Lecture 16:

Translation:

The tRNA and rRNA

Course 281

AIMS

- Understand the structure and function of tRNA.
- Understand the process in which the tRNA carries an amino acid.
- Understand the components and structures of the ribosomes of prokaryotes and eukaryotes.
- Understand the process of making the ribosome from genes to their final structure.

Translation – the process

What is translation?

Use the genetic code in the mRNA that reads 5’ ➔ 3’ to make a protein that reads N ➔ C.

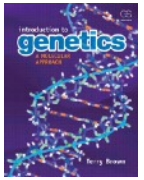
Translation – the process

What do we need to translate the genetic code?

1. mRNA
2. tRNA
3. Amino acids
4. Ribosomes

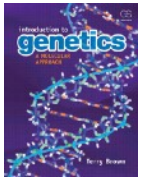
Transfer RNA

- Involved in protein synthesis
- They form the link between the mRNA that is being translated and the protein that is being synthesized



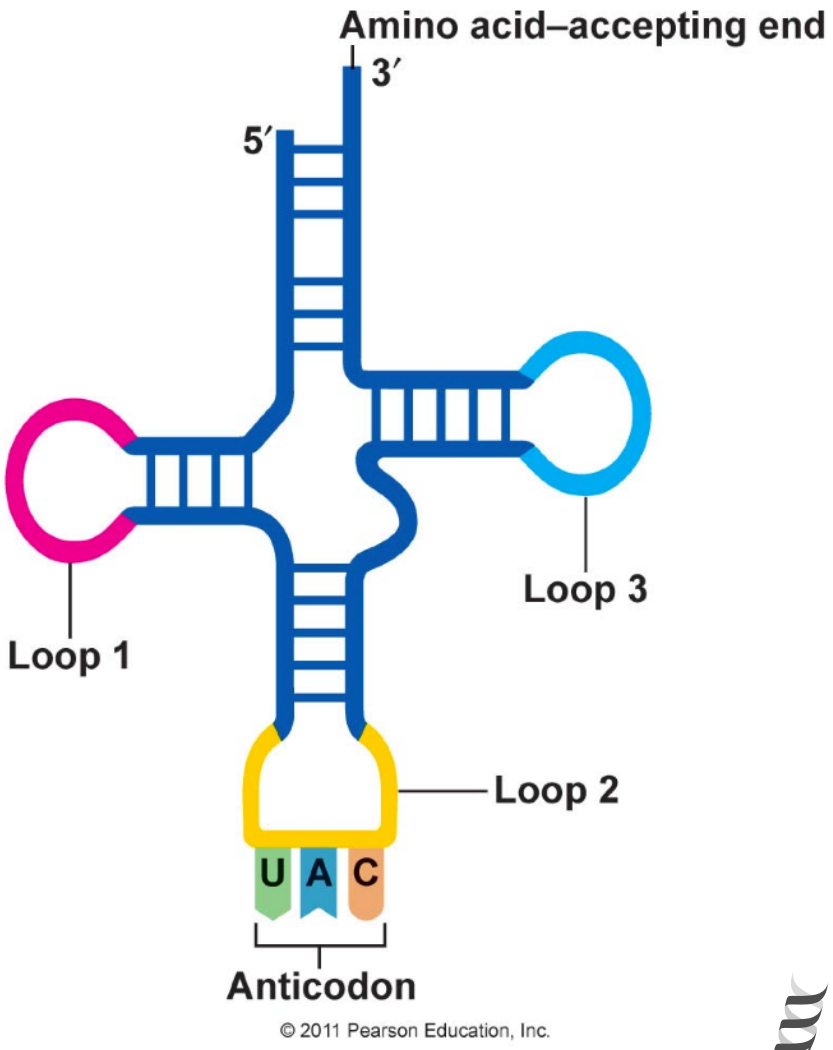
All tRNAs have a similar structure

- They are relatively small
- Most between 74 and 95 nucleotides in length
- Each organism synthesizes a number of different tRNAs, each in multiple copies
- Every tRNA molecule in every organism can be folded into a similar base-paired structure referred to as the **cloverleaf**



Transfer RNA (tRNA)

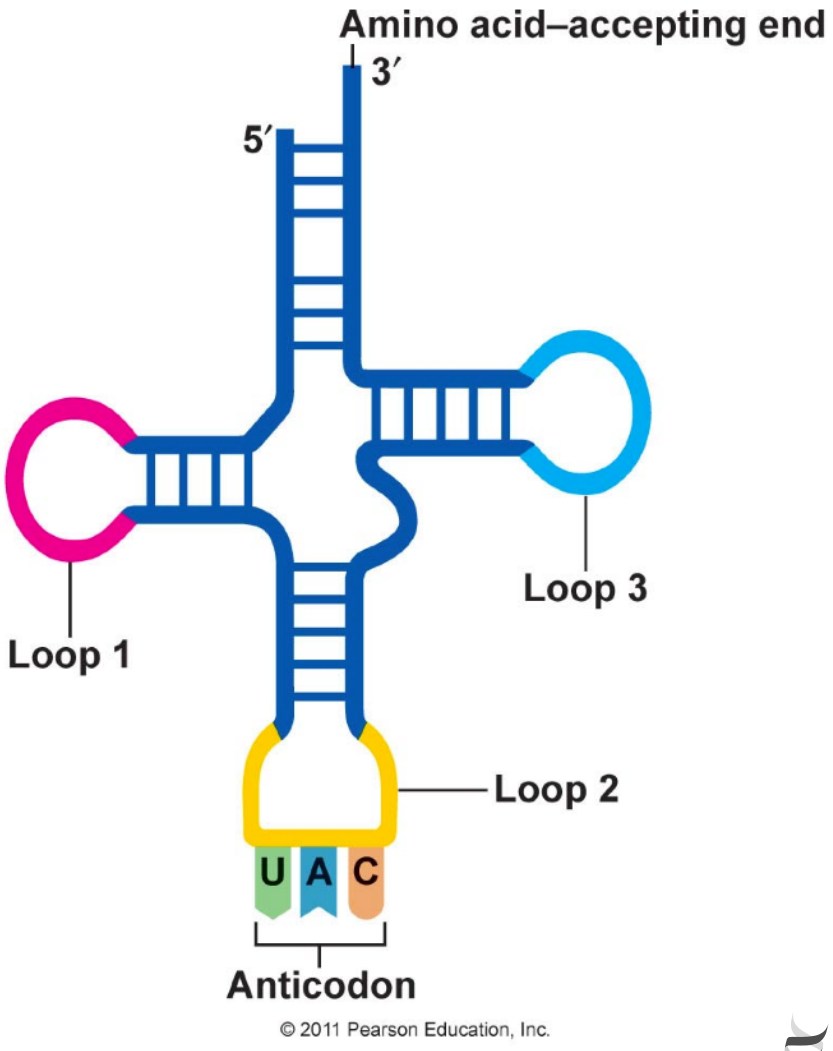
- tRNA carries the amino acid to the ribosome to make protein.
- There are specific tRNA for each codon and amino acid.



Transfer RNA (tRNA)

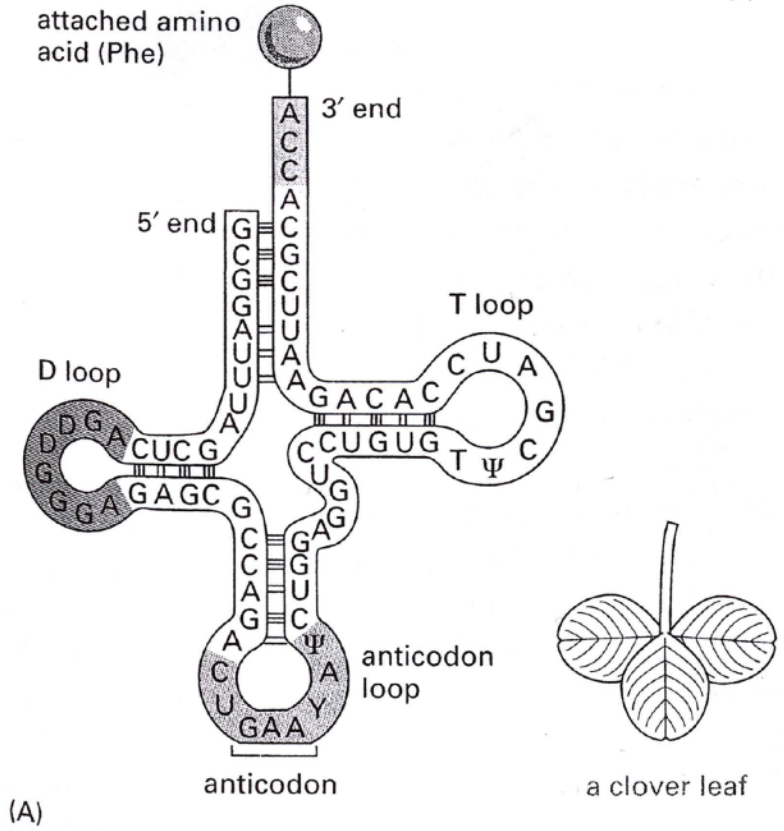
- The codon in the mRNA has a complementary sequence in the tRNA and it is called **Anti-codon.**

- **Why is it called anti-codon?**



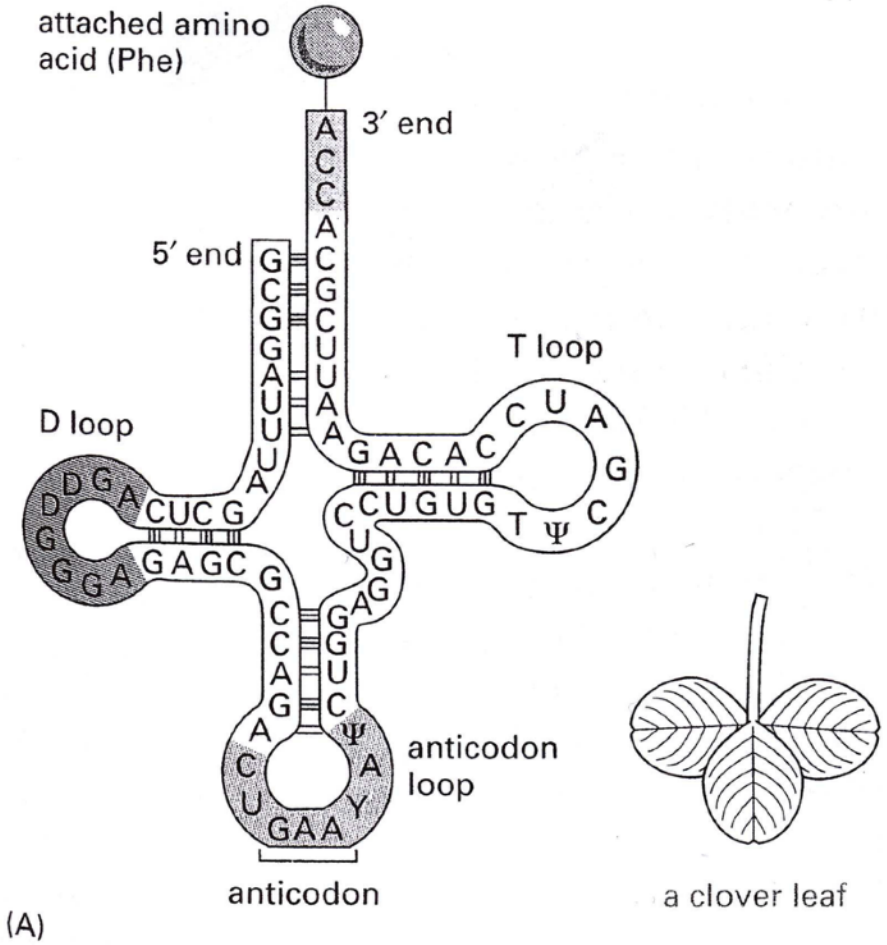
tRNA characteristics

- It is 75-90 nucleotide in sequence.
- tRNA folds to form a specific shape called **cloverleaf.**



tRNA characteristics

- **How is the shape of tRNA formed?**
- Contains three loops and the loop that contain the anticodon is called **anticodon loop.**



tRNA characteristics

- There are two ends in the tRNA:
  - 5’ end
  - 3’ end
- The 3’ end is where the amino acid is attached and it is called the **amino acid attachment site.**

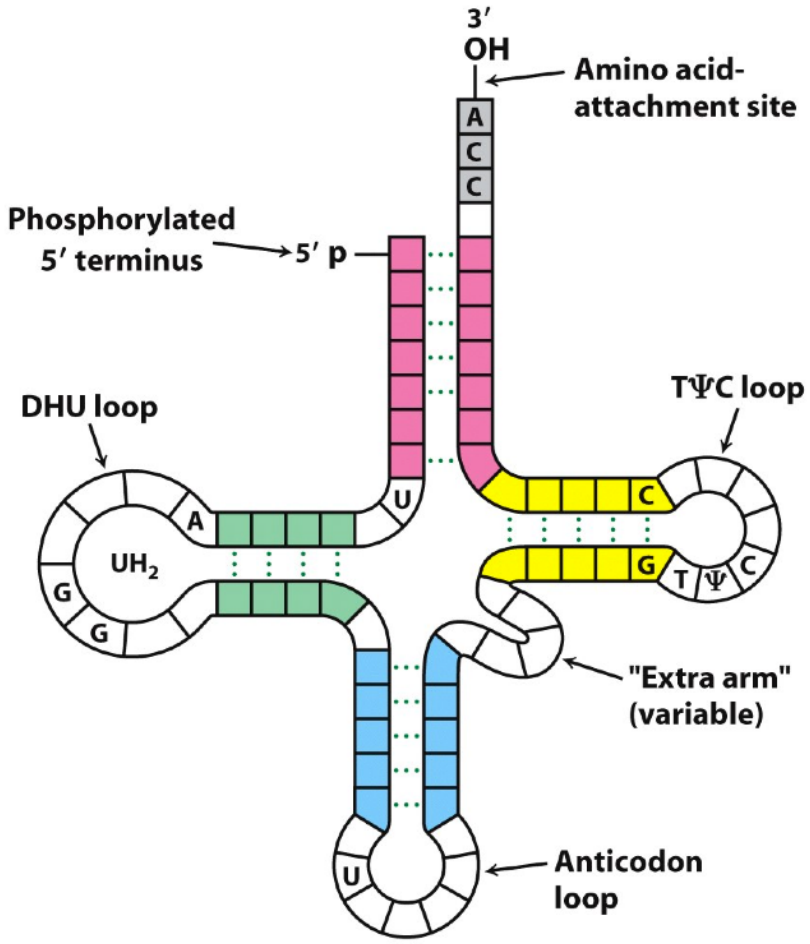


Figure 30.3
Biochemistry, Seventh Edition

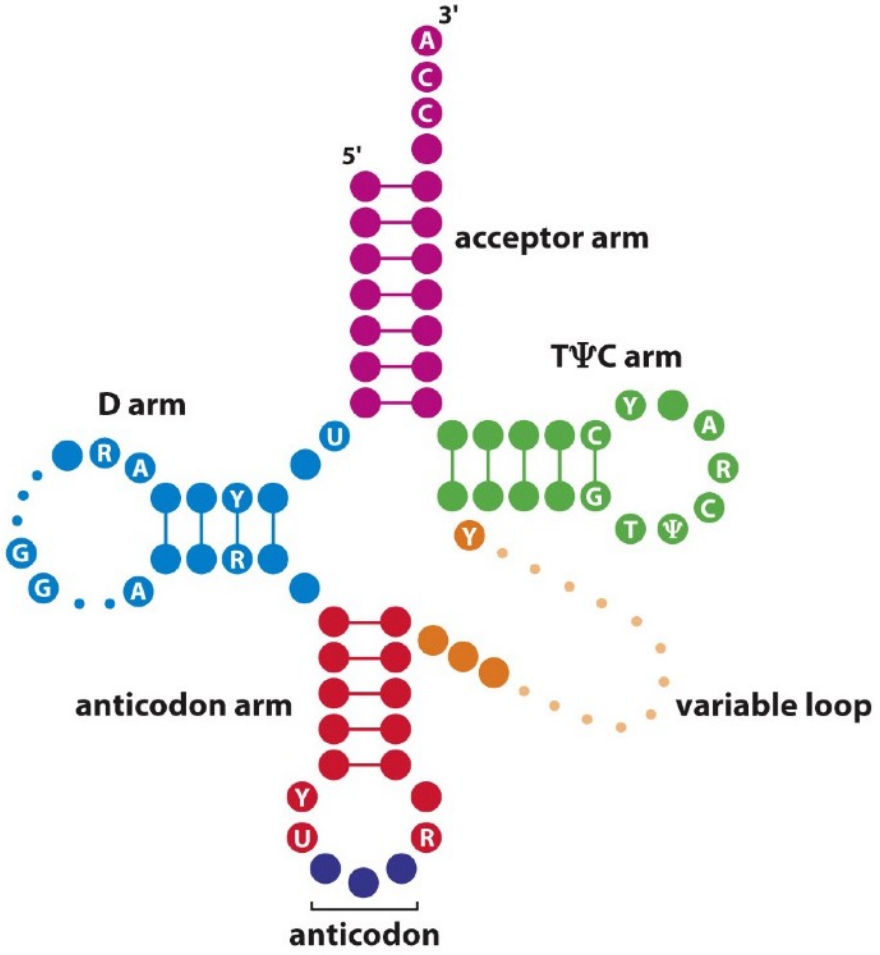
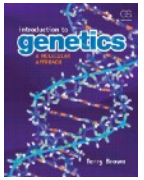
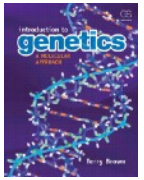


Figure 6.10 Introduction to Genetics (© Garland Science 2012)

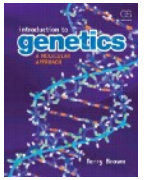


The cloverleaf structure has five components

- **Acceptor arm**
- **D arm**
- **anticodon arm**
- the **extra** (or **optional**, or **variable**) **loop**
- the **TψC arm**



- **Acceptor arm**
  - which is formed by seven base pairs between the 5’ and 3’ ends of the molecule.
  - During protein synthesis an amino acid is attached to the 3’ end to the adenosine of the invariant CCA terminal sequence
- **D arm**
  - Named after the modified nucleotide dihydrouridine
  - Which is always present in this structure



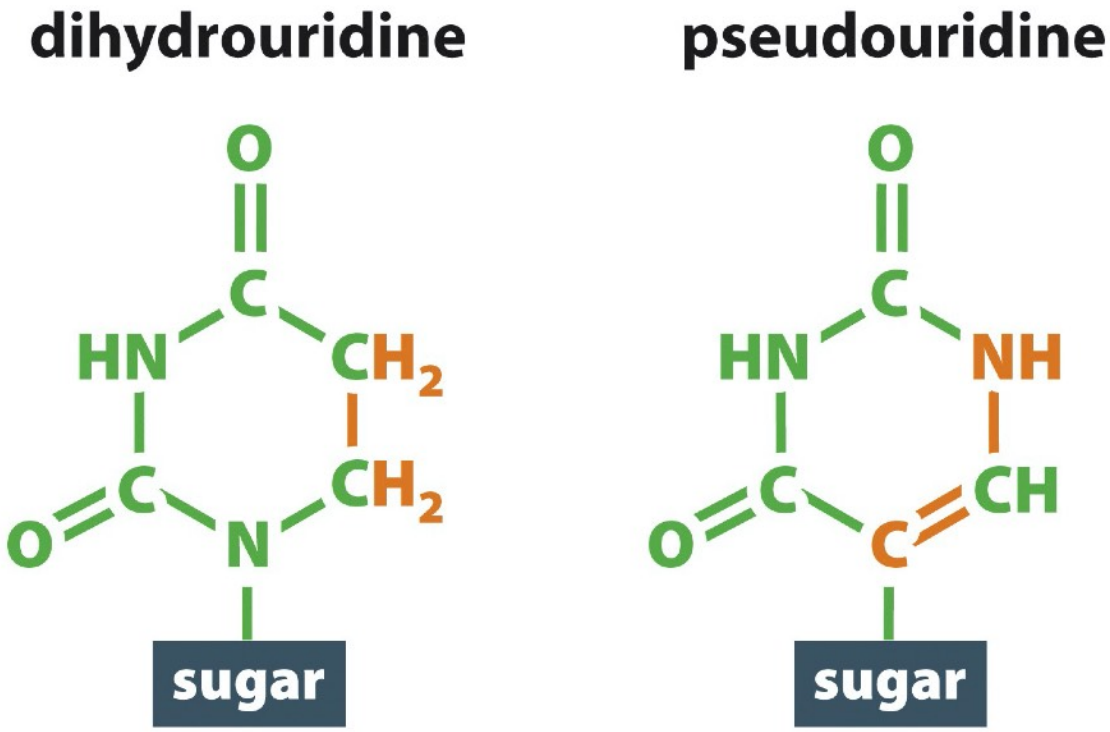
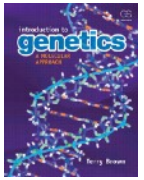


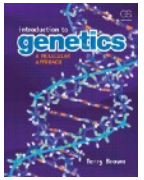
Figure 6.11 Introduction to Genetics (© Garland Science 2012)

Figure . The structures of two modified nucleotides found in tRNAs. Both are modified versions of uridine, the standard U nucleotide found in RNA.

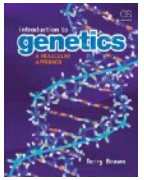
Chapter6



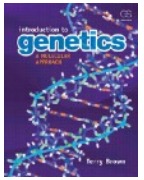
- **Anticodon arm**
  - This part play essential role in protein synthesis
- **Extra** (or **optional**, or **variable**) **loop**
  - which may be a loop of just three to five nucleotides
  - or a much larger hairpin structure of 13 to 21 nucleotides with up to five base pairs in the stem.
  - Types of tRNA with the smaller loop are called class I, and make up 75% of all tRNAs
  - Those with the larger loop are class II.



- The **TψC arm**
  - Named after the sequence thymidine– pseudouridine– cytosine, which is always present
  - Pseudouridine is another modified nucleotide



- The cloverleaf structure can be formed by virtually all tRNAs
- In addition to having this common secondary structure, different tRNAs also display a certain amount of nucleotide sequence conservation
- Some positions are invariant and in all tRNAs they are occupied by the same nucleotide
- Others are semi-invariant and always contain the same type of nucleotide
- Either one of the pyrimidine nucleotides or one of the purine nucleotides



- In the cell, tRNAs have a different three-dimensional structure
- This structure has been determined by X-ray diffraction analysis

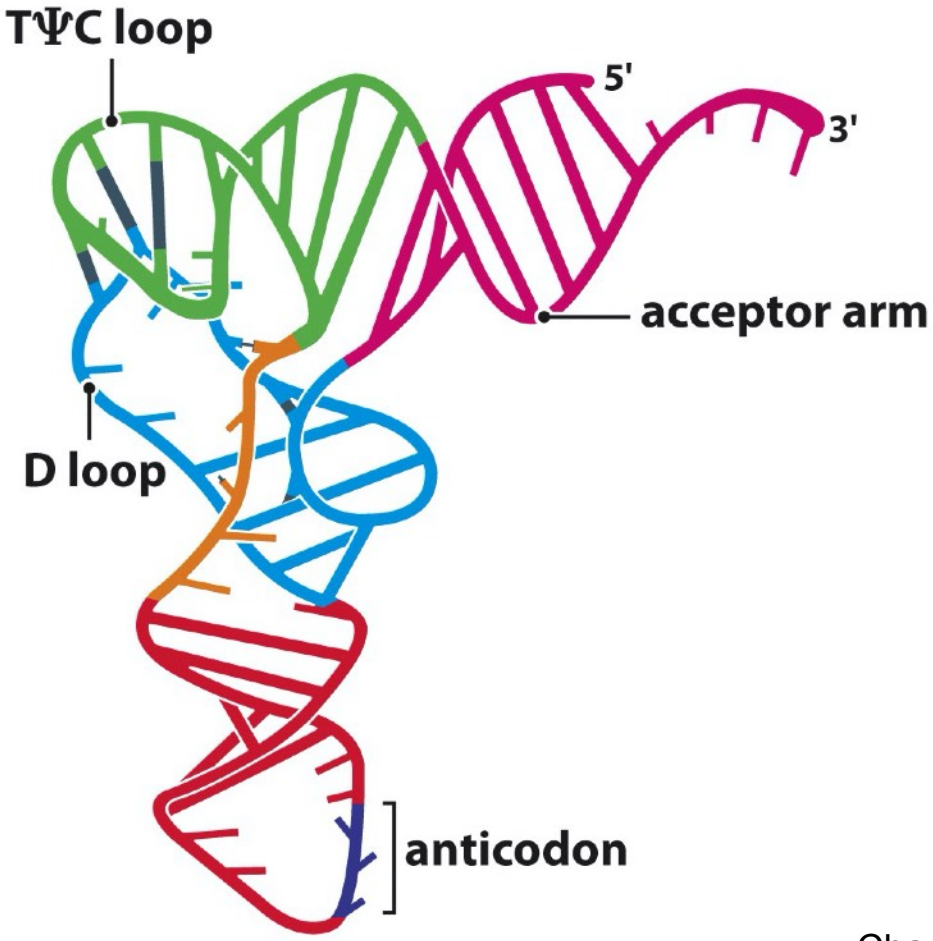
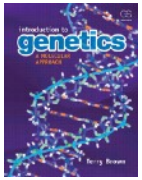
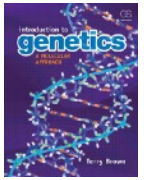


Figure 6.12 Introduction to Genetics (© Garland Science 2012)



- Several additional base pairs form between nucleotides in the D-loop cause the molecule to be folded into a compact L-shaped conformation.
- Many of the nucleotides involved in these extra base pairs are the invariant or semi-invariant ones that are the same in different tRNAs.
- The three-dimensional conformation places the acceptor arm and the anticodon loop at opposite ends of the molecule



tRNA characteristics

tRNA genes are found in multiple copies in the cell

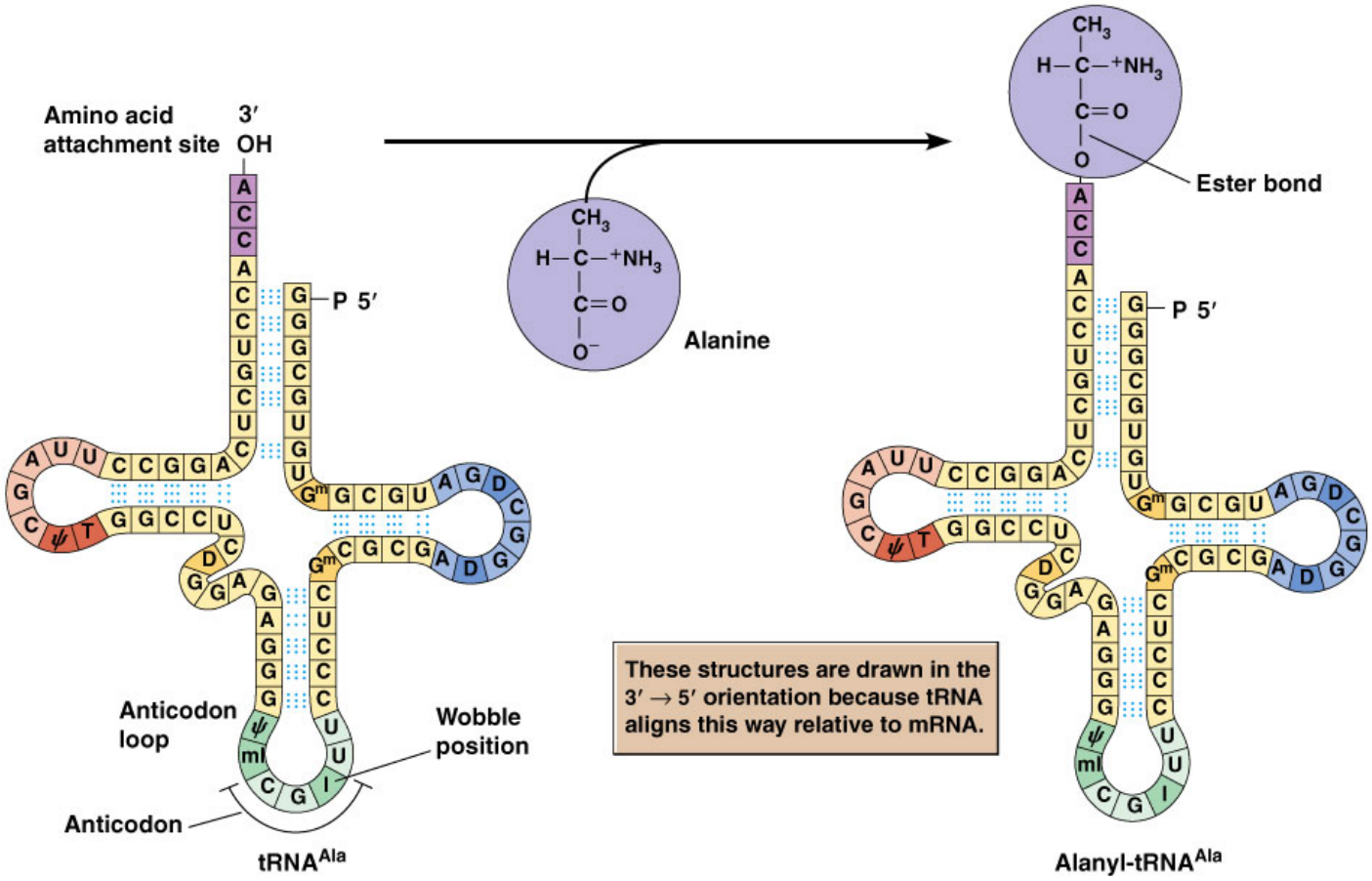
(Why?)

tRNA-amino acid

- Adding an amino acid to a tRNA is called **aminoacylation or tRNA charging.**
- An enzyme called **aminoacyl-tRNA synthetase** adds the correct amino acid to the corresponding tRNA.
- The process produces a **charged tRNA or aminoacyl tRNA.**

tRNA-amino acid

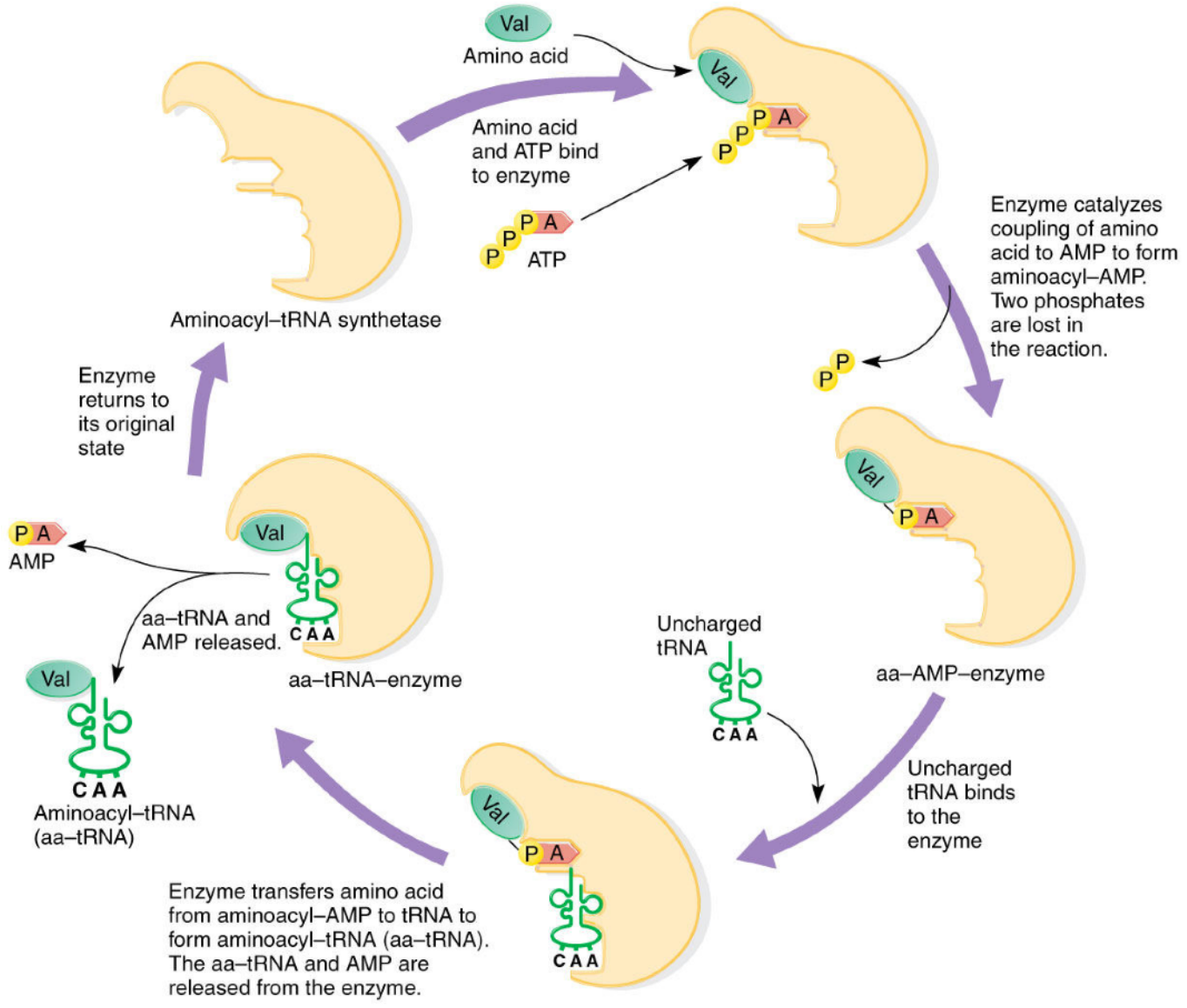
Aminoacylation or tRNA charging



tRNA-charging

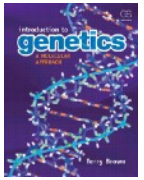
- tRNA charging uses ATP as a source of energy.
- Each amino acid has a specific **aminoacyltransferase**.
- The 3’ nucleotides of tRNA is always CCA in all tRNAs.
- The amino acid binds to the 2’ or 3’ sugar of adenine (A) of the 3’ CCA.

tRNA-charging



The role of tRNAs in protein synthesis

- tRNAs form a physical link between the mRNA and the protein that is being synthesized
- Binding to both the mRNA and the growing protein



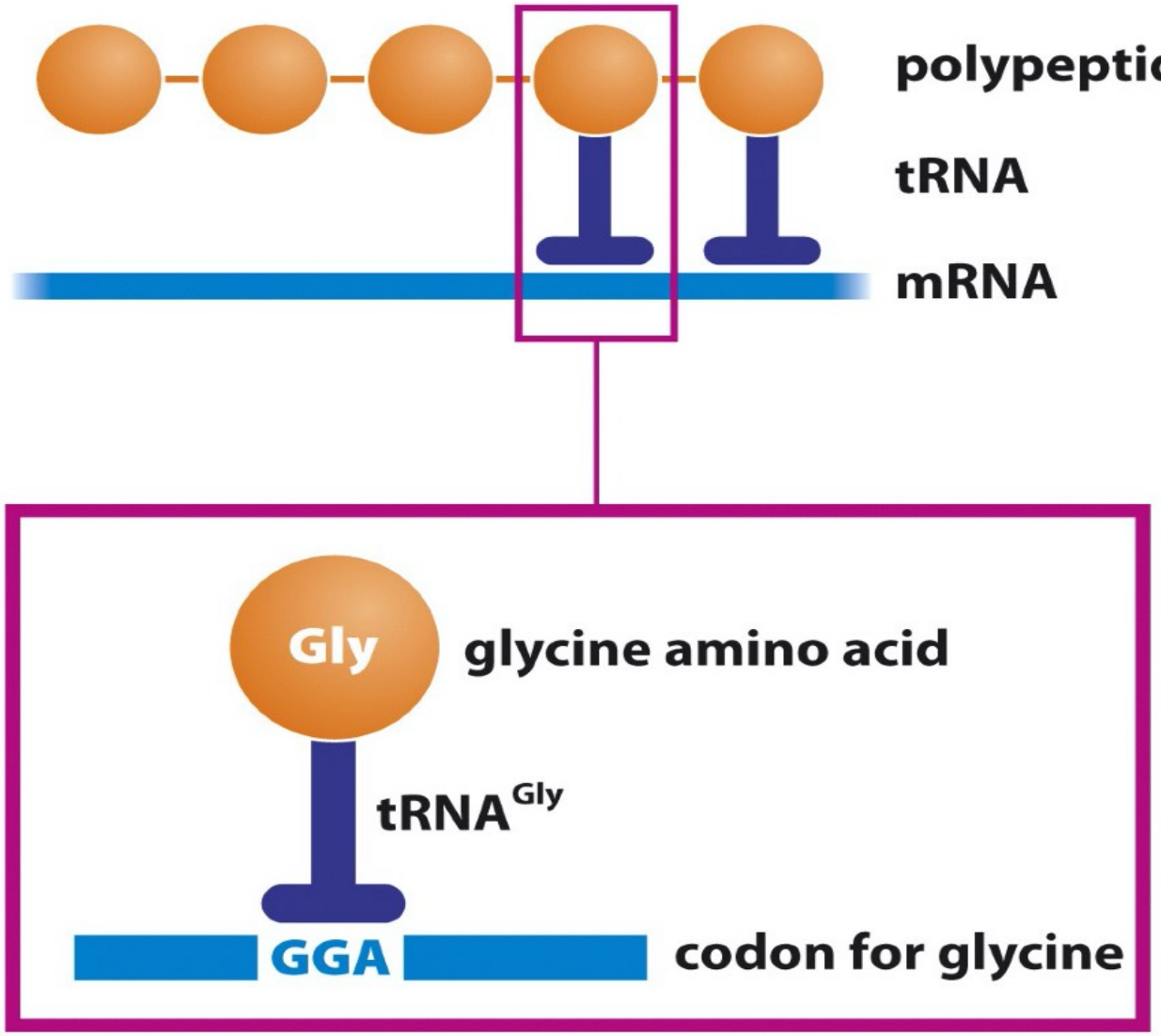
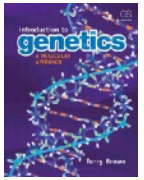
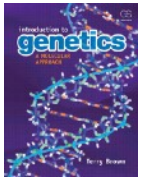


Figure. The role of tRNA in translation



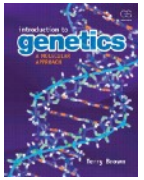
Aminoacyl-tRNA synthetases attach amino acids to tRNAs

- Bacteria contain 30 to 45 different tRNAs
- Eukaryotes have up to 50
- As only 20 amino acids are designated by the genetic code
- All organisms have at least some **isoaccepting tRNAs**
  - different tRNAs that are specific for the same amino acid
  - Two tRNAs specific for glycine would be written as $tRNA^{Gly1}$ and $tRNA^{Gly2}$

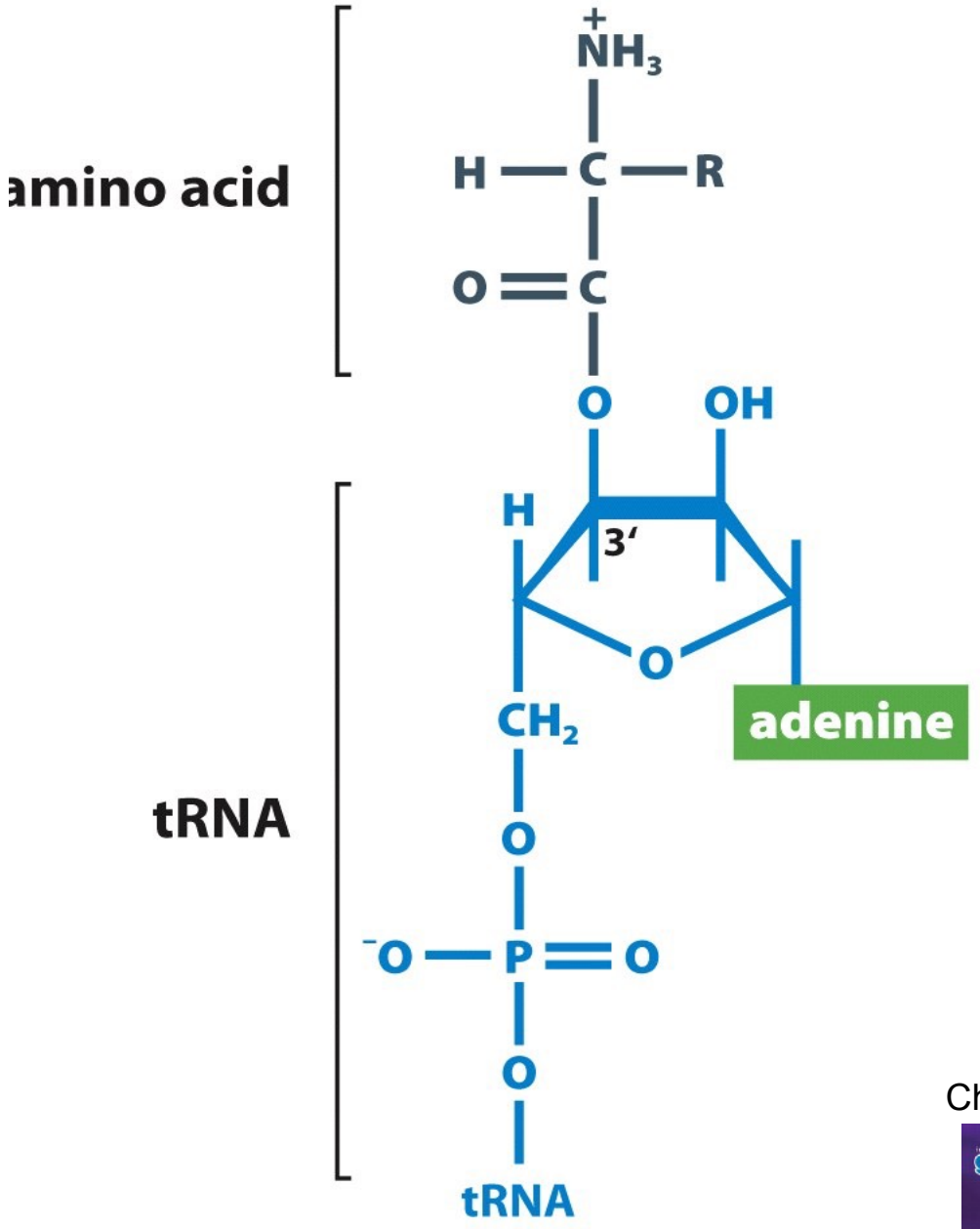


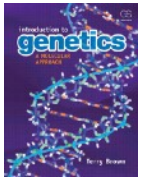
Aminoacylation
(charging)

- A process by which each tRNA molecule forms a covalent linkage with its specific amino acid
- The amino acid becomes attached to the end of the acceptor arm of the tRNA cloverleaf
- The linkage forms between the carboxyl group of the amino acid and the 2’-OH or 3’-OH group of the terminal nucleotide of the tRNA

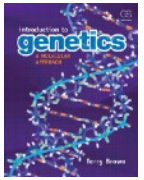


- All tRNAs have the sequence 5’-CCA-3’ at their 3’ ends

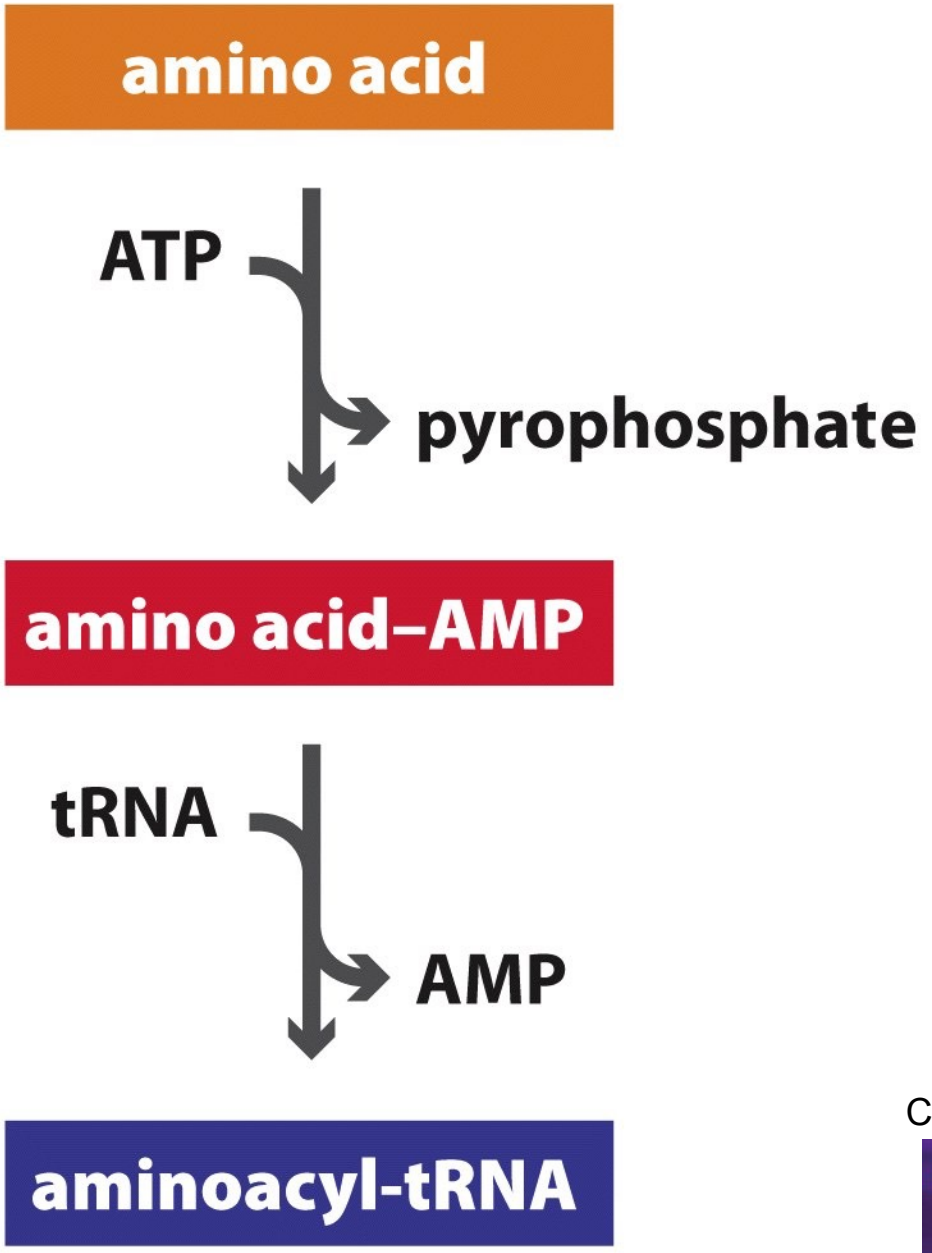


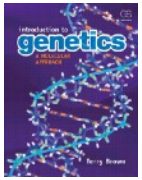


- Aminoacylation is catalyzed by a group of enzymes called the **aminoacyl-tRNA synthetases**.
- In most cells there is a single aminoacyl-tRNA synthetase for each amino acid

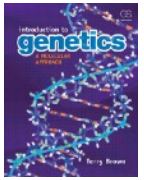


- The energy required to attach the amino acid to the tRNA is provided by:
  - cleavage of ATP to adenosine monophosphate (AMP) and pyrophosphate.

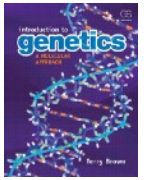




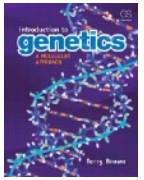
- Aminoacylation must be carried out accurately.
- The correct amino acid must be attached to the correct tRNA
- Each aminoacyl-tRNA synthetase forms an extensive interaction with its tRNA
- With contacts made to the acceptor arm and anticodon loop as well as to individual nucleotides in the D and T [?] C arms.



- These interactions enable the enzyme to distinguish the specific sequence features of different tRNAs and recognize the correct one.
- The interaction between enzyme and amino acid is, of necessity, less extensive
- Amino acids being much smaller than tRNAs, and presents a greater problem with regard to specificity
- Because several pairs of amino acids are structurally similar

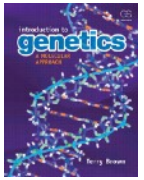


- Errors do therefore occur, at a very low rate for most amino acids
- But possibly as frequently as one aminoacylation in 80 for difficult pairs such as isoleucine and valine.
- Most of these errors are corrected by the aminoacyl-tRNA synthetase before the charged tRNA is released

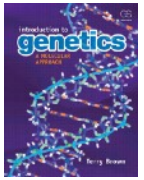


Codon–anticodon recognition

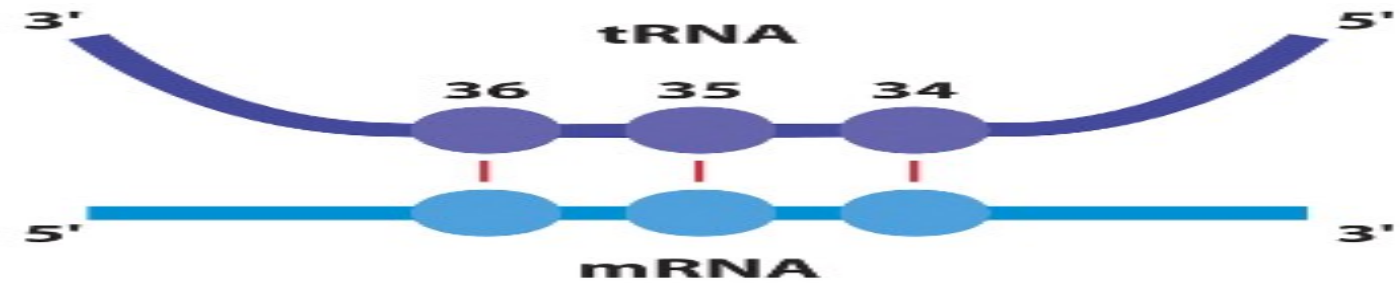
- Once the correct amino acid has been attached to the acceptor arm of the tRNA
- The aminoacylated molecule must complete the link between mRNA and protein
- By recognizing and attaching to the correct codon
- One coding for the amino acid that it carries

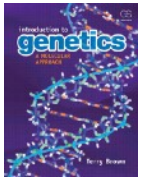


- Codon recognition is a function of the anticodon loop of the tRNA
- Specifically, of the triplet of nucleotides called the anticodon
- This triplet is complementary to the codon
- Can therefore attach to it by base pairing



- The specificity of the genetic code is ensured
- The anticodon present on a particular tRNA is is complementary to a codon for the amino acid with which the tRNA is charged





Ribosomes

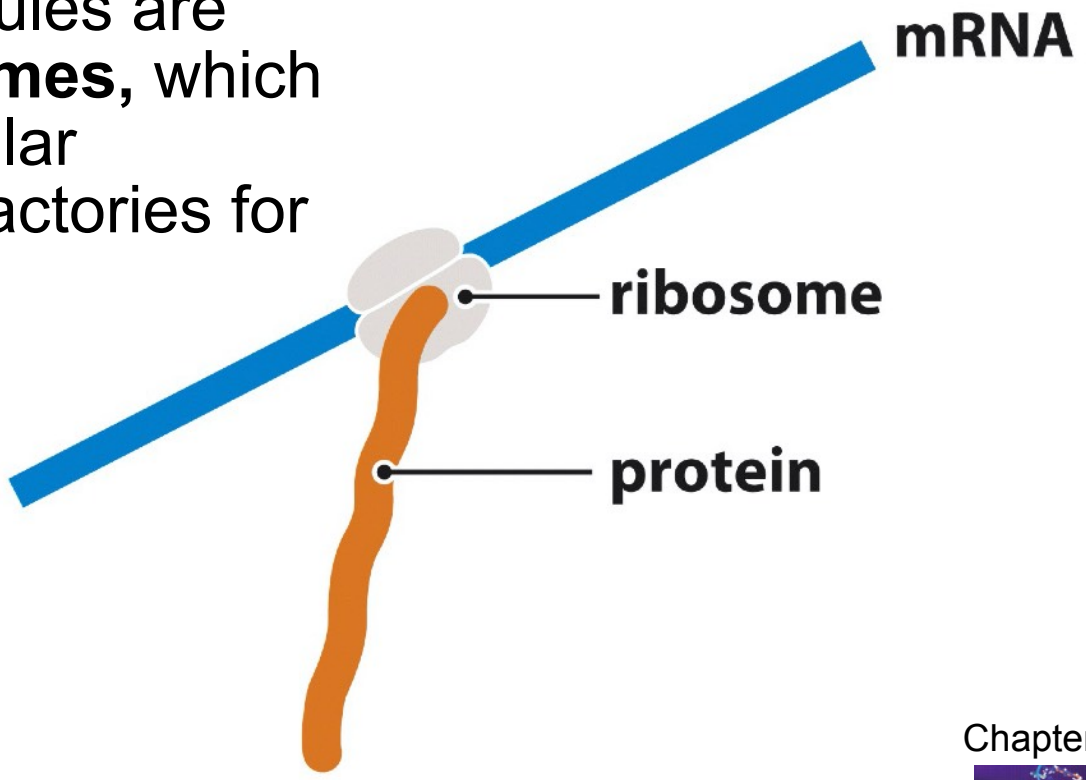
- Peptide synthesis and translation of the genetic code takes place on ribosomes.
- Ribosomes attach to mRNA and charged tRNA to make polypeptide chains.
- Both in prokaryotes and in eukaryotes the ribosome is made of:

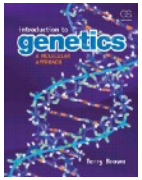
  Large subunit
  Small subunit

- Each subunit is composed of rRNA and ribosomal proteins.

Ribosomal RNA

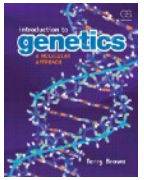
- Ribosomal RNA molecules are components of **ribosomes,** which are large, multi-molecular structures that act as factories for protein synthesis.





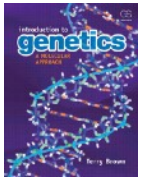
Ribosomes

- Ribosomes play an active role in protein translation
- Made up of rRNA molecules and proteins
- They are extremely numerous in most cells
  - over 20,000 ribosomes found in an actively growing bacterium
  - about 80% of the total cell RNA and 10% of the total protein
- One of the rRNAs in the ribosome catalyze the synthesis of bonds between amino acids



Ribosomes and their components were first studied by density gradient centrifugation

- Originally called “microsomes”
- The first electron micrographs showed that:
  - Bacterial ribosomes are oval-shaped (dimensions 29 nm x 21 nm)
  - Eukaryotic ribosomes are slightly larger
    - varying a little in size depending on species (averaging about 32nm x 22nm)



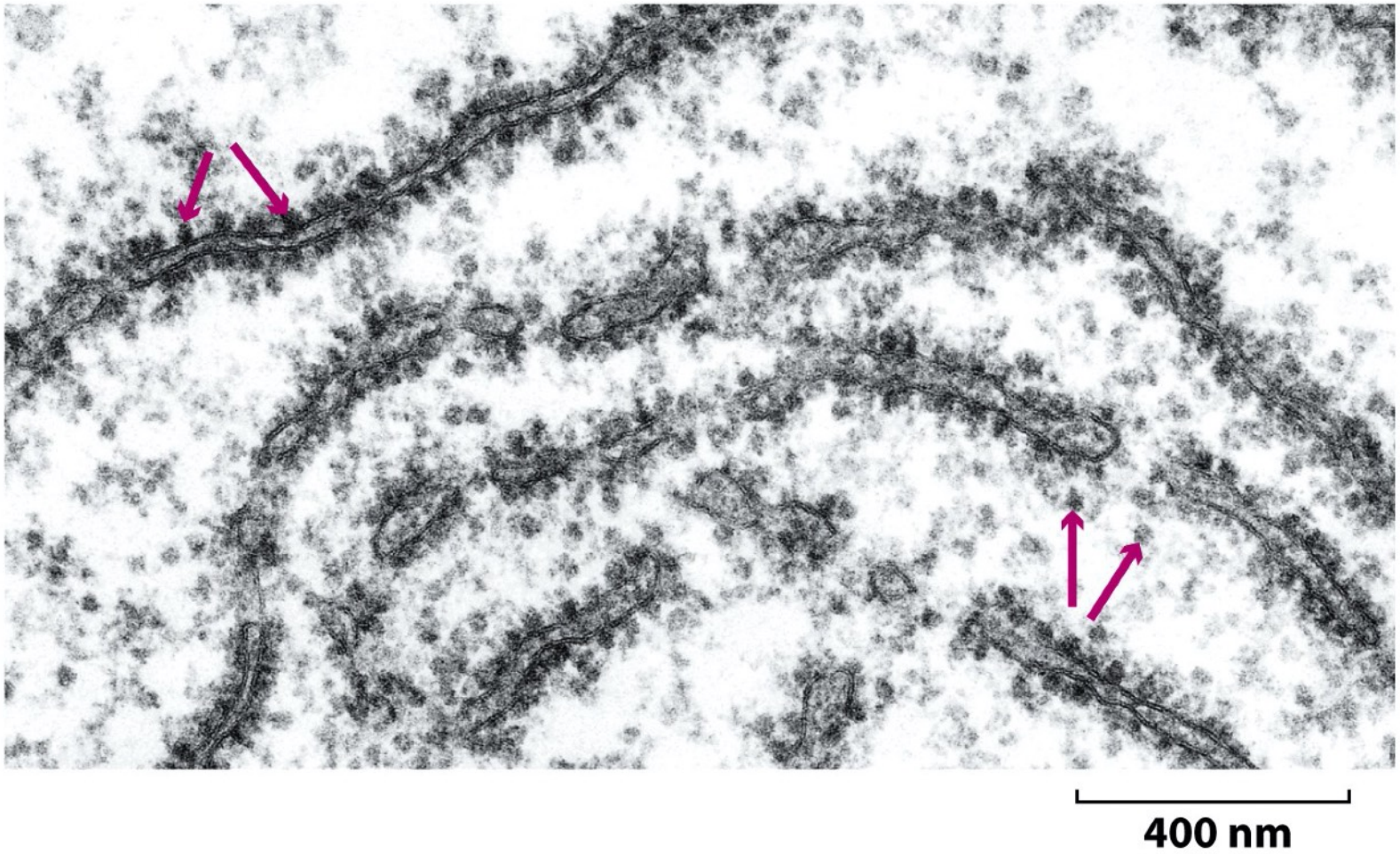
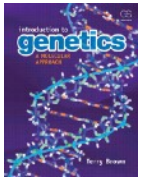


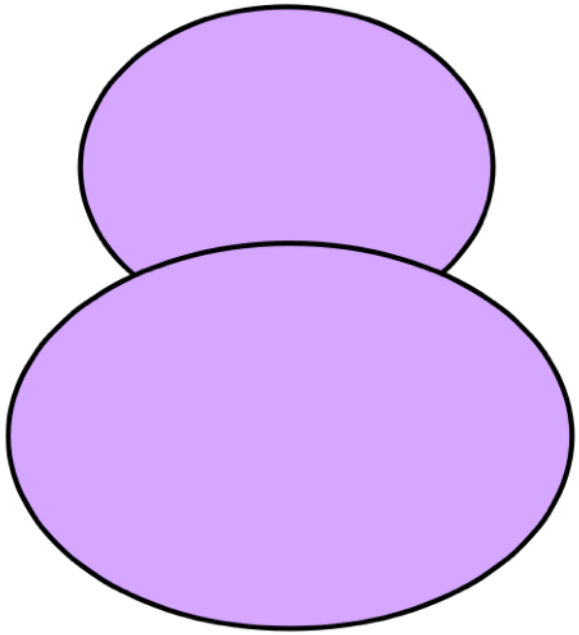
Figure. Electron micrograph showing ribosomes inside an animal cell. The ribosomes appear as black dots, indicated by the red arrows. Some occur free in the cytoplasm, and others are attached to membranes.

Chapter6



Bacterial ribosomes

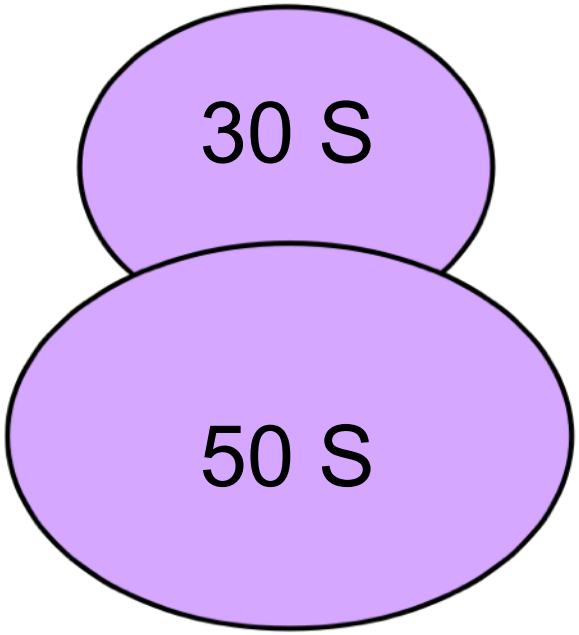
- Bacterial ribosomes are called 70S ribosomes.
- The 70S ribosome is composed of two subunits:
  - Large subunit (50S):
    - 23S rRNA
    - 5S rRNA
  - Small subunit (30S):
    - 16S rRNA



70S

Bacterial ribosomes

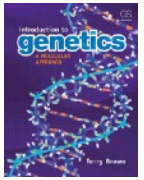
- The S numbers do not add up correct?
- **WHY?**



70S

Density Gradient Centrifugation

- The detailed structure of the ribosome was made by analyzing the particles by **density gradient centrifugation**
- In which the rate of migration of a cell component through the gradient depends on its **sedimentation coefficient**
- The sedimentation coefficient is expressed as a svedberg (S) value
- The S value is dependent on several factors, mainly molecular mass and shape



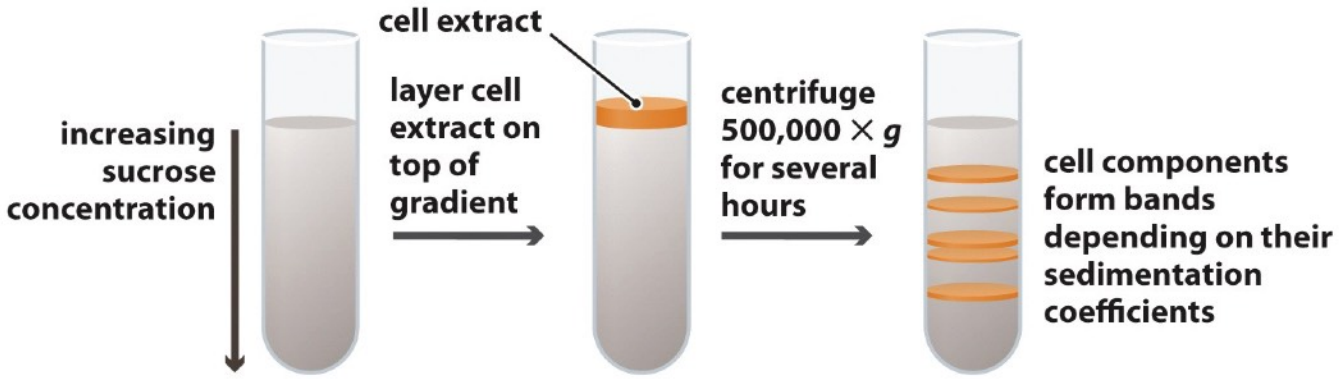
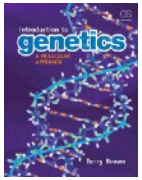
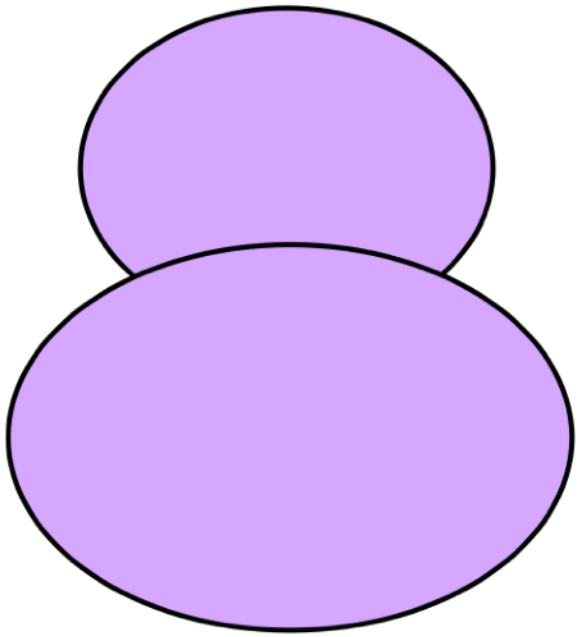


Figure 6.3 Introduction to Genetics (© Garland Science 2012)



Eukaryotic ribosomes

- Eukaryotic ribosomes are called 80S ribosomes.
- The 80S ribosome is composed of two subunits:
  - Large subunit (60S):
    - 28S rRNA
    - 5.8S rRNA
    - 5S rRNA
  - Small subunit (40S):
    - 18S rRNA



80 S

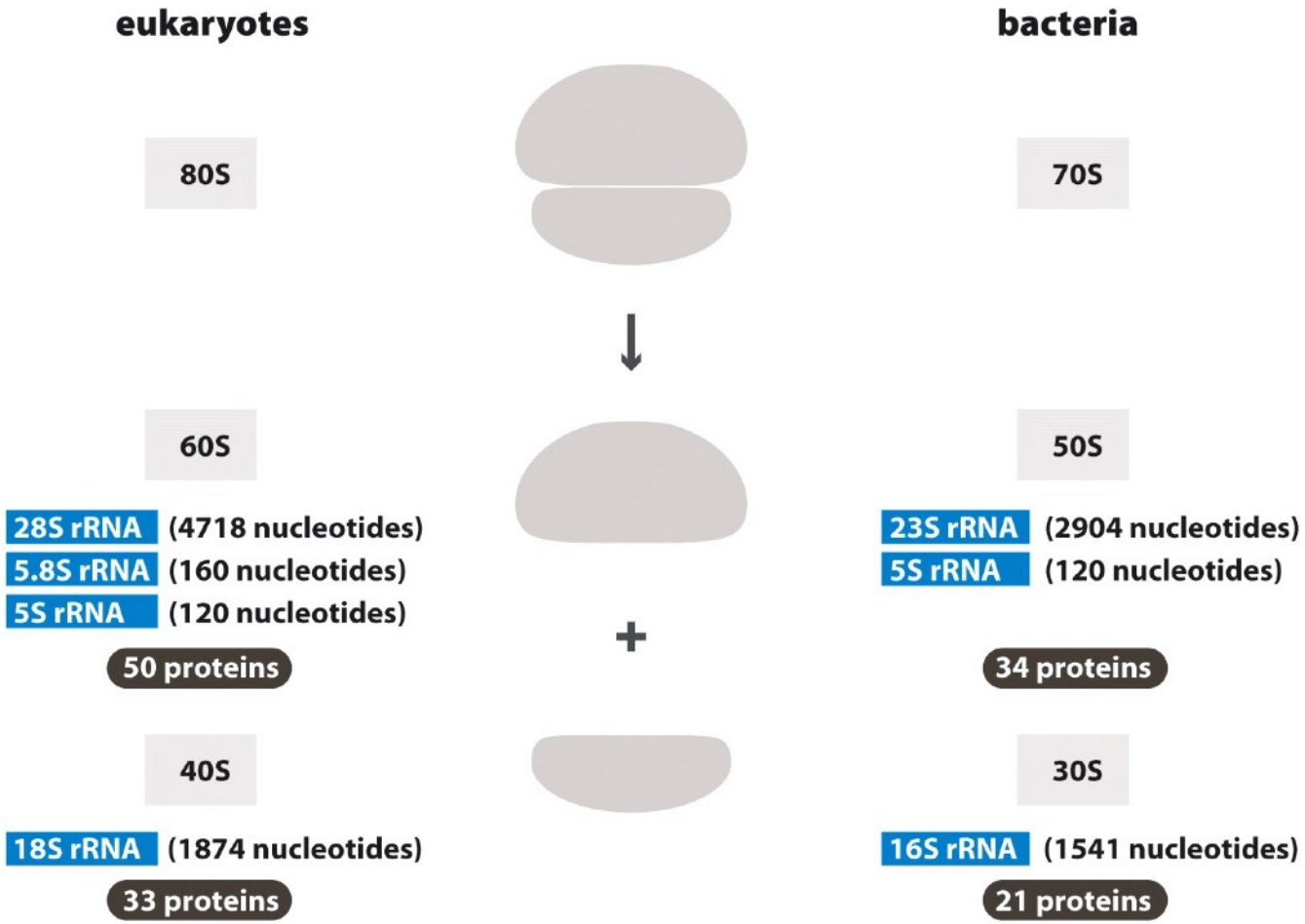
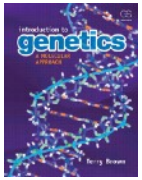
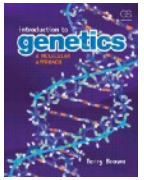


Figure 6.4 Introduction to Genetics (© Garland Science 2012)

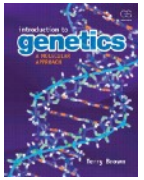


Each type of ribosome is made up of two subunits

- In eukaryotes these subunits are 60S and 40S
- in bacteria they are 50S and 30S.
- Both subunits contain a variety of **ribosomal proteins**
- The small subunit contains just a single rRNA in both eukaryotes and bacteria and
- Sedimentation coefficients are not additive because they depend on shape as well as mass



- The ribosomal proteins of the small subunit are called S1, S2, etc.
- Those of the large subunit are L1, L2, etc.
- There is just one of each protein per ribosome, except for L7 and L12, which are present as dimers.



The rRNA contributes to the structure and function of the ribosomes.

Bacterial ribosomal genes

- Both prokaryotic and eukaryotic rRNA is coded in the DNA by genes called **ribosomal DNA (rDNA) or rRNA transcription units.**
- In bacteria (*E. coli*), 7 rRNA transcription units are scattered through out the chromosome.
- **Why many copies?**

Bacterial ribosomal genes

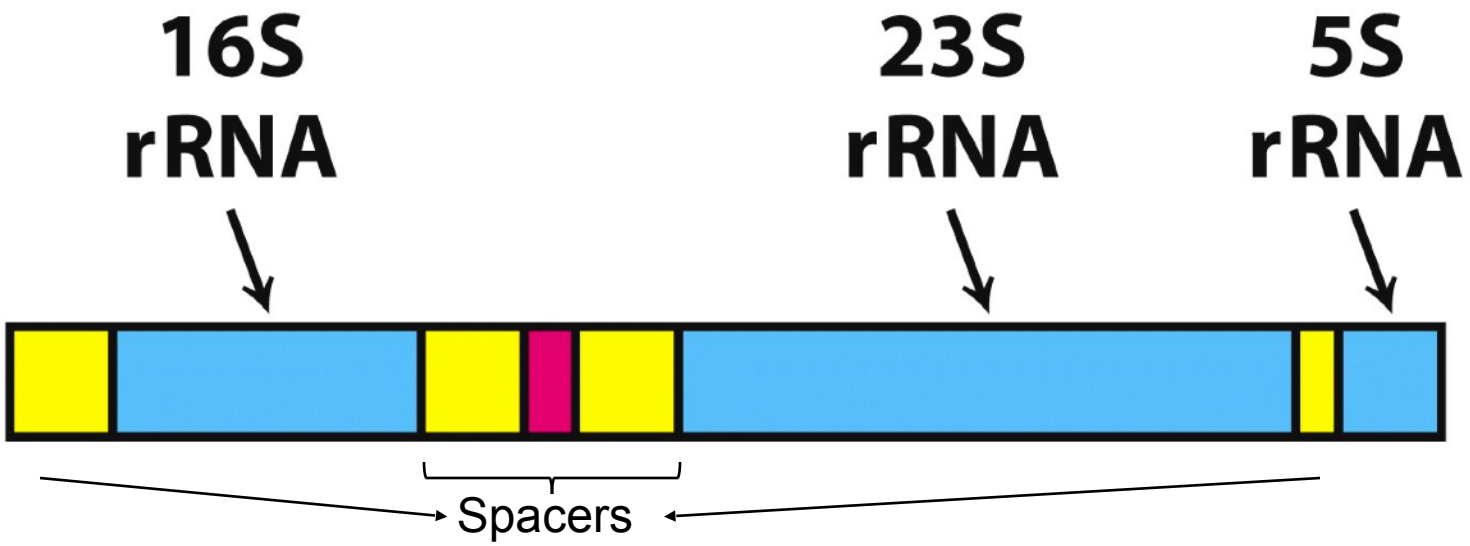
- Each rRNA transcription unit is composed of:

16S
23S
5S

- The transcription of these genes produces a **precursor rRNA (pre-rRNA).**

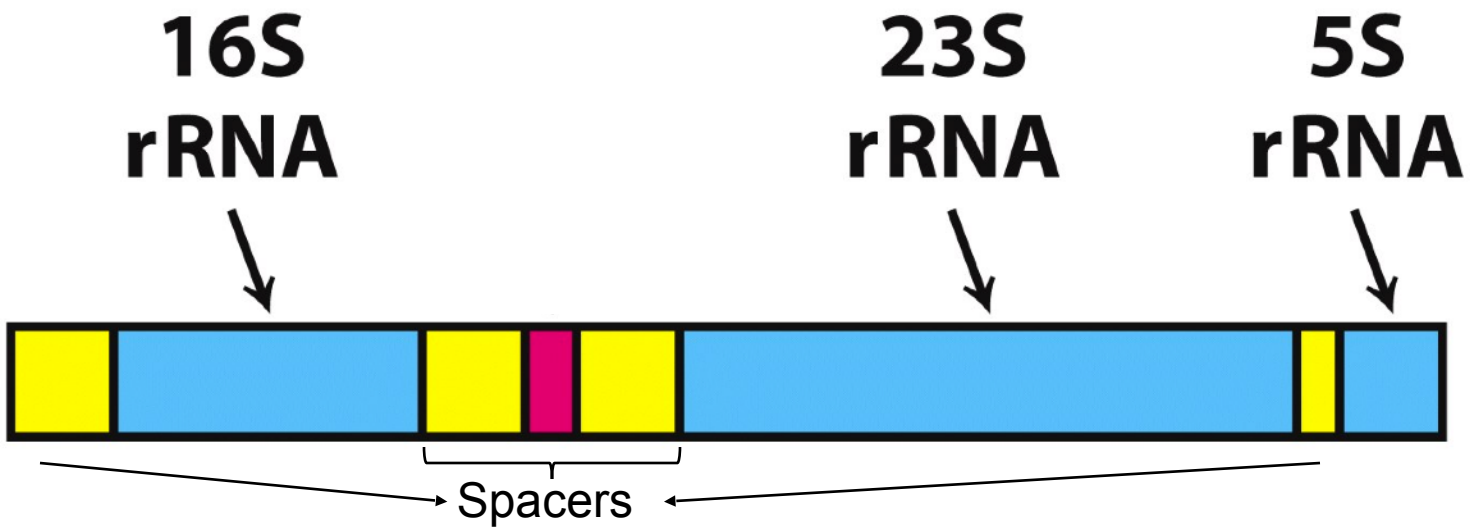
Bacterial ribosomal genes

- The pre-rRNA transcribed is 5’ 16S-23S-5S 3’ with non-rRNA sequences in between.
- The non-rRNA sequences are called **spacers.**



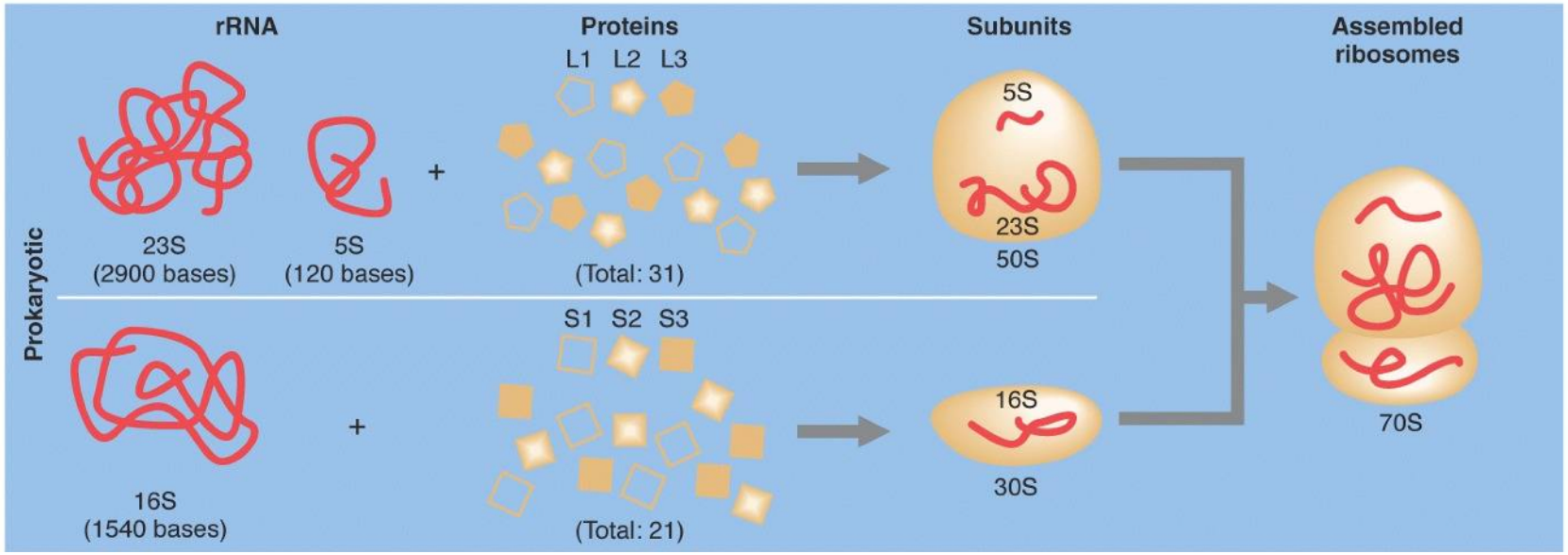
Bacterial ribosomal genes

- **Ribonucleases** remove the spacers and release three rRNA separate molecules.
- **Is this like intron splicing?**



Prokaryotic ribosome

Ribosomal proteins with the three rRNA make the ribosome two subunits.



Eukaryotic ribosomal genes

- Eukaryotic rRNA is coded by rDNA genes.
- The rDNA genes are composed of units containing:

18S-5.8s-28S

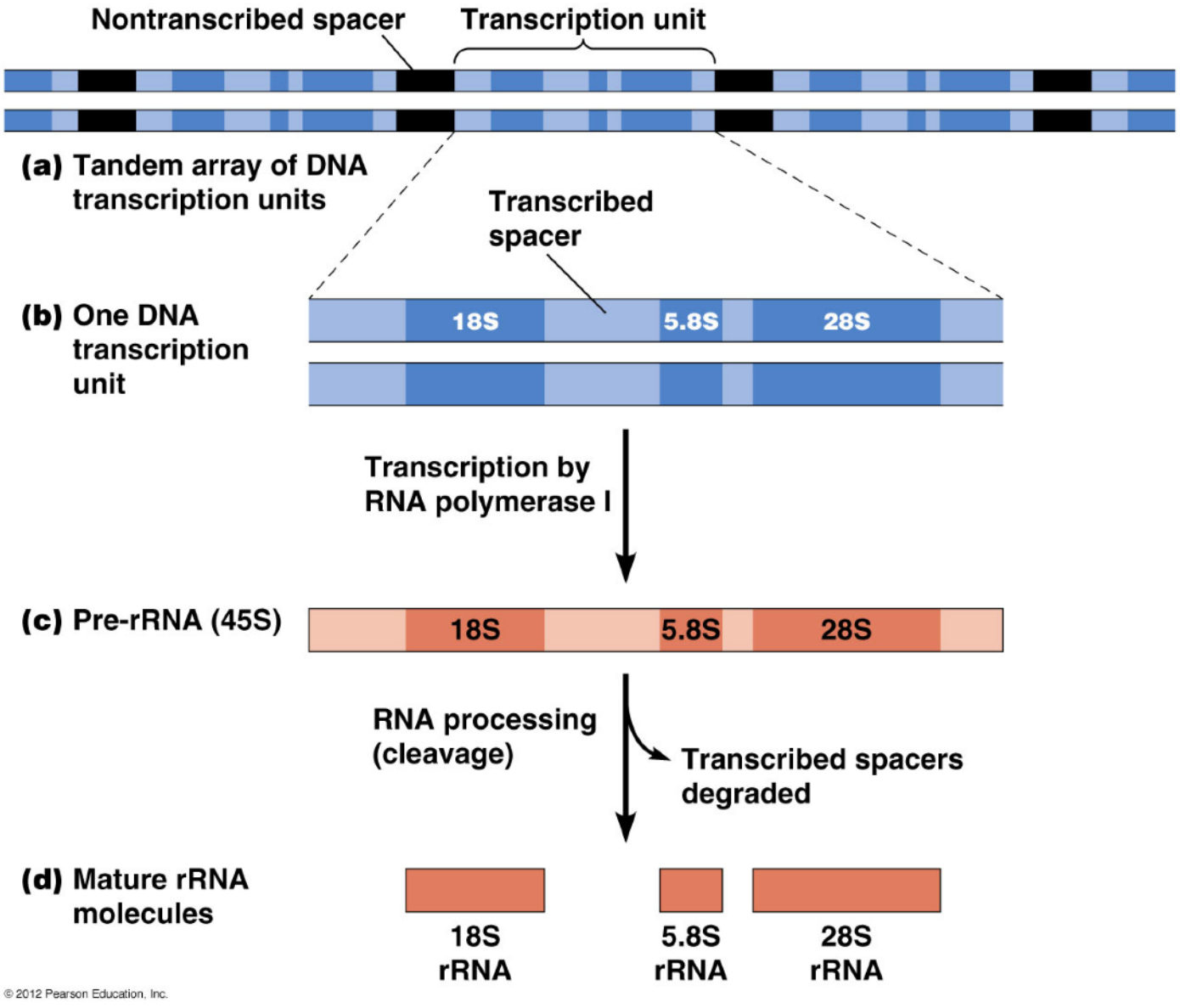
- This unit is repeated in eukaryotic genomes 100-1000 times.
- **Why?**

Eukaryotic ribosomal genes

- The rDNA repeat units get transcribed by RNA Pol I producing a pre-rRNA with spacers.
- Pre-rRNA:

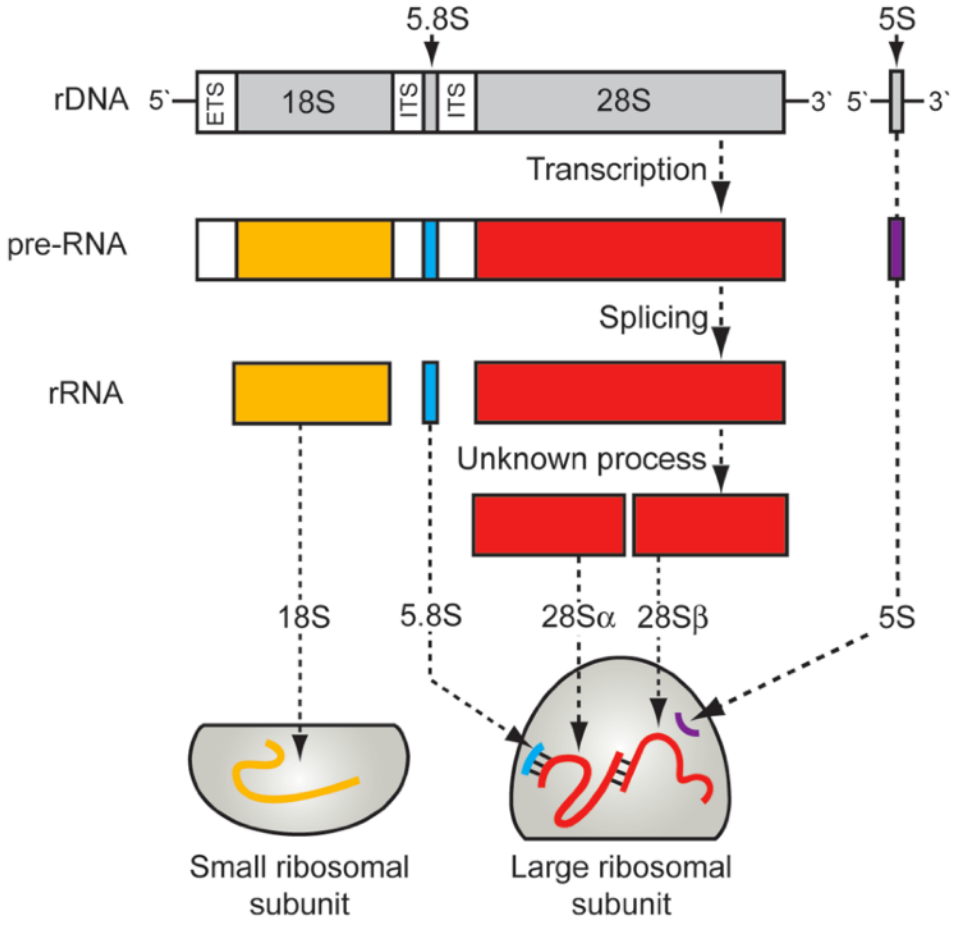
5’ 18S-5.8S-28S 3’

Eukaryotic ribosomal genes



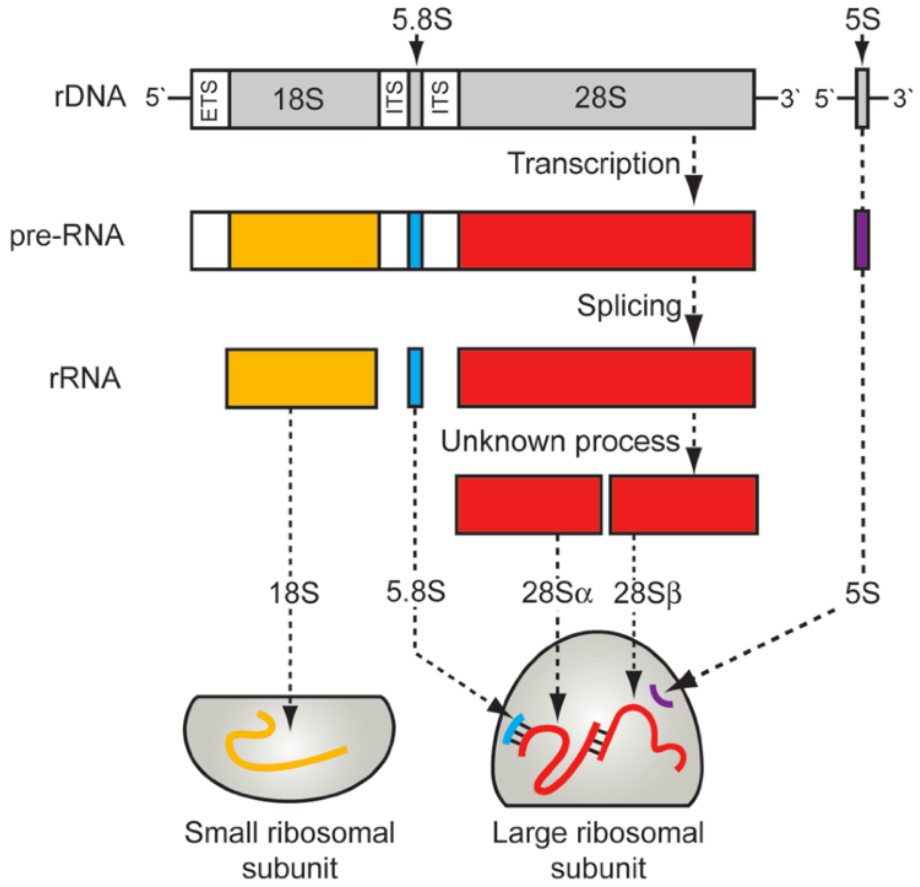
Eukaryotic ribosomal genes

- **Ribonucleases** process the rRNA unit and remove spacers.
- 5S rRNA is located in other location than the repeat unit.
- **What is the effect of the location 5S gene on its transcription?**



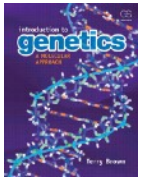
Eukaryotic ribosomal genes

- 5S rRNA is transcribed independently by RNA Pol III.
- The ribosomal proteins and the four rRNA molecules make the eukaryotic ribosome.



Processing of precursor rRNA and tRNA molecules

- The rRNAs and tRNAs that play active roles in protein synthesis are quite different from the RNA molecules that are initially transcribed from the rRNA and tRNA genes.
- These initial transcripts are precursor molecules:
  - longer than the mature RNAs
  - Often contain more than one rRNA and/or tRNA sequence
- These precursors must therefore be cut into smaller pieces to release the rRNAs and tRNAs



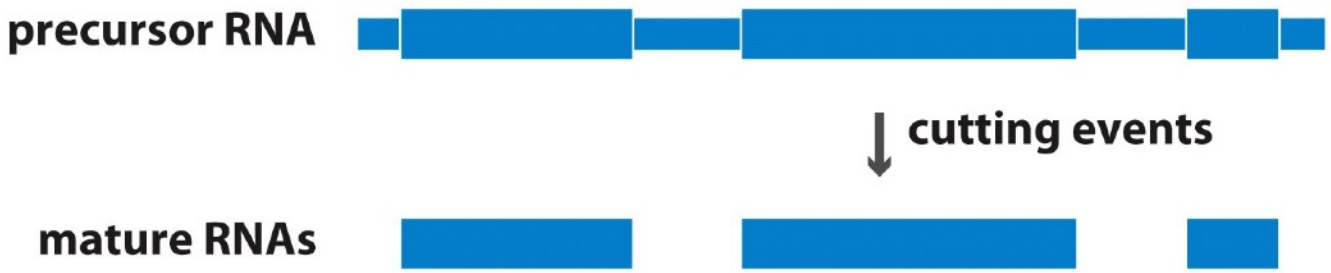


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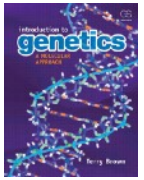
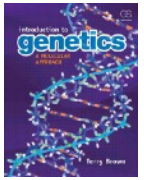
Figure . The initial transcripts of rRNA and tRNA genes are precursor molecules that must be cut into smaller pieces to release the mature RNAs

Chapter6

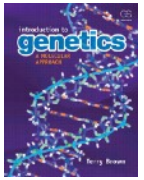


- Most rRNAs and tRNAs also contain unusual nucleotides that are not present in the initial transcripts.
- These unusual nucleotides are produced by chemical modification of the initial transcripts
- All of these processing reactions must be carried out with precision.
- The cuts must be made at exactly the right positions in the precursor molecules
- The chemical modifications must be equally precise.

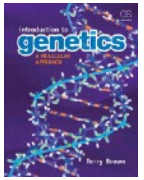


Ribosomal RNAs are transcribed as long precursor molecules

- Each ribosome contains one copy of each of the different rRNA molecules
- Three rRNAs for the bacterial ribosome or four for the eukaryotic version
- The entire complement of rRNA molecules transcribed together as a single unit



- The product of transcription, the primary transcript, is a long RNA precursor
- The **pre-rRNA**, containing each rRNA separated from the next by a short spacer
- In bacteria all three rRNAs are transcribed into a single pre-rRNA containing the mature molecules in the order: 16S–23S–5S
- For eukaryotic rRNA only the 28S, 18S, and 5.8S genes are transcribed together
  - The 5S genes occur elsewhere on the eukaryotic chromosomes and are transcribed independently of the main unit.



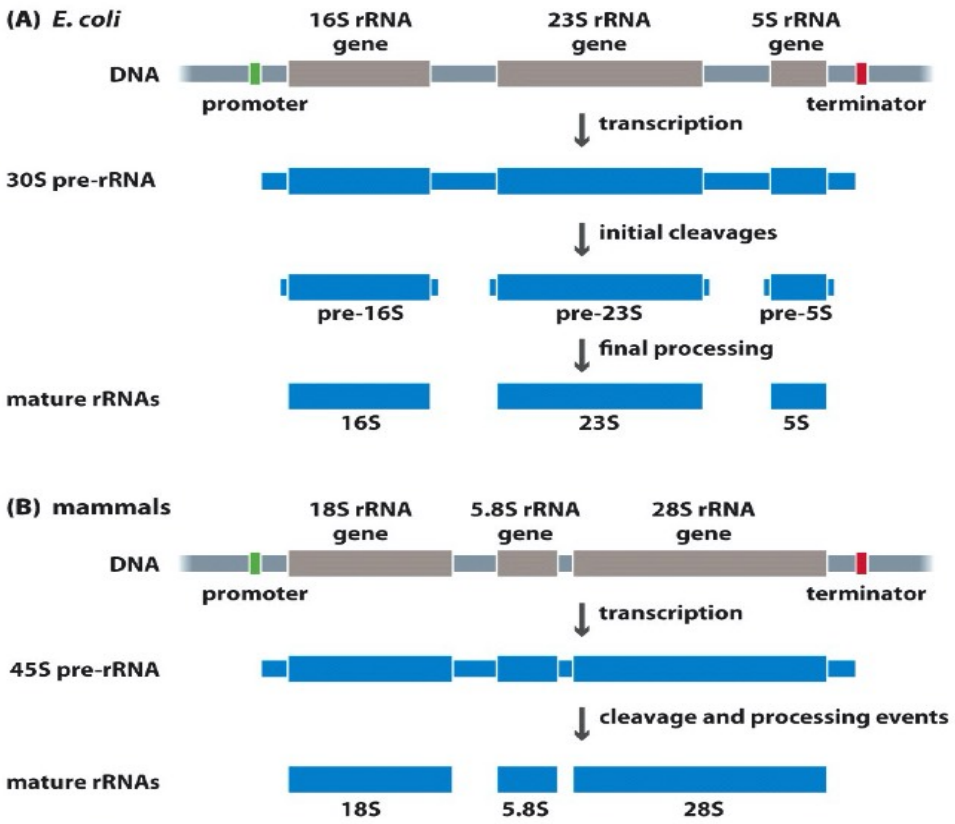
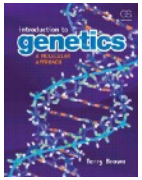
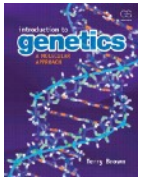


Figure . Processing of pre-rRNA in (A) *E. coli* and (B) mammals

Chapter6



- A variety of ribonucleases are involved in cutting the pre-rRNA molecules
- Most of these are double-strand– specific
- They cut the pre-rRNA by digesting short segments of double-stranded RNA formed by base pairing between different parts of the precursor
- This specific base pairing ensures that these cuts are made at the correct positions



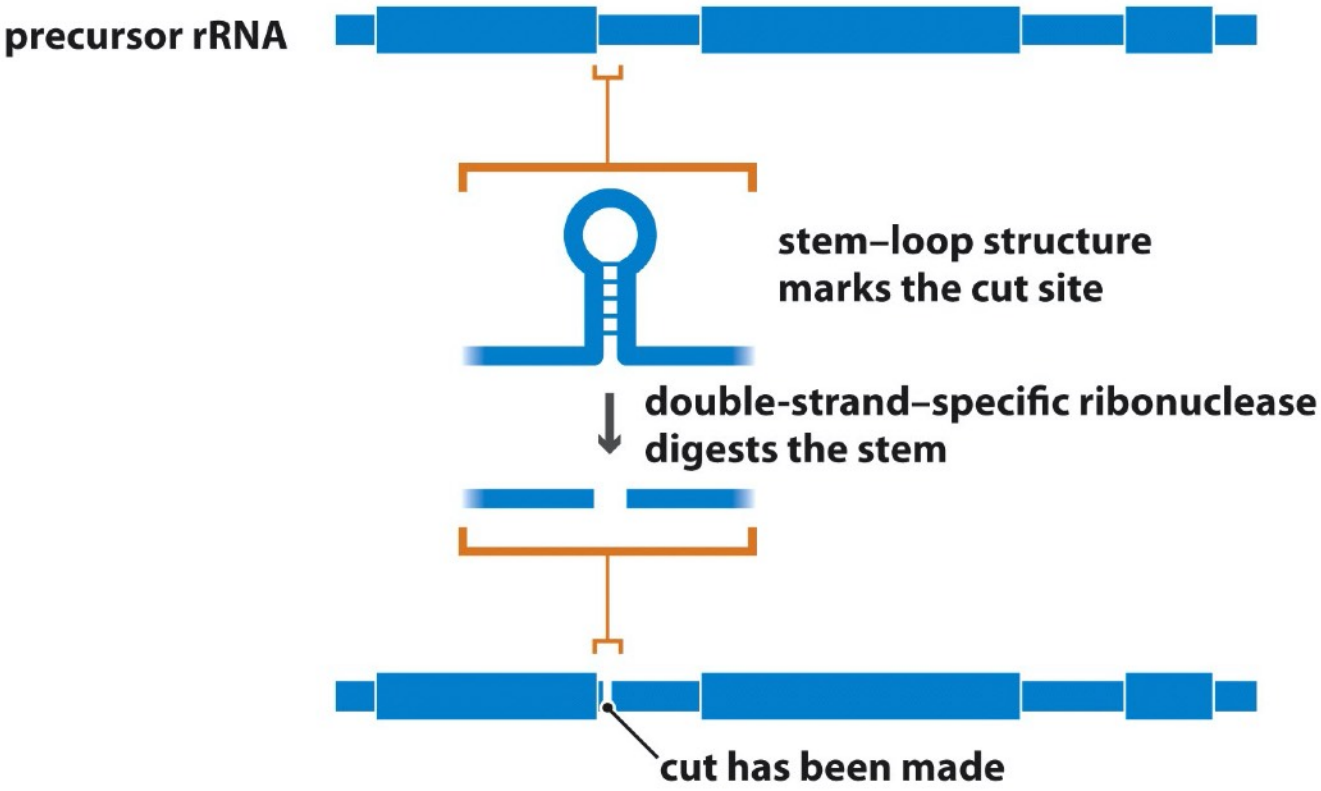
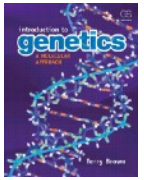
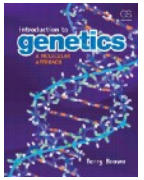


Figure. The role of a double strand–specific ribonuclease in cutting a precursor rRNA molecule.



- Cells not only need equal numbers of each rRNA but also need lots of them
- An actively growing *E. coli* cell contains 20,000 ribosomes and divides once every 20 minutes or so
- The *E. coli* chromosome contains seven copies of the rRNA transcription unit



In eukaryotes

- There are 50 to 5000 identical copies of the rRNA transcription unit present depending on species.
- These units are usually arranged into multigene families
- with large numbers of copies following one after the other, separated by non transcribed spacers

Figure 6.16 Introduction to Genetics (© Garland Science 2012)

Figure. A tandem array of rRNA transcription units. Each green box is a transcription unit comprising one set of 18S, 5.8S, and 28S rRNA genes.

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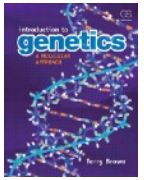
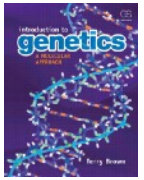


Gene amplification

- Occur in some eukaryotic cells (e.g. amphibian oocytes)
- Involves replication of rRNA genes into multiple DNA copies
- These copies subsequently exist as independent molecules not attached to the chromosomes
- Transcription of the amplified copies then produces additional rRNA molecules
- Gene amplification is not restricted to rRNA genes
- It also occurs with a few other genes whose transcription is required at a greatly enhanced rate in certain situations



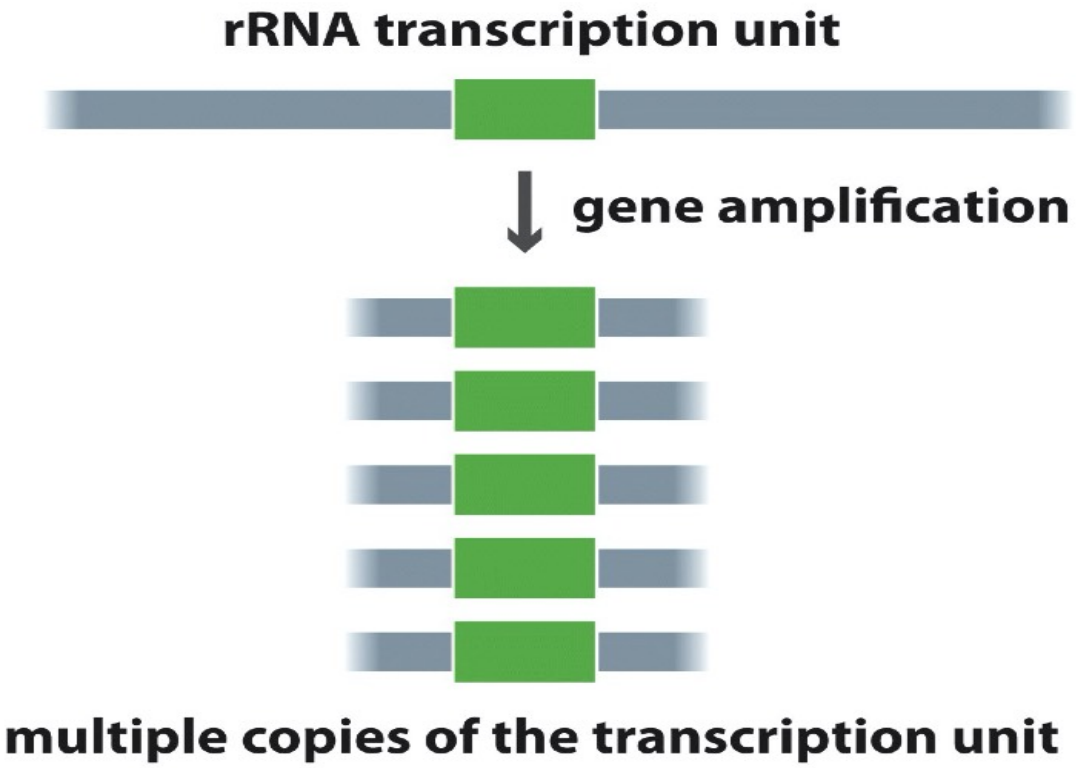
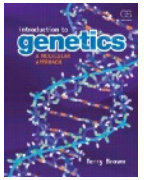
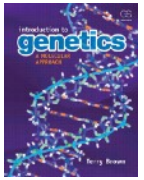


Figure. Production of multiple copies of rRNA genes by gene amplification. The amplified DNA copies exist as independent molecules and are not attached to any of the chromosomes.

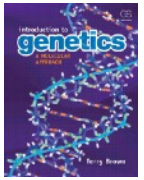


Transfer RNAs are also cut out of longer transcription units

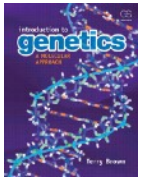
- In both bacteria and eukaryotes tRNAs are transcribed initially as precursor tRNA
- Which is subsequently processed to release the mature molecules.
- In *E. coli* there are several separate tRNA transcription units
- Some containing just one tRNA gene and some with as many as seven different tRNA genes in a cluster



- In some bacteria, tRNA genes also occur as infiltrators in the rRNA transcription units
- This is the case with *E. coli*, which has either one or two tRNA genes between the 16S and 23S genes in each of its seven rRNA transcription units



- All pre-tRNAs are processed in a similar though not identical way
- The tRNA sequence within the precursor molecule adopts its base-paired cloverleaf structure
- And two additional hairpin structures form, one on either side of the tRNA
- Processing begins with a cut by ribonuclease E or F, forming a new 3’ end just upstream of one of the hairpins



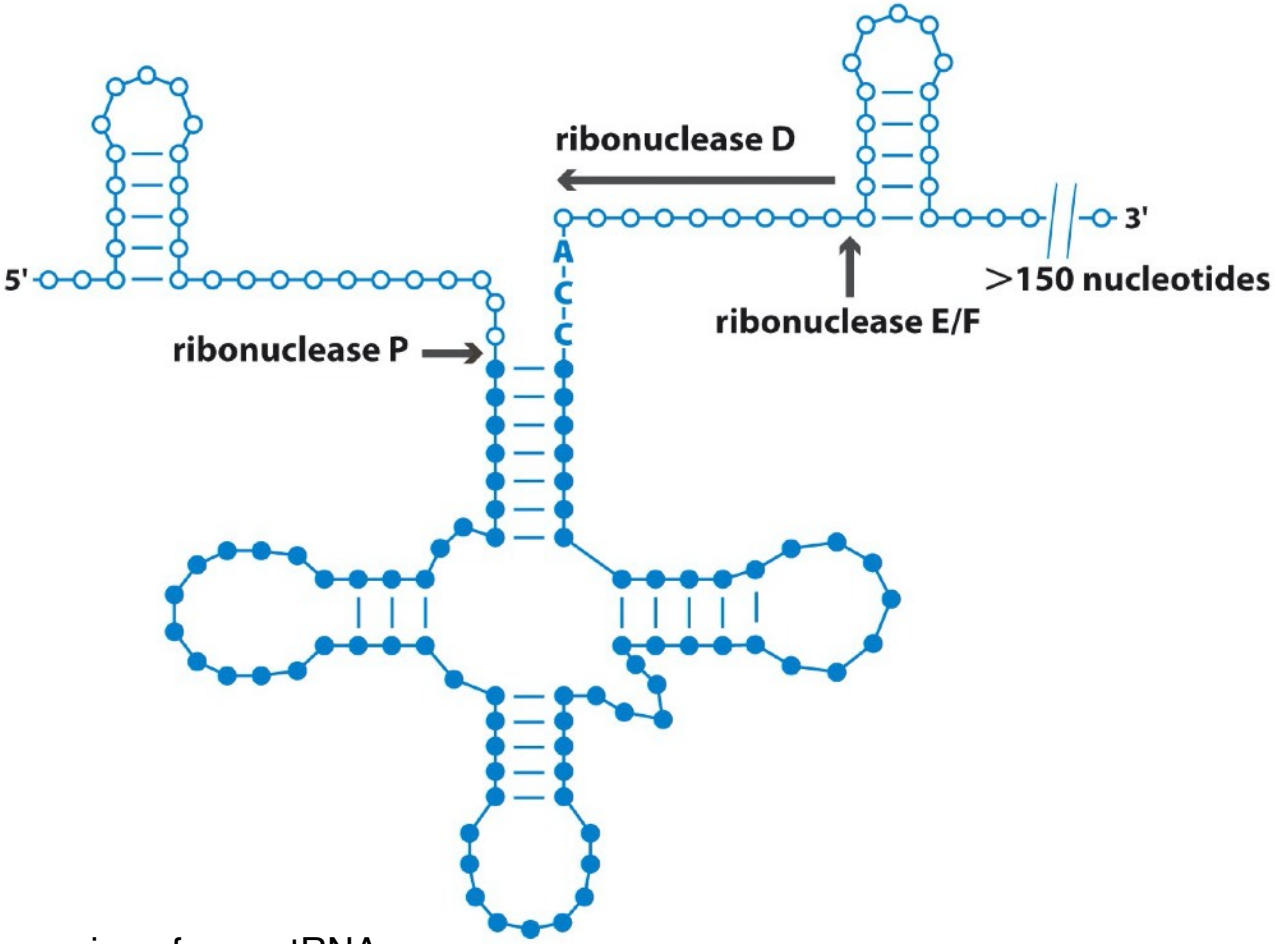
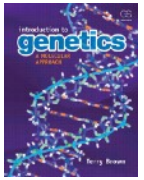
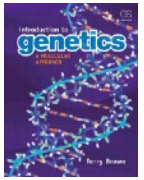


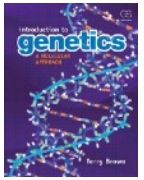
Figure. Processing of a pre-tRNA



- Ribonuclease D, which is an exonuclease, trims seven nucleotides from this new 3’ end
- Then pauses while ribonuclease P makes a cut at the start of the cloverleaf, forming the 5’ end of the mature tRNA.
- Ribonuclease D then removes two more nucleotides, creating the 3’ end of the mature molecule

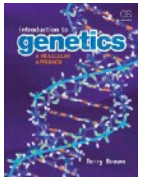


- All mature tRNAs must end with the trinucleotide 5'-CCA-3'.
- With some tRNAs the terminal CCA is present in the pre-RNA and is not removed by ribonuclease D
- But with some other pre-tRNAs this sequence is absent, or is removed by the processing ribonucleases
- If the CCA is absent or removed during processing, it has to be added by one or more template-independent RNA polymerases such as **tRNA nucleotidyltransferase**.

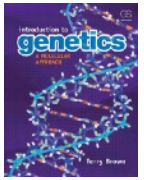


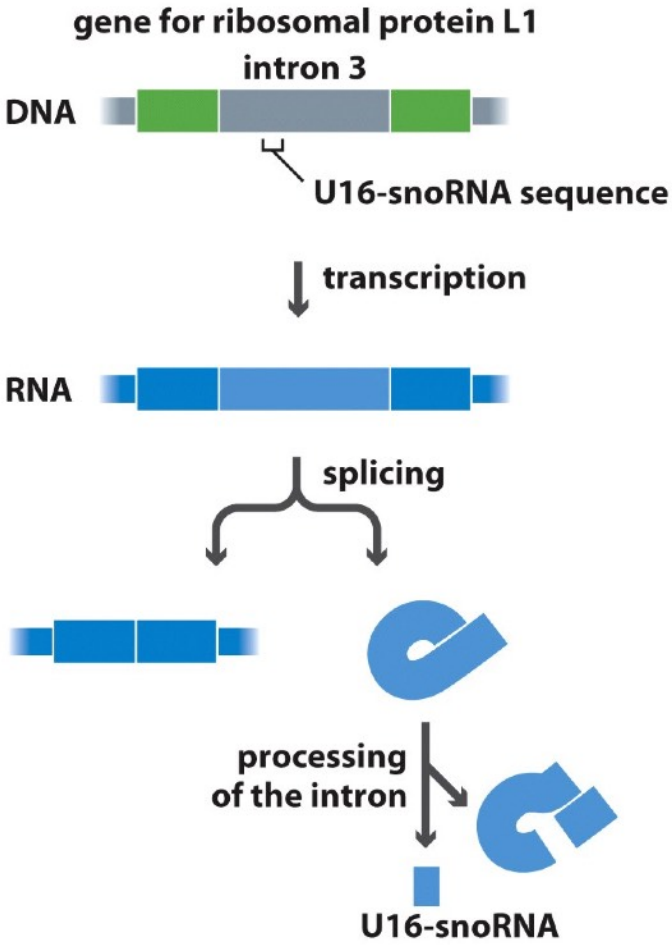
Removal of introns from pre-rRNAs and pre-tRNAs

- Introns are found not only in genes that are transcribed into mRNA, but also in some eukaryotic rRNA and tRNA genes.
- These introns are not the same as those found in mRNA:
  - They lack the characteristic consensus sequences, such as GU and AG at the splice sites
  - They are not associated with spliceosomes
- The mechanisms by which they are spliced are therefore different



- Splicing of pre-rRNAs and pre-tRNAs appears simply to be a part of the series of processing events needed to produce the mature molecules
- There is no equivalent of alternative splicing with rRNA and tRNA transcripts





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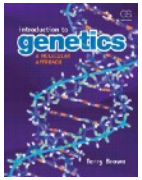
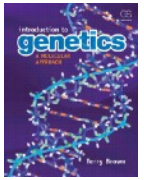
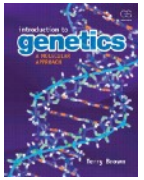


Some rRNA introns are enzymes

- Not only proteins can have enzymatic activity and catalyze biochemical reactions.
- The introns present in some pre-rRNAs are enzymes
- The biochemical reaction that they catalyze is their own splicing



- Introns are not common in rRNA genes but are found in certain protozoa such as *Tetrahymena*
- The introns of these organisms are able to fold up by intramolecular base pairing into a complex structure
- In which the two splice sites are brought close together
- The intron is then cut out and the two exons joined together in the complete absence of any protein molecules
- The intron catalyzes the reaction by acting as an RNA enzyme, or **ribozyme**



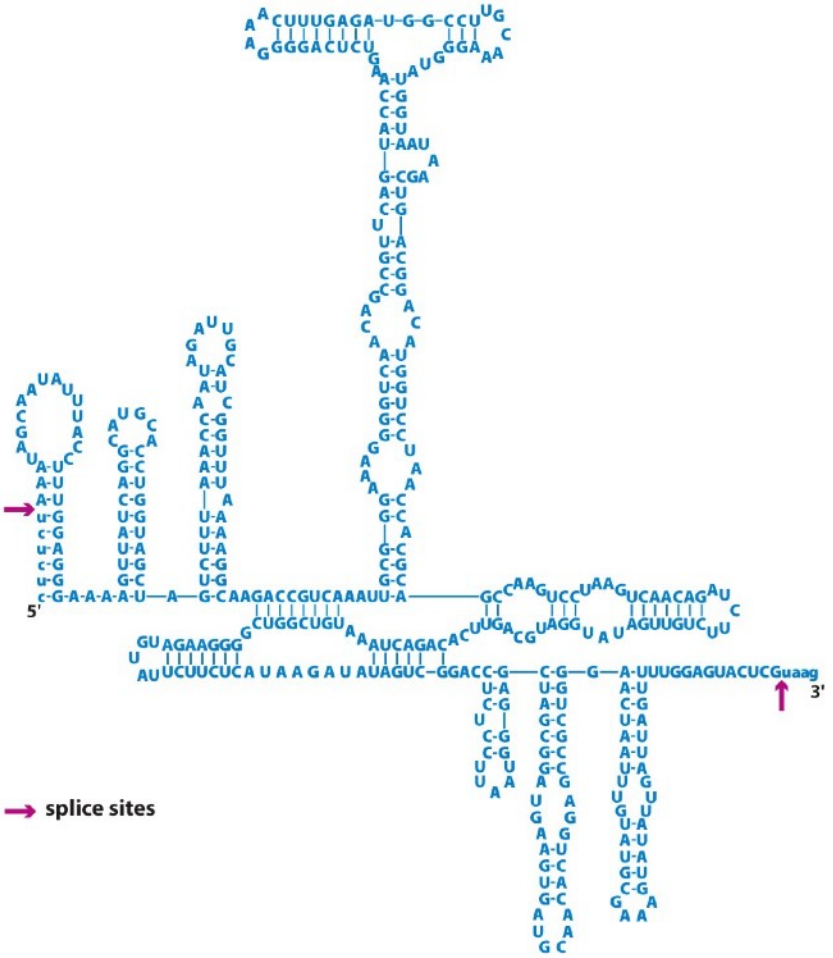
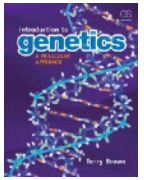
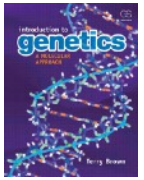


Figure. The base-paired structure of the *Tetrahymena* rRNA intron

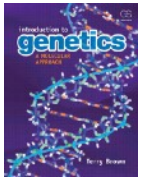
Chapter6



- The *Tetrahymena* self-splicing intron was the first known example of a ribozyme
- The self-splicing intron is a member of the “Group I” class of introns.
- Group I introns are also found in the rRNA genes of other protozoa and the mitochondrial DNA of fungi and yeast
- They are characterized by their ability to take up the base-paired structure displayed by the *Tetrahymena* intron

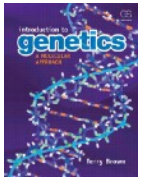


- Only the *Tetrahymena* intron has been shown to splice efficiently in the absence of proteins
- This does not mean that the other Group I introns are not ribozymes
- The splicing reaction might still be catalyzed by the intron itself
- With the proteins that are required in the cell acting only to stabilize the base-paired structure.

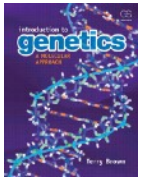


Some eukaryotic pre-tRNAs contain introns

- Transfer RNA introns are relatively common in lower eukaryotes
- But less frequent in vertebrates
- introns are present in only 6% of all human tRNA genes.
- Introns in eukaryotic pre-tRNAs are 14 to 60 nucleotides in length
- They are usually found at the same position in the transcript within the anticodon arm.



- The intron sequence is variable
- But includes a short region complementary to part of the anticodon arm.
- Base pairing between the complementary sequences forms a short stem between two loops in the unspliced pre-tRNA



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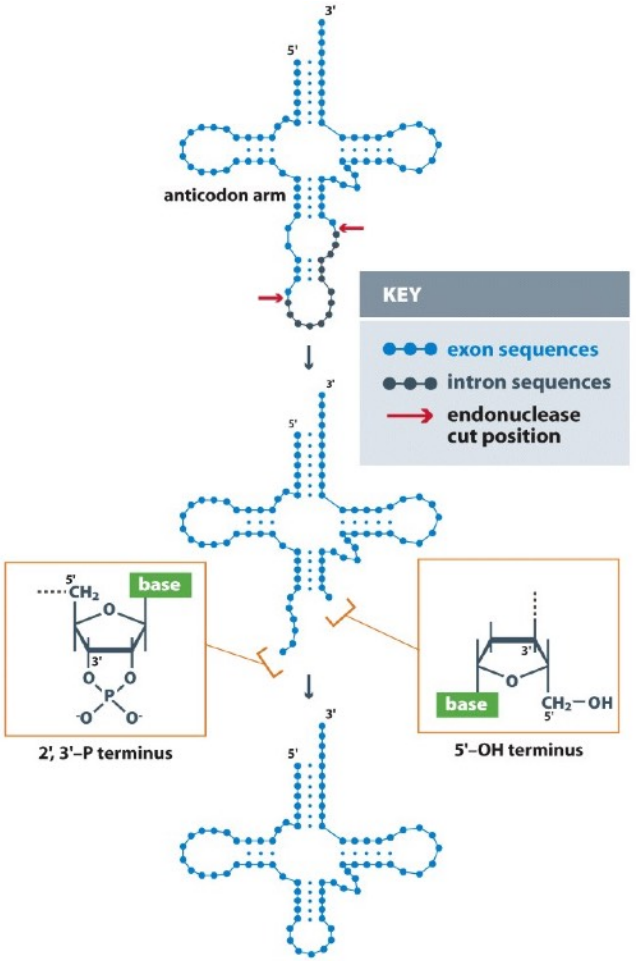
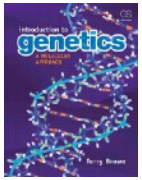
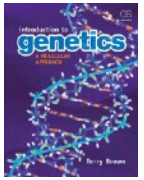


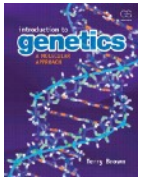
Chapter6



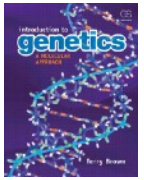
- Unlike the mRNA and Group I introns, removal of pre-tRNA introns involves an endonuclease.
- This enzyme contains four nonidentical subunits
- one of which uses the structure of the base-paired intron as a guide to identify the correct positions at which the RNA should be cut



- The upstream and downstream cuts are then made by two of the other enzyme subunits.
- Cleavage leaves :
  - an unusual cyclic phosphate structure attached to the 3’ end of the upstream exon
  - a hydroxyl group at the 5’ end of the downstream exon
- Before the ends can be joined, the cyclic phosphate must be converted to a 3’–OH end, and the 5’–OH terminus to 5’–P



- The two ends are held in proximity by the natural base pairing adopted by the tRNA sequence, and are ligated together
- The enzymatic activities needed to convert the ends and join them together are all provided by a single protein



To think about

- **Where does the polymerase come from?**
- **The number of copies of rDNA genes in prokaryotic and eukaryotic genomes.**
- **The difference between intron splicing in eukaryotic genes and spacer removal in prokaryotic and eukaryotic pre-rRNA processing.**

Stuff to know

Aminoacylation

Ribosomal DNA

rDNA

CCA

80S ribosome

5S rRNA

tRNA

tRNA loops

Ribosomal small subunit

rRNA transcription unit

23S rRNA

Aminoacyl-tRNA synthetase

70S ribosome

5.8S rRNA

Anticodon loop

Ribosomal large subunit

Pre-rRNA

28S rRNA

16S rRNA

tRNA charging

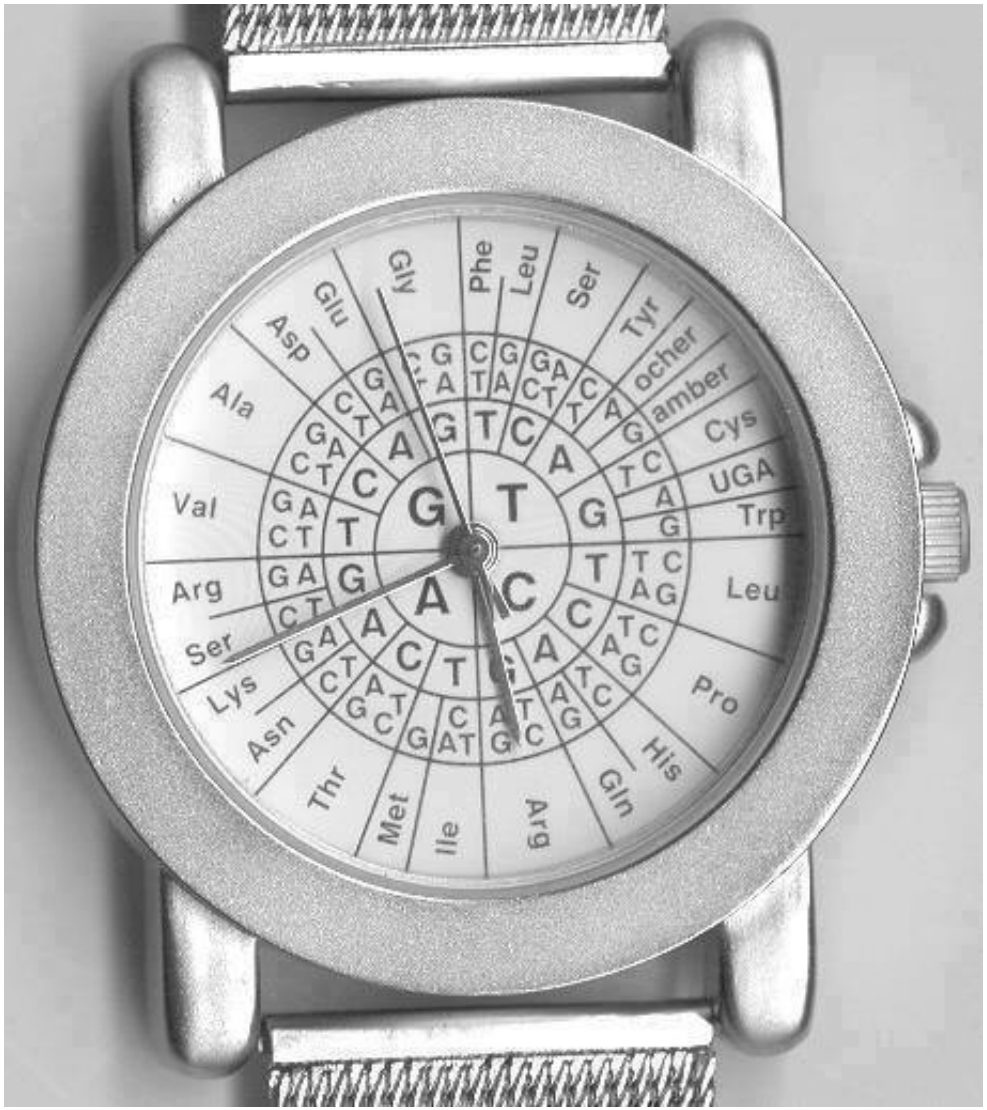
Ribosomes

Cloverleaf shape

Expectations

- You know the structure of tRNA and the process of charging the molecule with amino acids.
- You know the ribosomes of prokaryotes and eukaryotes:
  - Components
  - Genes
  - Structure

For a smile


Gly
Phe
Leu
Ser
Tyr
ocher
amber
Cys
UGA
Trp
Leu
Pro
His
Gln
Arg
Ile
Met
Thr
Asn
Lys
Ser
Arg
Val
Ala
Asp
Glu