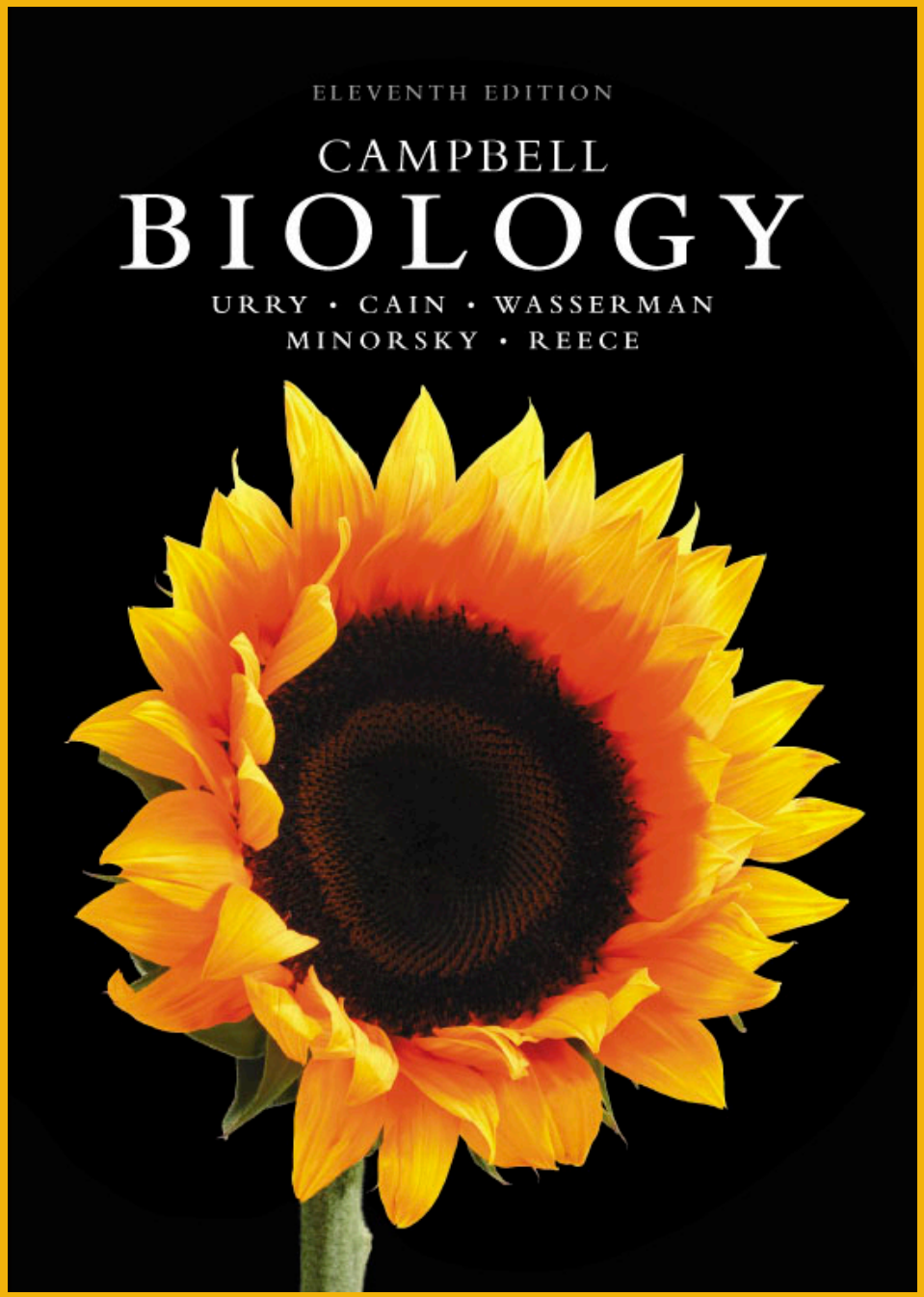


# Chapter 26

# Phylogeny and the Tree of Life

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

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# Investigating the Tree of Life

- **Phylogeny** is the evolutionary history of a species or group of related species
  - For example, a phylogeny shows that legless lizards and snakes evolved from different lineages of legged lizards
- The discipline of **systematics** classifies organisms and determines their evolutionary relationships

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Figure 26.1

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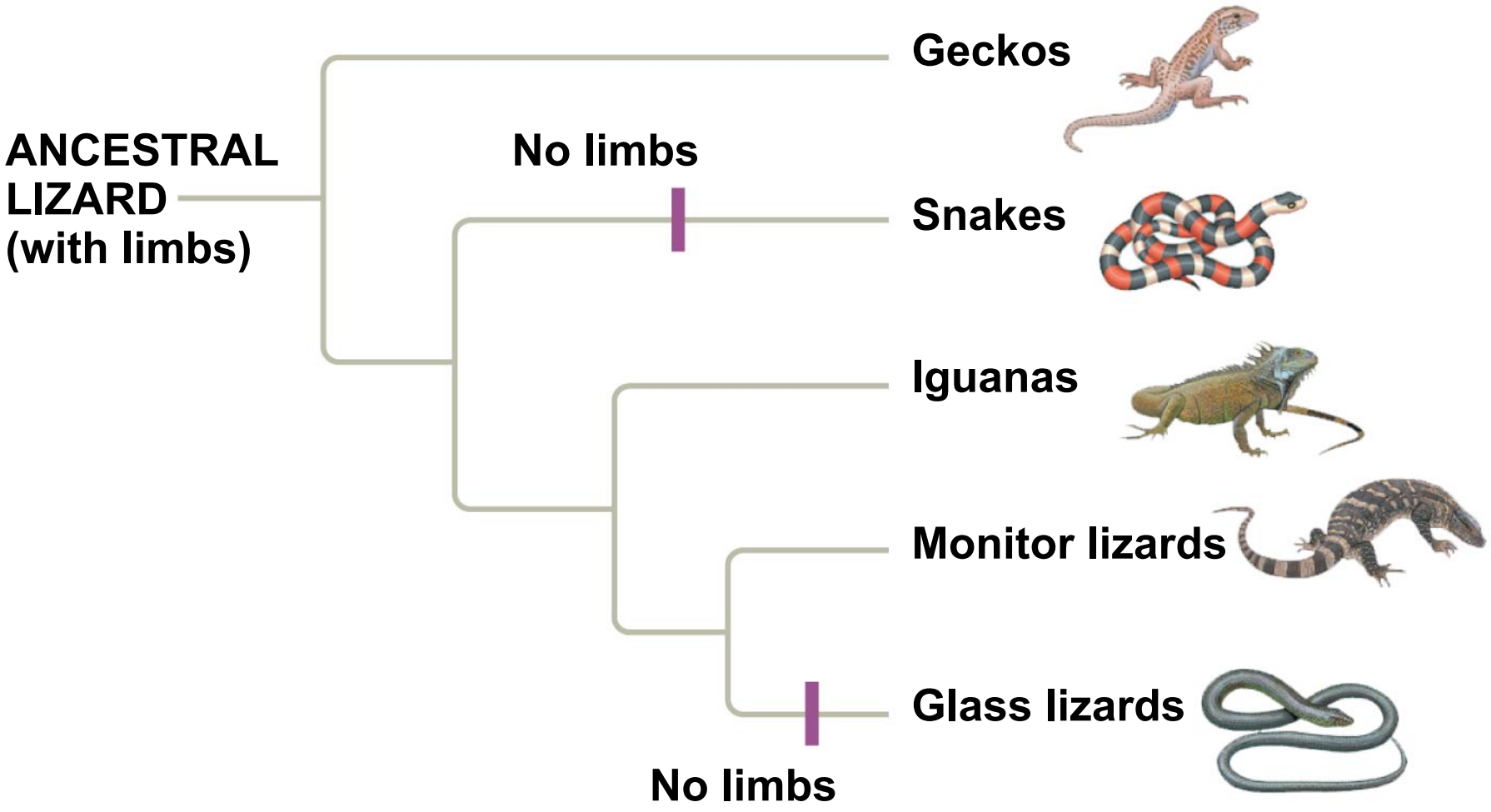
Figure 26.2

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# Binomial Nomenclature

- In the 18th century, Carolus Linnaeus published a system of taxonomy based on resemblances
- Two key features of his system remain useful today: two-part names for species and hierarchical classification

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- The two-part scientific name of a species is called a **binomial**
- The first part of the name is the **genus**
- The second part, called the specific epithet, is unique for each species within the genus
- The first letter of the genus is capitalized, and the entire species name is italicized
- Both parts together name the species (not the specific epithet alone)

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# Hierarchical Classification

- Linnaeus introduced a system for grouping species in increasingly inclusive categories
- The taxonomic groups from broad to narrow are **domain**, **kingdom**, **phylum**, **class**, **order**, **family**, genus, and species
- A taxonomic unit at any level of hierarchy is called a **taxon**
- The broader taxa are not comparable between lineages
  - For example, an order of snails has less genetic diversity than an order of mammals

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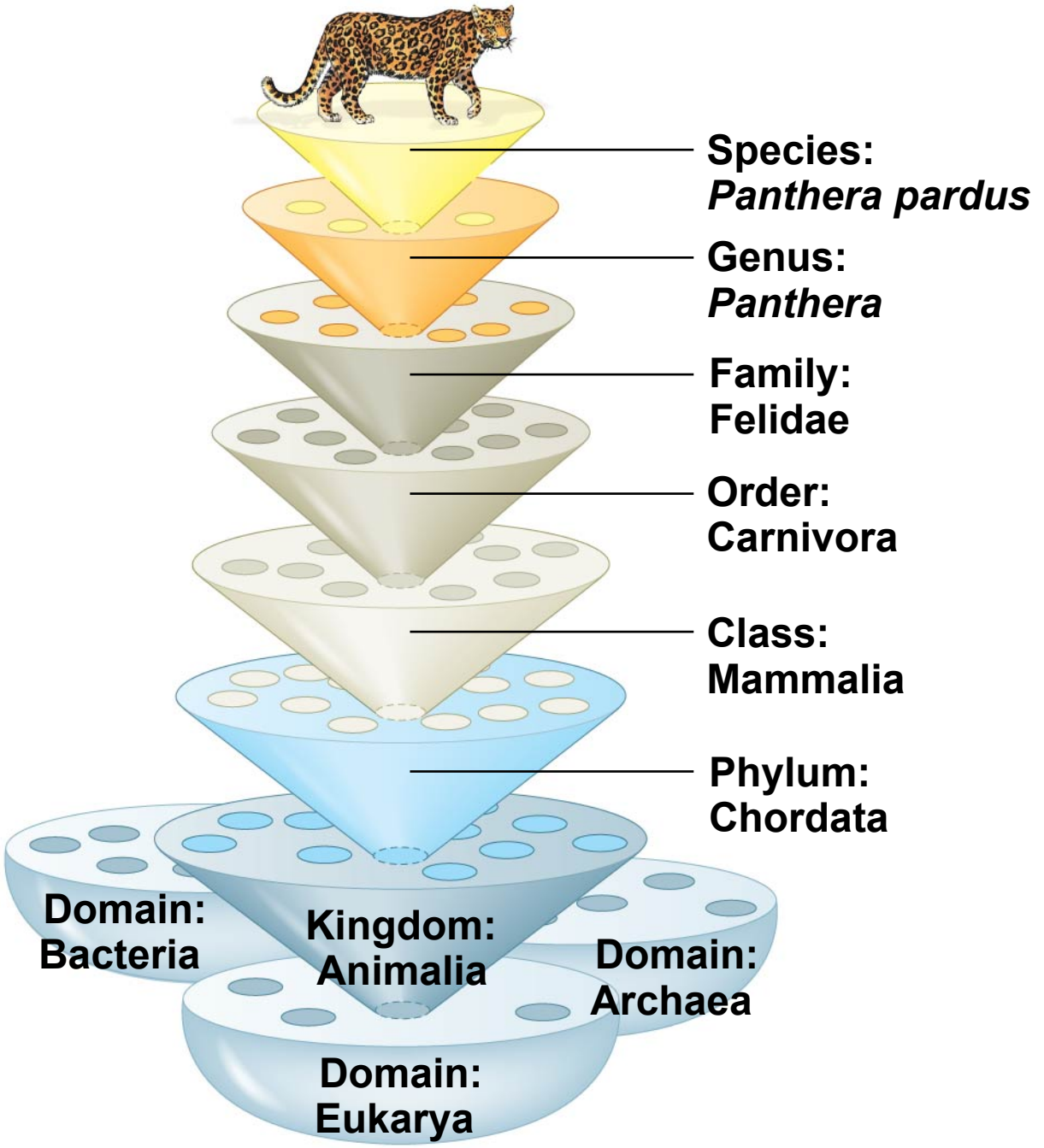
Figure 26.3

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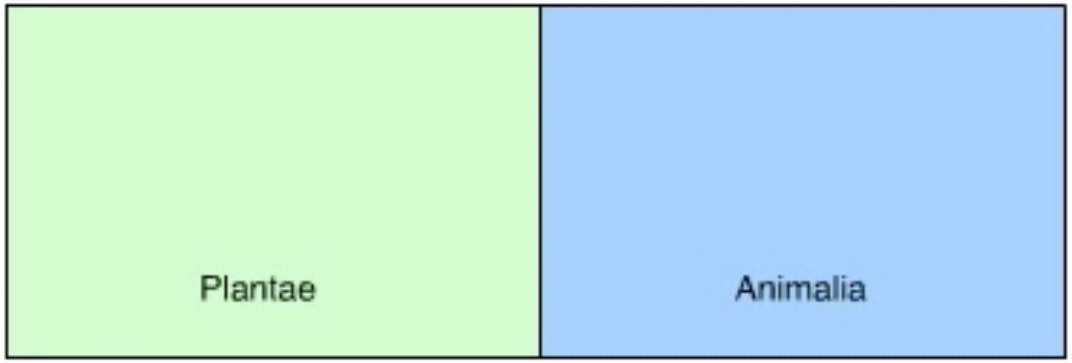
# Animation: Classification Schemes

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# Linking Classification and Phylogeny

- The evolutionary history of a group of organisms can be represented in a branching **phylogenetic tree**

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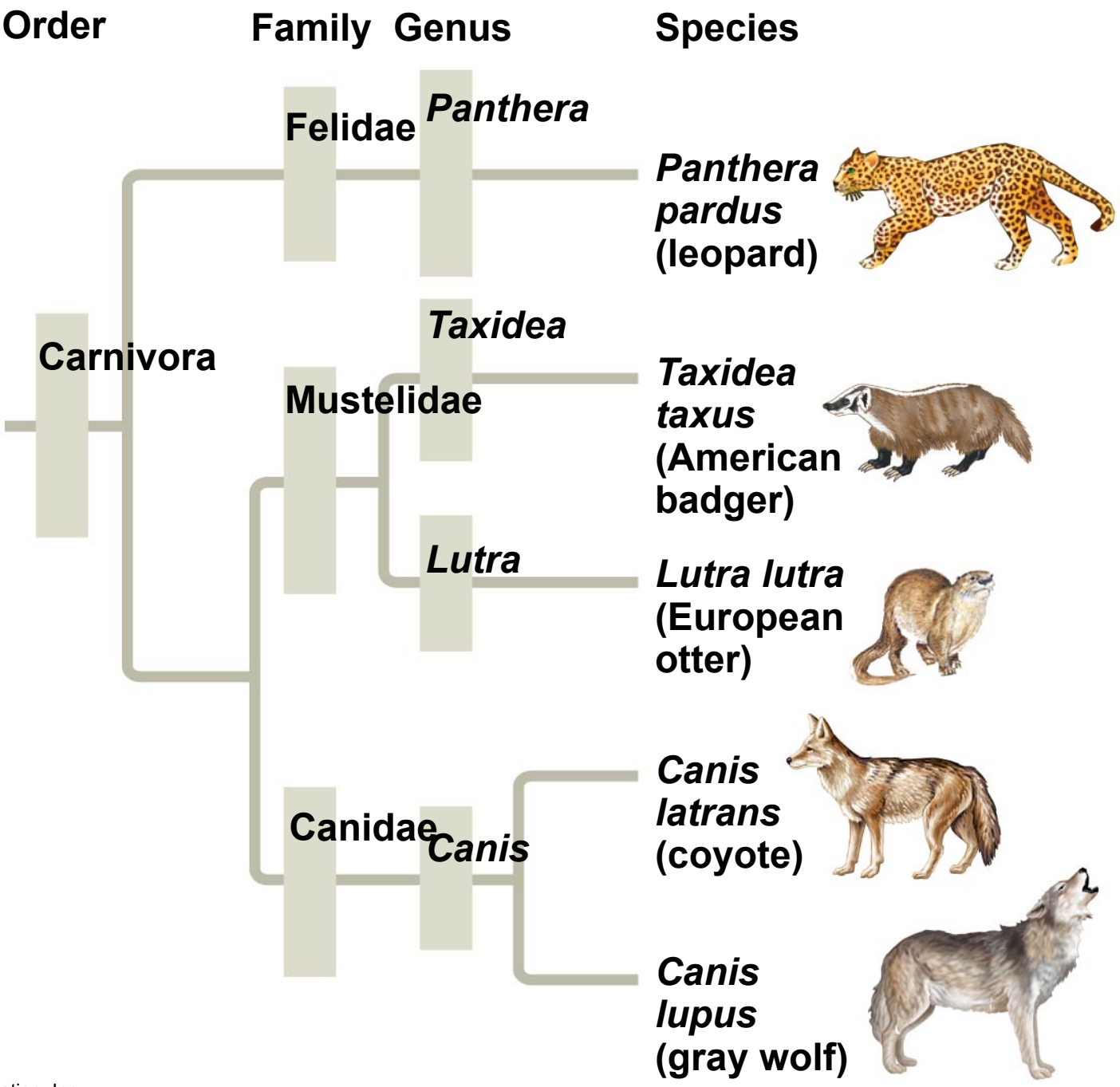
Figure 26.4

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- Linnaean classification and phylogeny can differ from each other
- Systematists have proposed a classification system that would recognize only groups that include a common ancestor and all its descendants

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# What We Can and Cannot Learn from Phylogenetic Trees

- A phylogenetic tree represents a hypothesis about evolutionary relationships
- Each **branch point** represents the divergence of two evolutionary lineages from a common ancestor
- **Sister taxa** are groups that share an immediate common ancestor that is not shared by any other group

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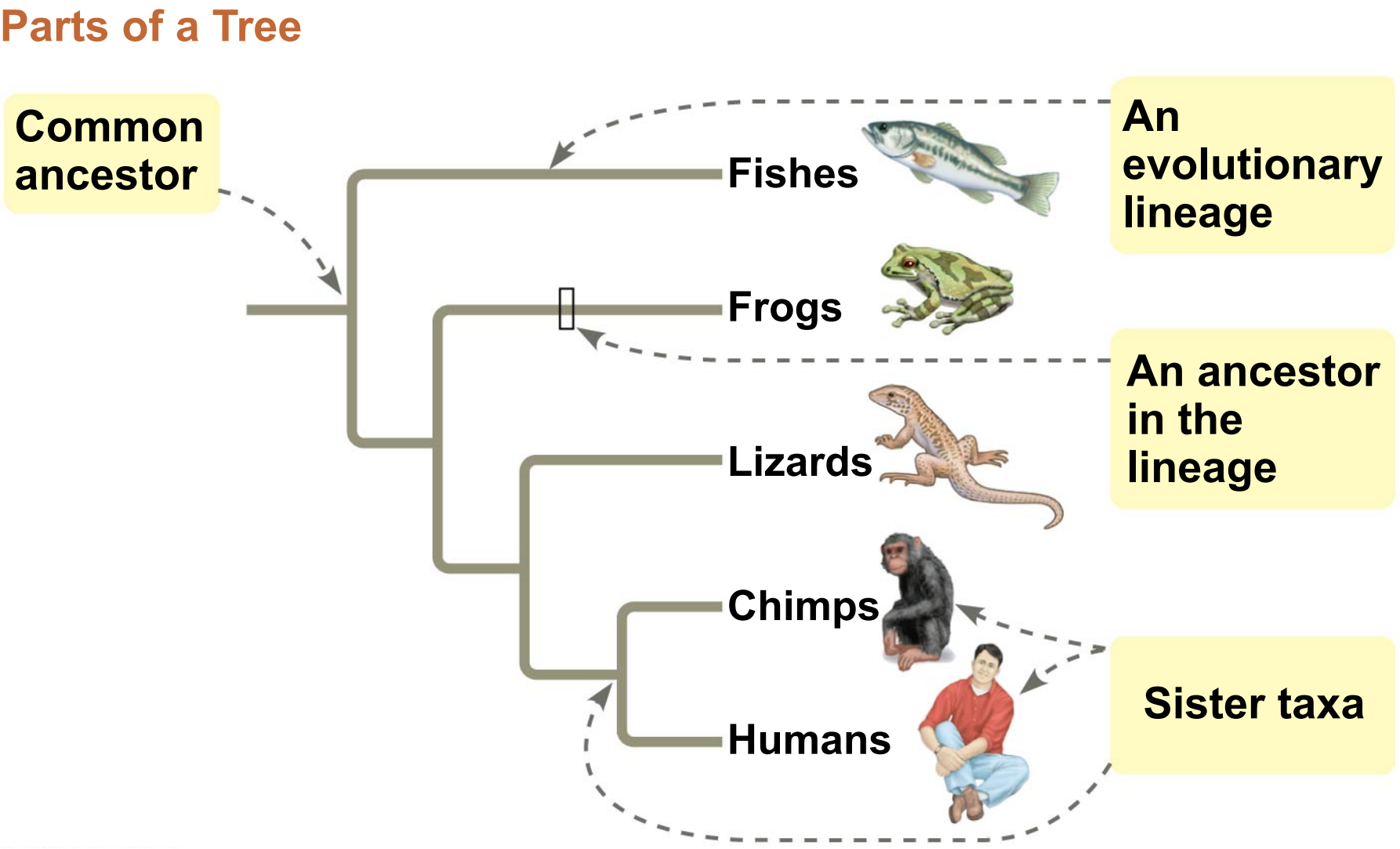
Figure 26.5a

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- Phylogenetic trees can be drawn horizontally, vertically, or diagonally without changing the relationships between groups

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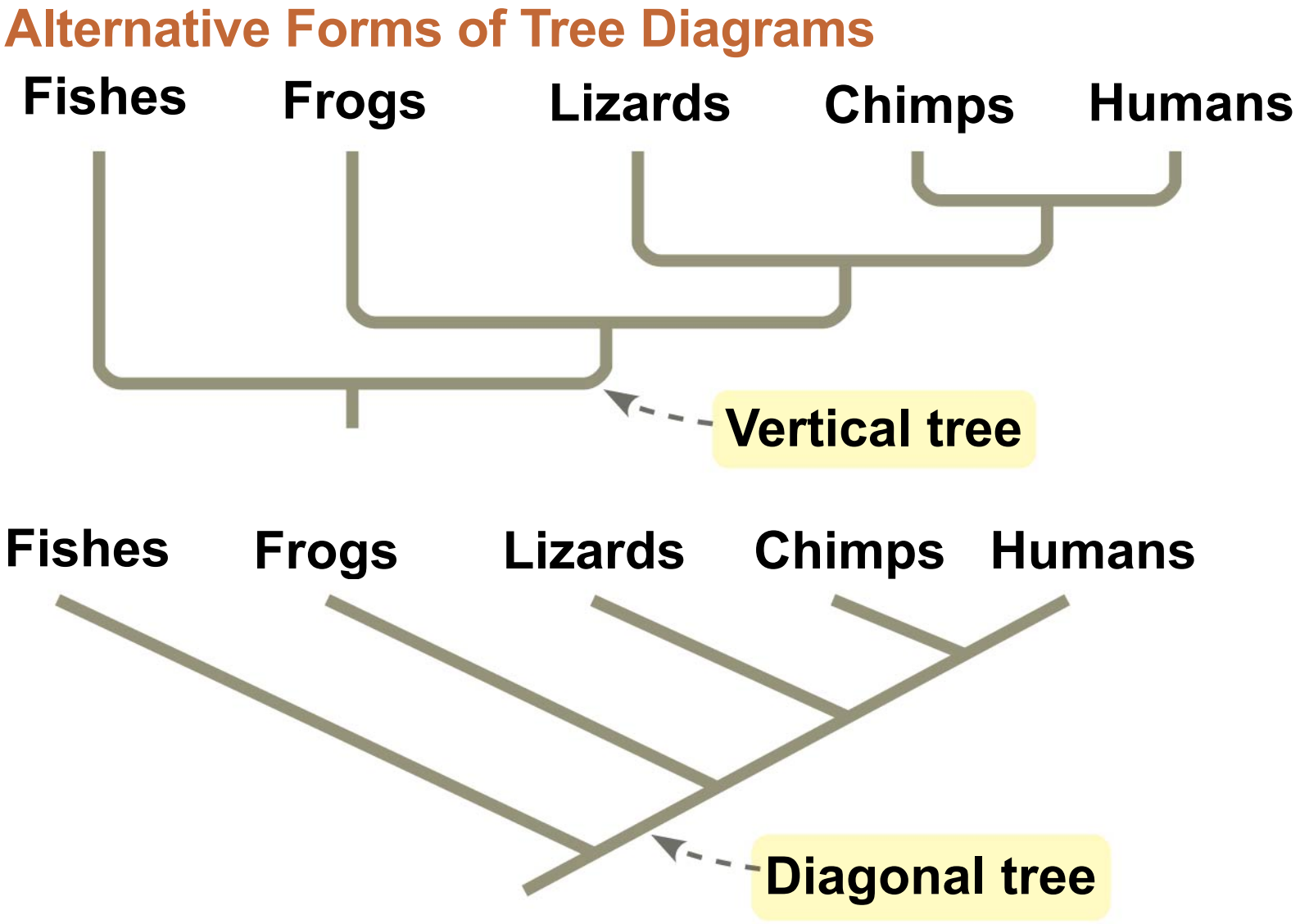
Figure 26.5b

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- Tree branches can be rotated around a branch point without changing the evolutionary relationships

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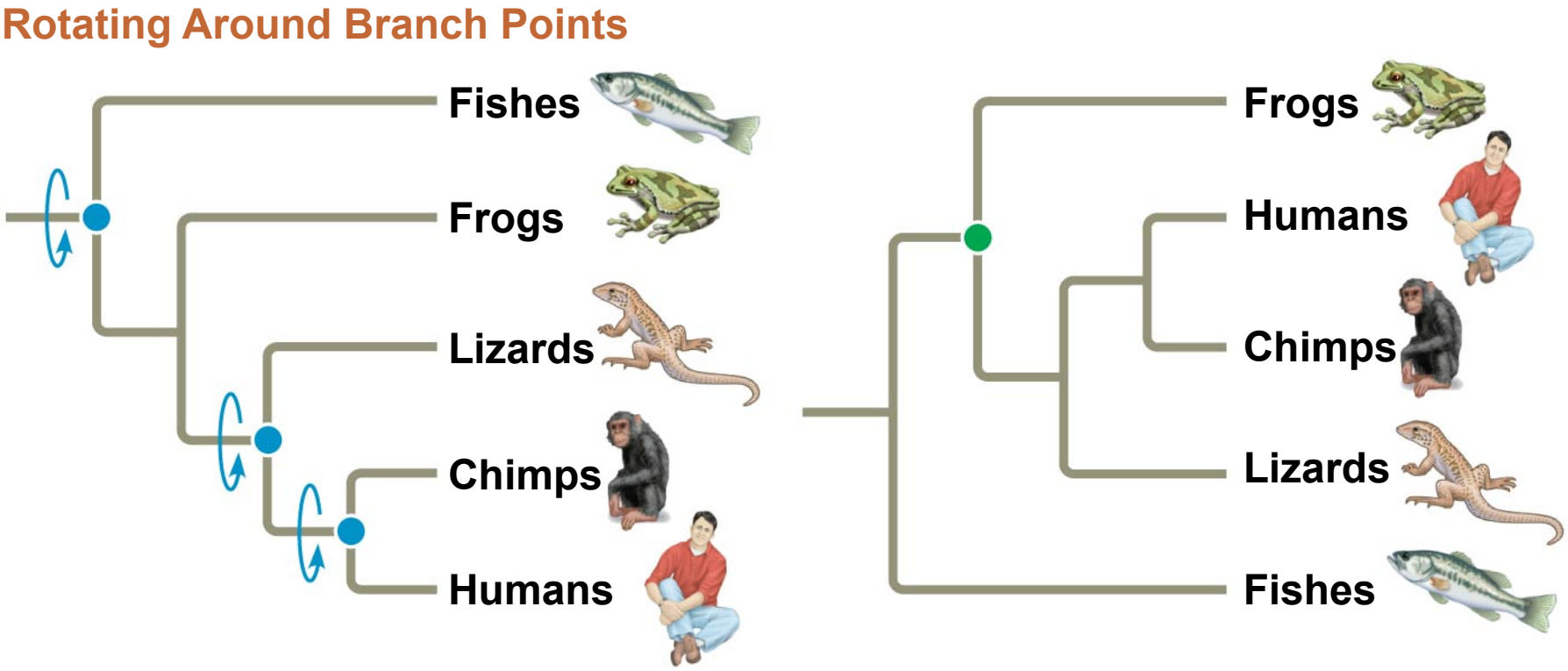
Figure 26.5c

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- A **rooted** tree includes a branch to represent the most recent common ancestor of all taxa in the tree
- A **basal taxon** diverges early in the history of a group and originates near the common ancestor of the group

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- Phylogenetic trees show patterns of descent, not phenotypic similarity
- Phylogenetic trees do not indicate when species evolved or how much change occurred in a lineage
- It should not be assumed that a taxon evolved from the taxon next to it

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# Applying Phylogenies

- Phylogeny provides important information about similar characteristics in closely related species
- A phylogeny was used to identify the species of whale from which “whale meat” originated to discover if the whale was harvested illegally

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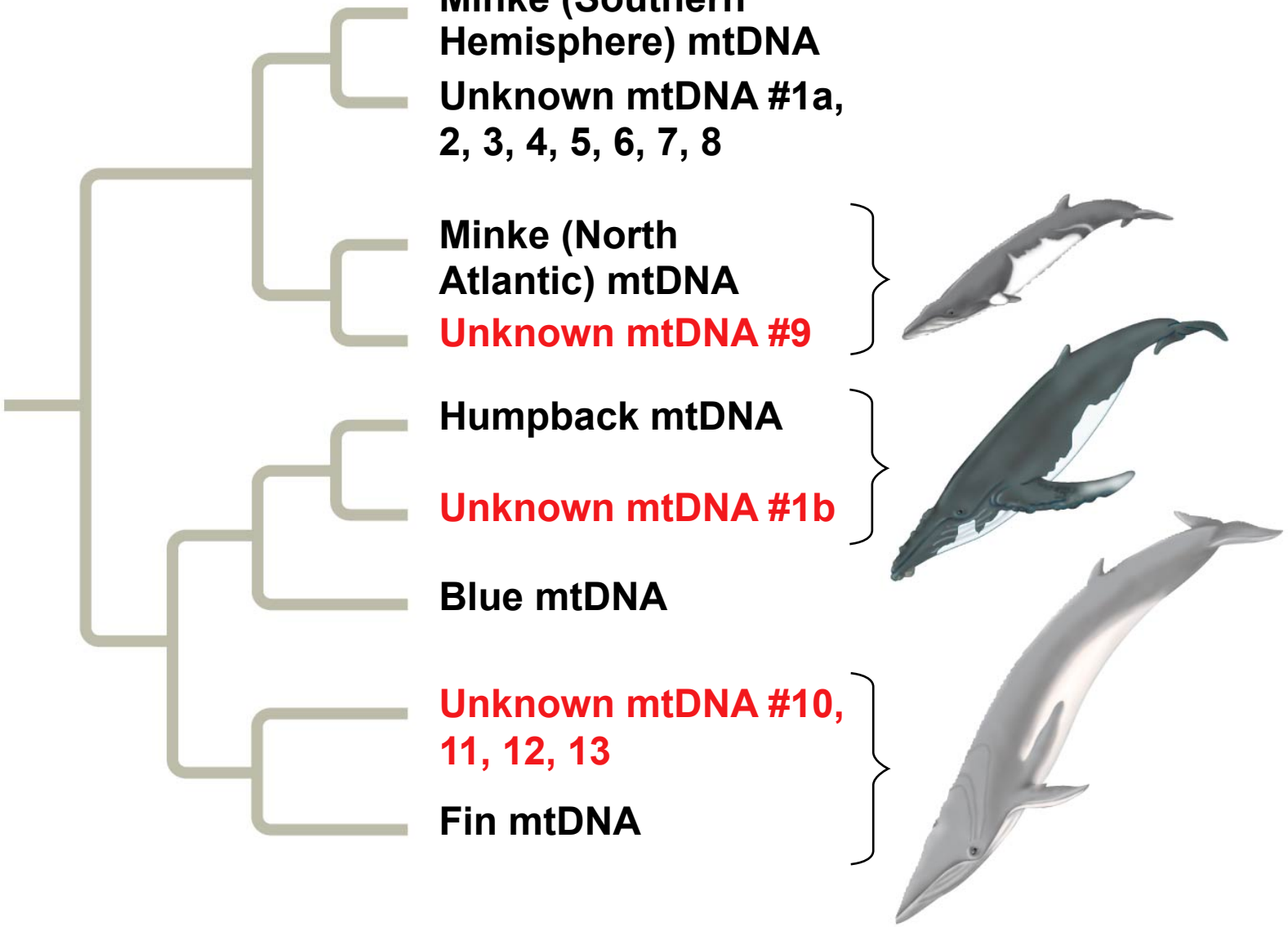
Figure 26.6 **Results**




Data from C. S. Baker and S. R. Palumbi, Which whales are hunted? A molecular genetic approach to monitoring whaling, *Science* 265:1538–1539 (1994). Reprinted with permission from AAAS.

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# Concept 26.2: Phylogenies are inferred from morphological and molecular data

- To infer phylogenies, systematists gather information about the morphologies, genes, and biochemistry of living organisms

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# Morphological and Molecular Homologies

- Phenotypic and genetic similarities due to shared ancestry are called **homologies**
- Organisms with similar morphologies or DNA sequences are likely to be more closely related than organisms with different structures or sequences

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# Sorting Homology from Analogy

- When constructing a phylogeny, systematists need to distinguish whether a similarity is the result of homology or **analogy**
- Homology is similarity due to shared ancestry
- Analogy is similarity due to convergent evolution

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- Convergent evolution occurs when similar environmental pressures and natural selection produce similar (analogous) adaptations in organisms from different evolutionary lineages

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Figure 26.7

Australian “mole”

African golden mole

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- Homology can be distinguished from analogy by comparing fossil evidence and the degree of complexity
- The more elements that are similar in two complex structures, the more likely it is that they are homologous
- If the genes in two organisms share many portions of nucleotide sequence, it is likely they are homologous

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# Evaluating Molecular Homologies

- Systematists use computer programs and mathematical tools when analyzing comparable DNA segments from different organisms

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Figure 26.8_1

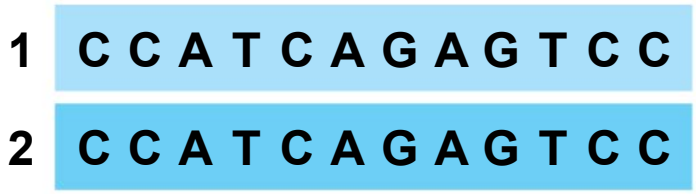


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Figure 26.8_2

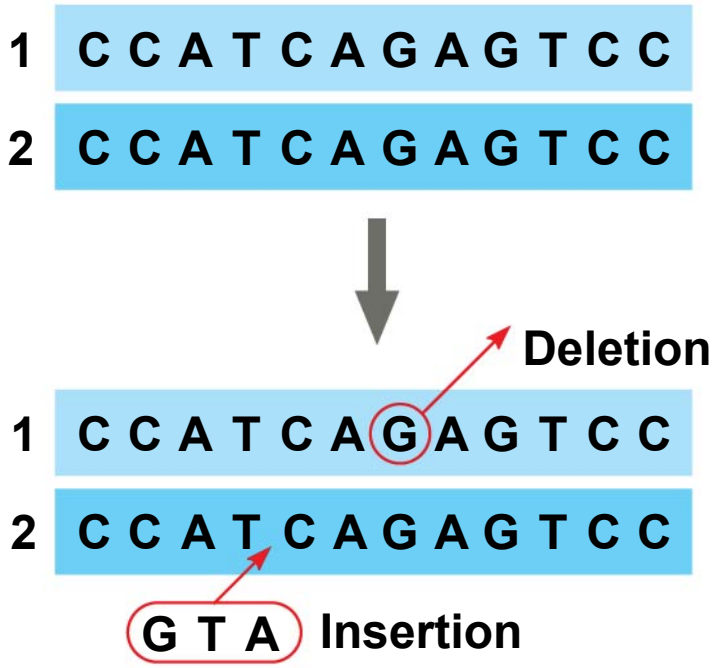


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Figure 26.8_3

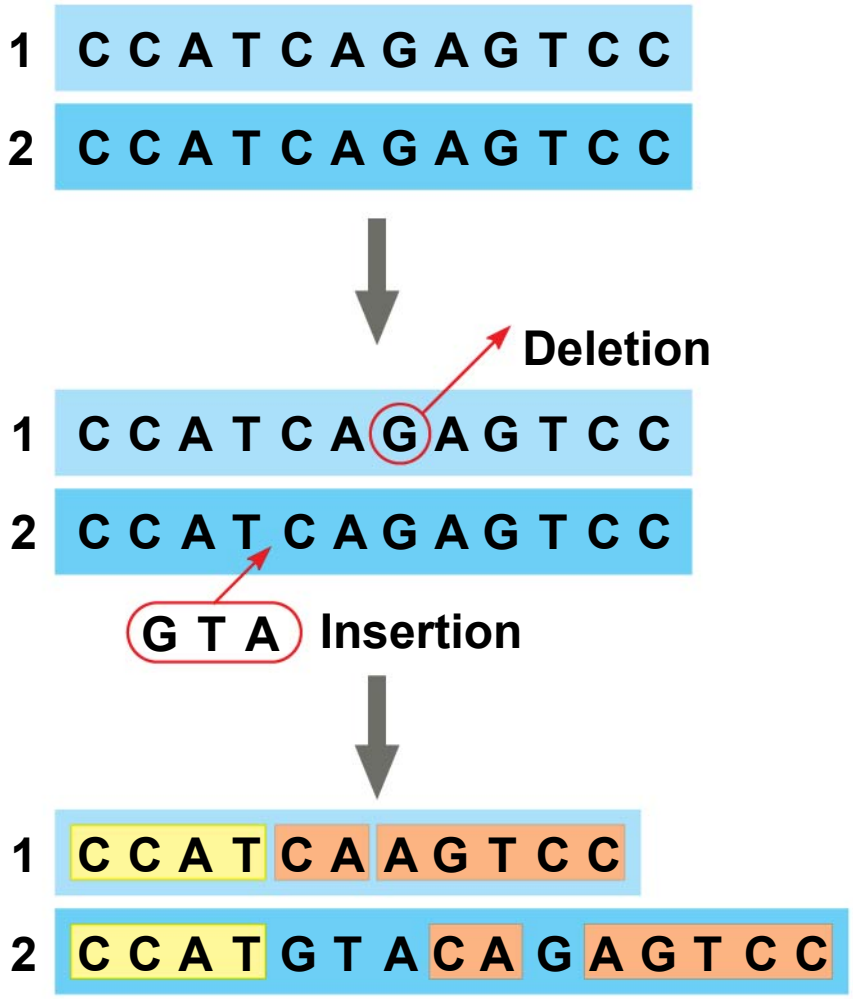


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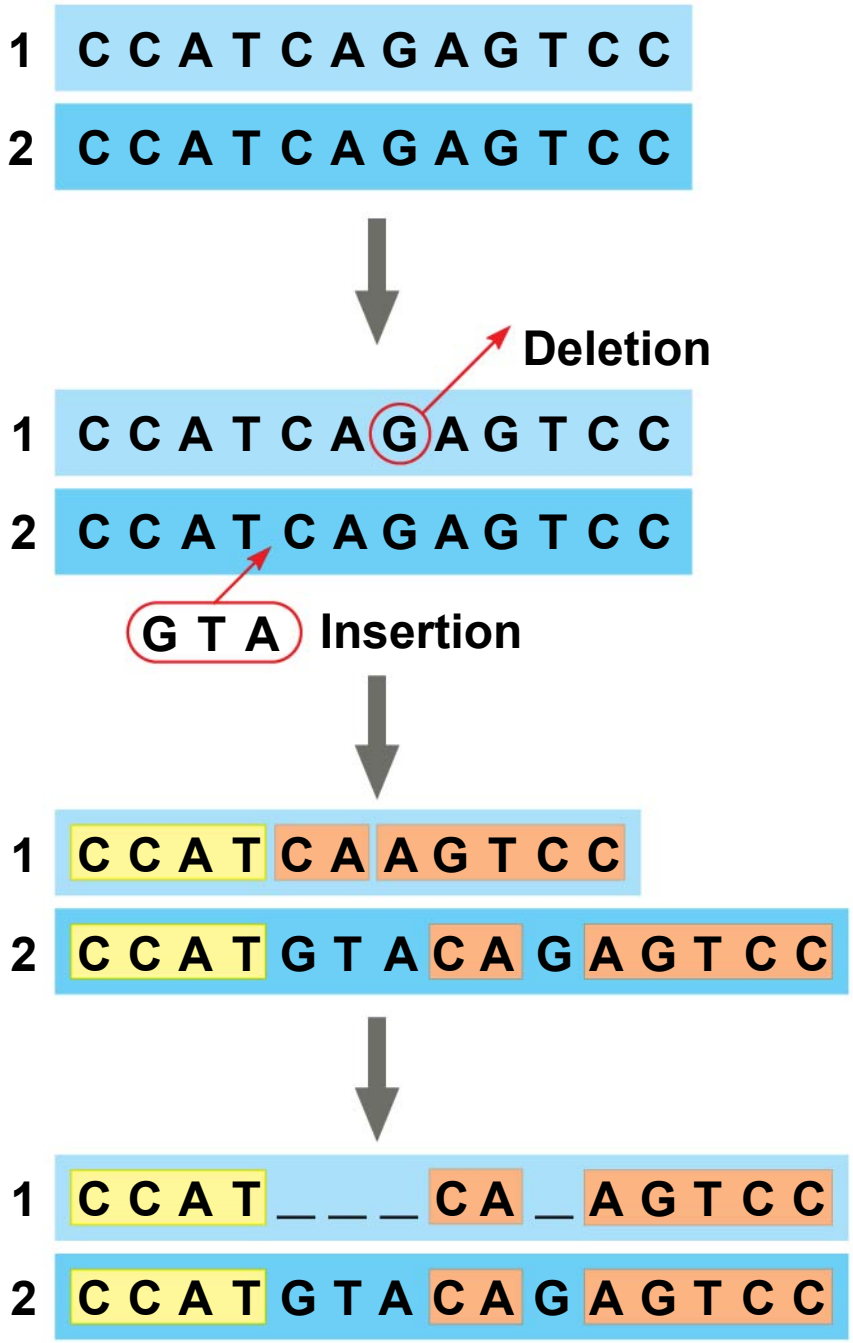
Figure 26.8_4

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- It is also important to distinguish homology from analogy in molecular similarities
- Mathematical tools help to identify molecular homoplasies, or coincidental similarities

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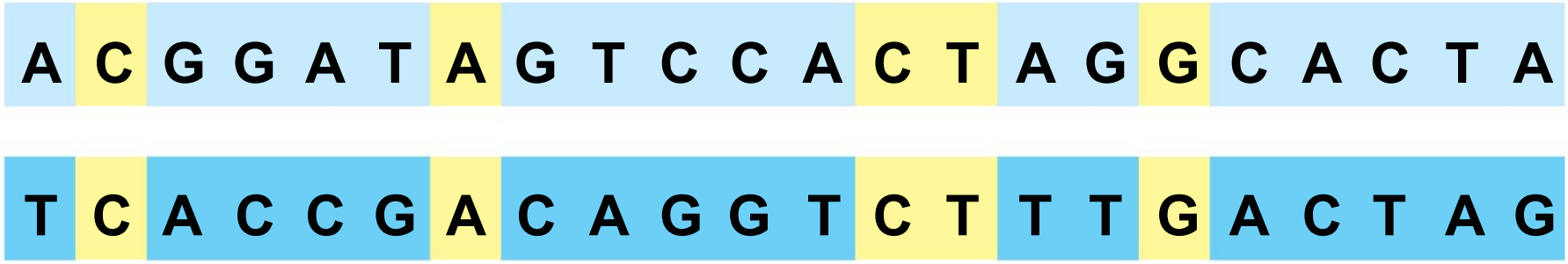
Figure 26.9

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# Concept 26.3: Shared characters are used to construct phylogenetic trees

- Once homologous characters have been identified, they can be used to infer a phylogeny

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# Cladistics

- **Cladistics** groups organisms by common ancestry
- A **clade** is a group of species that includes an ancestral species and all its descendants
- Clades can be nested in larger clades, but not all groupings of organisms qualify as clades

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- A valid clade is **monophyletic**, signifying that it consists of the ancestor species and all its descendants
- A **paraphyletic** grouping consists of an ancestral species and some, but not all, of the descendants
- A **polyphyletic** grouping includes distantly related species but does not include their most recent common ancestor

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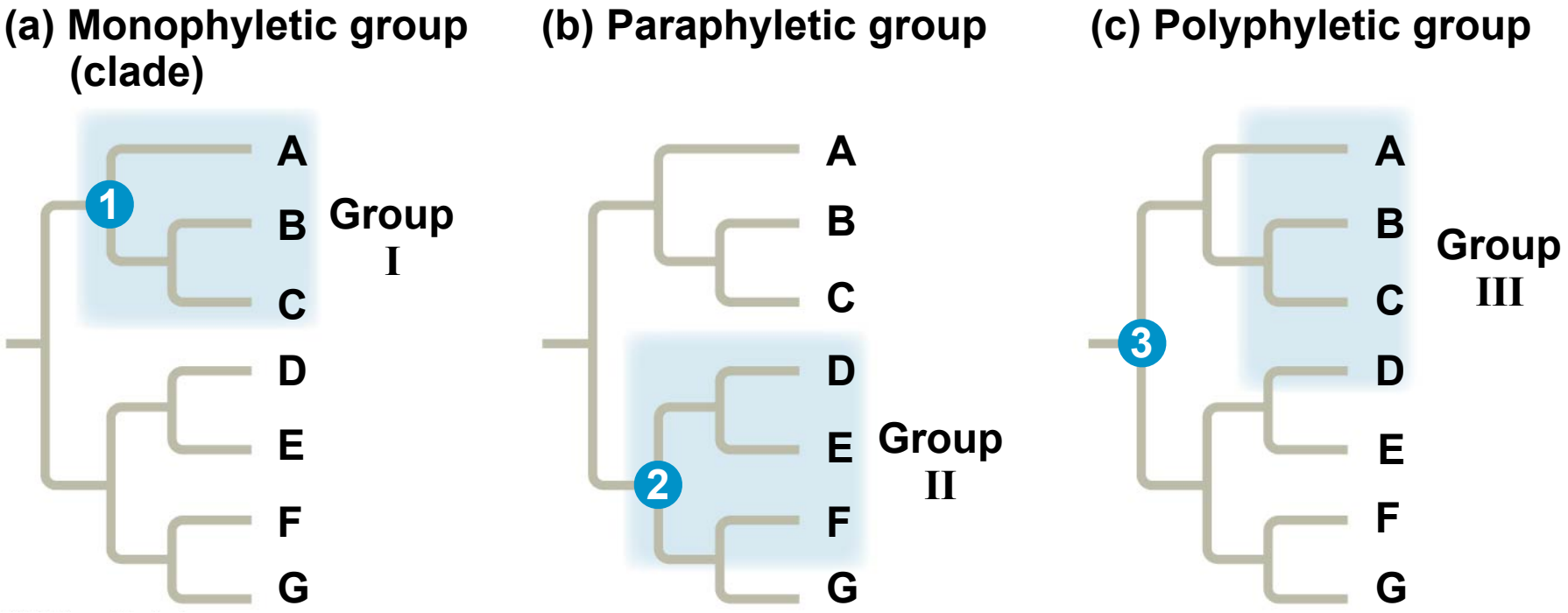
Figure 26.10

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- Polyphyletic groups are distinguished from paraphyletic groups by the fact that they do not include the most recent common ancestor
- Biologists avoid defining polyphyletic groups and instead reclassify organisms if evidence suggests they are polyphyletic

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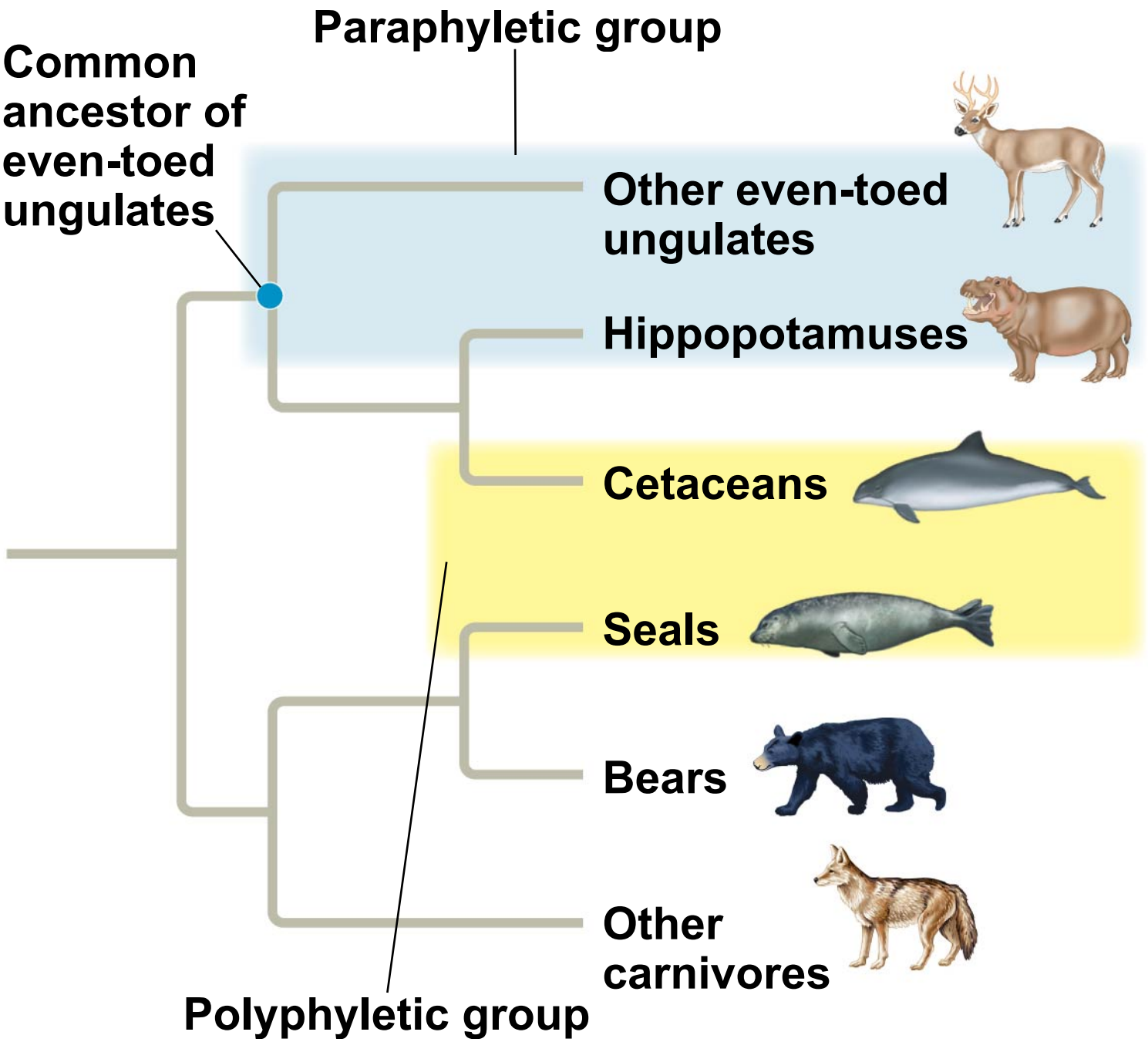
Figure 26.11

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# *Shared Ancestral and Shared Derived Characters*

- In comparison with its ancestor, an organism has both shared and different characters
- A **shared ancestral character** is a character that originated in an ancestor of the taxon
- A **shared derived character** is an evolutionary novelty unique to a particular clade
- A character can be both ancestral and derived, depending on the context

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# *Inferring Phylogenies Using Derived Characters*

- When inferring evolutionary relationships, it is useful to know in which clade a shared derived character first appeared

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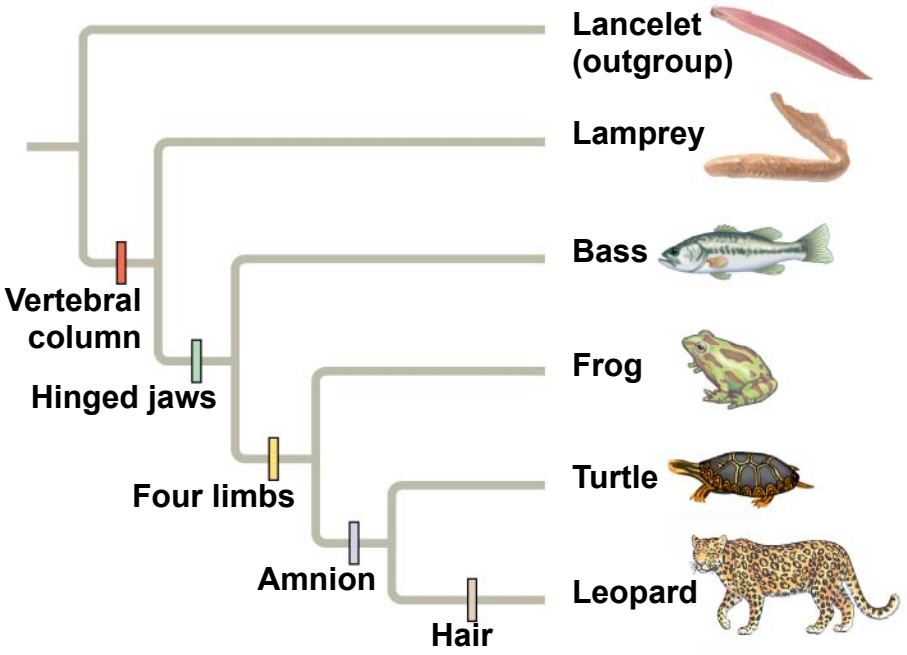
Figure 26.12

TAXA

| CHARACTERS | Lancelet (outgroup) | Lamprey | Bass | Frog | Turtle | Leopard |
|---|---|---|---|---|---|---|
| Vertebral column (backbone) | 0 | 1 | 1 | 1 | 1 | 1 |
| Hinged jaws | 0 | 0 | 1 | 1 | 1 | 1 |
| Four limbs | 0 | 0 | 0 | 1 | 1 | 1 |
| Amnion | 0 | 0 | 0 | 0 | 1 | 1 |
| Hair | 0 | 0 | 0 | 0 | 0 | 1 |

(a) Character table




(b) Phylogenetic tree

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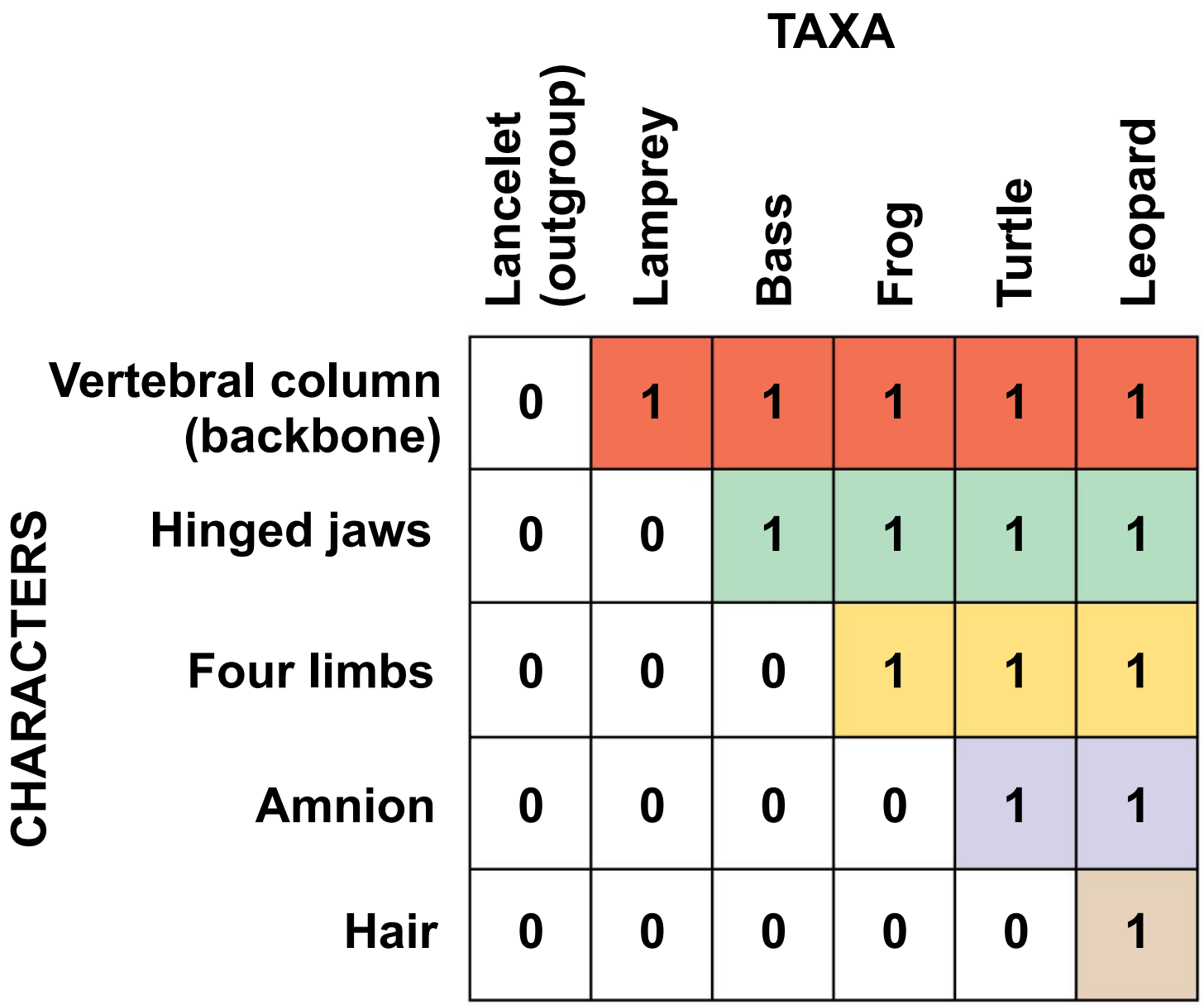
Figure 26.12a




(a) Character table

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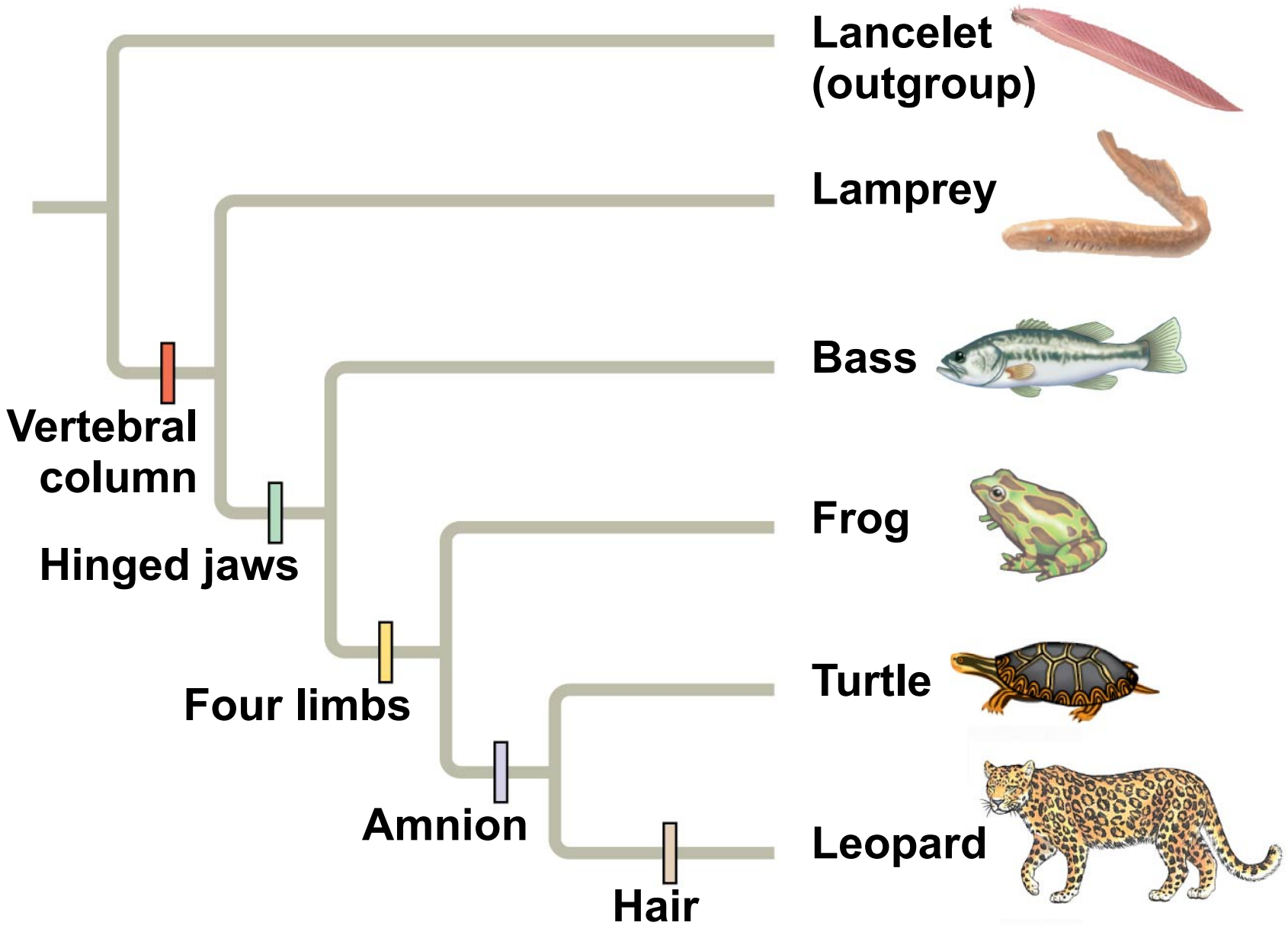
Figure 26.12b




(b) Phylogenetic tree

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- An **outgroup** is a species or group of species that is closely related to the **ingroup**, the various species being studied
- The outgroup is a group that has diverged before the ingroup
- Systematists compare each ingroup species with the outgroup to differentiate between shared derived and shared ancestral characters

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- Characters shared by the outgroup and ingroup are ancestral characters that predate the divergence of both groups from a common ancestor

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# Phylogenetic Trees with Proportional Branch Lengths

- In some trees, the length of a branch can reflect the number of genetic changes that have taken place in a particular DNA sequence in that lineage

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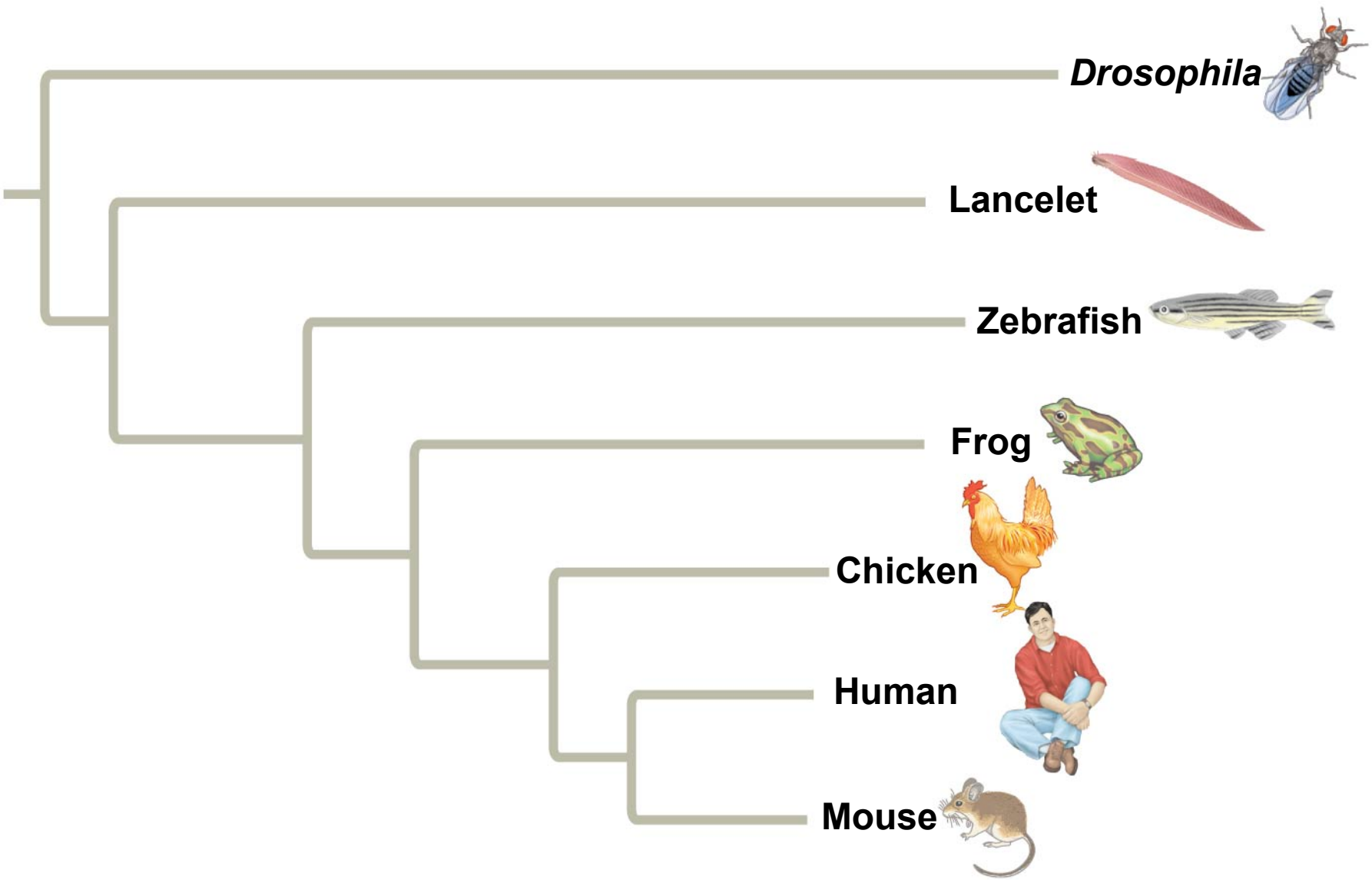
Figure 26.13

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- In other trees, branch length can be proportional to time, and branching points can be determined from the fossil record

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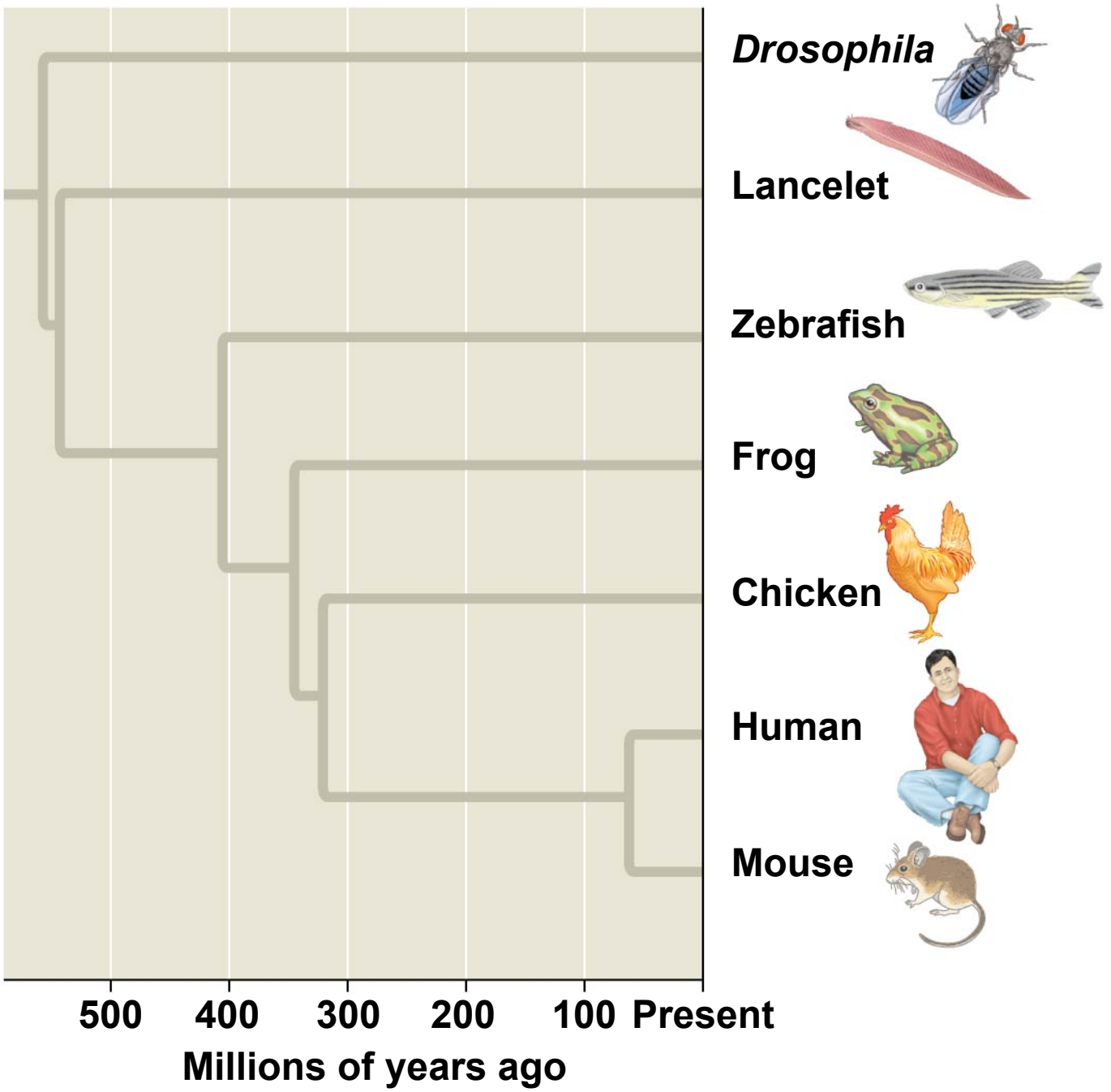
Figure 26.14

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# Maximum Parsimony and Maximum Likelihood

- Systematists can never be sure of finding the best tree in a large data set
- They narrow possibilities by applying the principles of maximum parsimony and maximum likelihood

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- **Maximum parsimony** assumes that the tree that requires the fewest evolutionary events (appearances of shared derived characters) is the most likely
- **Maximum likelihood** is based on probability rules about how DNA changes over time and assumes a tree can be found that reflects the most likely sequence of evolutionary events
- Computer programs are used to search for trees that are parsimonious and likely

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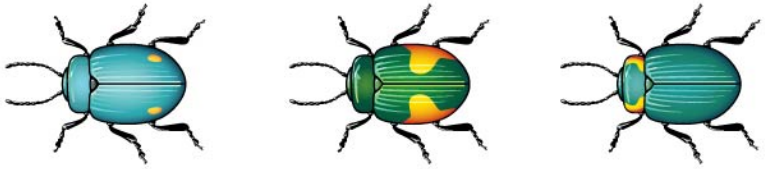
Figure 26.15

## Technique

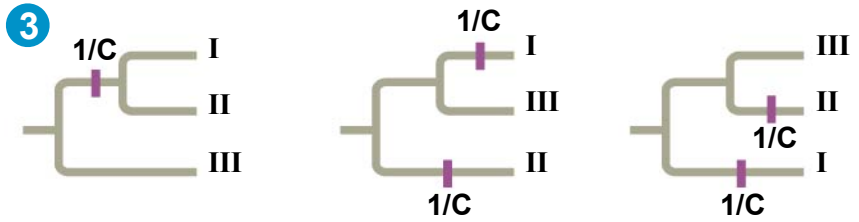



**1** Three phylogenetic hypotheses:

**2**

| | Site 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Species I | C | T | A | T |
| Species II | C | T | T | C |
| Species III | A | G | A | C |
| Ancestral sequence | A | G | T | T |

**3**

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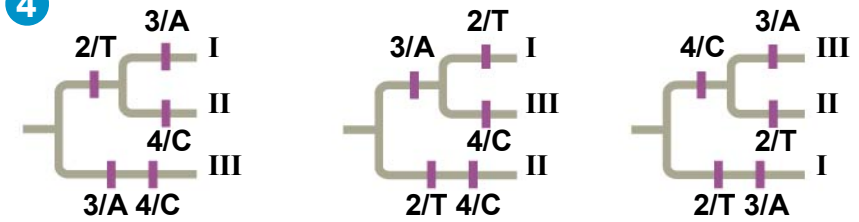


## Results

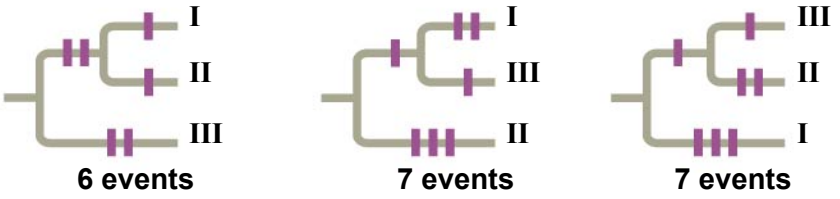


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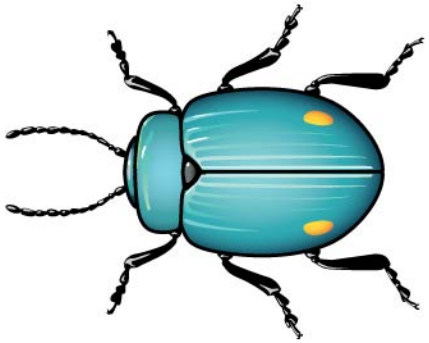
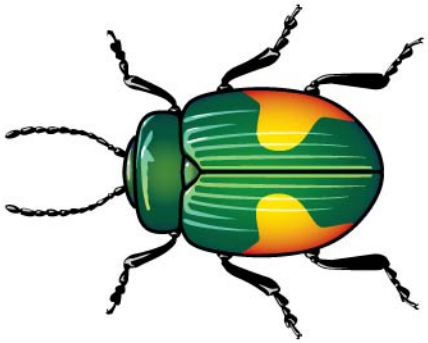
Figure 26.15a

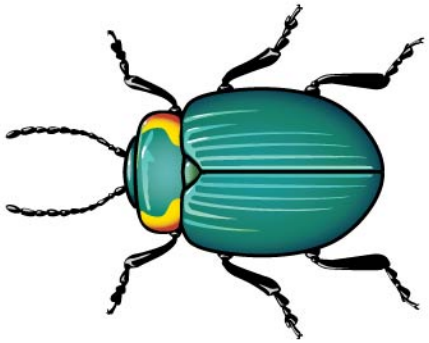
## Technique



Species I

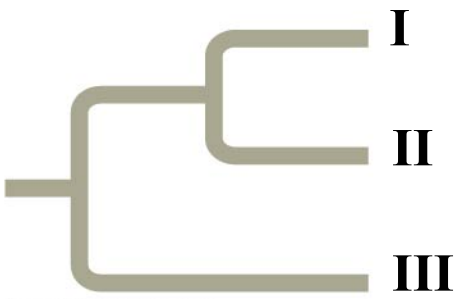


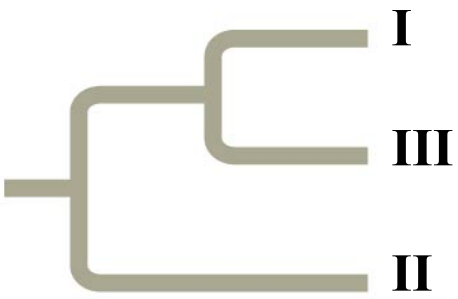
Species II



Species III

1 **Three phylogenetic hypotheses:**



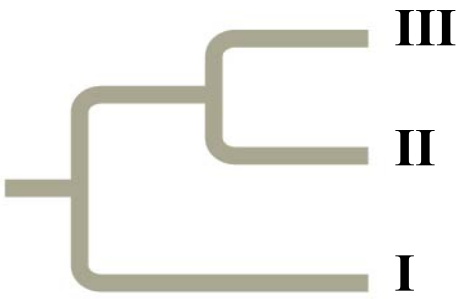




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Figure 26.15b

## Technique

2

| | Site 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Species I | C | T | A | T |
| Species II | C | T | T | C |
| Species III | A | G | A | C |
| Ancestral sequence | A | G | T | T |

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Figure 26.15c

## Technique

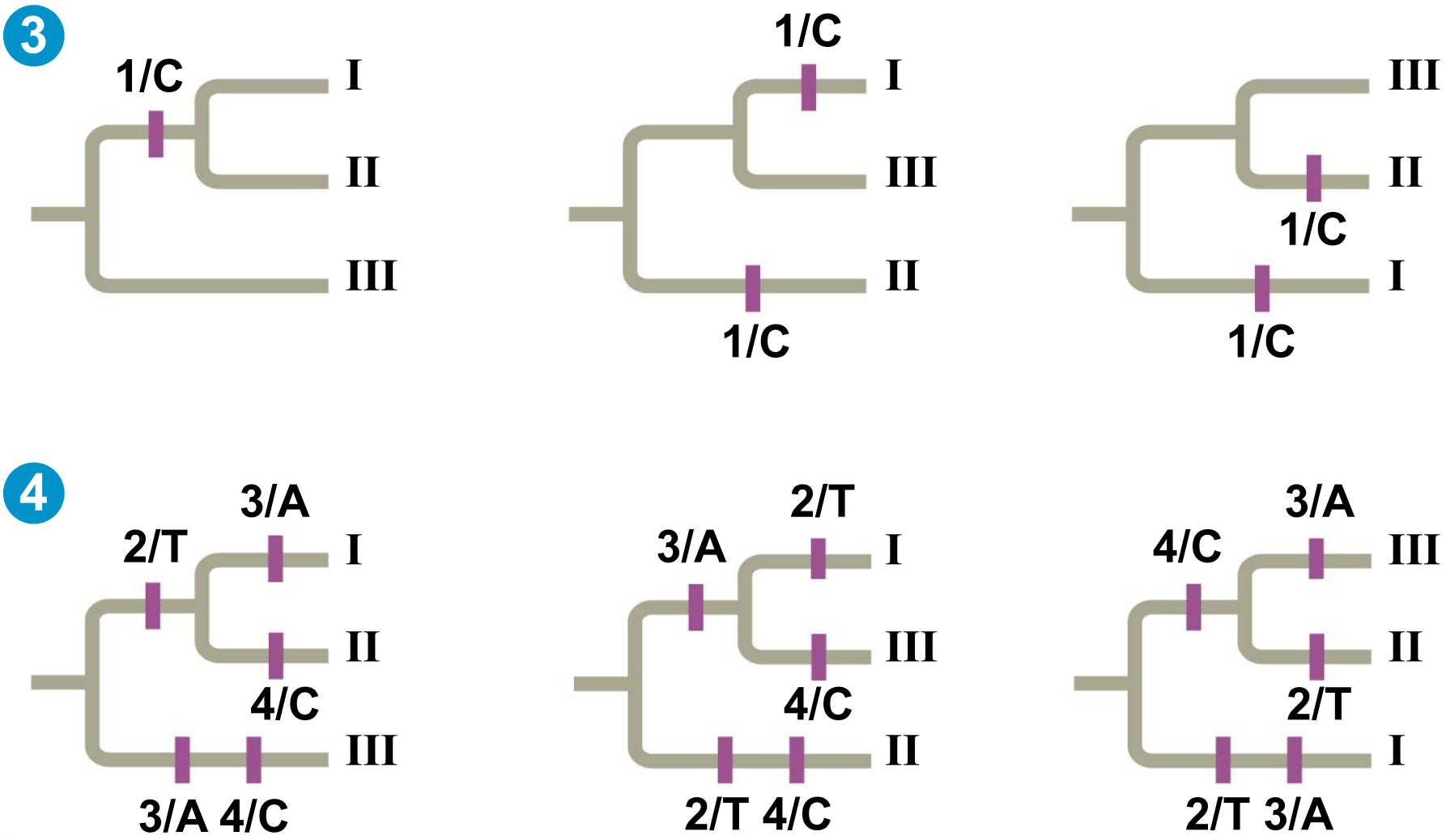


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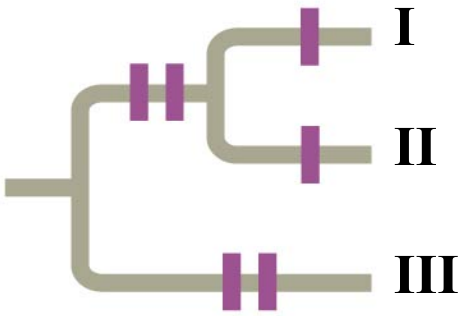
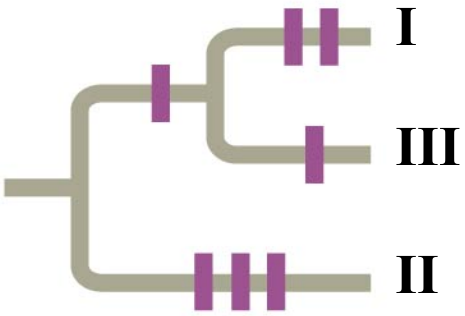
Figure 26.15d

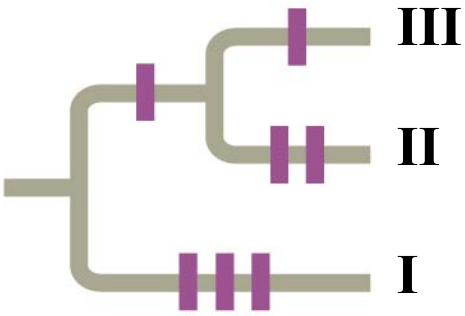
## Results




6 events




7 events




7 events

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# Phylogenetic Trees as Hypotheses

- The best hypothesis for a phylogenetic tree fits the most data: morphological, molecular, and fossil
- Phylogenetic bracketing allows us to predict features of an ancestor from features of its descendants
  - For example, phylogenetic bracketing allows us to infer characteristics of dinosaurs

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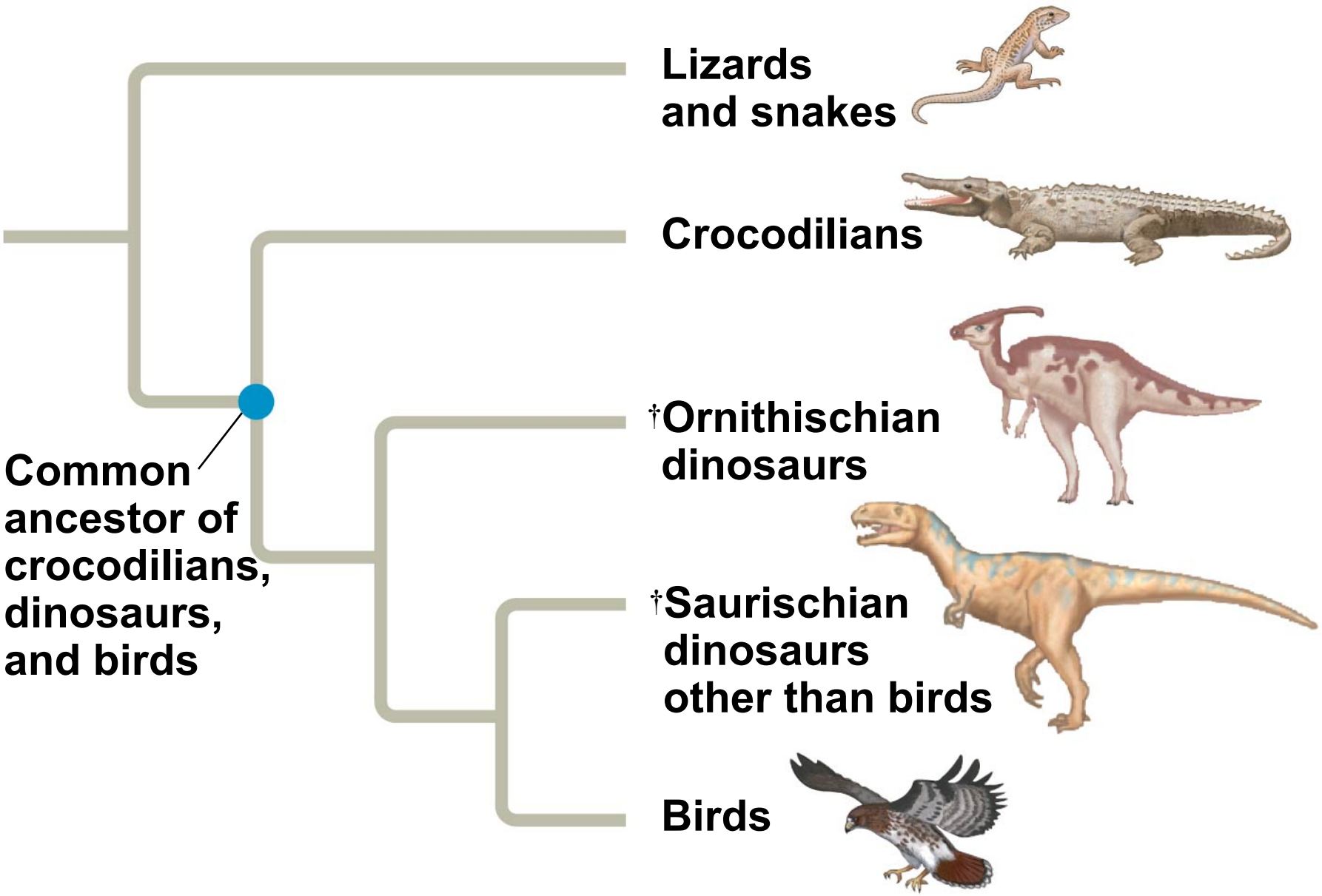
Figure 26.16

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- Birds and crocodiles share several features: four-chambered hearts, song, nest building, and brooding
- These features likely evolved in a common ancestor and were shared by all of its descendants, including dinosaurs
- The fossil record supports nest building and brooding in dinosaurs

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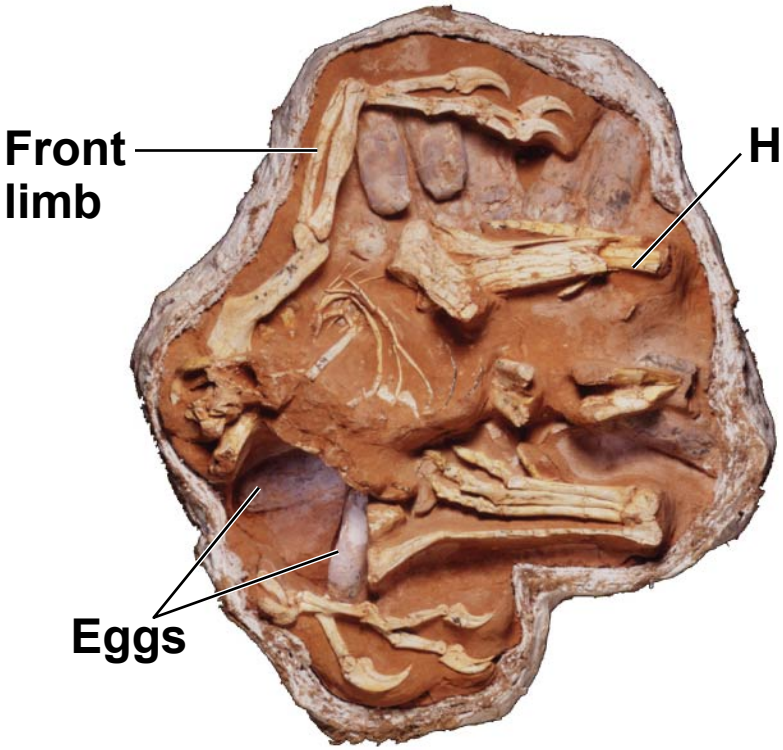
Figure 26.17




(a) Fossil remains of *Oviraptor* and eggs

(b) Artist's reconstruction of the dinosaur's posture based on the fossil findings

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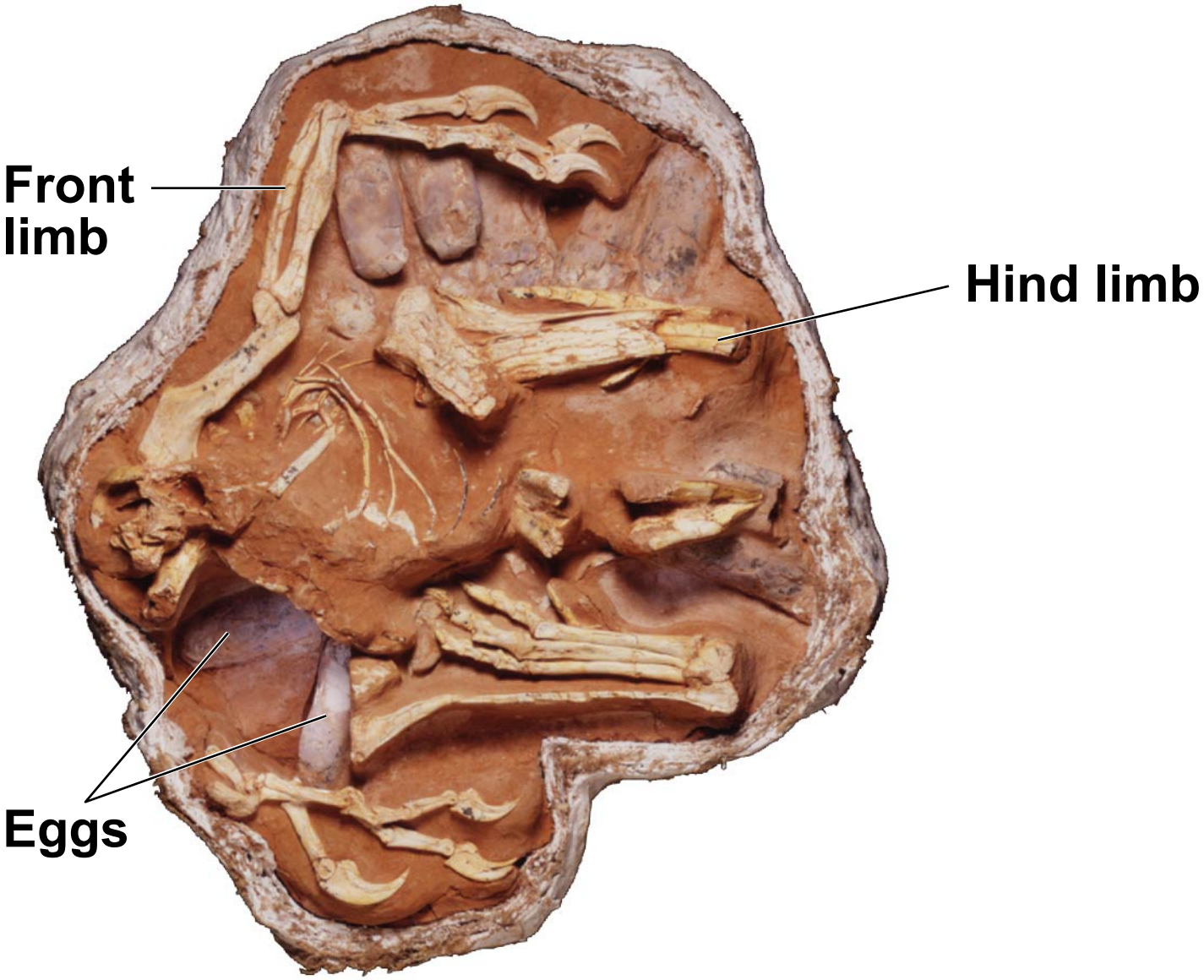
Figure 26.17a




(a) Fossil remains of *Oviraptor* and eggs

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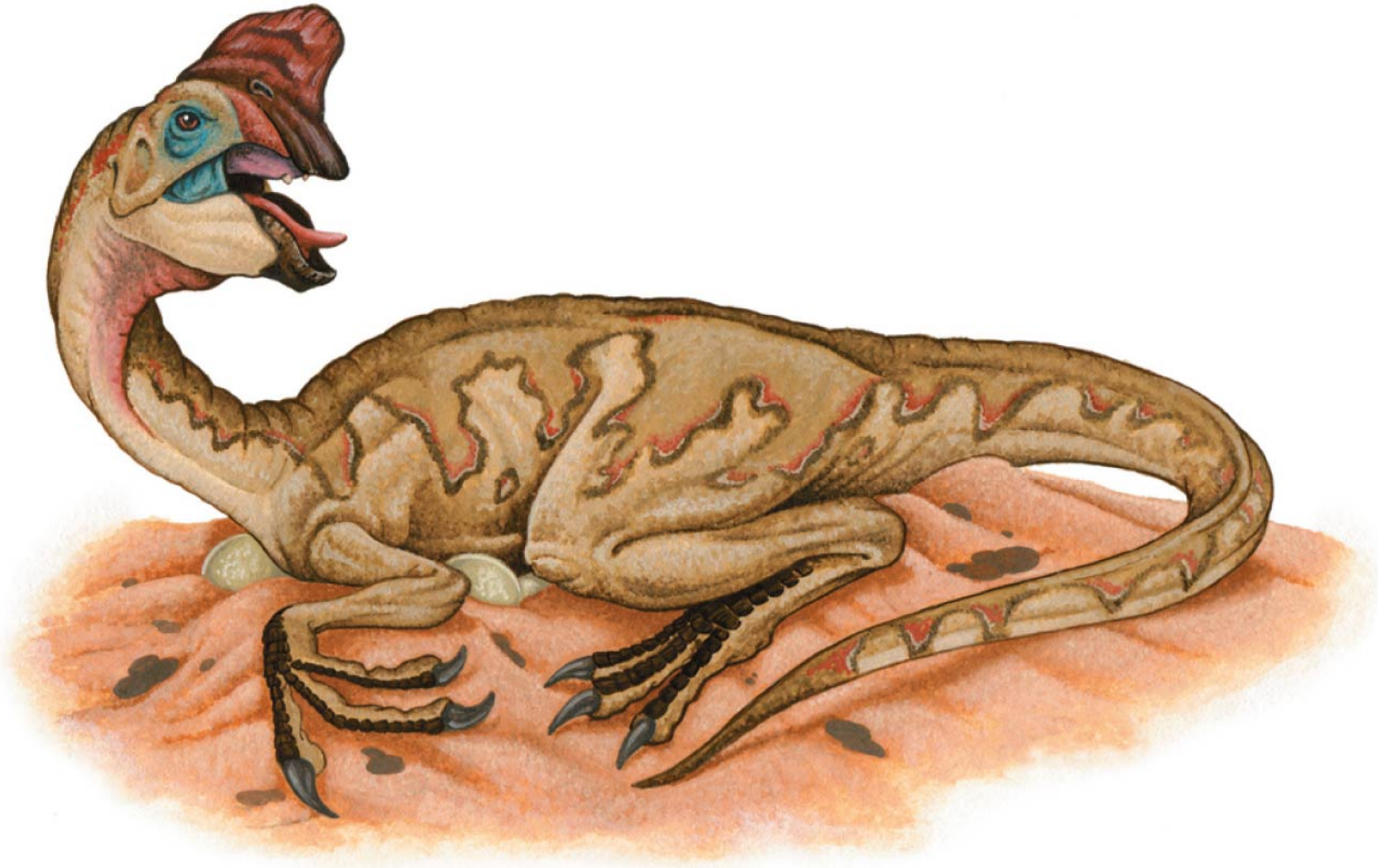
Figure 26.17b



**(b) Artist's reconstruction of the dinosaur's posture based on the fossil findings**

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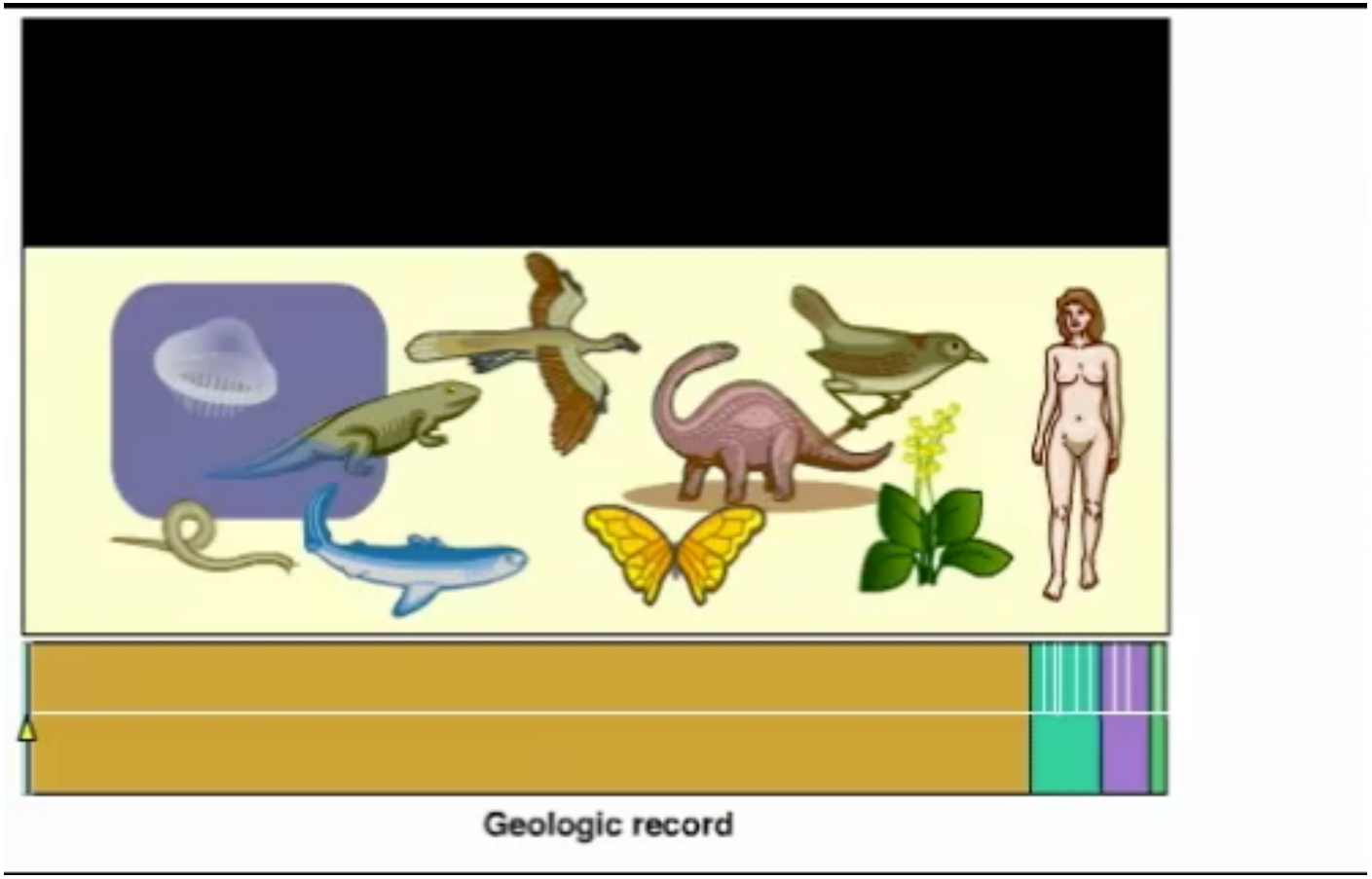
# Animation: The Geologic Record

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# Concept 26.4: An organism's evolutionary history is documented in its genome

- Comparing nucleic acids or other molecules to infer relatedness is a valuable approach for tracing organisms' evolutionary history
- DNA that codes for rRNA changes relatively slowly and is useful for investigating branching points that diverged hundreds of millions of years ago
- mtDNA evolves rapidly and can be used to explore recent evolutionary events

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# Gene Duplications and Gene Families

- Gene duplication increases the number of genes in the genome, providing more opportunities for evolutionary changes
- Repeated gene duplications result in gene families
- Like homologous genes, duplicated genes can be traced to a common ancestor

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- **Orthologous genes** are found in a single copy in the genome and are homologous between species
- They can diverge only after speciation occurs

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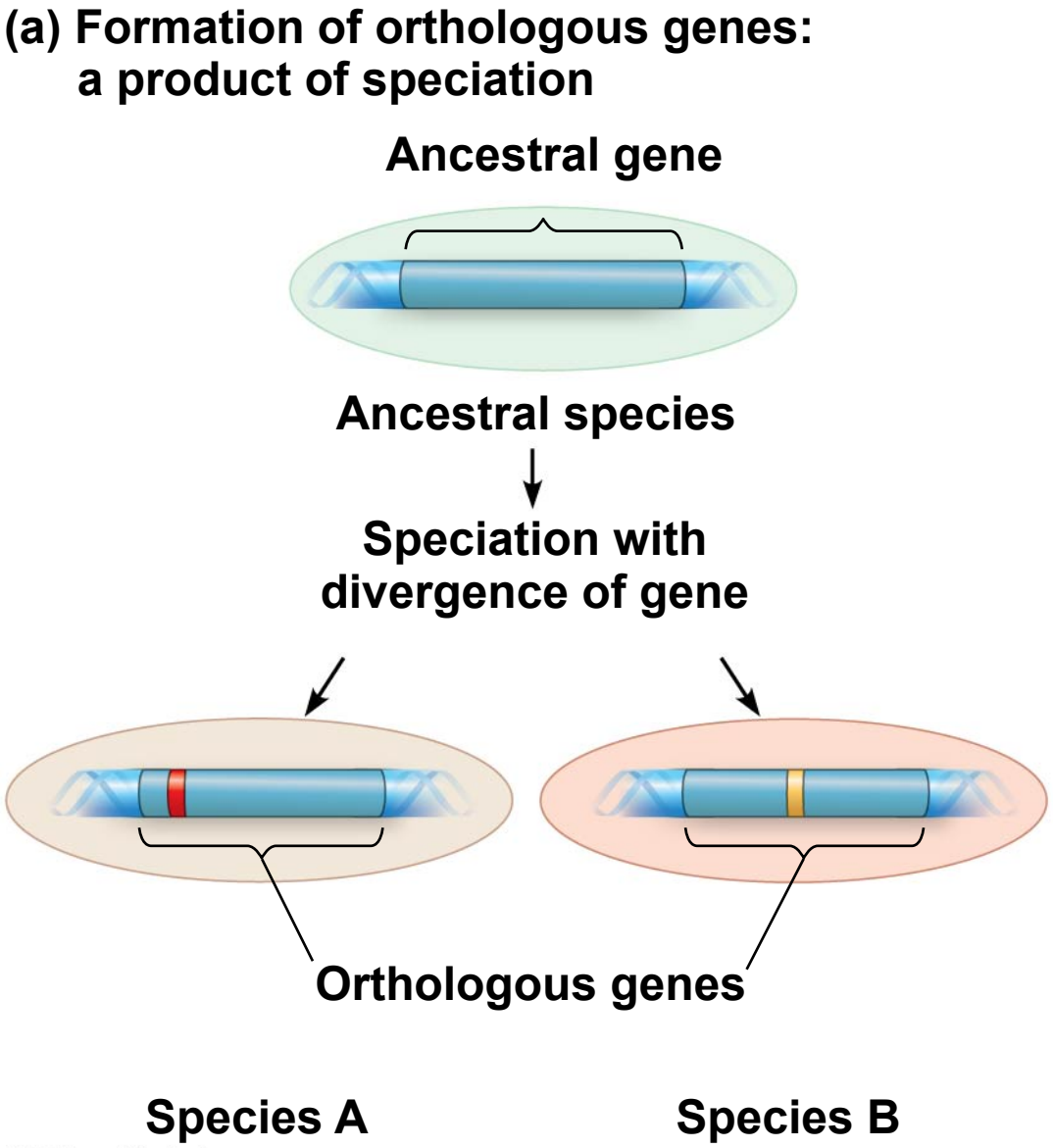
Figure 26.18a

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- **Paralogous genes** result from gene duplication so are found in more than one copy in the genome
- They can diverge within the species that carries them and often evolve new functions

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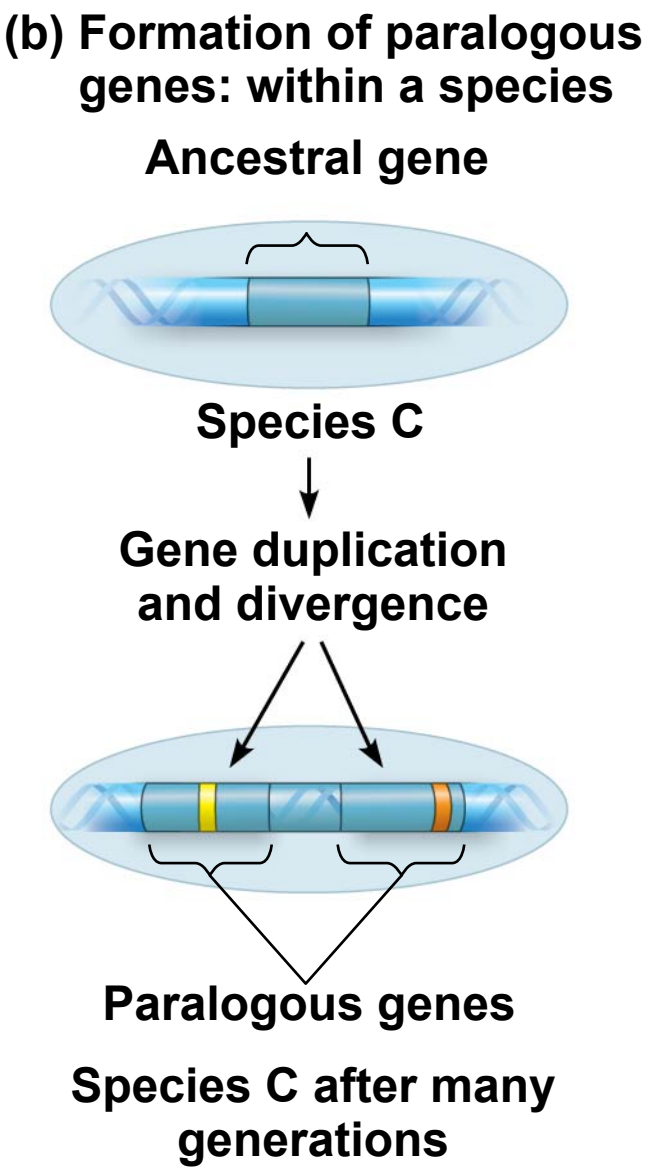
Figure 26.18b

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# Genome Evolution

- Orthologous genes are widespread and extend across many widely varied species
  - For example, humans and mice diverged about 65 million years ago, and 99% of our genes are orthologous

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- Gene number and the complexity of an organism are not strongly linked
  - For example, humans have only four times as many genes as yeast, a single-celled eukaryote
- Genes in complex organisms appear to be very versatile, and each gene can encode multiple proteins that perform many different functions

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# Concept 26.5: Molecular clocks help track evolutionary time

- To extend phylogenies beyond the fossil record, we must make an assumption about how molecular change occurs over time

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# Molecular Clocks

- A **molecular clock** uses constant rates of evolution in some genes to estimate the absolute time of evolutionary change
- In orthologous genes, nucleotide substitutions are assumed to be proportional to the time since they last shared a common ancestor
- In paralogous genes, nucleotide substitutions are proportional to the time since the genes became duplicated

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- Molecular clocks are calibrated against branches whose dates are known from the fossil record
- Individual genes vary in how clocklike they are

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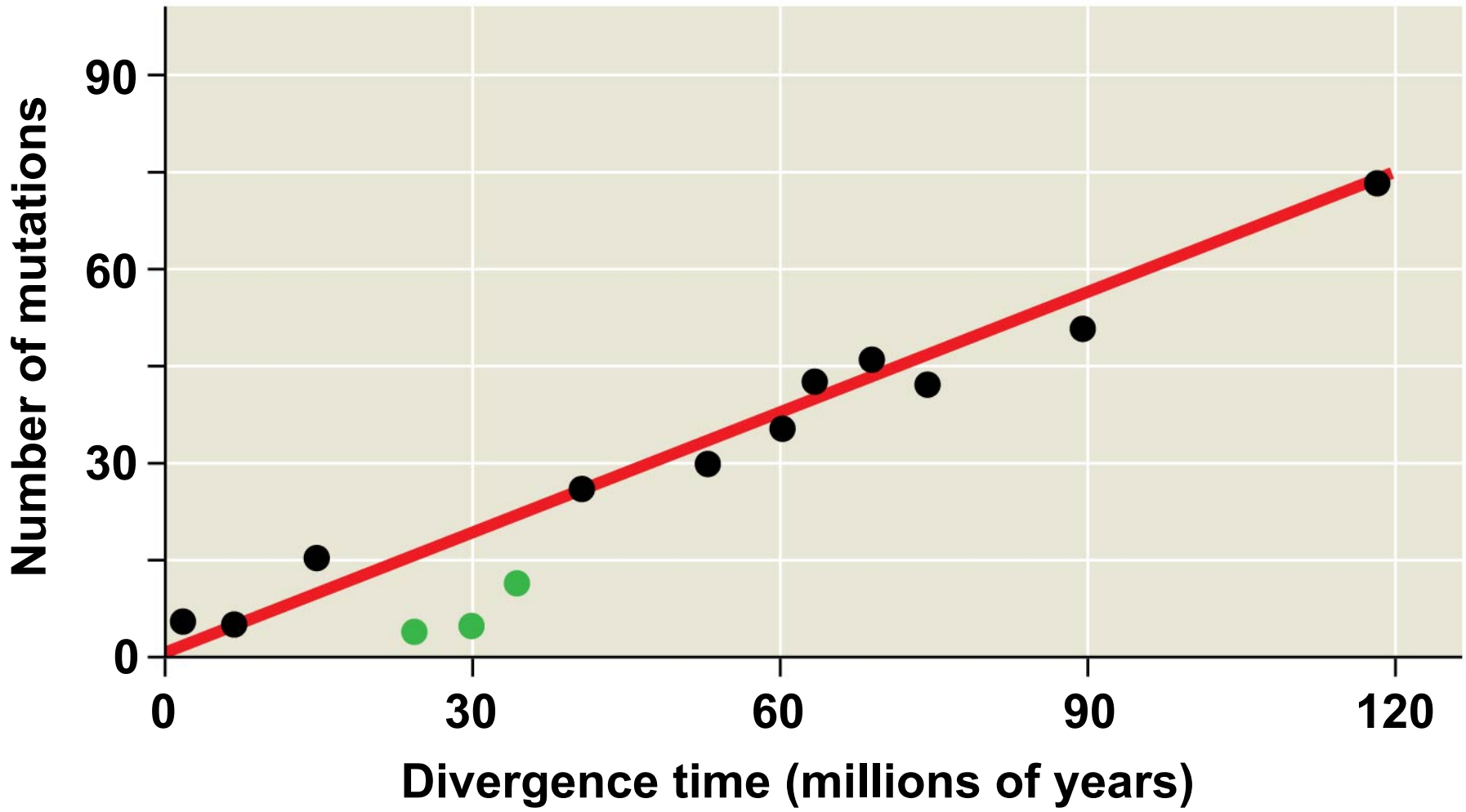
Figure 26.19

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# *Differences in Clock Speed*

- If most of the evolutionary change in genes and proteins has no effect on fitness, then the rate of molecular change should be regular, like a clock
- Differences in clock rate for different genes are a function of the importance of the gene and how critical the specific amino acid is to protein function

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# *Potential Problems with Molecular Clocks*

- The molecular clock does not run as smoothly as expected if mutations were neutral
- Irregularities result from natural selection in which some DNA changes are favored over others
- Estimates of evolutionary divergences older than the fossil record have a high degree of uncertainty
- The use of multiple genes or genes that evolved in different taxa may improve estimates

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# Applying a Molecular Clock: Dating the Origin of HIV

- Phylogenetic analysis shows that HIV is descended from viruses that infect chimpanzees and other primates
- HIV spread to humans more than once
- Comparison of HIV samples shows that the virus evolved in a very clocklike way

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- Application of a molecular clock to one strain of HIV suggests that the strain spread to humans during the 1930s
- A more advanced molecular clock approach estimated the first spread to humans around 1910

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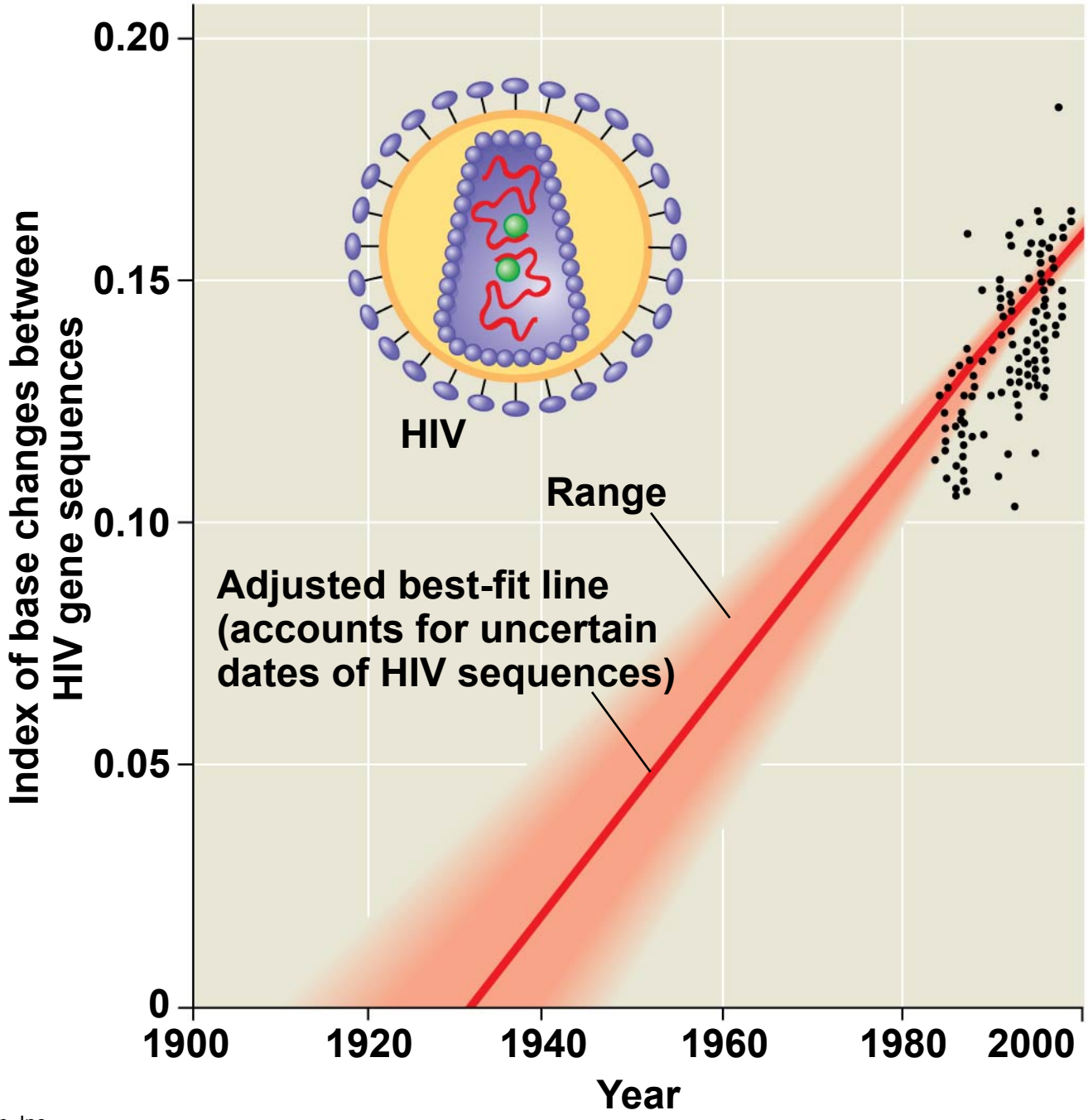
Figure 26.20

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## Concept 26.6: Our understanding of the tree of life continues to change based on new data

- Recently, we have gained insight into the very deepest branches of the tree of life through molecular systematics

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# From Two Kingdoms to Three Domains

- Early taxonomists classified all species as either plants or animals
- Later, five kingdoms were recognized: Monera (prokaryotes), Protista, Plantae, Fungi, and Animalia
- More recently, the three-domain system has been adopted: Bacteria, Archaea, and Eukarya
- The three-domain system is supported by data from many sequenced genomes

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Figure 26.21

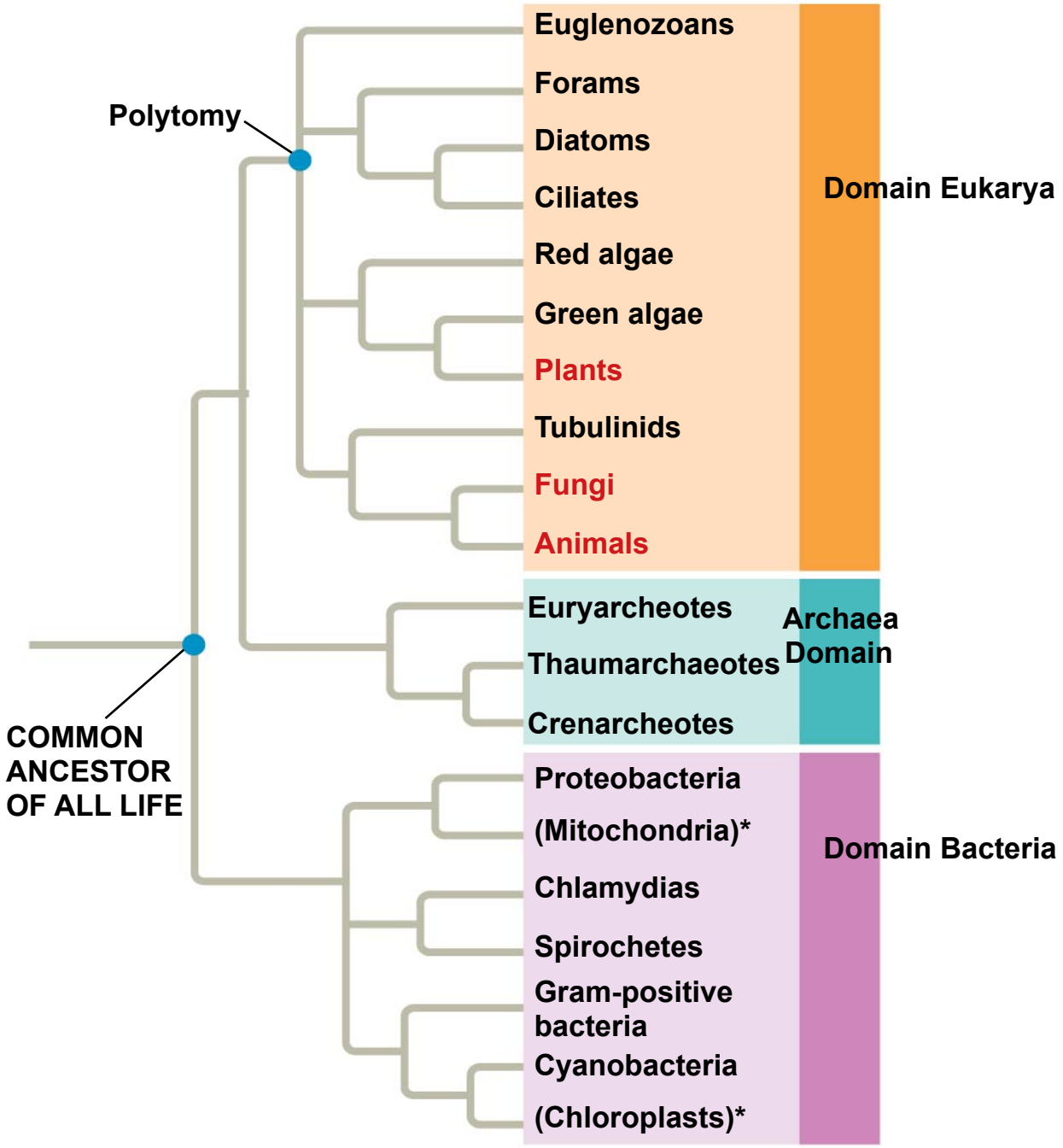


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Figure 26.21a

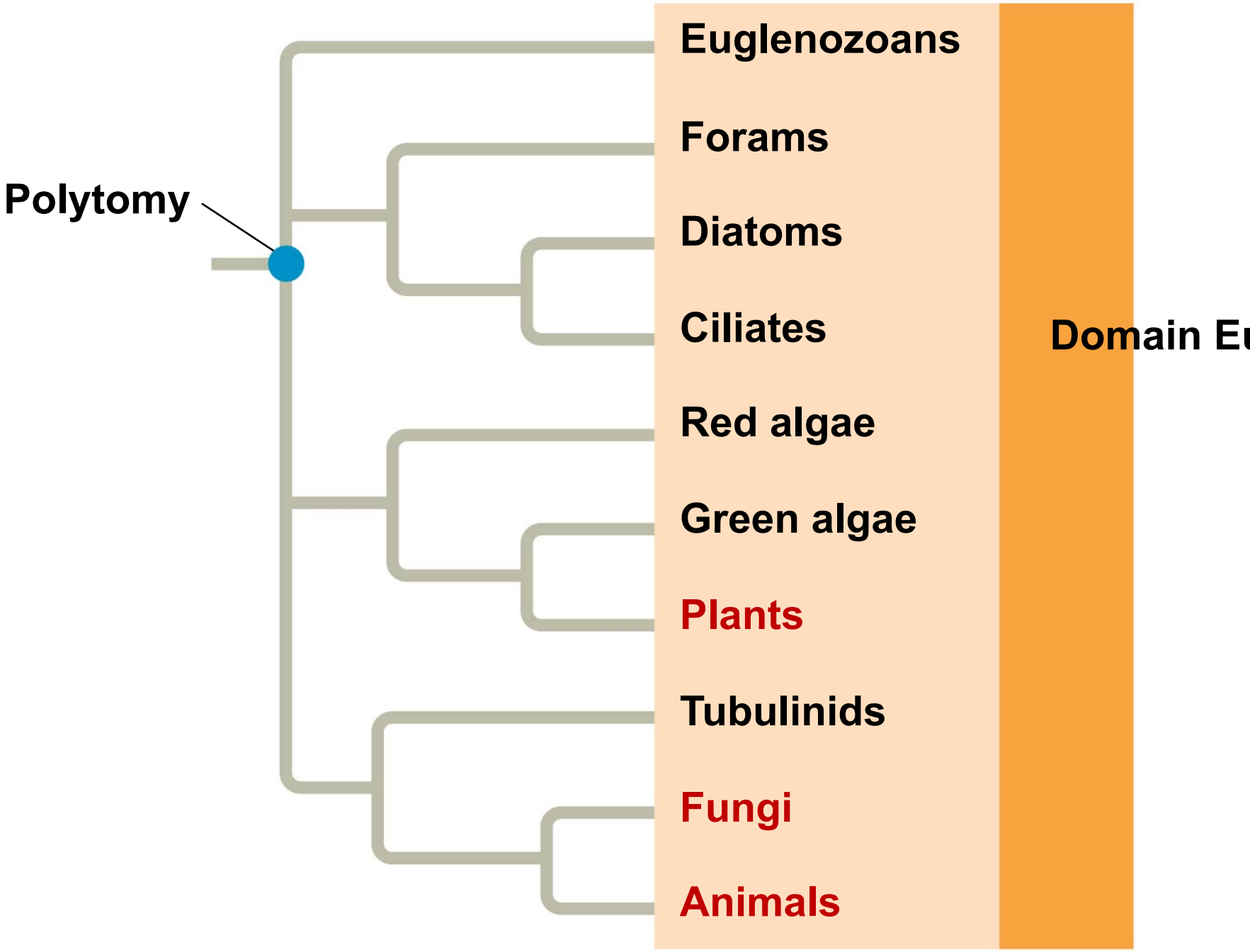


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Figure 26.21b

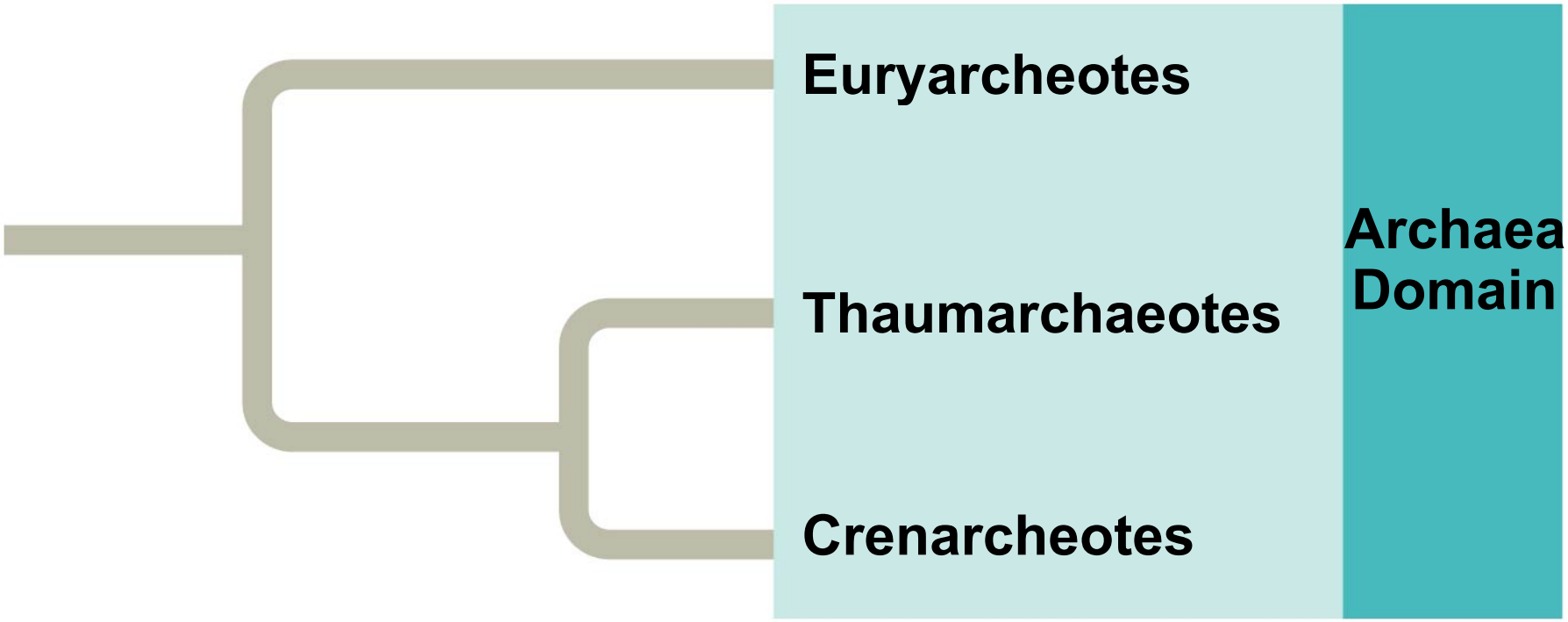


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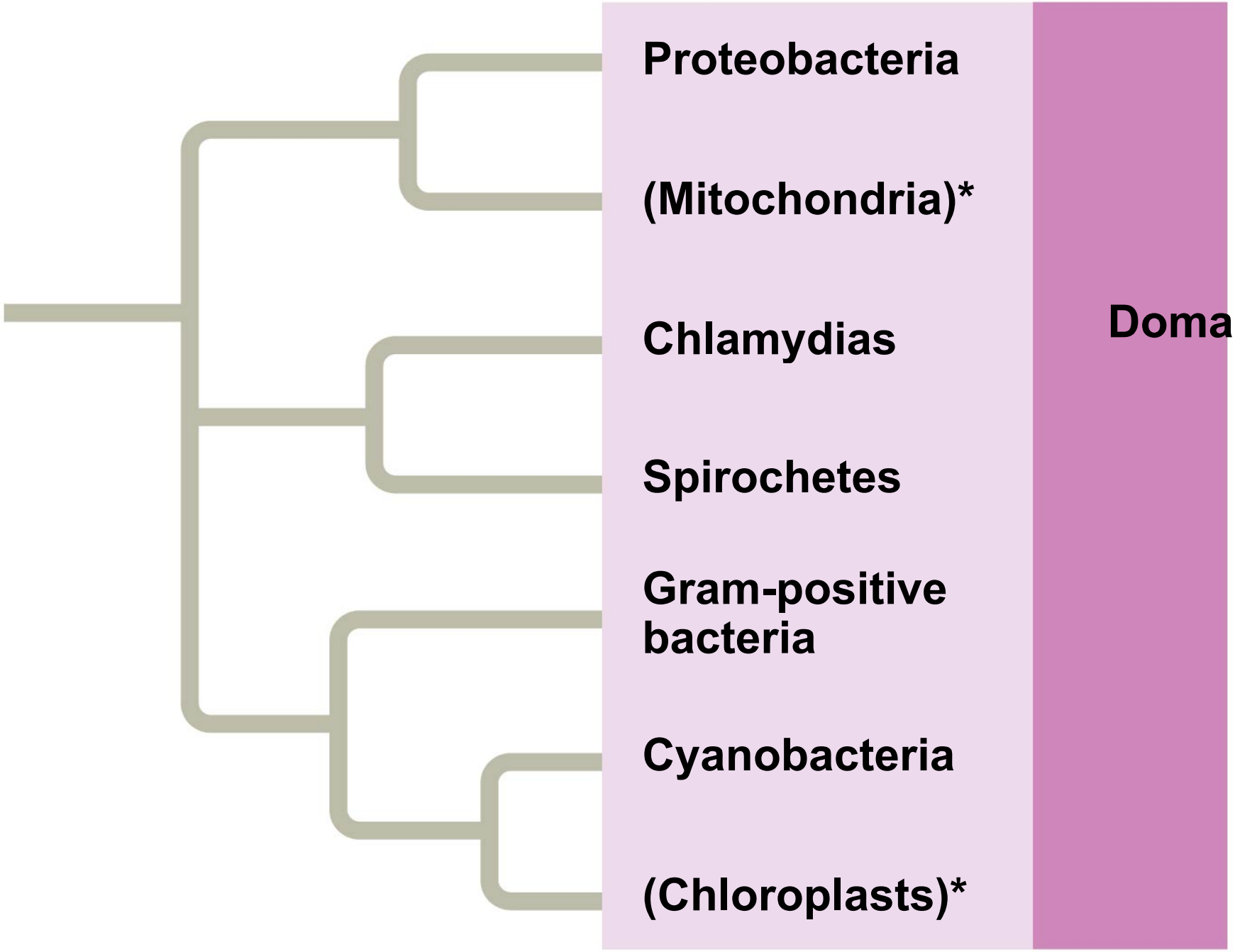
Figure 26.21c

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# The Important Role of Horizontal Gene Transfer

- The tree of life suggests that eukaryotes and archaea are more closely related to each other than to bacteria
- The tree of life is based largely on rRNA genes; however, some other genes reveal different relationships

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- There have been substantial interchanges of genes between organisms in different domains
- **Horizontal gene transfer** is the movement of genes from one genome to another
- Horizontal gene transfer occurs by exchange of transposable elements and plasmids, viral infection, and possibly fusion of organisms

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- Disparities between gene trees can be explained by the occurrence of horizontal gene transfer
- Horizontal gene transfer has played a key role in the evolution of both prokaryotes and eukaryotes
- Eukaryotes can acquire nuclear genes from bacteria and archaea
  - For example, the alga *Galdieria sulphuraria* acquired about 5% of its genes from bacterial and archaeal species

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Figure 26.22a

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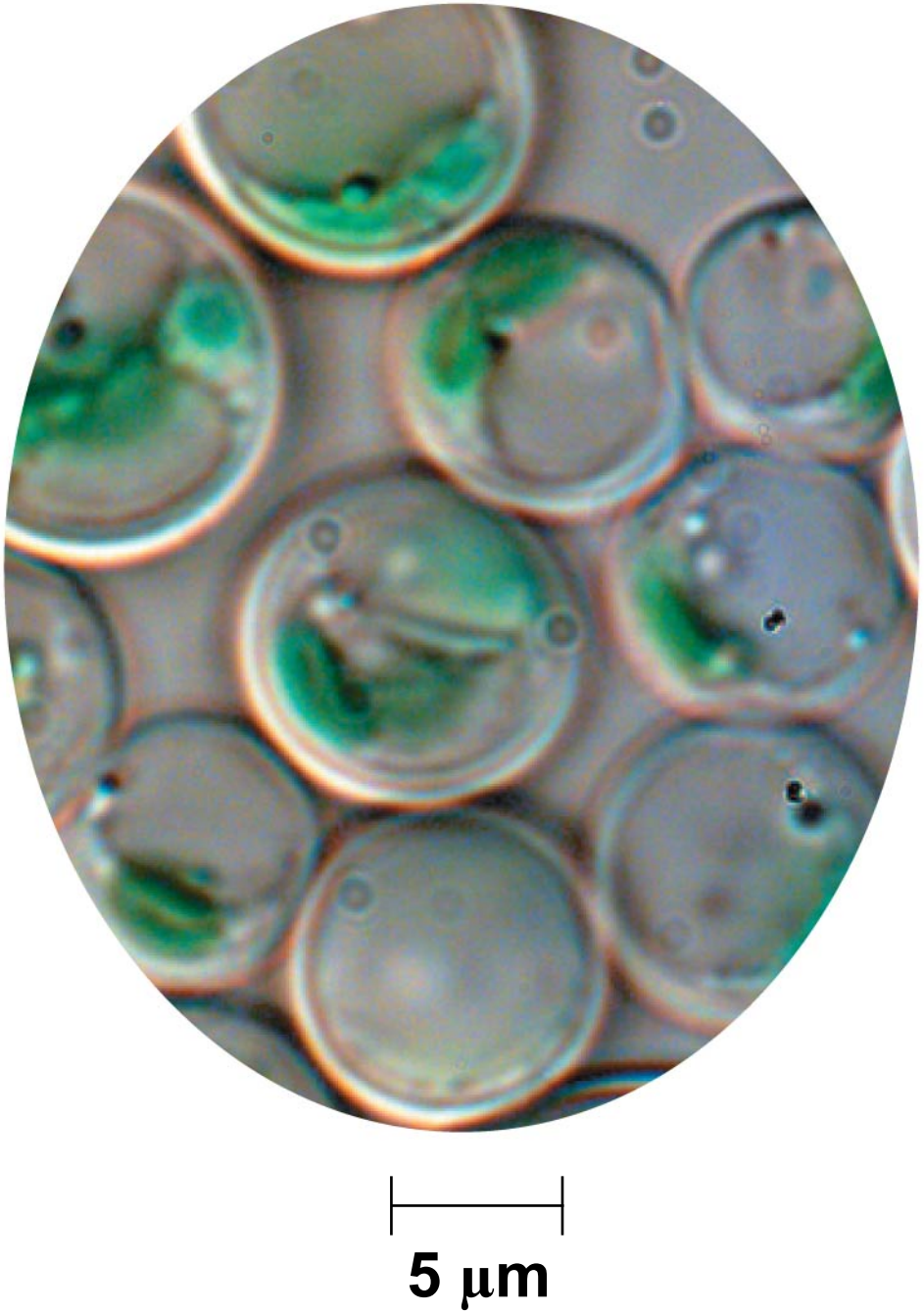


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- Some biologists argue that horizontal gene transfer was so common that the early history of life should be represented as a tangled network of connected branches

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Figure 26.23

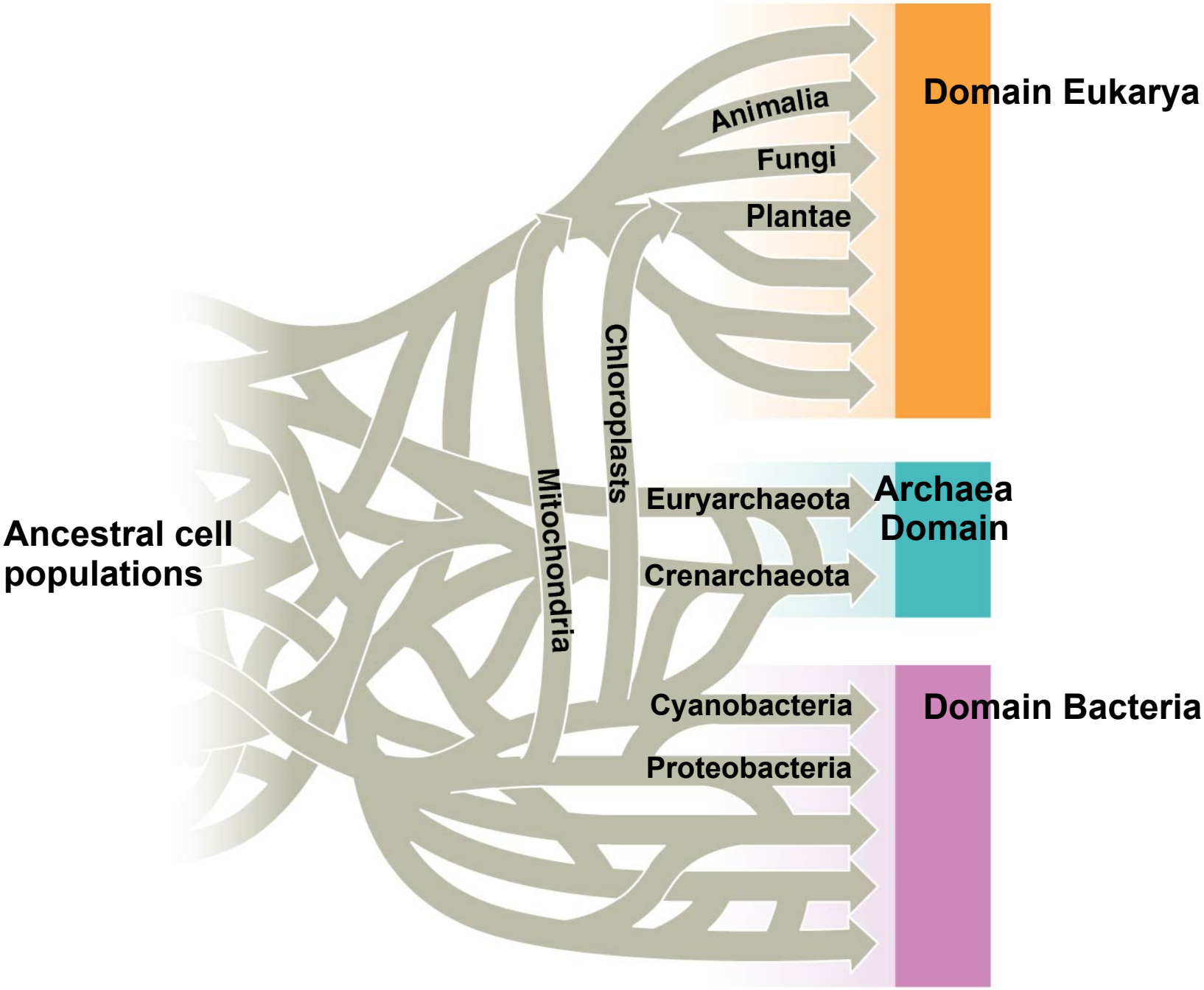


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Figure 26.23a

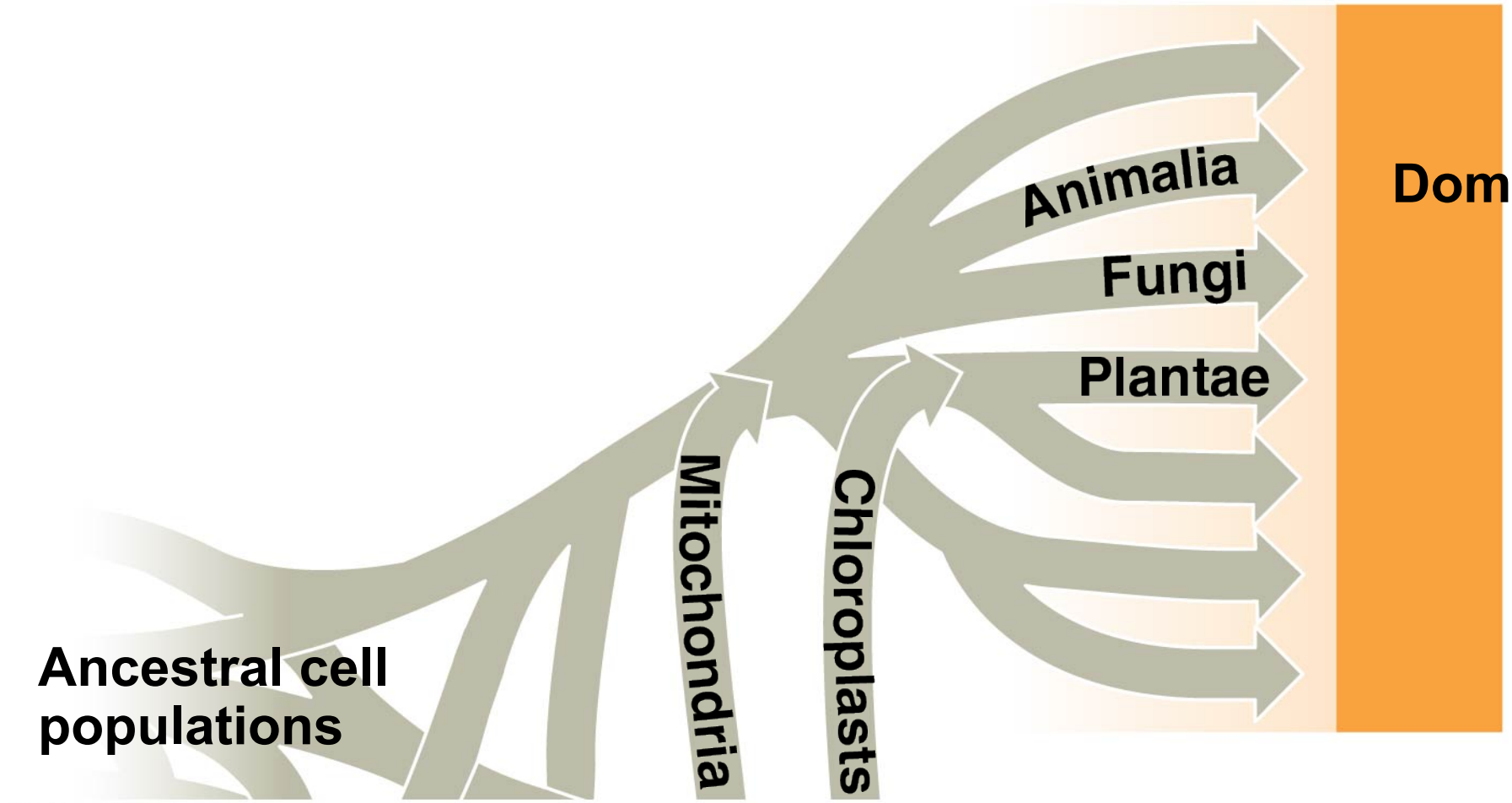


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Figure 26.23b

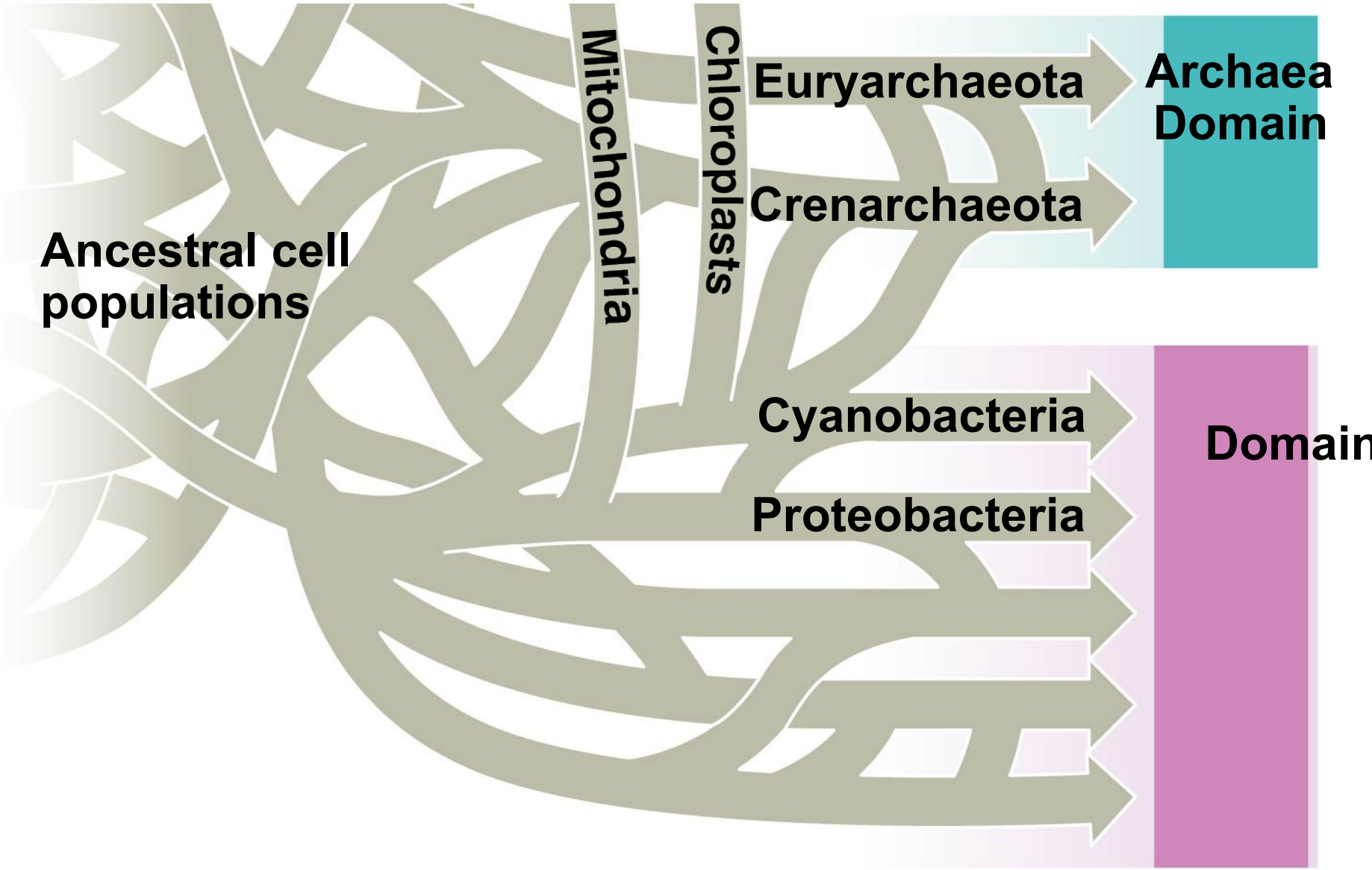


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Figure 26.0

# UNIT 5: THE EVOLUTIONARY HISTORY OF BIOLOGICAL DIVERSITY

Dr. Nancy Moran

Adult female pea aphids and asexually produced daughters. The reddish color is due to carotenoid pigments.

**"We sequenced these genes and determined that they came from a fungus. What a surprise—the carotenoid genes of a fungus had become part of the DNA of an aphid!"**

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Figure 26.0a

**Dr. Nancy Moran**

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Figure 26.0b

**Adult female pea aphids and asexually produced daughters. The reddish color is due to carotenoid pigments.**

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Figure 26.5

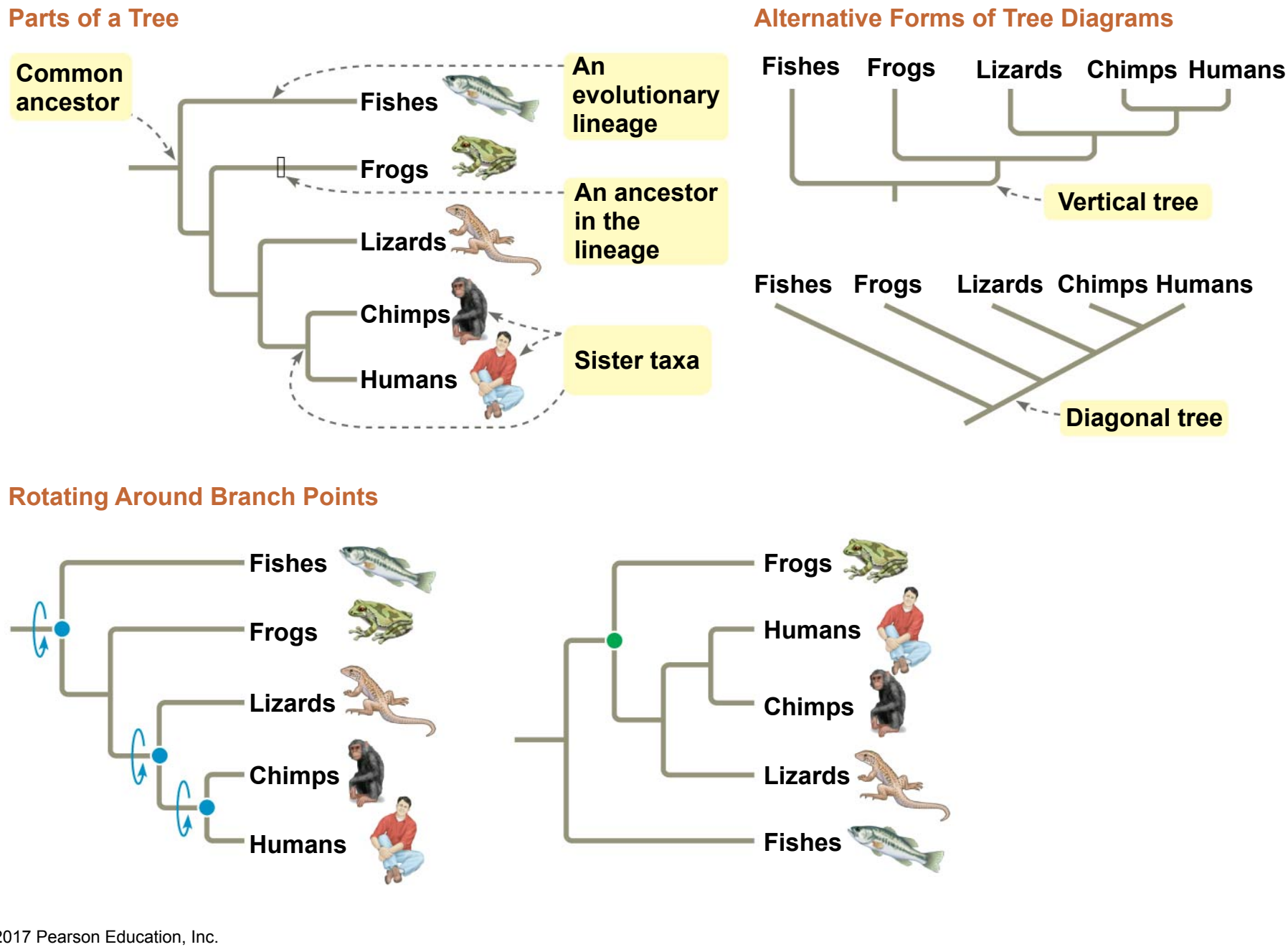


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Figure 26.UN01

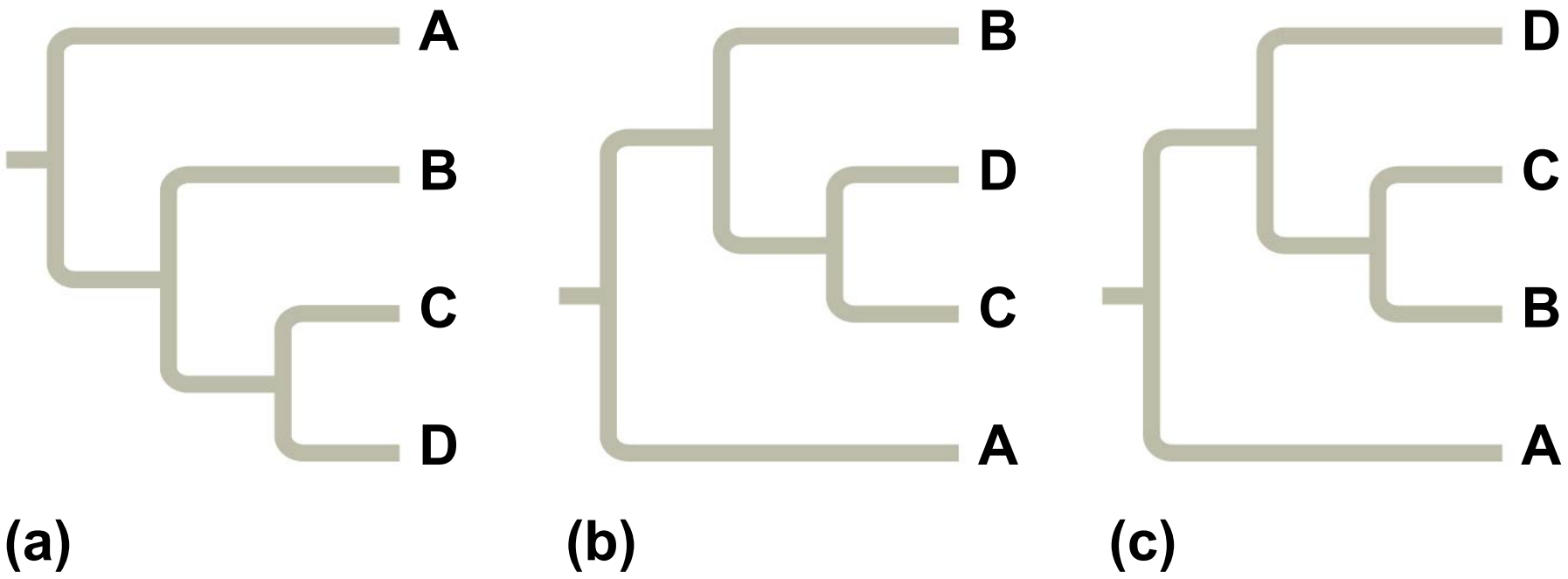


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Figure 26.UN02a

| Organism | Alignment of Amino Acid Sequences |
|---|---|
| *Acyrthosiphon* (aphid) | IKIIIIGSGV GGTAAAARLS KKGFQVEVYE KNSYNGGRCS IIR-HNGHRF DQGPSL--YL |
| *Ustilago* (fungus) | KKVVIIGAGA GGTALAARLG RRGYSVTVLE KNSFGGGRCS LIH-HDGHRW DQGPSL--YL |
| *Gibberella* (fungus) | KSVIVIGAGV GGVSTAARLA KAGFKVTILE KNDFTGGRCS LIH-NDGHRF DQGPSL--LL |
| *Staphylococcus* (bacterium) | MKIAVIGAGV TGLAAAARIA SQGHEVTIFE KNNNVGGRMN QLK-KDGFTF DMGPTI--VM |
| *Pantoea* (bacterium) | KRTFVIGAGF GGLALAIRLQ AAGIATTVLE QHDKPGGRAY VWQ-DQGFTF DAGPTV--IT |
| *Arabidopsis* (plant) | WDAVVIGGGH NGLTAAAYLA RGGLSVAVLE RRHVIGGAAV TEEIVPGFKF SRCSYLQGLL |

**Data from Nancy A. Moran, Yale University. See N. A. Moran and T. Jarvik, Lateral transfer of genes from fungi underlies carotenoid production in aphids, *Science* 328:624–627 (2010).**

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Figure 26.UN02b

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Figure 26.UN03

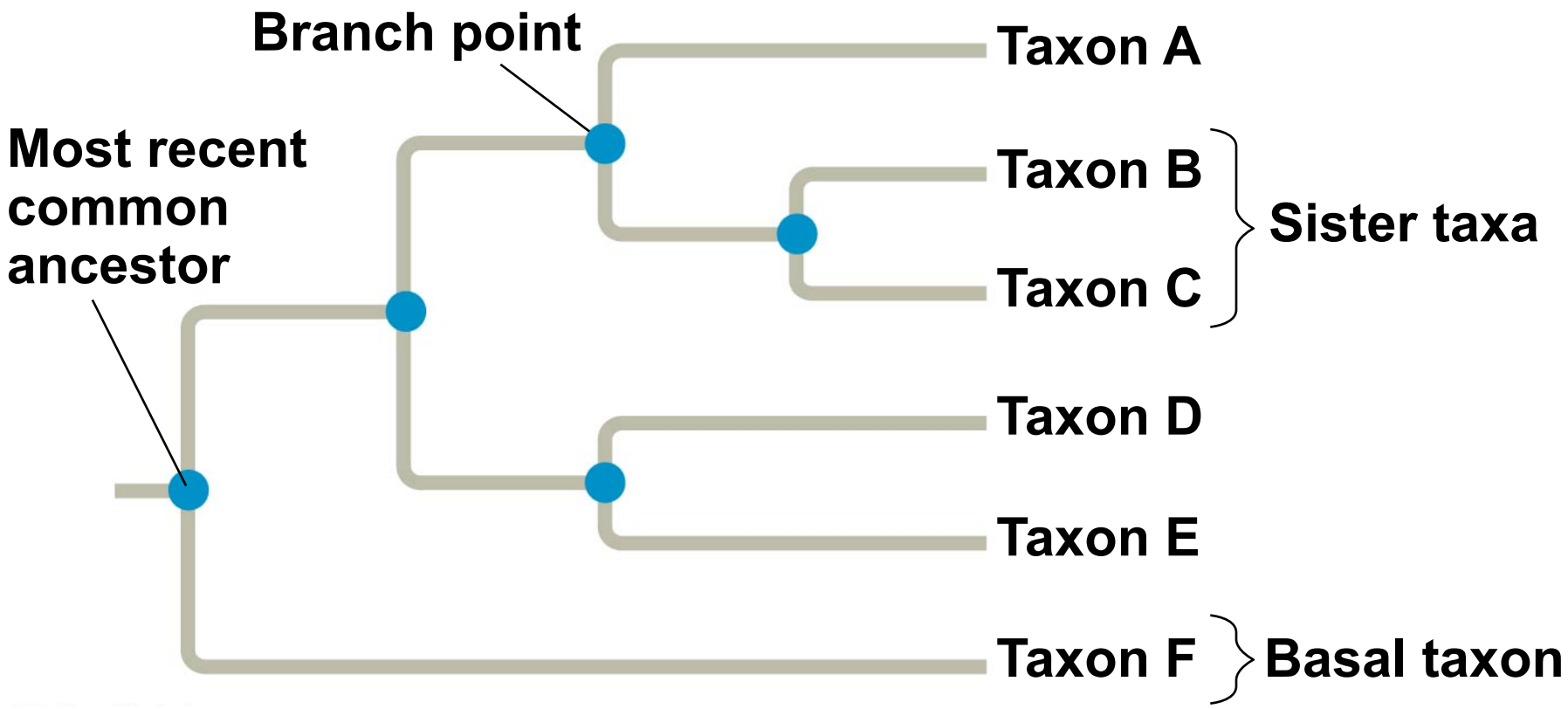


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Figure 26.UN04

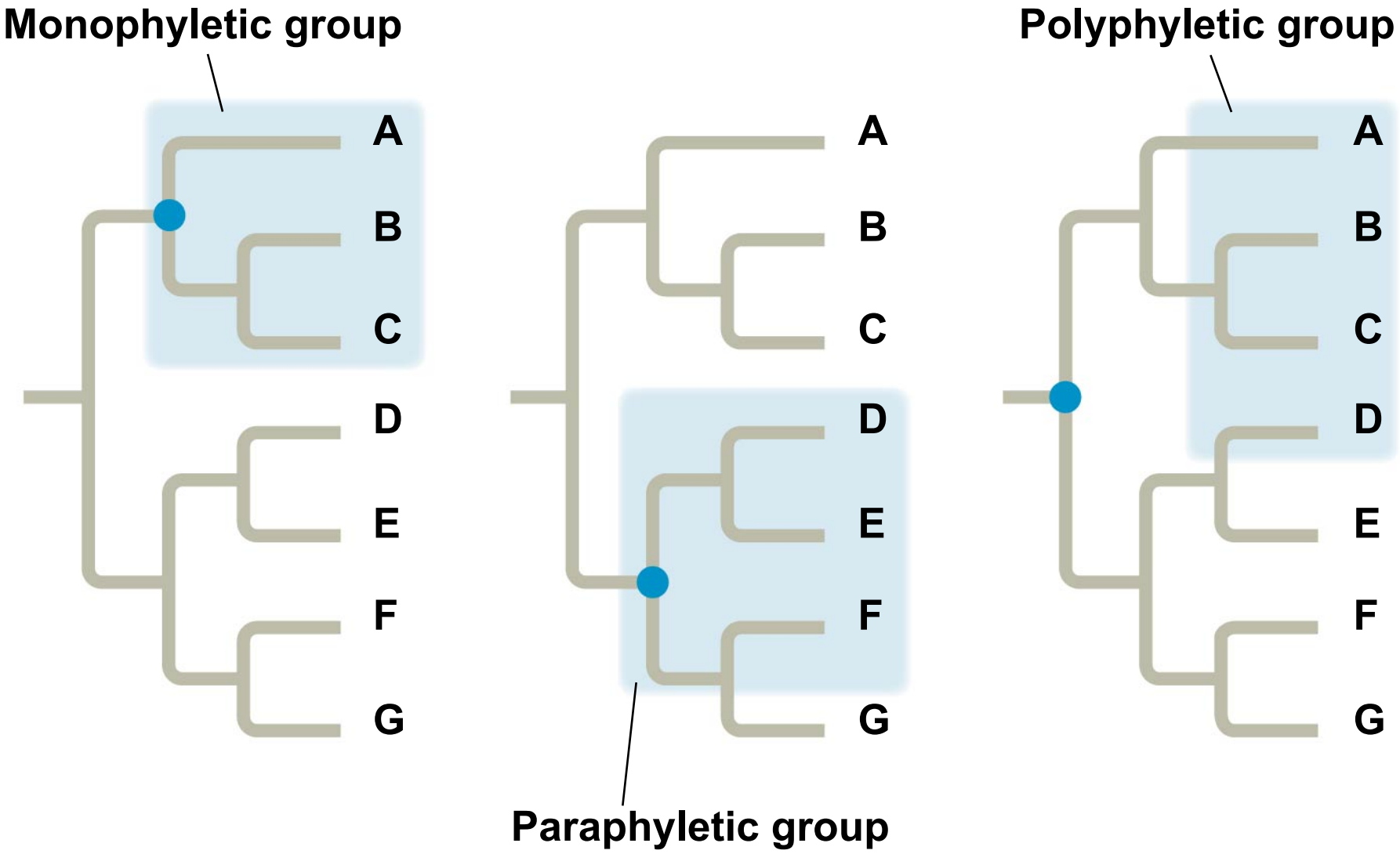


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Figure 26.UN05

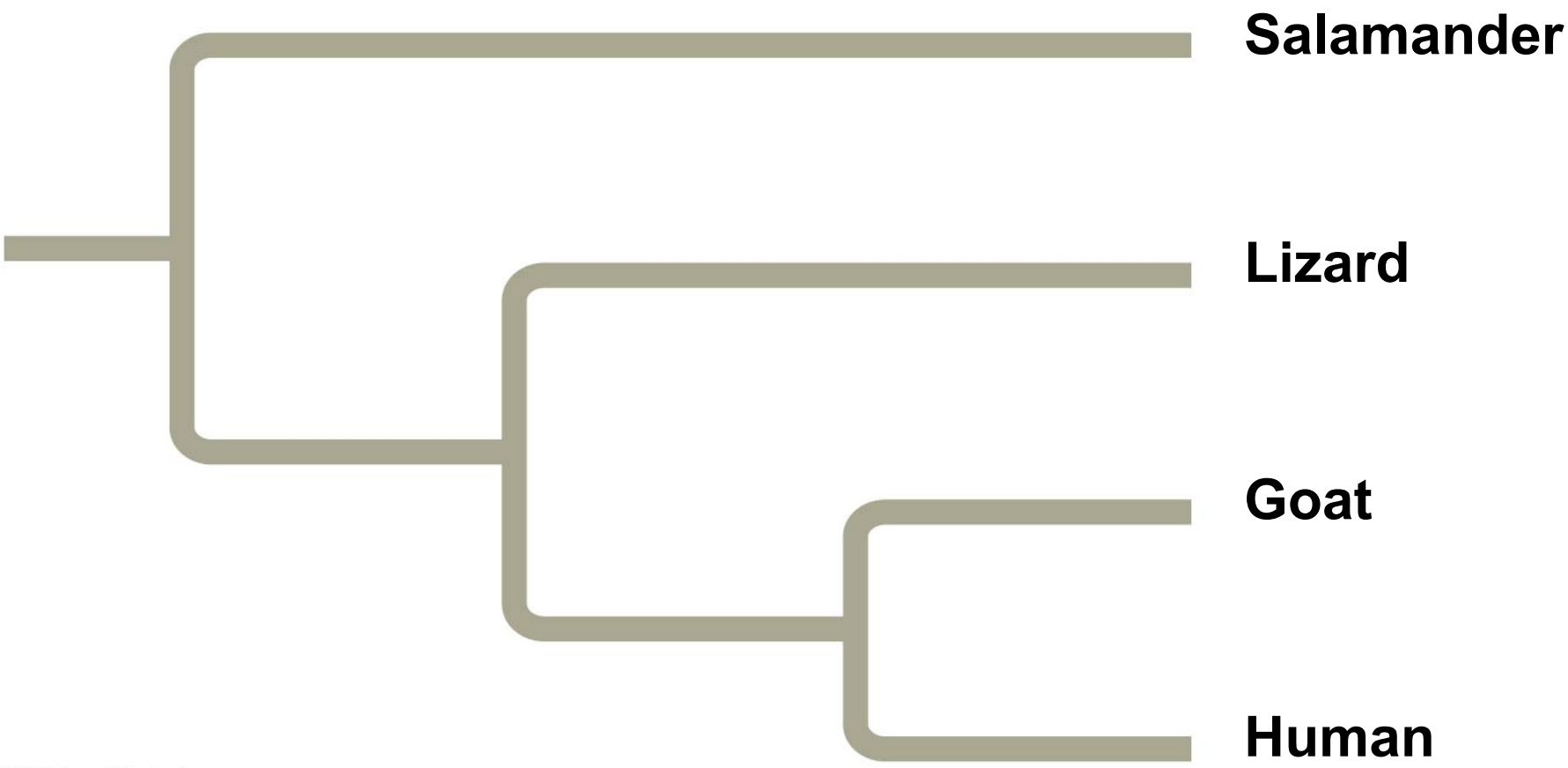


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Figure 26.UN06

| Character | Lancelet (outgroup) | Lamprey | Tuna | Salamander | Turtle | Leopard | Dolphin |
|---|---|---|---|---|---|---|---|
| (1) Backbone | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| (2) Hinged jaw | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| (3) Four limbs | 0 | 0 | 0 | 1 | 1 | 1 | 1* |
| (4) Amnion | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| (5) Milk | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| (6) Dorsal fin | 0 | 0 | 1 | 0 | 0 | 0 | 1 |

*Although adult dolphins have only two obvious limbs (their flippers), as embryos they have two hind-limb buds, for a total of four limbs.

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Figure 26.UN07

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