CAMPBELL BIOLOGY IN FOCUS

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20

Phylogeny

Lecture Presentations by
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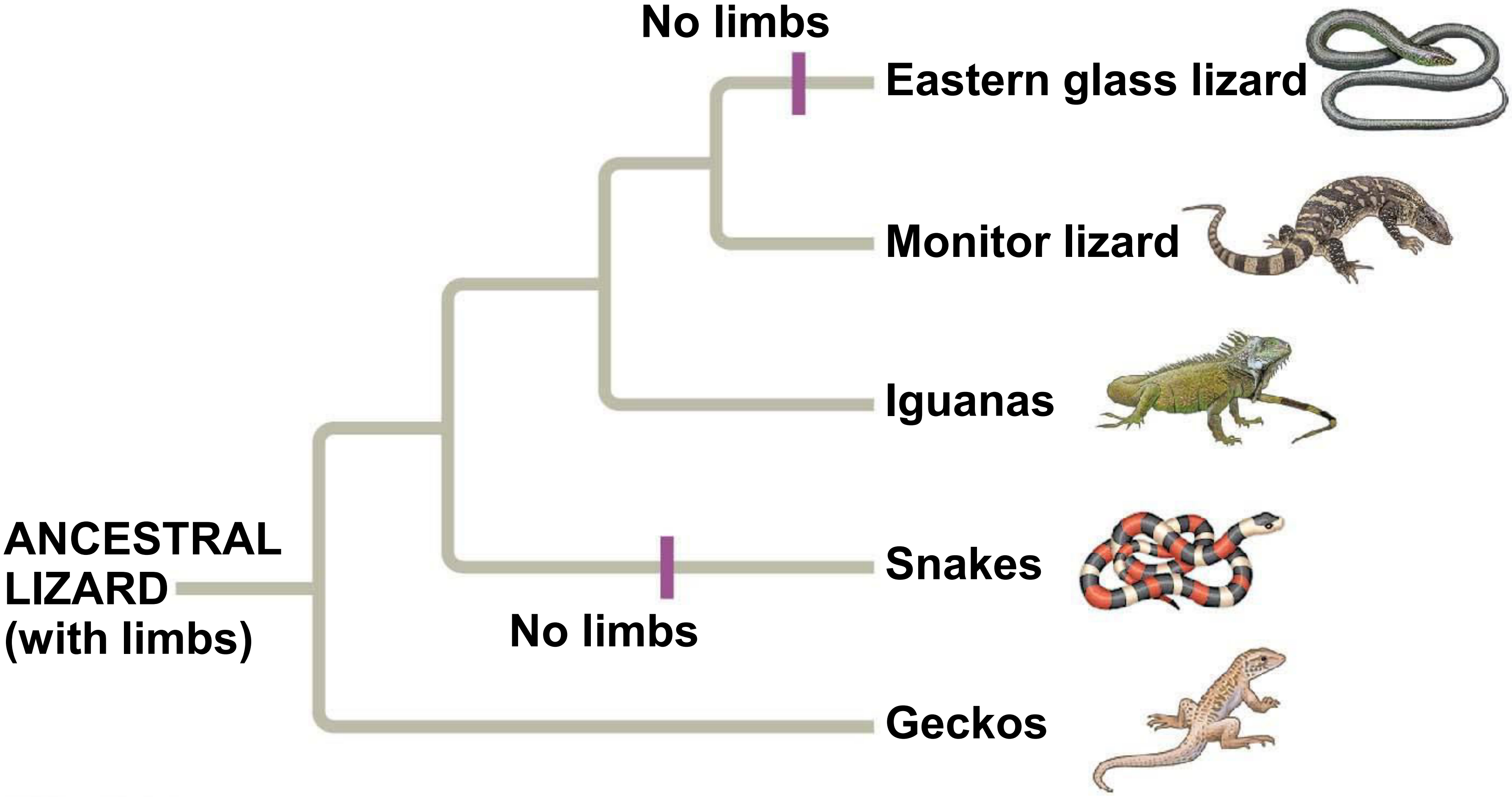
SECOND EDITION

Investigating the Evolutionary History of Life

- Legless lizards and snakes evolved from different lineages of lizards with legs
- Legless lizards have evolved independently in several different groups through adaptation to similar environments

Figure 20.1

Figure 20.2


No limbs
Eastern glass lizard
Monitor lizard
Iguanas
ANCESTRAL
LIZARD
(with limbs)
Snakes
No limbs
Geckos

- **Phylogeny** is the evolutionary history of a species or group of related species
- The discipline of **systematics** classifies organisms and determines their evolutionary relationships

Concept 20.1: Phylogenies show evolutionary relationships

- Organisms share many characteristics because of common ancestry
- **Taxonomy** is the ordered division and naming of organisms

Binomial Nomenclature

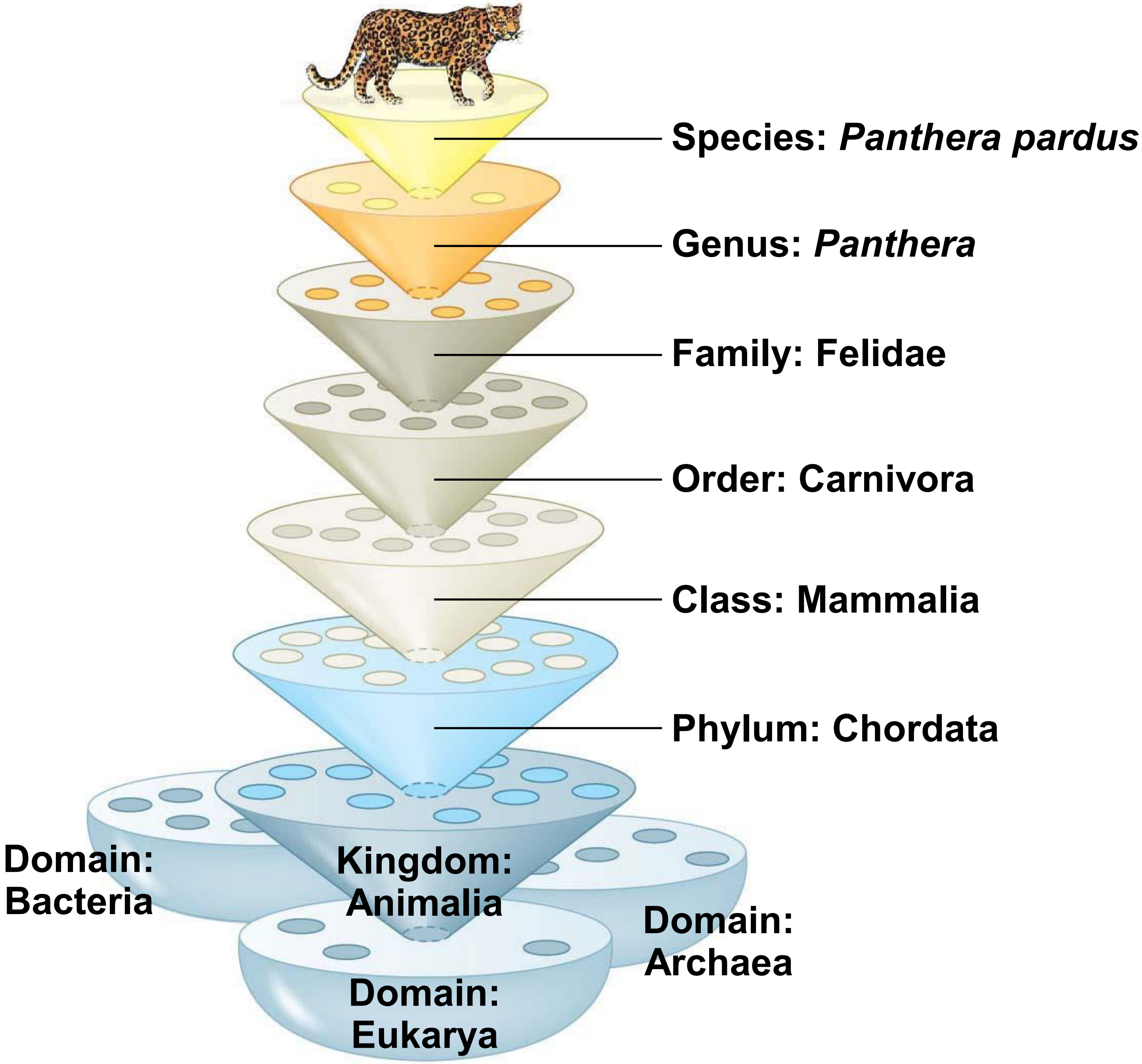
- In the 18th century, Carolus Linnaeus published a system of taxonomy based on resemblances
- Two key features of his system remain useful today: two-part names for species and hierarchical classification

- 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)

Hierarchical Classification

- Linnaeus introduced a system for grouping species in increasingly broad categories
- The taxonomic groups from narrow to broad are species, genus, **family**, **order**, **class**, **phylum**, **kingdom**, and **domain**

Figure 20.3

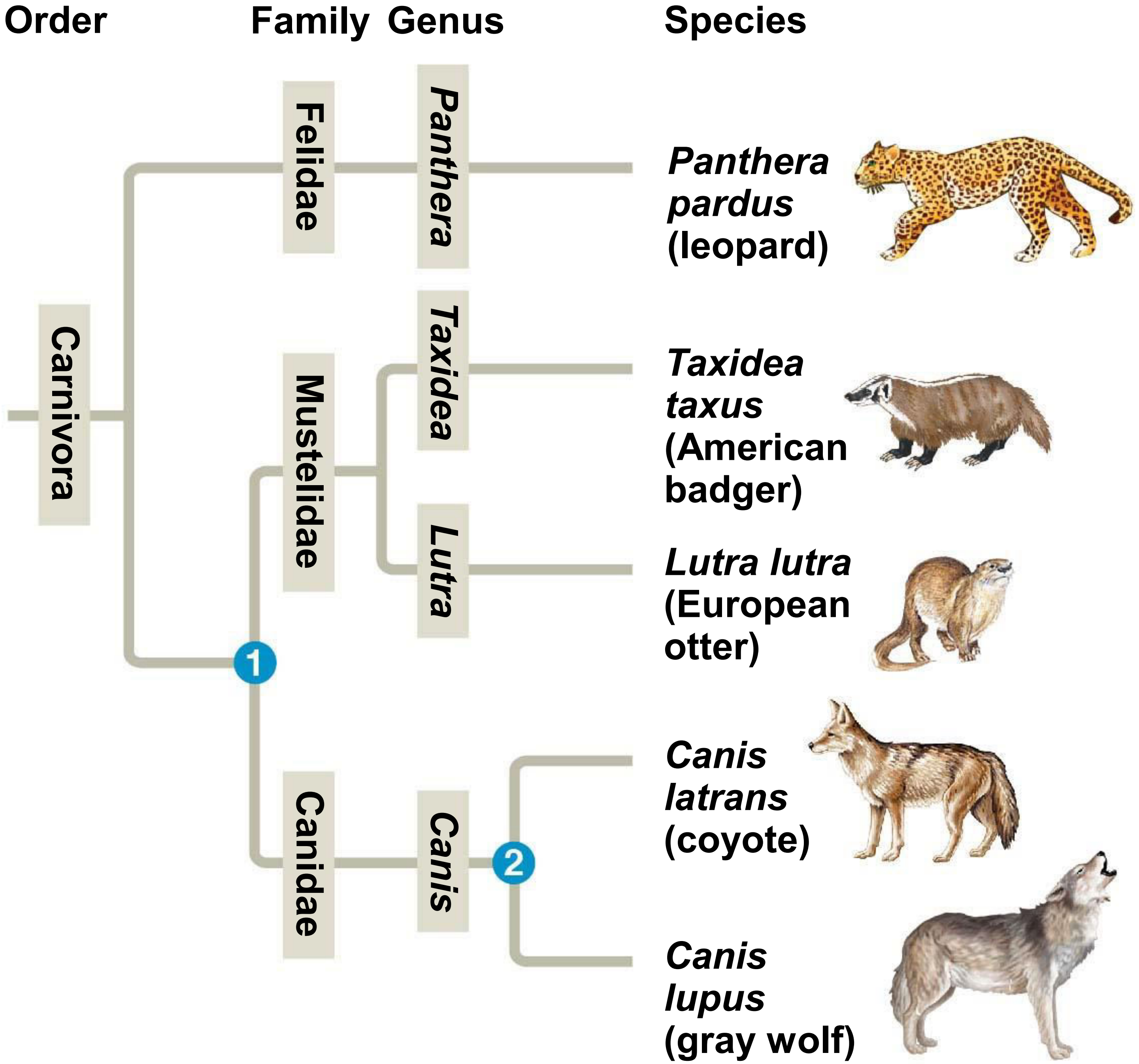

Species: ***Panthera pardus***
Genus: ***Panthera***
Family: Felidae
Order: Carnivora
Class: Mammalia
Phylum: Chordata
Domain: Bacteria
Kingdom: Animalia
Domain: Archaea
Domain: Eukarya

- 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

Linking Classification and Phylogeny

- Systematists depict evolutionary relationships in branching **phylogenetic trees**

Figure 20.4



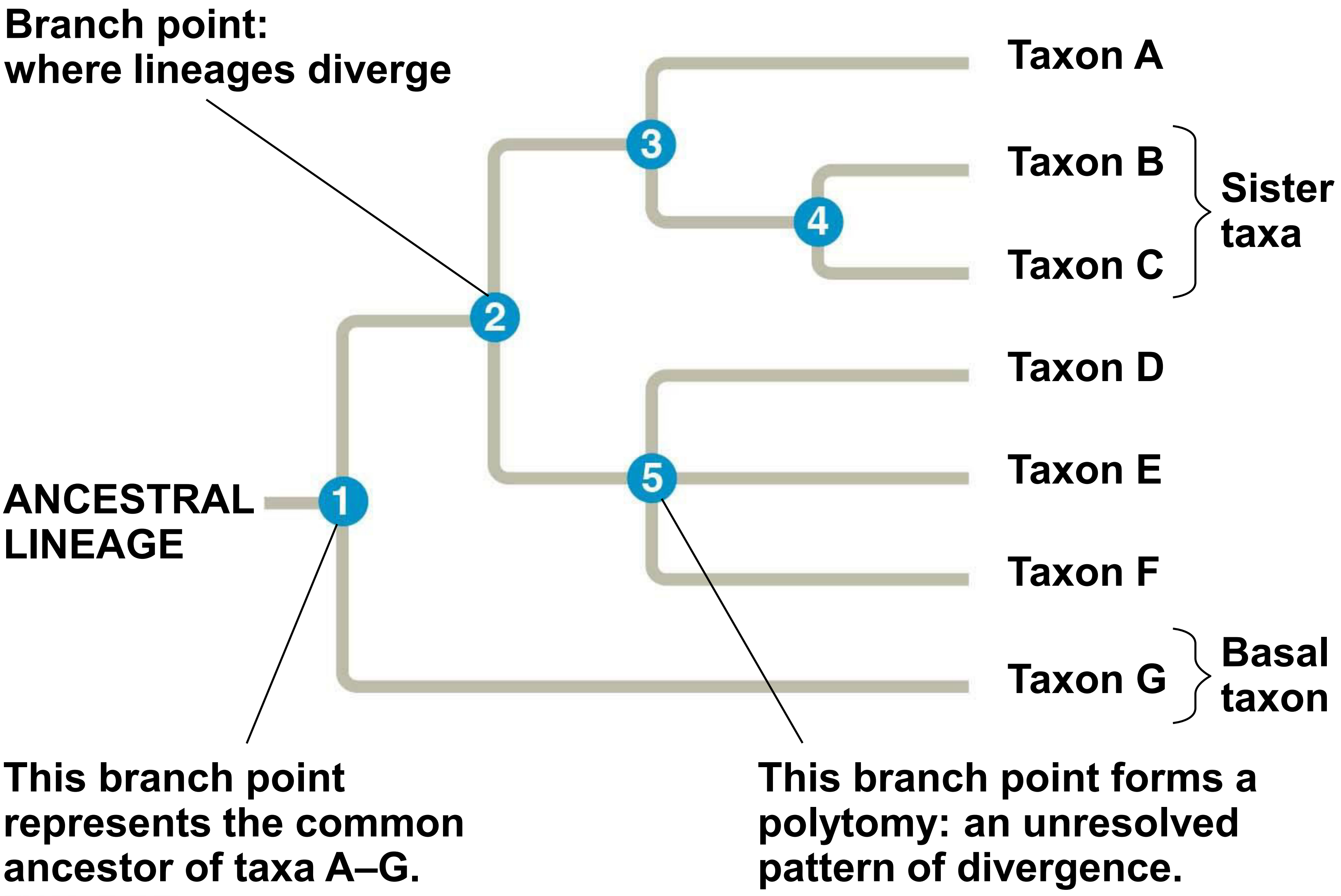
Order
Family
Genus
Species
Carnivora
Felidae
Panthera
Mustelidae
Taxidea
Lutra
Canidae
Canis
1
2
Panthera pardus (leopard)
Taxidea taxus (American badger)
Lutra lutra (European otter)
Canis latrans (coyote)
Canis lupus (gray wolf)

- Linnaean classification and phylogeny can differ from each other
- Systematists have proposed that classification be based entirely on evolutionary relationships

- A phylogenetic tree represents a hypothesis about evolutionary relationships
- Each **branch point** represents the divergence of two taxa from a common ancestor
- **Sister taxa** are groups that share an immediate common ancestor

- 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
- A **polytomy** is a branch from which more than two groups emerge

Figure 20.5



Branch point: where lineages diverge

ANCESTRAL LINEAGE

1

2

3

4

5

Taxon A

Taxon B

Taxon C

Sister taxa

Taxon D

Taxon E

Taxon F

Taxon G

Basal taxon

This branch point represents the common ancestor of taxa A–G.

This branch point forms a polytomy: an unresolved pattern of divergence.

What We Can and Cannot Learn from Phylogenetic Trees

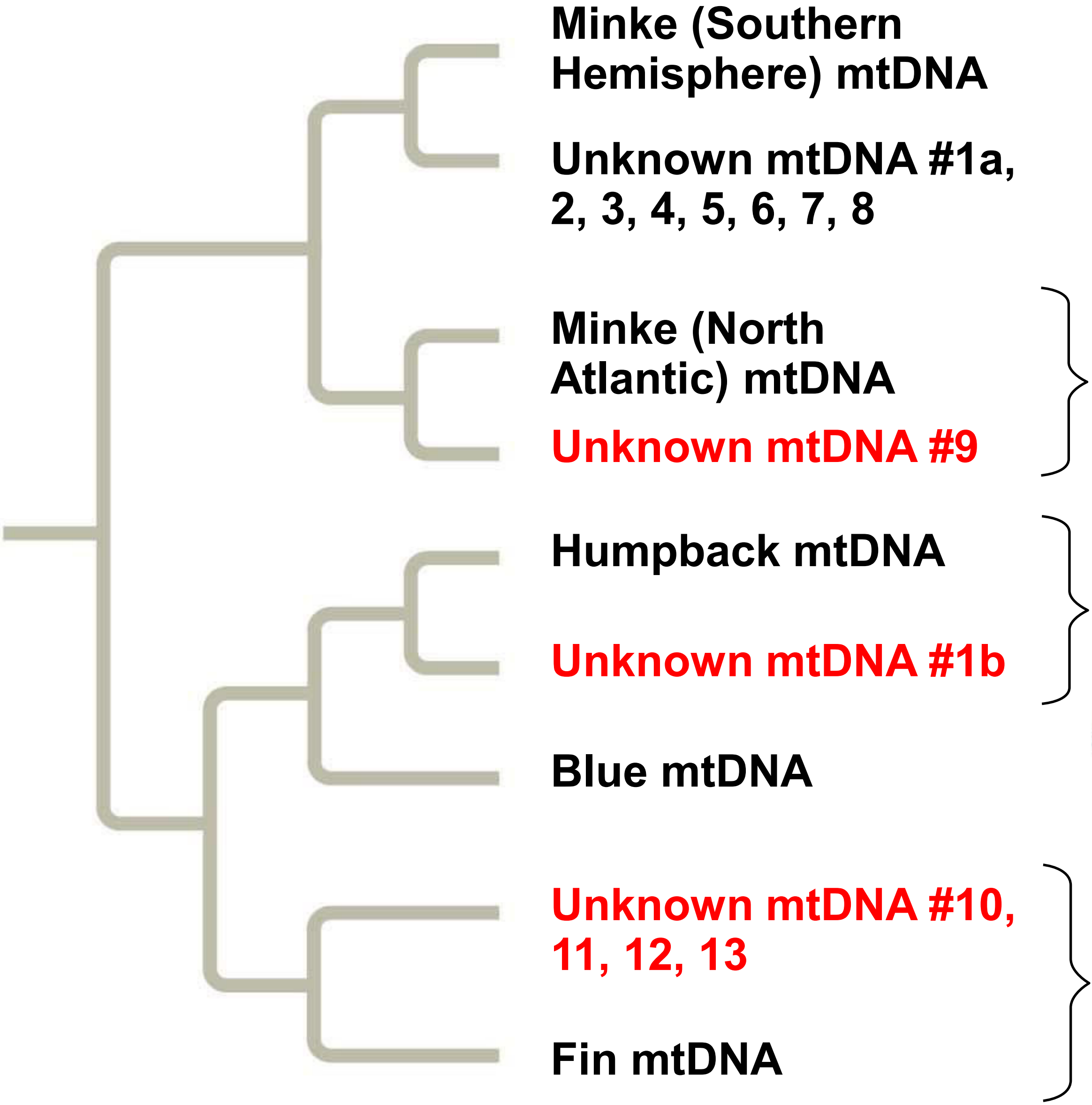
- Phylogenetic trees show patterns of descent, not phenotypic similarity
- Phylogenetic trees do not generally indicate when a species evolved or how much change occurred in a lineage
- It should not be assumed that a taxon evolved from the taxon next to it

Applying Phylogenies

- Phylogeny provides important information about similar characteristics in closely related species
- Phylogenetic trees based on DNA sequences can be used to infer species identities
  - For example: A phylogeny was used to identify the species of whale from which “whale meat” originated

Figure 20.6

Results


Minke (Southern Hemisphere) mtDNA

Unknown mtDNA #1a, 2, 3, 4, 5, 6, 7, 8

Minke (North Atlantic) mtDNA

Unknown mtDNA #9

Humpback mtDNA

Unknown mtDNA #1b

Blue mtDNA

Unknown mtDNA #10, 11, 12, 13

Fin mtDNA

Concept 20.2: Phylogenies are inferred from morphological and molecular data

- To infer phylogeny, systematists gather information about morphologies, genes, and biochemistry of the relevant organisms
- The similarities used to infer phylogenies must result from shared ancestry

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

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

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

Figure 20.7

Australian marsupial mole

North American eutherian mole

- Bat and bird wings are homologous as forelimbs, but analogous as functional wings
- Analogous structures or molecular sequences that evolved independently are also called **homoplasies**
- Homology can be distinguished from analogy by comparing fossil evidence and the degree of complexity
- The more complex two similar structures are, the more likely it is that they are homologous

Evaluating Molecular Homologies

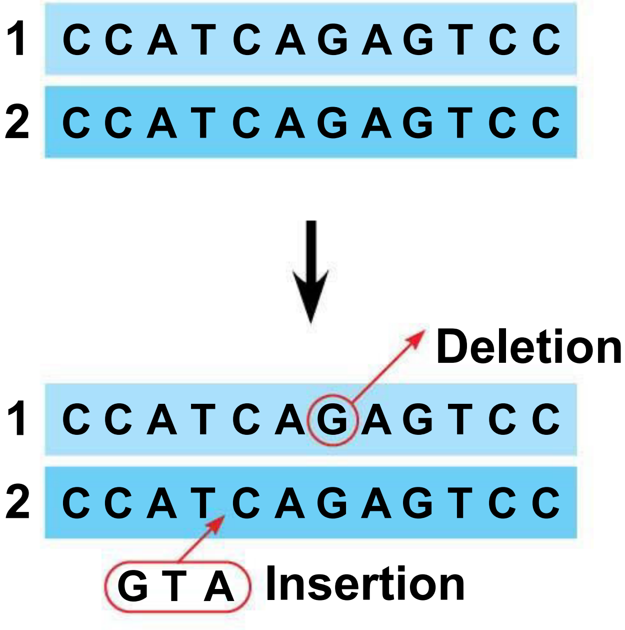
- Molecular homologies are determined based on the degree of similarity in nucleotide sequence between taxa
- Systematists use computer programs when analyzing comparable DNA segments from different organisms

Figure 20.8-s1

1 C C A T C A G A G T C C

2 C C A T C A G A G T C C

Figure 20.8-s2



1 C C A T C A G A G T C C

2 C C A T C A G A G T C C

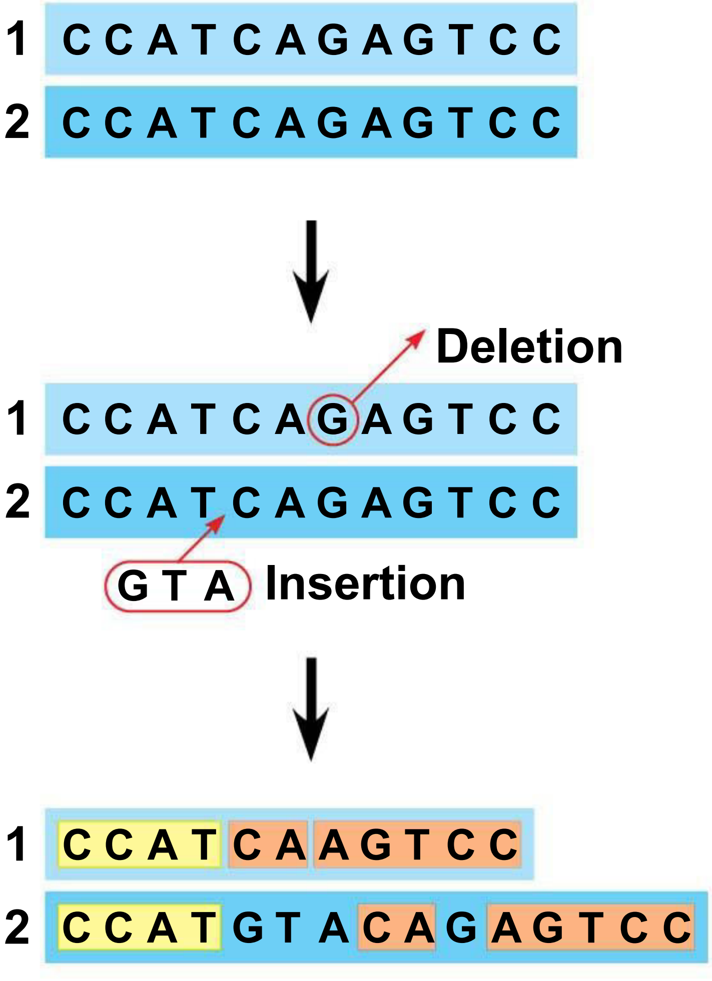
Deletion

1 C C A T C A G A G T C C

2 C C A T C A G A G T C C

G T A Insertion

Figure 20.8-s3



1 C C A T C A G A G T C C

2 C C A T C A G A G T C C

Deletion

1 C C A T C A G A G T C C

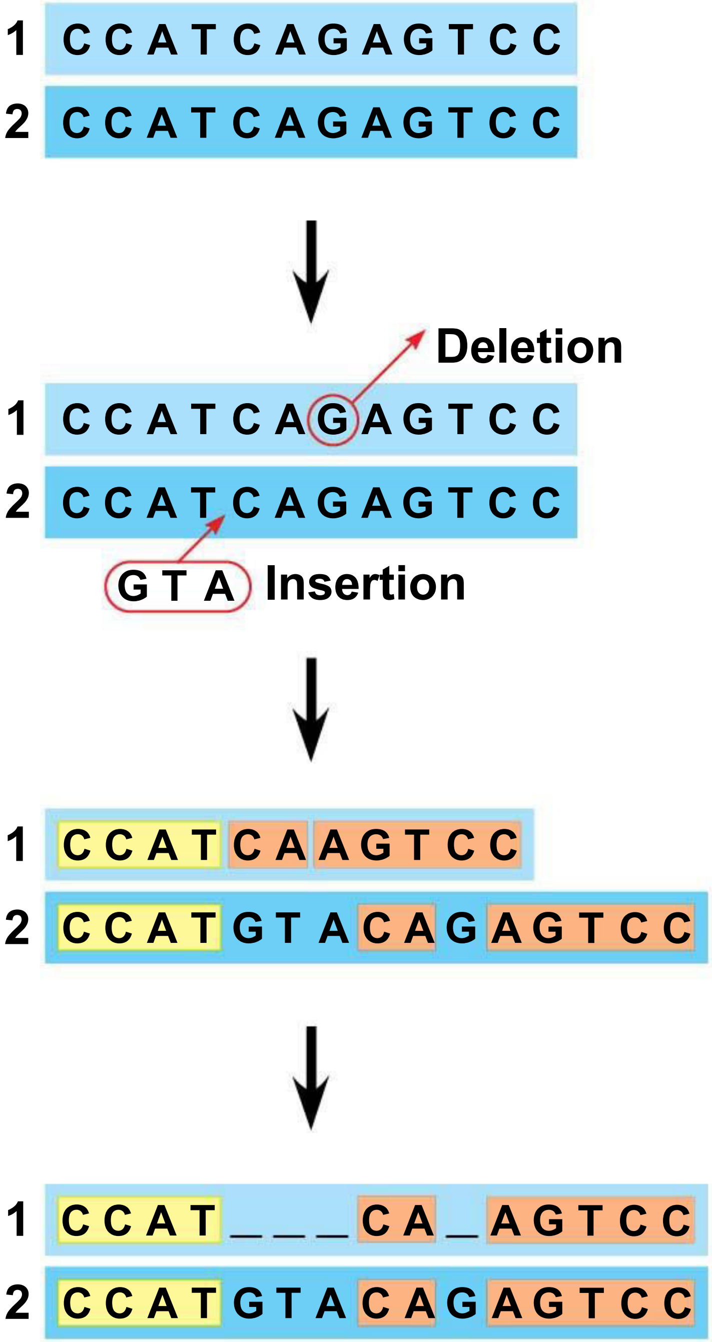
2 C C A T C A G A G T C C

G T A Insertion

1 C C A T C A A G T C C

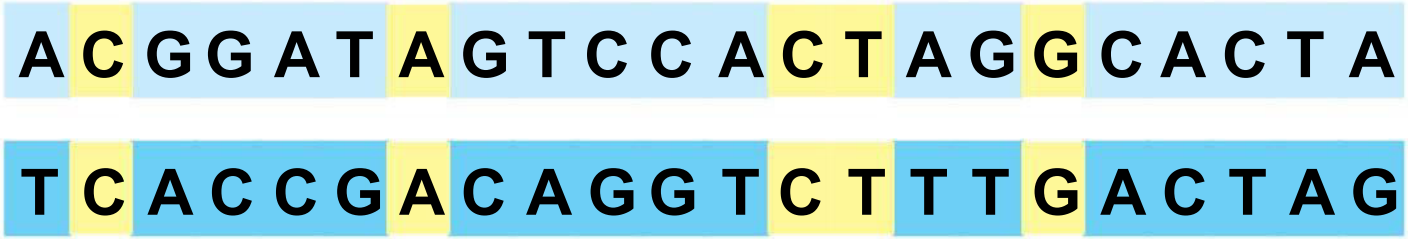
2 C C A T G T A C A G A G T C C

Figure 20.8-s4



- Shared bases in nucleotide sequences that are otherwise very dissimilar are called molecular homoplasies

Figure 20.9



A C G G A T A G T C C A C T A G G C A C T A

T C A C C G A C A G G T C T T T G A C T A G

Concept 20.3: Shared characters are used to construct phylogenetic trees

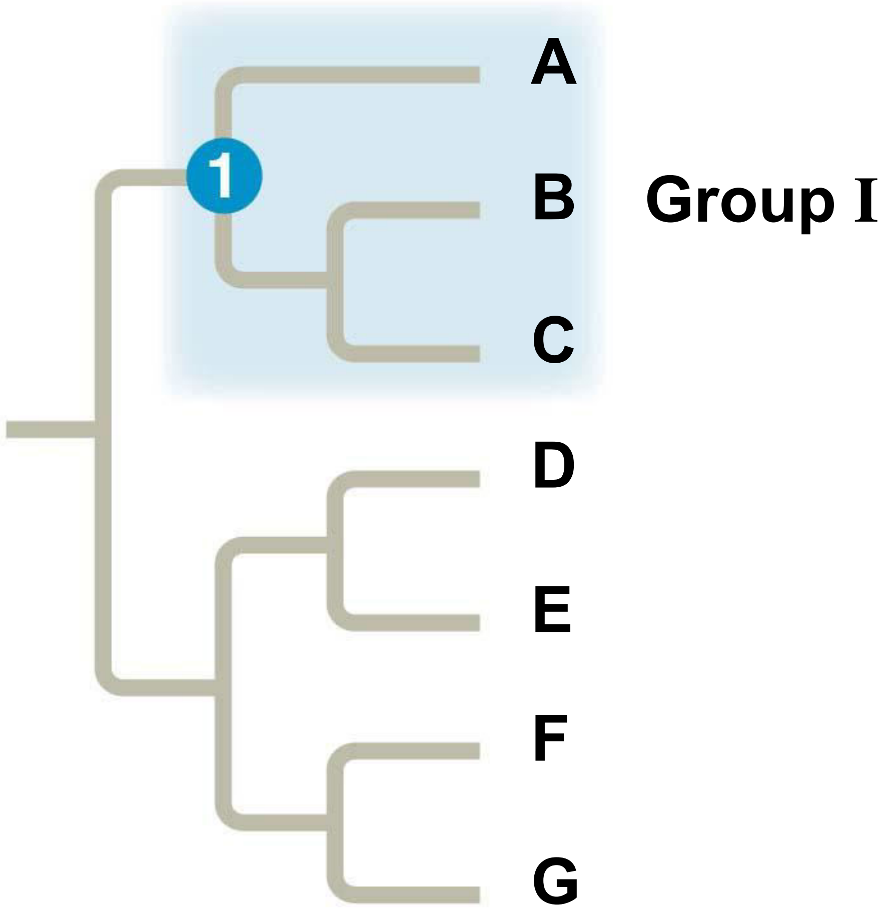
- Once homologous characters have been identified, they can be used to infer a phylogeny

Cladistics

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

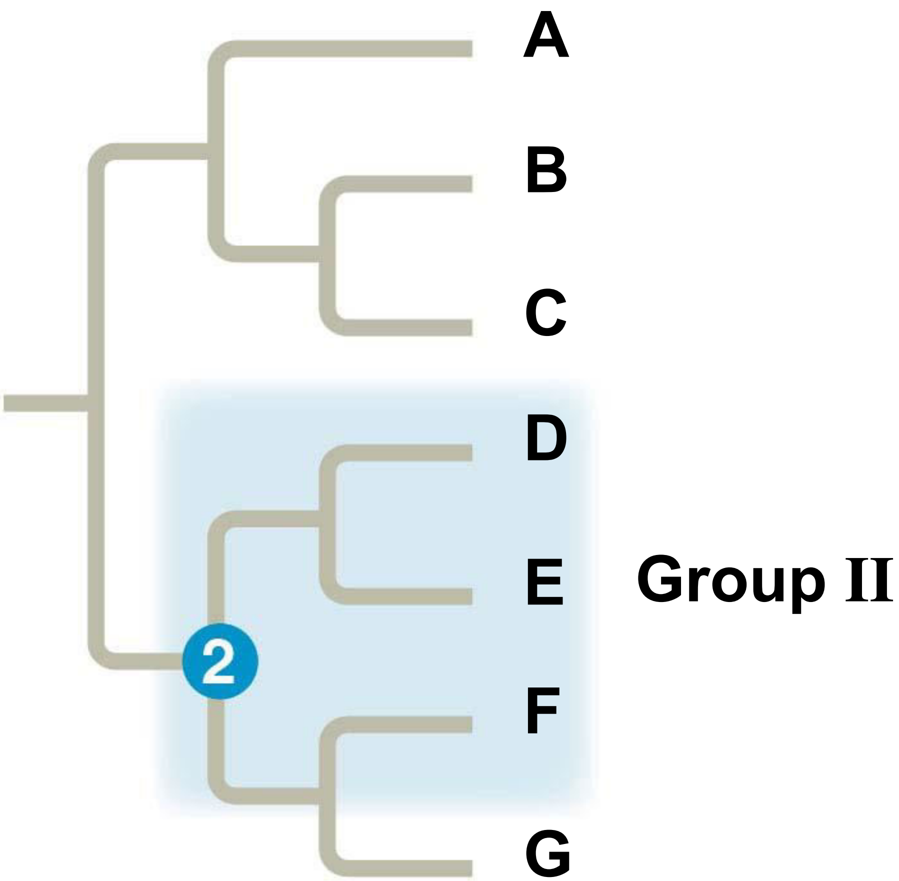
- A valid clade is **monophyletic**, signifying that it consists of the ancestor species and all its descendants

(a) Monophyletic group (clade)



- A **paraphyletic** grouping consists of an ancestral species and some, but not all, of the descendants

(b) Paraphyletic group



- A **polyphyletic** grouping consists of various taxa with different ancestors

(c) Polyphyletic group

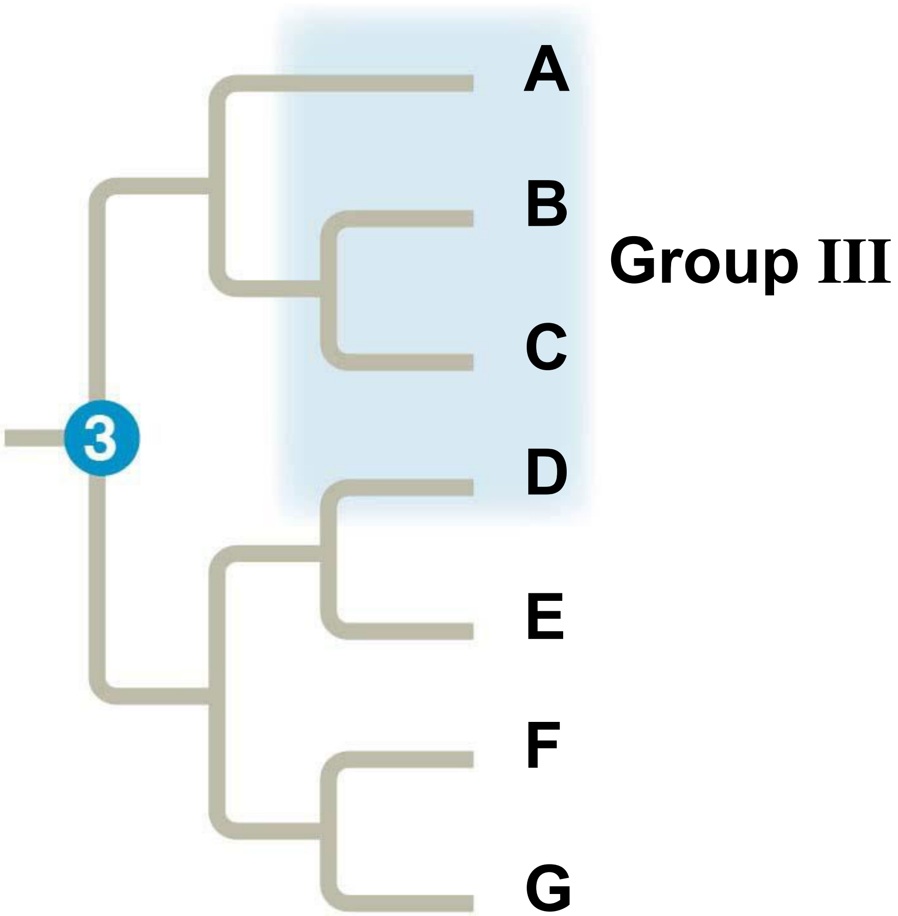
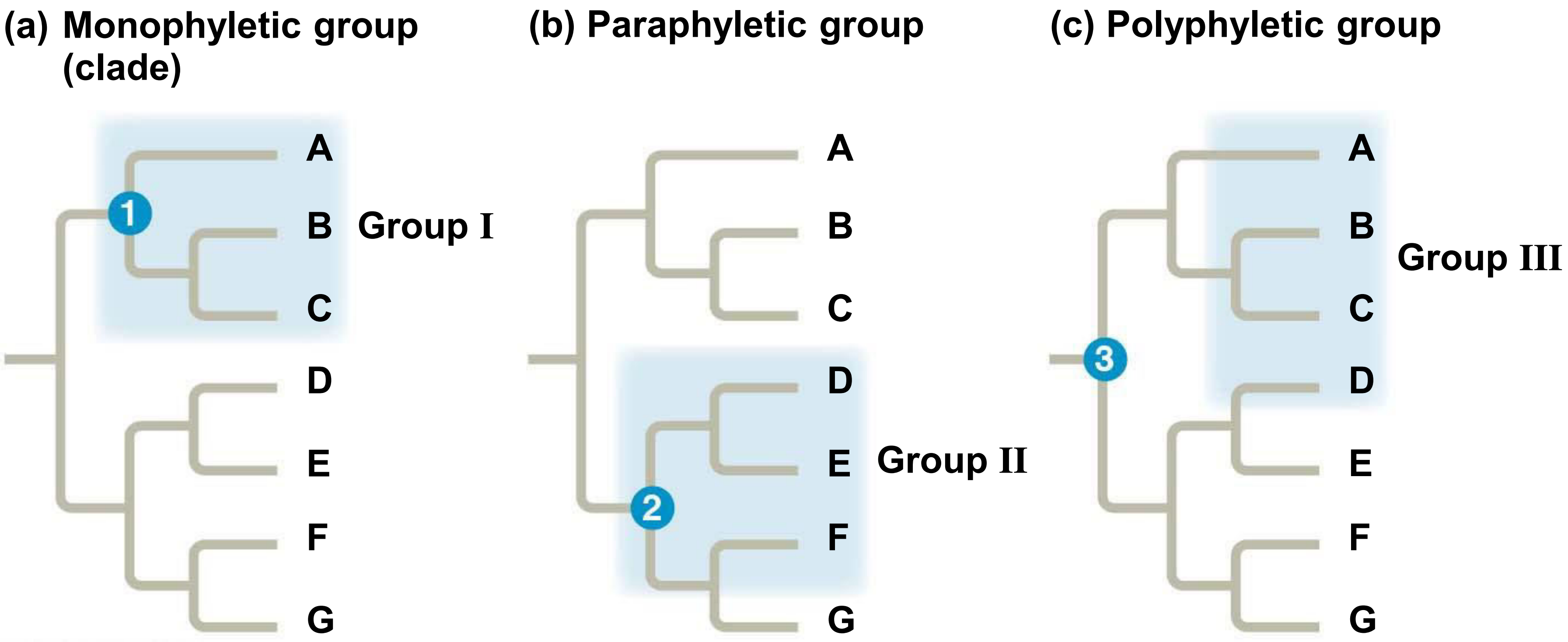


Figure 20.10



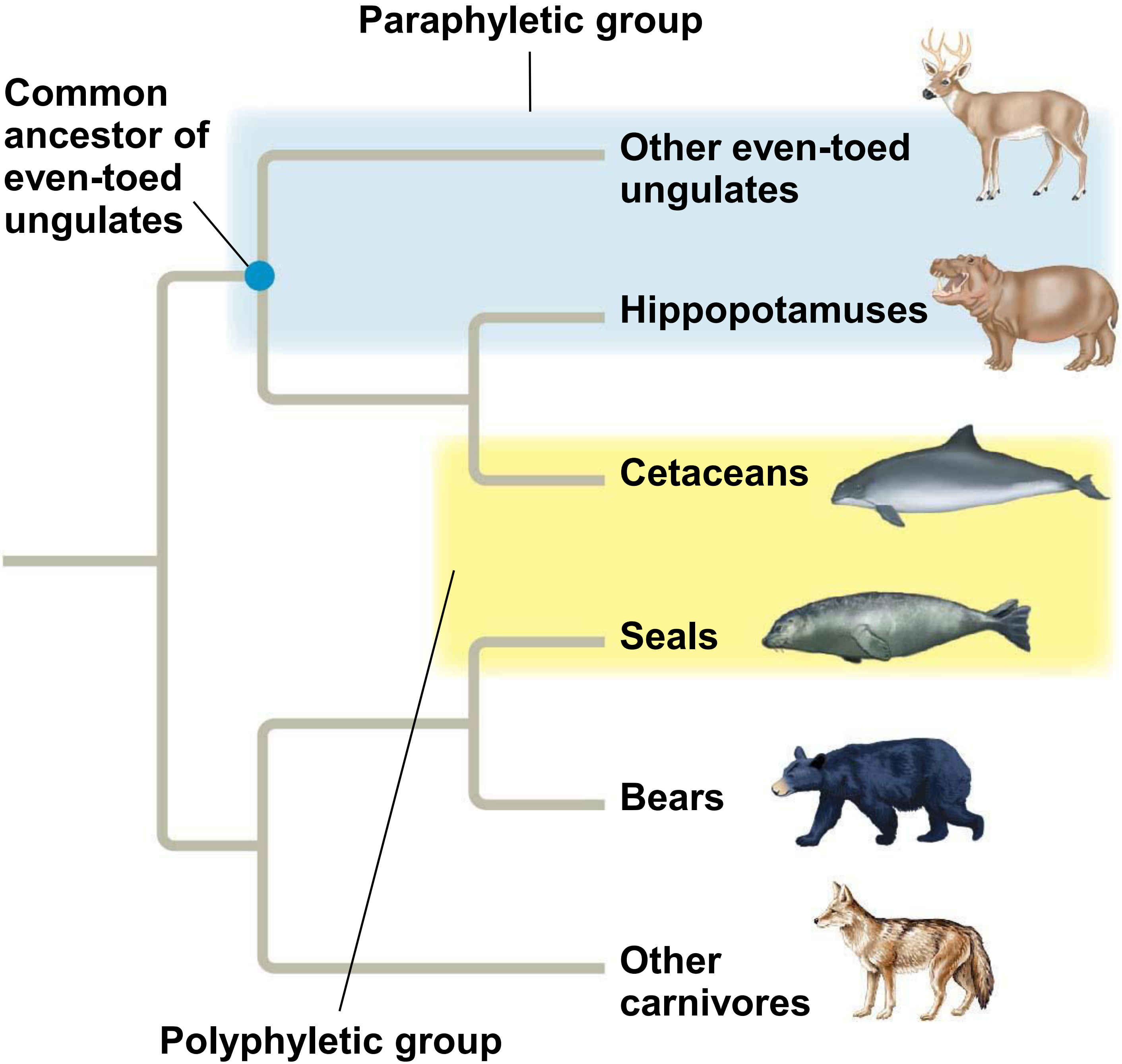
(a) Monophyletic group (clade)

(b) Paraphyletic group

(c) Polyphyletic group

- In a paraphyletic group, the most recent common ancestor of all members of the group *is* part of the group
- In a polyphyletic group, the most recent common ancestor *is not* part of the group

Figure 20.11



Paraphyletic group
Common ancestor of even-toed ungulates
Other even-toed ungulates
Hippopotamuses
Cetaceans
Seals
Bears
Other carnivores
Polyphyletic group

Shared Ancestral and Shared Derived Characters

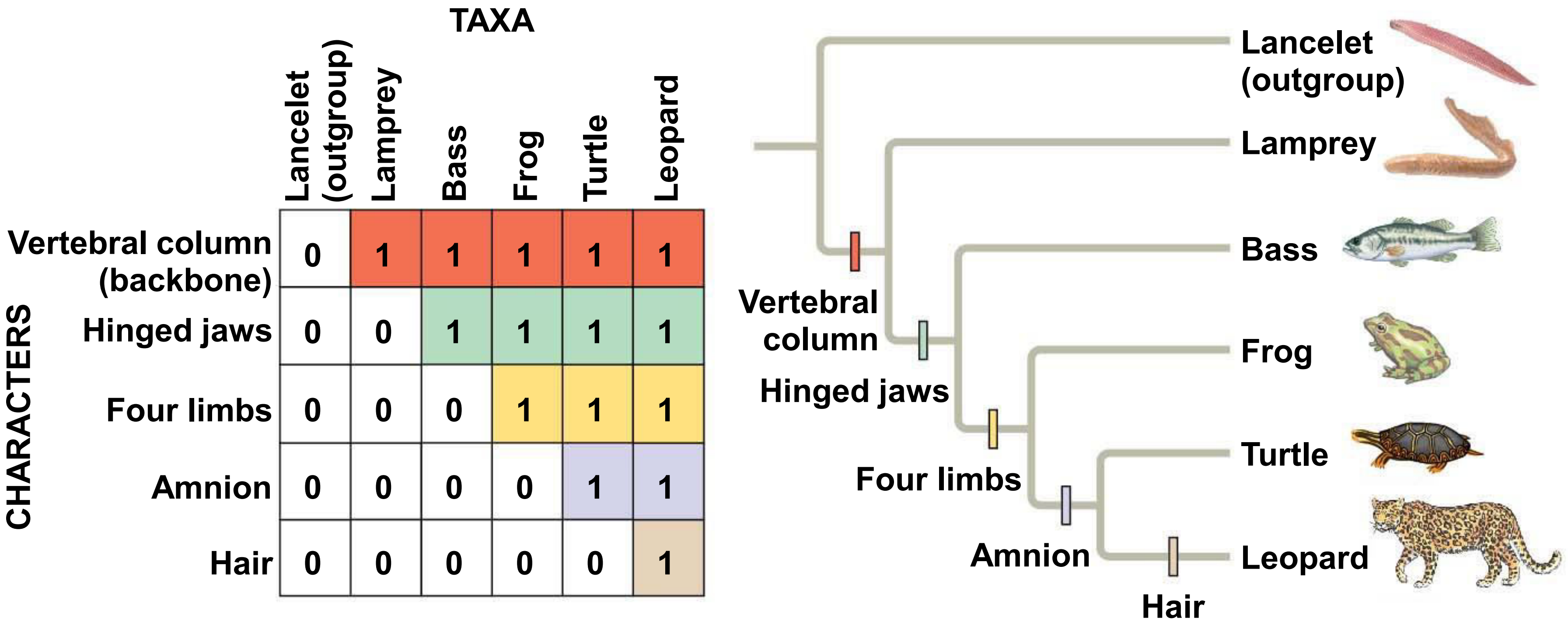
- In comparison with its ancestor, an organism has both shared and different characteristics

- 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

Inferring Phylogenies Using Derived Characters

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

Figure 20.12



(a) Character table

CHARACTERS	Lancelet (outgroup)	Lamprey	Bass	Frog	Turtle	Leopard
	TAXA					
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

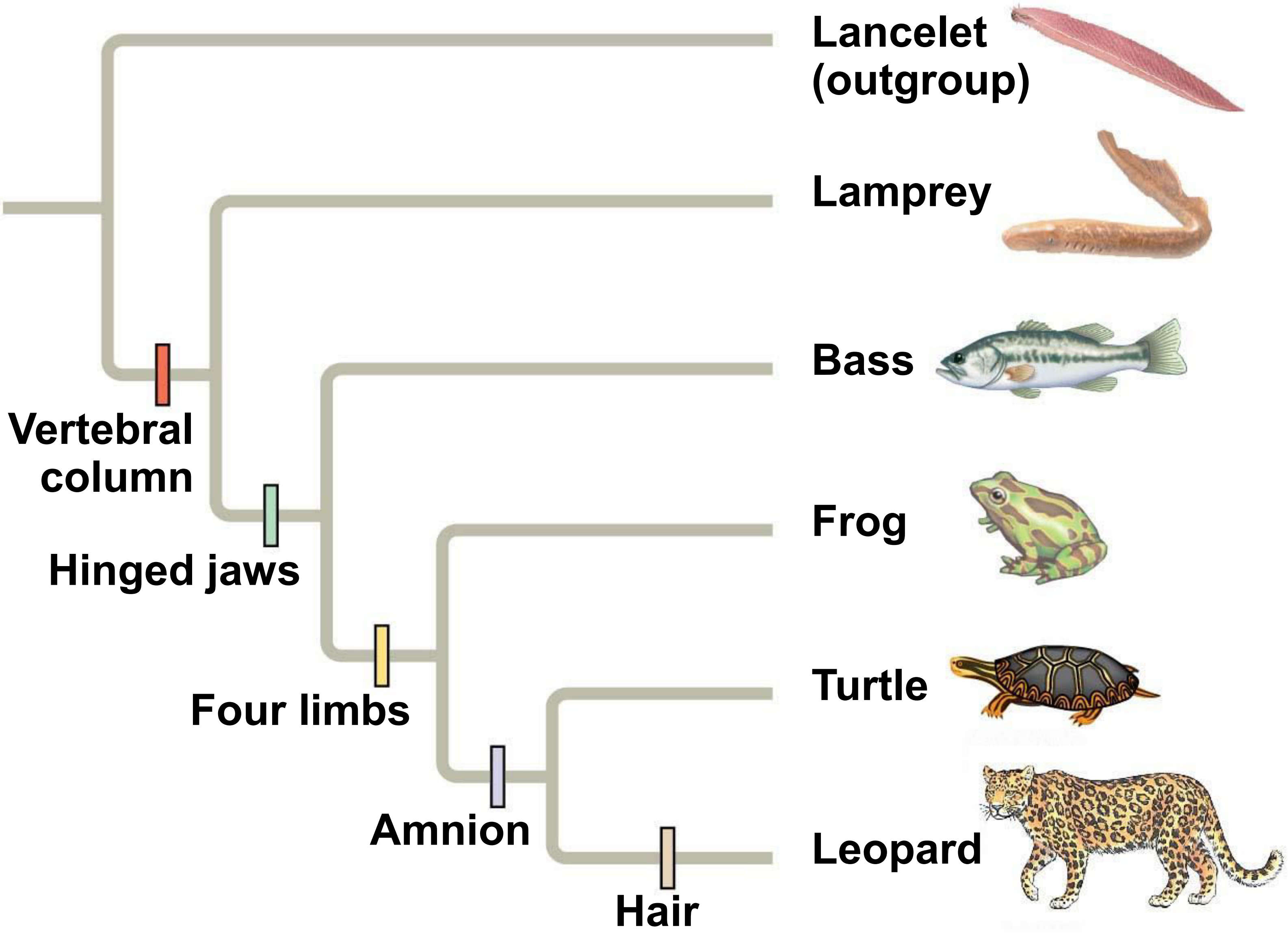
(b) Phylogenetic tree

Figure 20.12-1

	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

Figure 20.12-2



(b) Phylogenetic tree

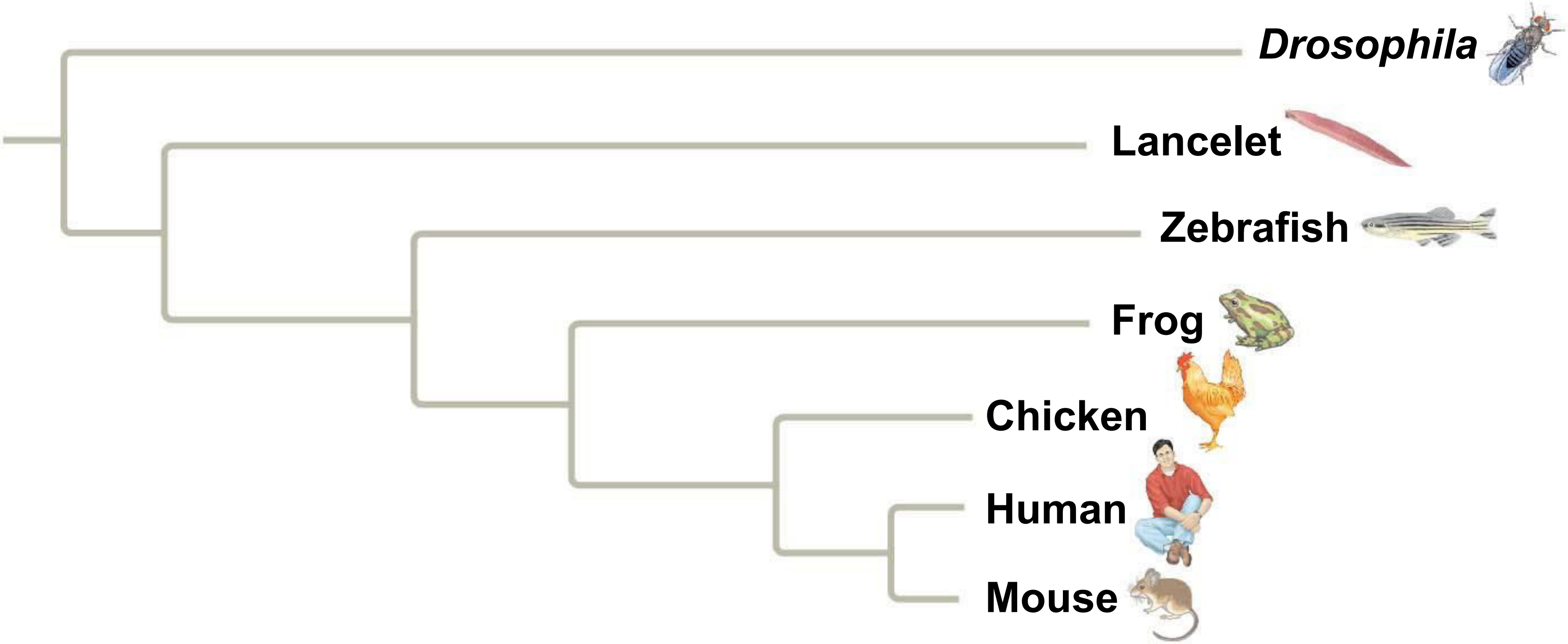
- An **outgroup** is a species or group of species that is closely related to the **ingroup**, the various species being studied
- The outgroup is a group that has diverged before the ingroup
- Systematists compare each ingroup species with the outgroup to differentiate between shared derived and shared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

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

Phylogenetic Trees with Proportional Branch Lengths

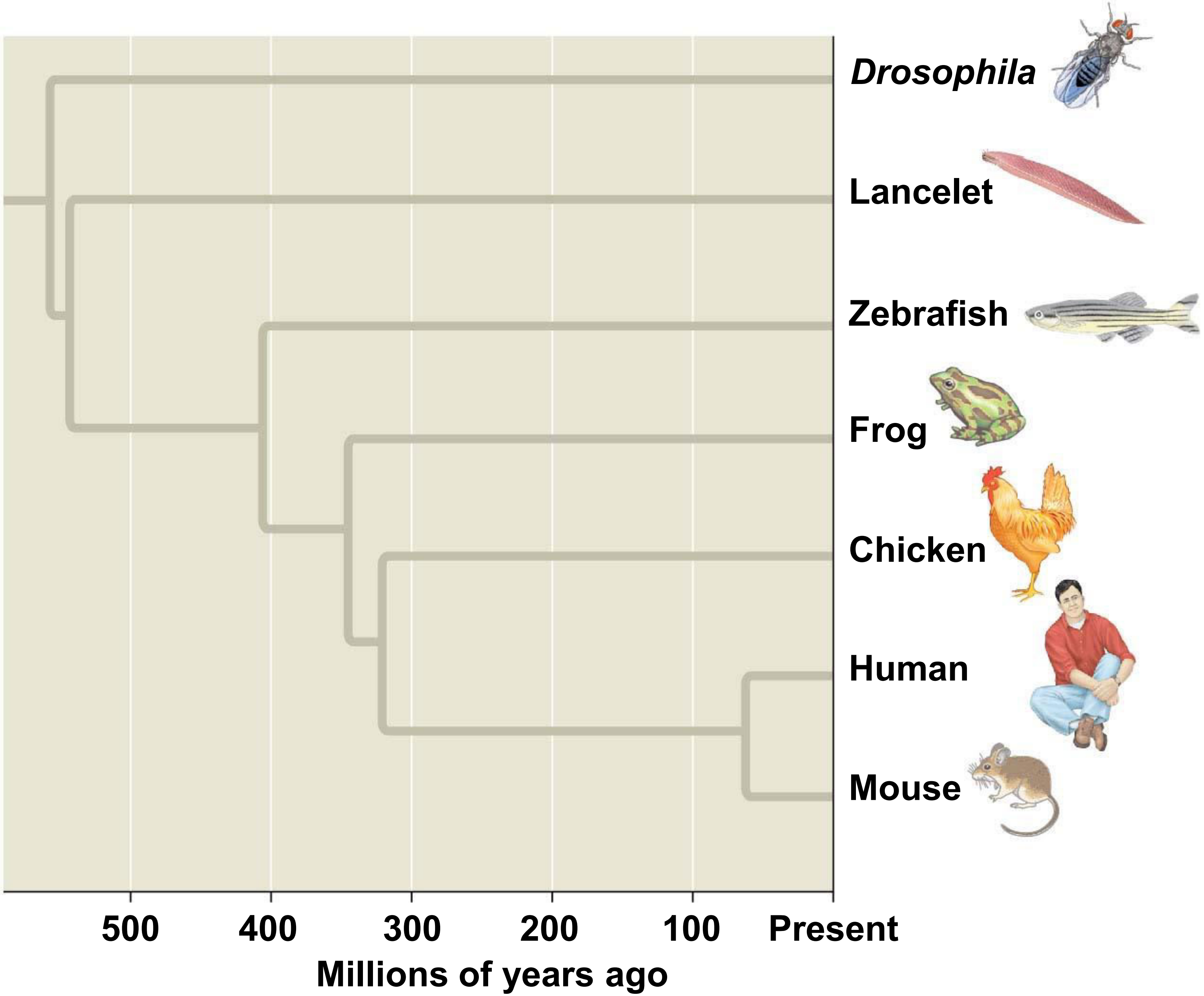
- In some trees, the length of a branch can reflect the number of genetic changes that have taken place in a particular DNA sequence in that lineage

Figure 20.13



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

Figure 20.14


Drosophila
Lancelet
Zebrafish
Frog
Chicken
Human
Mouse
500
400
300
200
100
Present
Millions of years ago

Maximum Parsimony

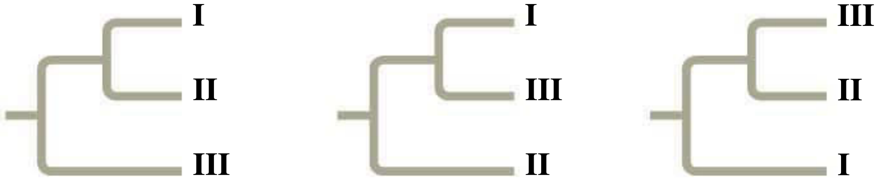
- Systematists can never be sure of finding the best tree in a large data set
- They narrow possibilities by applying the principle of maximum parsimony

- **Maximum parsimony** assumes that the tree that requires the fewest evolutionary events (appearances of shared derived characters) is the most likely
- Computer programs are used to search for trees that are parsimonious

Figure 20.15

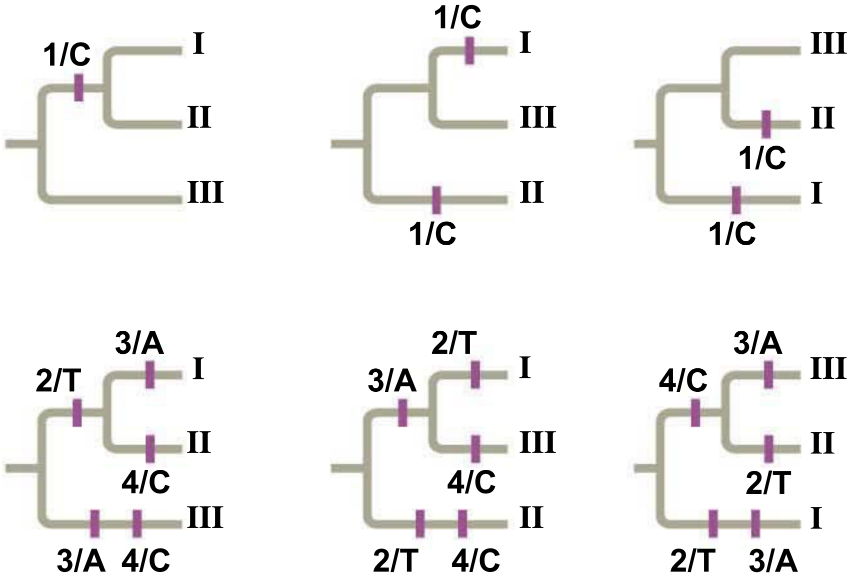
Technique

Three phylogenetic hypotheses:



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



Results

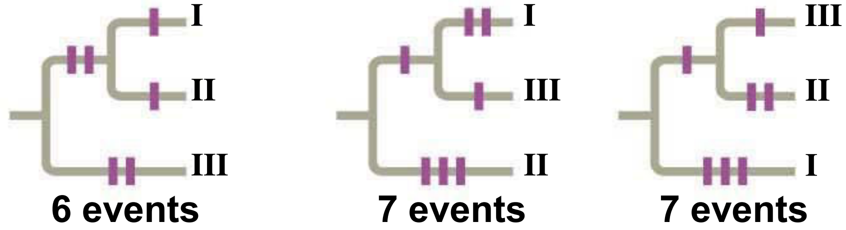


Figure 20.15-1

Technique

Species I **Species II** **Species III**

Three phylogenetic hypotheses:

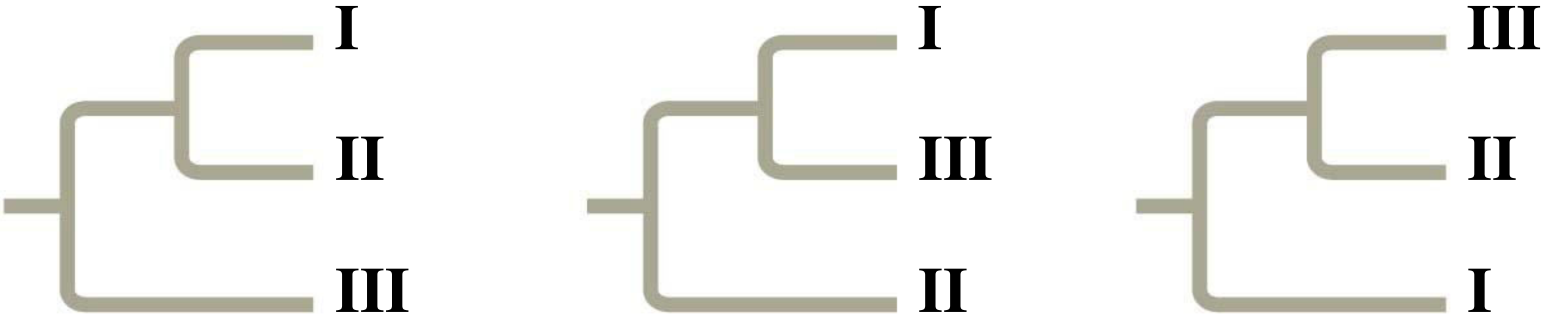


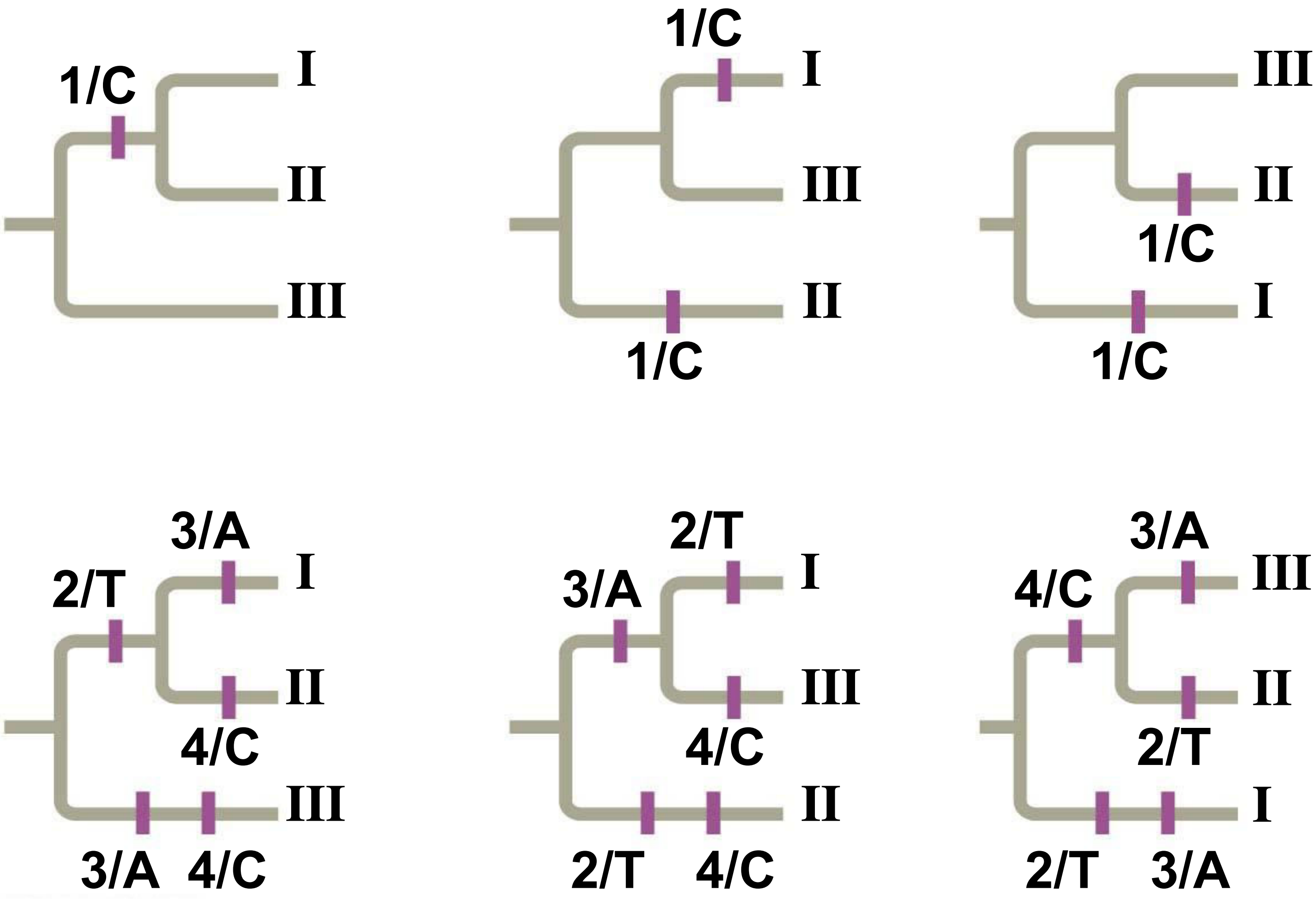
Figure 20.15-2

Technique

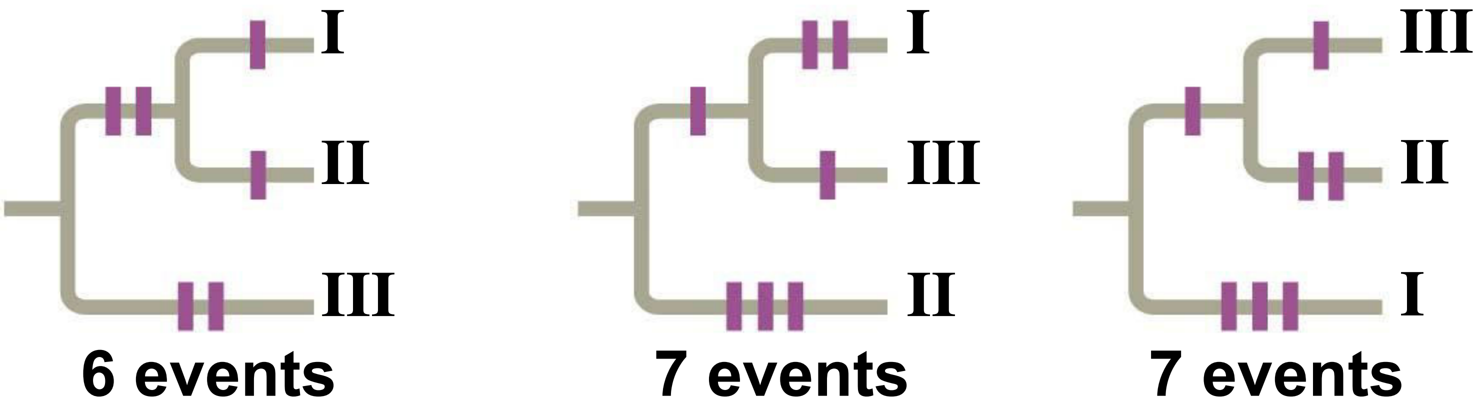
	Site			
	1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

Figure 20.15-3

Technique



Results

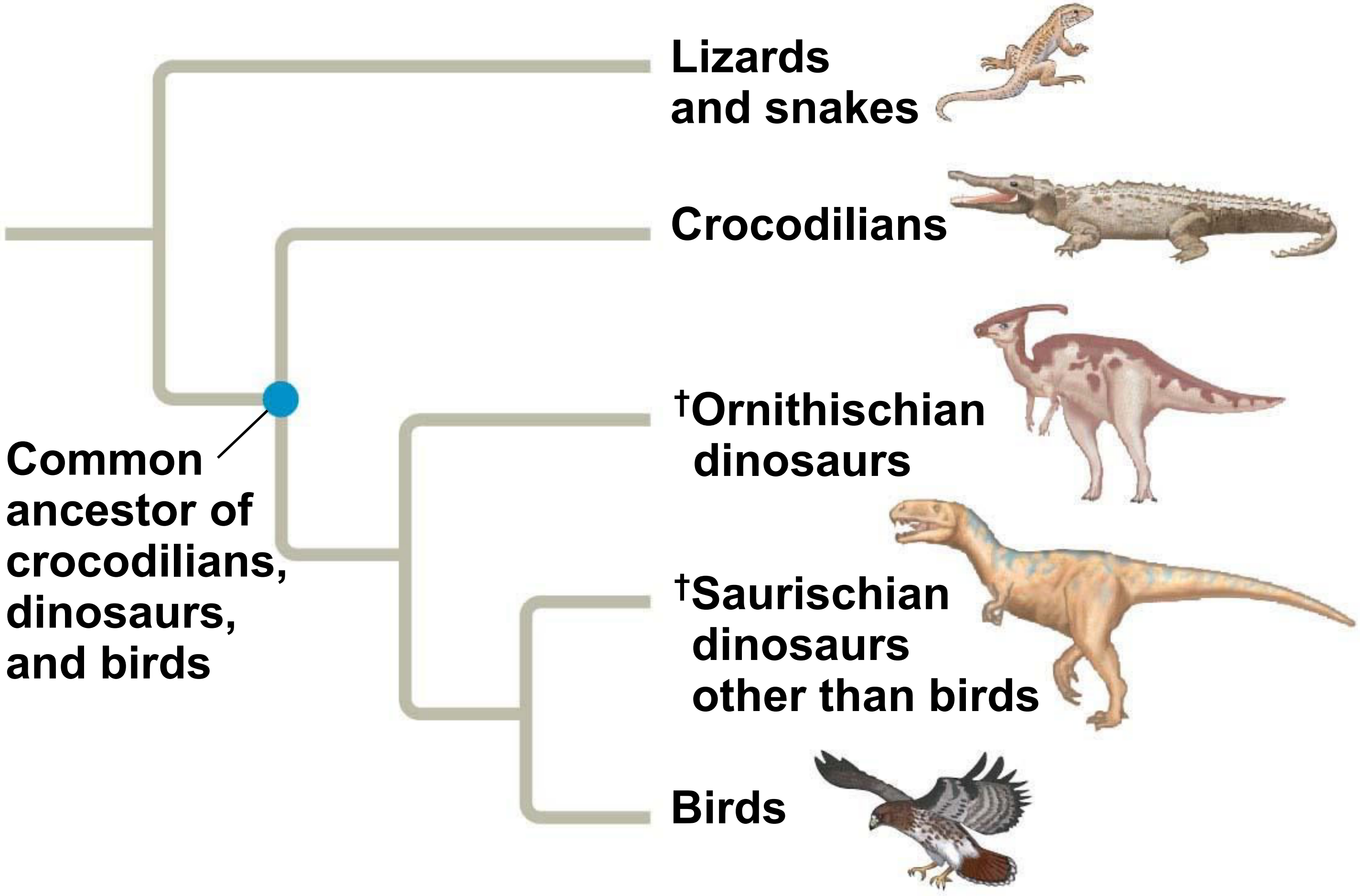


Phylogenetic Trees as Hypotheses

- The best hypothesized phylogenetic tree fits the most data: morphological, molecular, and fossil
- Phylogenetic hypotheses are modified when new evidence arises

- Phylogenetic bracketing allows us to predict features of ancestors and their extinct descendants based on the features of closely related living descendants
  - For example, phylogenetic bracketing allows us to infer characteristics of dinosaurs based on shared characters in modern birds and crocodiles

Figure 20.16

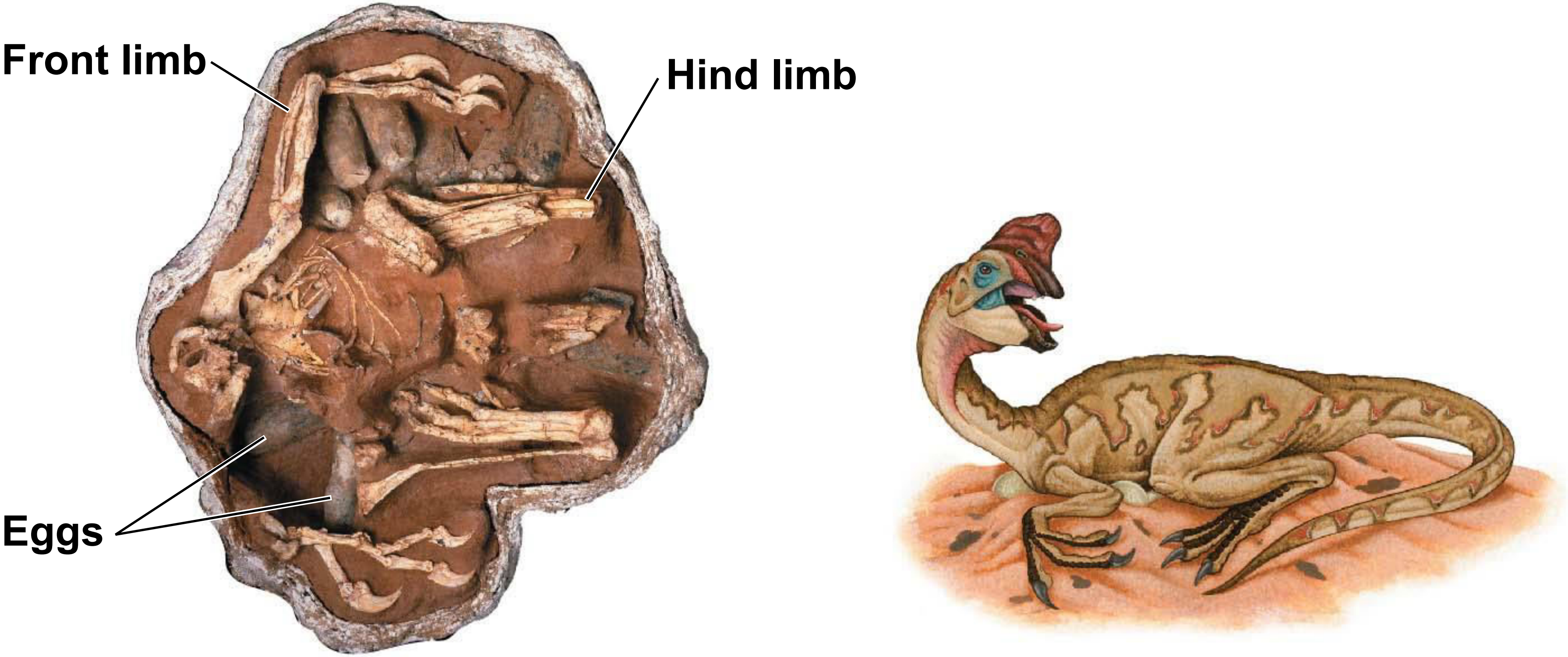

Lizards
and snakes
Crocodilians
†Ornithischian
dinosaurs
†Saurischian
dinosaurs
other than birds
Birds
Common
ancestor of
crocodilians,
dinosaurs,
and birds

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

Figure 20.17

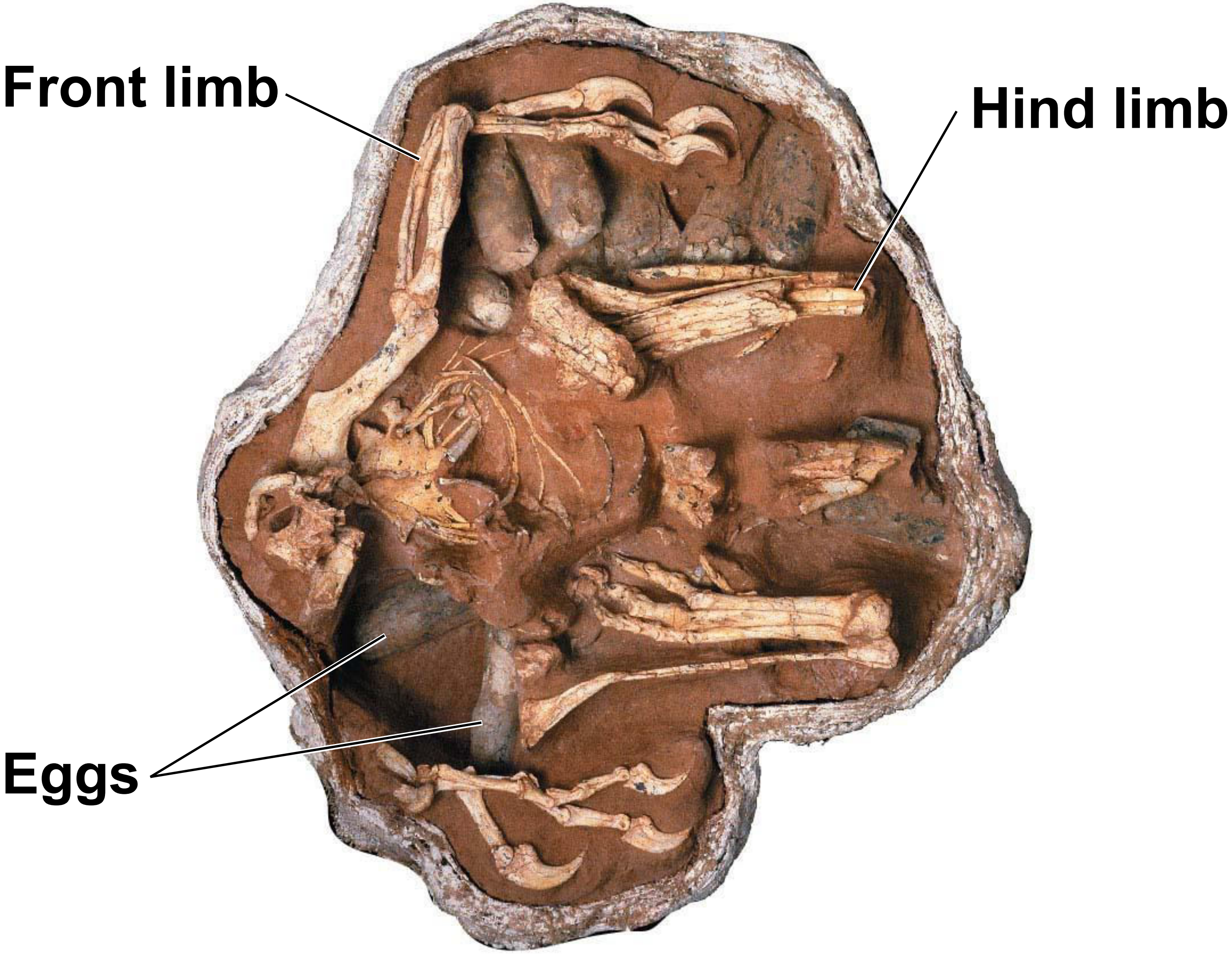
- The fossil record supports nest building and brooding in dinosaurs

Figure 20.18



(a) Fossil remains of *Oviraptor* and eggs

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



(a) Fossil remains of *Oviraptor* and eggs

Concept 20.4: Molecular clocks help track evolutionary time

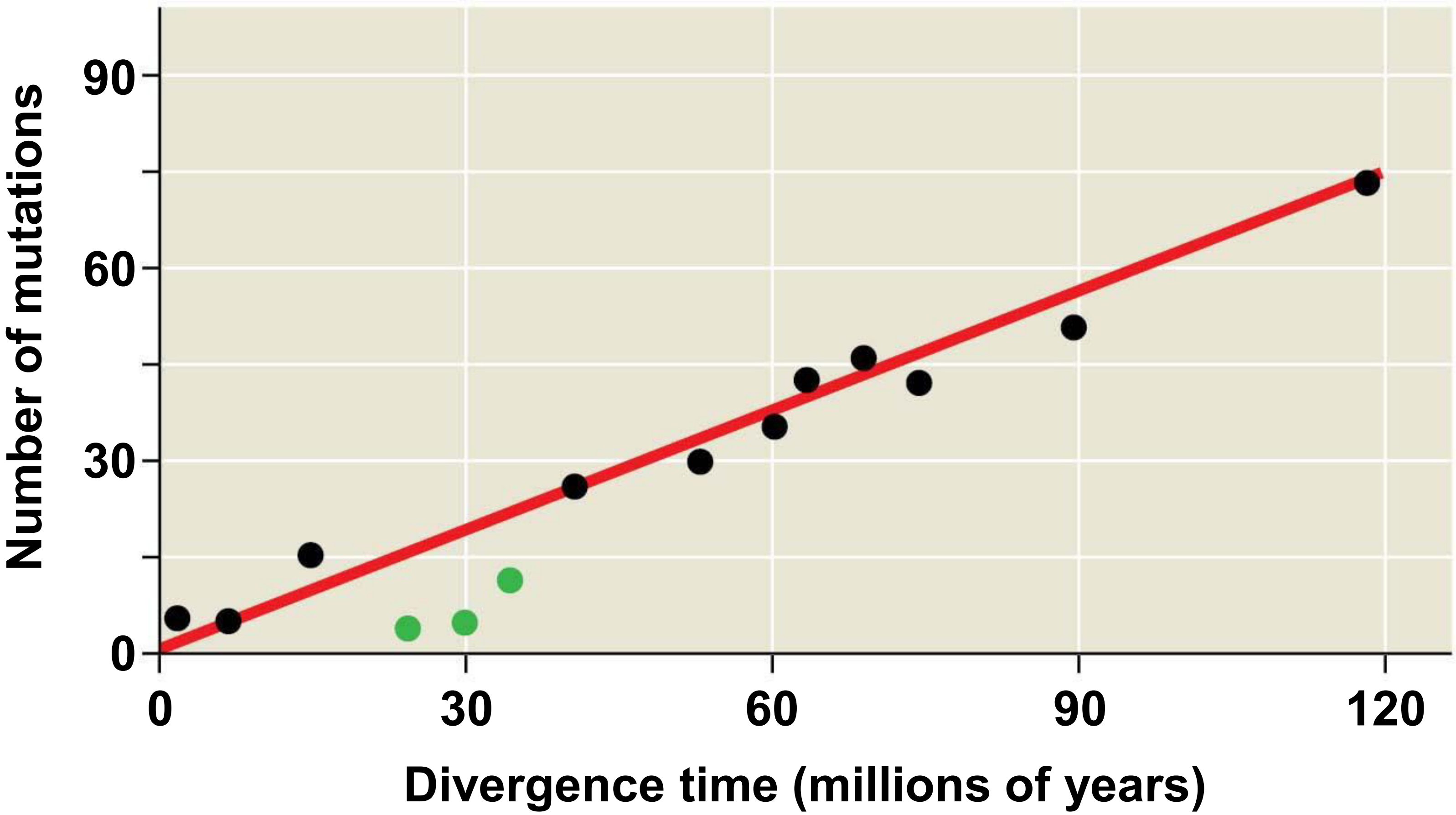
- To extend molecular phylogenies beyond the fossil record, we must make an assumption about how molecular change occurs over time

Molecular Clocks

- A **molecular clock** uses constant rates of evolution in some genes to estimate the absolute time of evolutionary change
- The number of nucleotide substitutions in related genes is assumed to be proportional to the time since they last shared a common ancestor

- Molecular clocks are calibrated by plotting the number of genetic changes against the dates of branch points known from the fossil record
- Individual genes vary in how clocklike they are

Figure 20.19


Number of mutations
90
60
30
0
0
30
60
90
120
Divergence time (millions of years)

Differences in Clock Speed

- Some mutations are selectively neutral and have little or no effect on fitness
- Neutral mutations should be regular like a clock
- The mutation rate is dependent on how critical a gene’s amino acid sequence is to survival

Potential Problems with Molecular Clocks

- Molecular clocks do not run as smoothly as expected if mutations were selectively 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 may improve estimates

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

Animation: Class Schemes

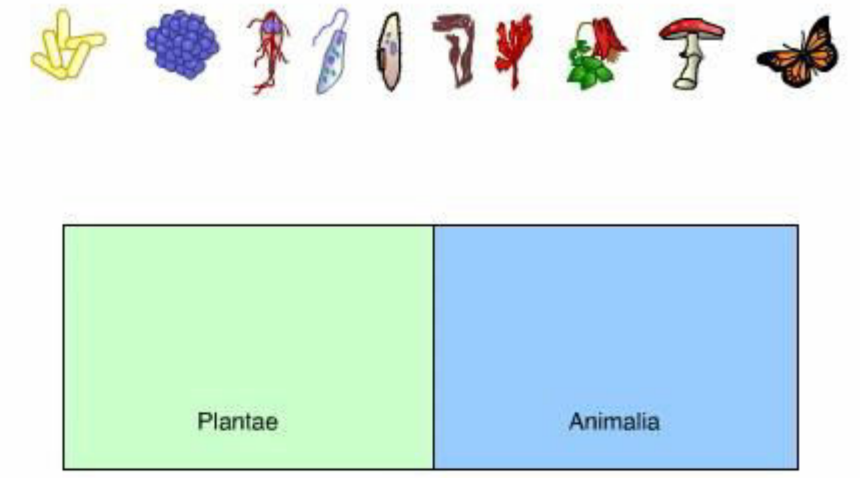
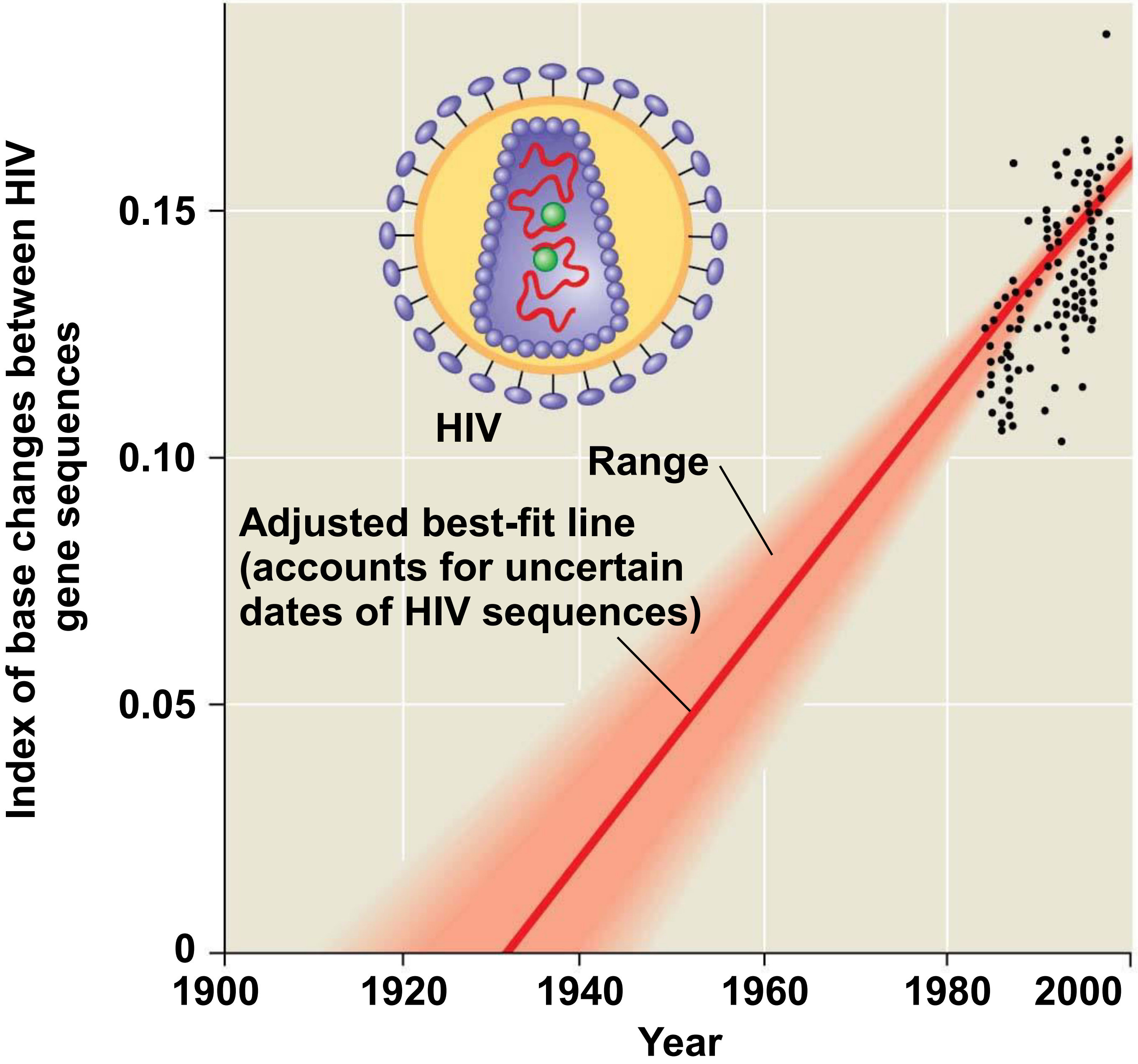


Figure 20.20


Index of base changes between HIV gene sequences
0.15
0.10
0.05
0
1900
1920
1940
1960
1980
2000
Year
HIV
Range
Adjusted best-fit line (accounts for uncertain dates of HIV sequences)

- Application of a molecular clock to one strain of HIV suggests that that strain spread to humans during the 1930s
- A more advanced molecular clock approach has dated the origin of that strain to about 1910

Concept 20.5: New information continues to revise our understanding of evolutionary history

- Recently, systematists have gained insight into the very deepest branches of the tree of life through analysis of DNA sequence data

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

Figure 20.21

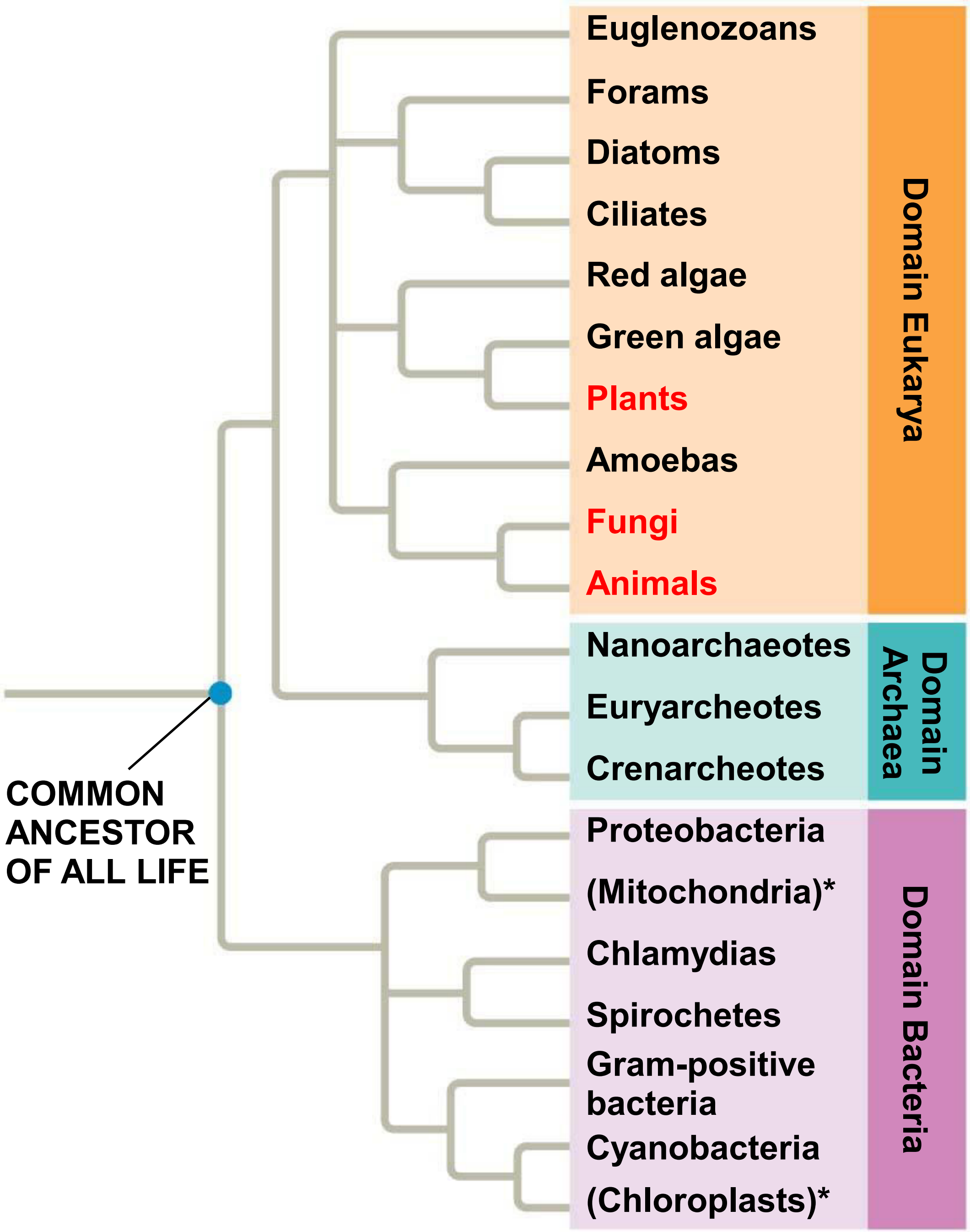
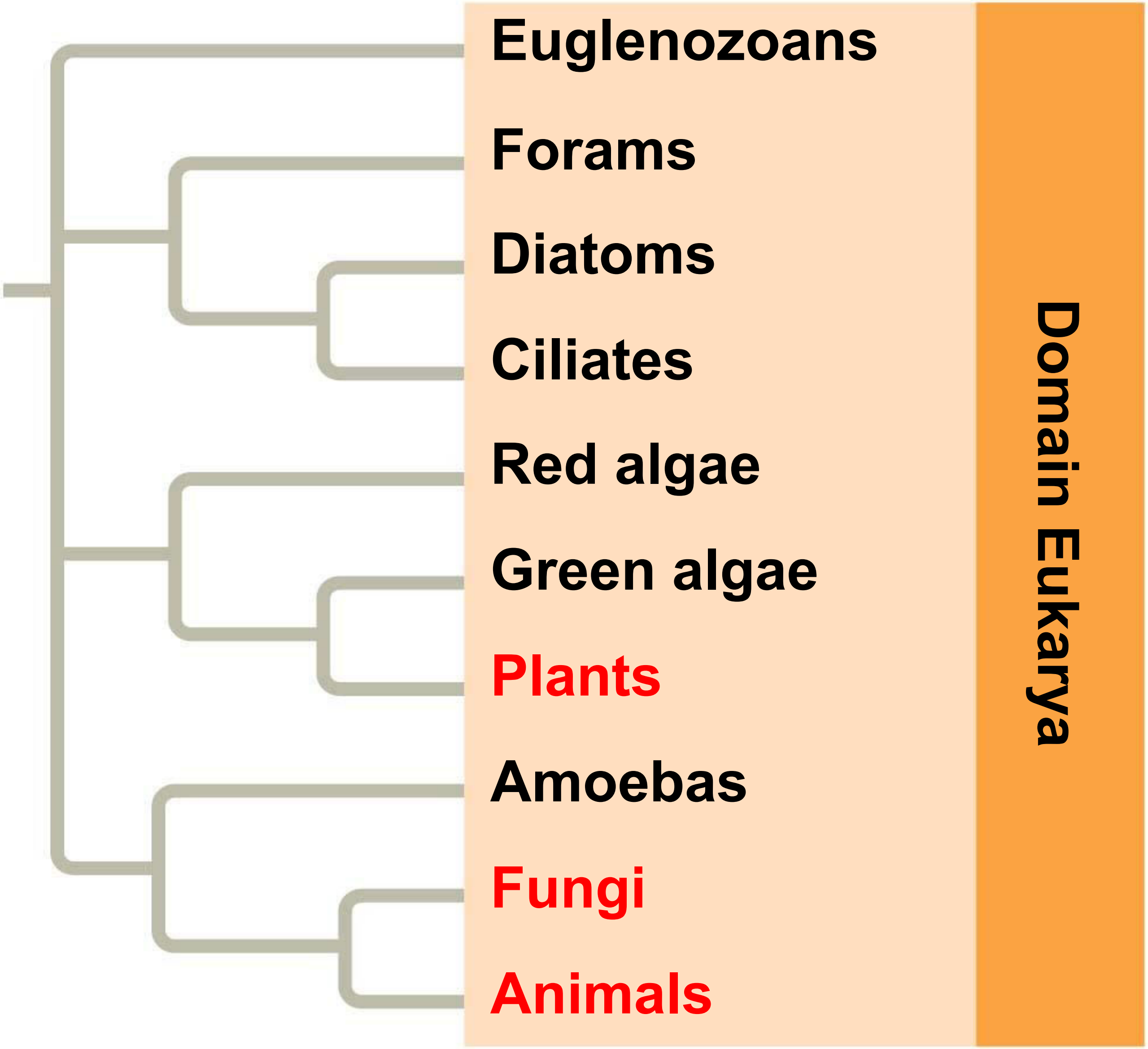

Euglenozoans
Forams
Diatoms
Ciliates
Red algae
Green algae
Plants
Amoebas
Fungi
Animals
Domain Eukarya
Nanoarchaeotes
Euryarcheotes
Crenarcheotes
Domain Archaea
Proteobacteria
(Mitochondria)*
Chlamydias
Spirochetes
Gram-positive bacteria
Cyanobacteria
(Chloroplasts)*
Domain Bacteria
COMMON ANCESTOR OF ALL LIFE

Figure 20.21-1



Euglenozoans

Forams

Diatoms

Ciliates

Red algae

Green algae

Plants

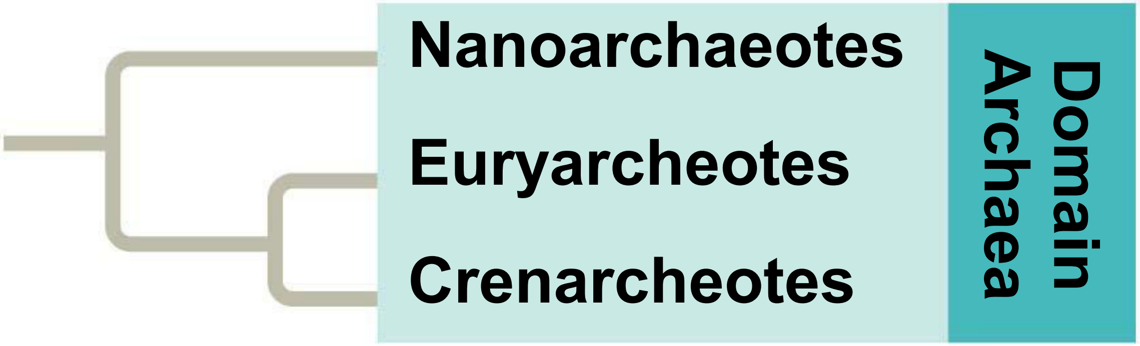
Amoebas

Fungi

Animals

Domain Eukarya

Figure 20.21-2



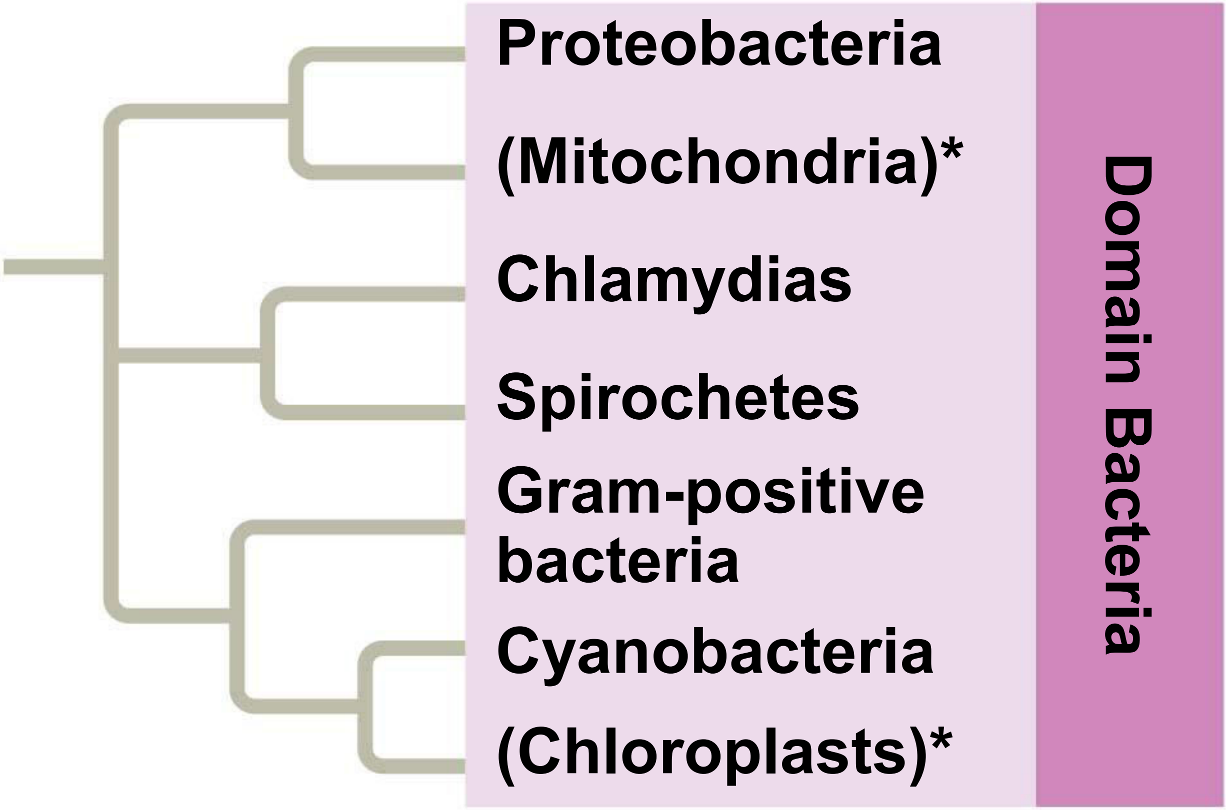
Nanoarchaeotes

Euryarcheotes

Crenarcheotes

Domain Archaea

Figure 20.21-3



Proteobacteria

(Mitochondria)*

Chlamydias

Spirochetes

Gram-positive bacteria

Cyanobacteria

(Chloroplasts)*

Domain Bacteria

- The three-domain system highlights the importance of single-celled organisms in the history of life
- Domains Bacteria and Archaea are single-celled prokaryotes
- Only three lineages in the domain Eukarya are dominated by multicellular organisms, kingdoms Plantae, Fungi, and Animalia

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, which have evolved slowly, allowing detection of homologies between distantly related organisms
- Other genes indicate different evolutionary relationships

- 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 fusion of organisms
- Horizontal gene transfer complicates efforts to build a tree of life

- Horizontal gene transfer may have been common enough that the early history of life is better depicted by a tangled web than a branching tree

Figure 20.22

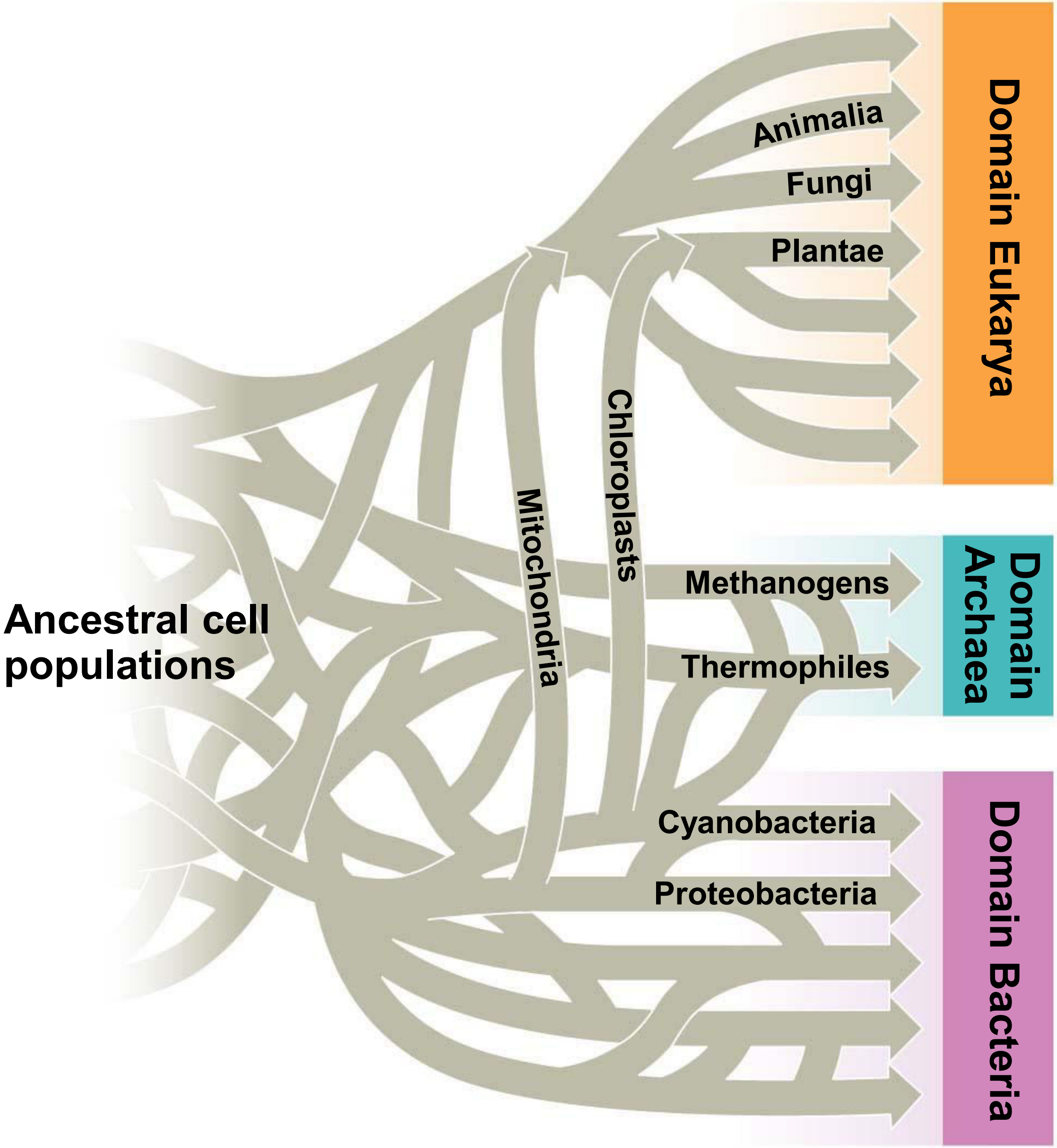

Animalia
Fungi
Plantae
Domain Eukarya
Chloroplasts
Mitochondria
Methanogens
Thermophiles
Domain Archaea
Ancestral cell populations
Cyanobacteria
Proteobacteria
Domain Bacteria

Figure 20.22-1

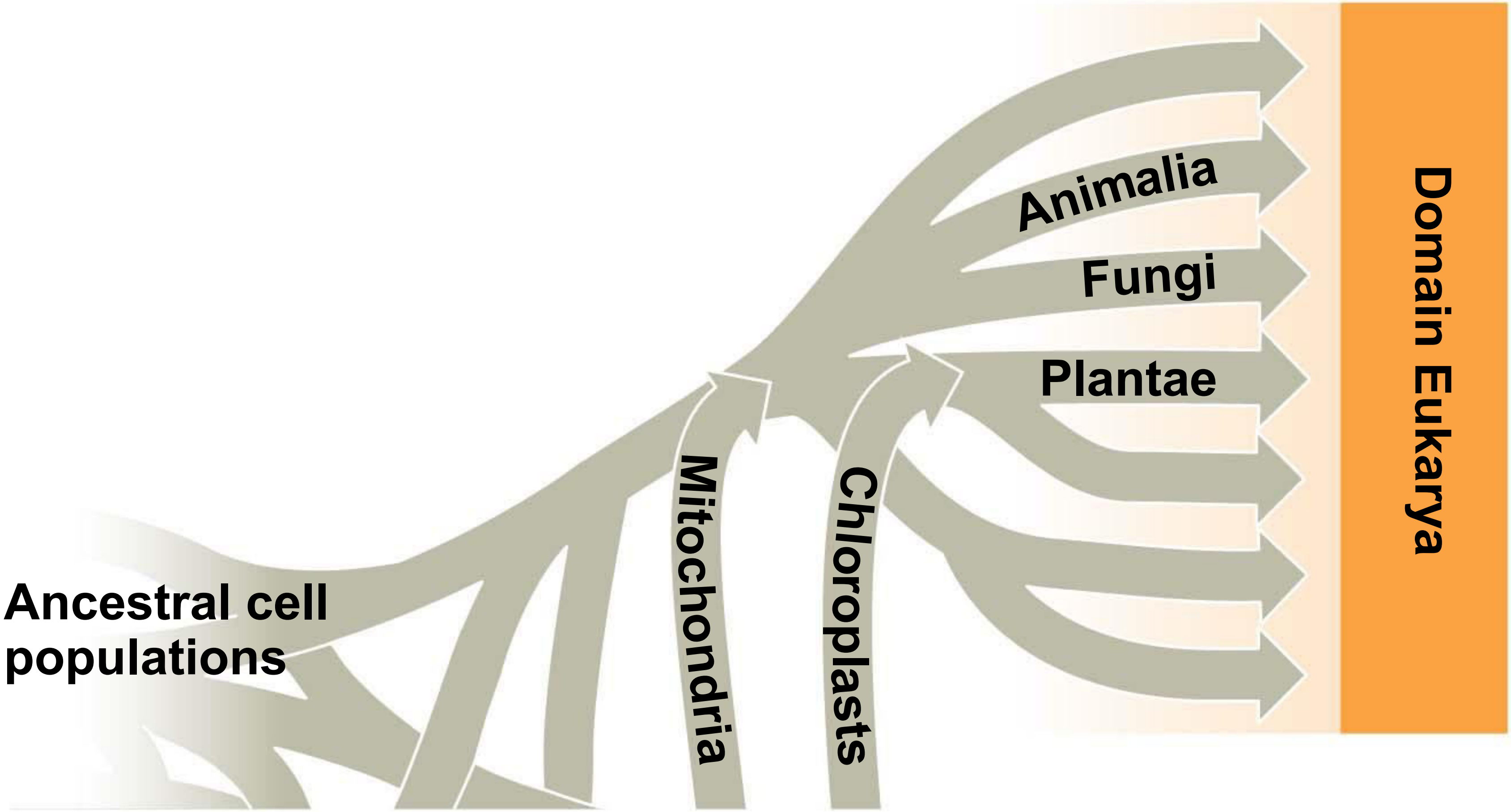


Figure 20.22-2

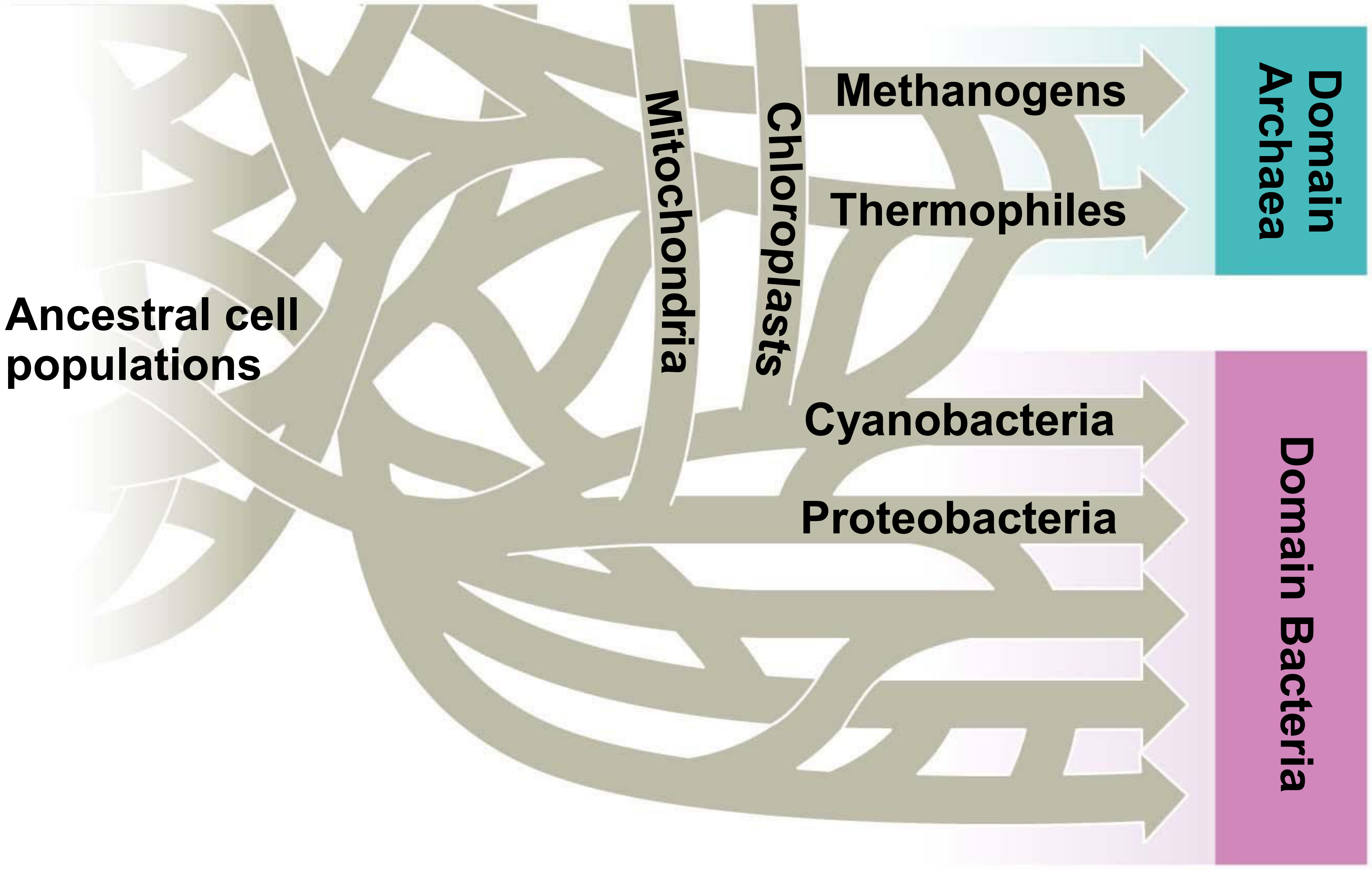
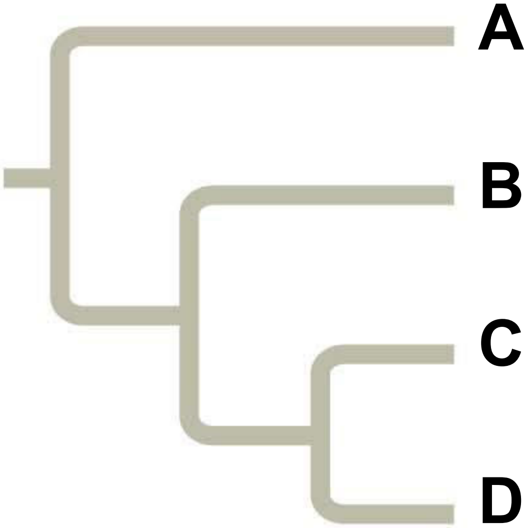
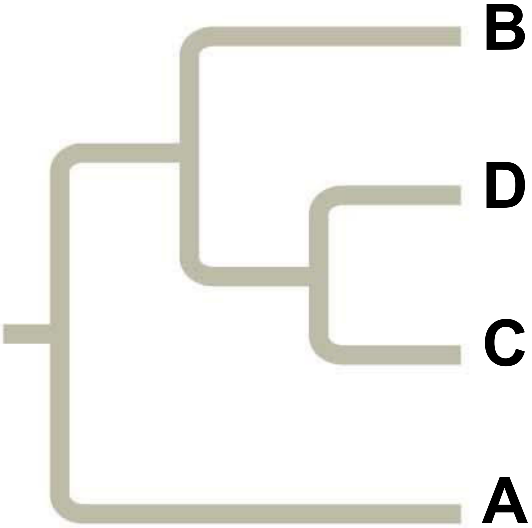


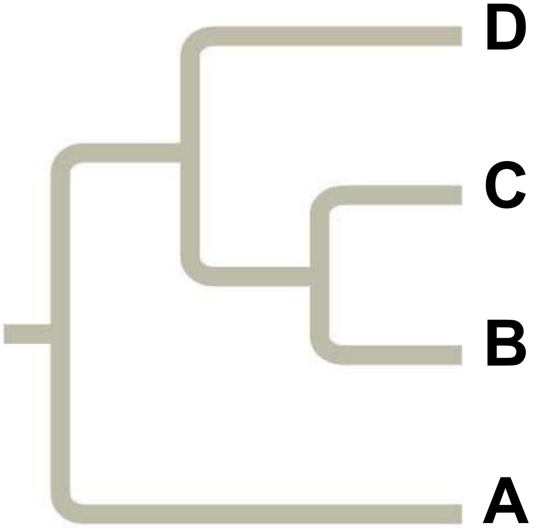
Figure 20.UN01



(a)



(b)



(c)

Figure 20.UN02

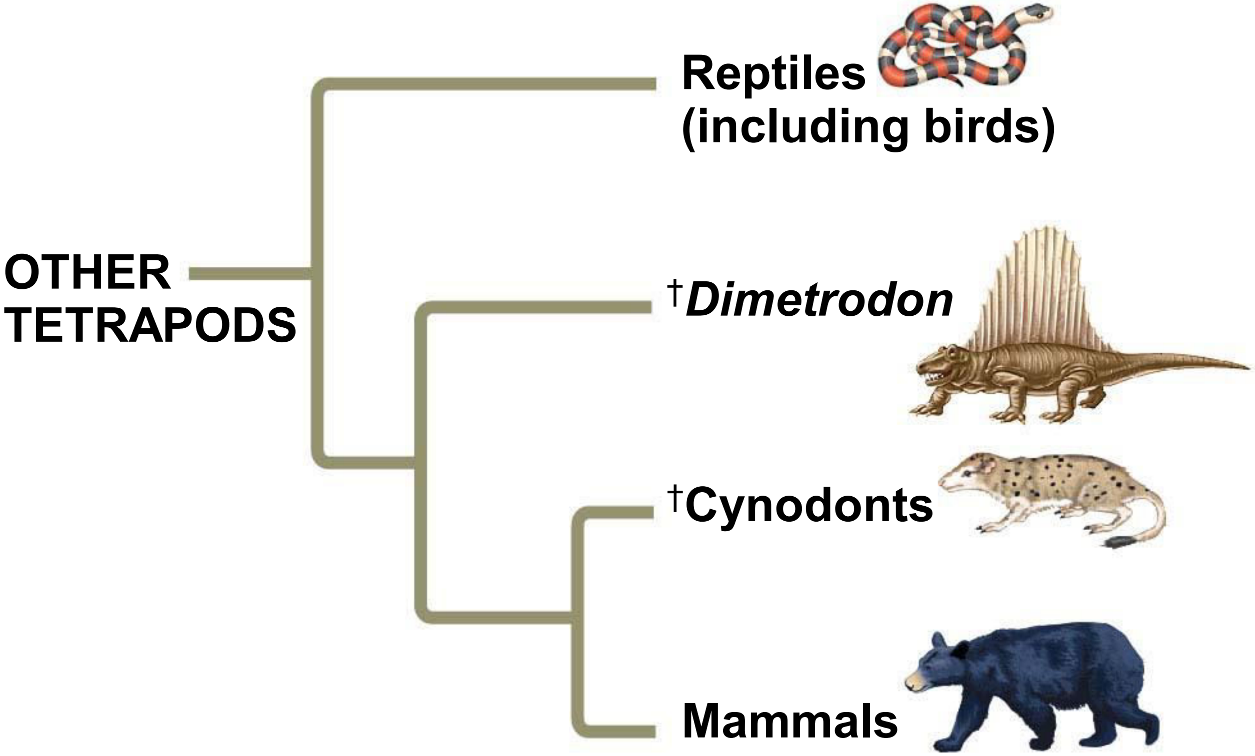


Figure 20.UN03-1

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

Figure 20.UN03-2

Figure 20.UN04

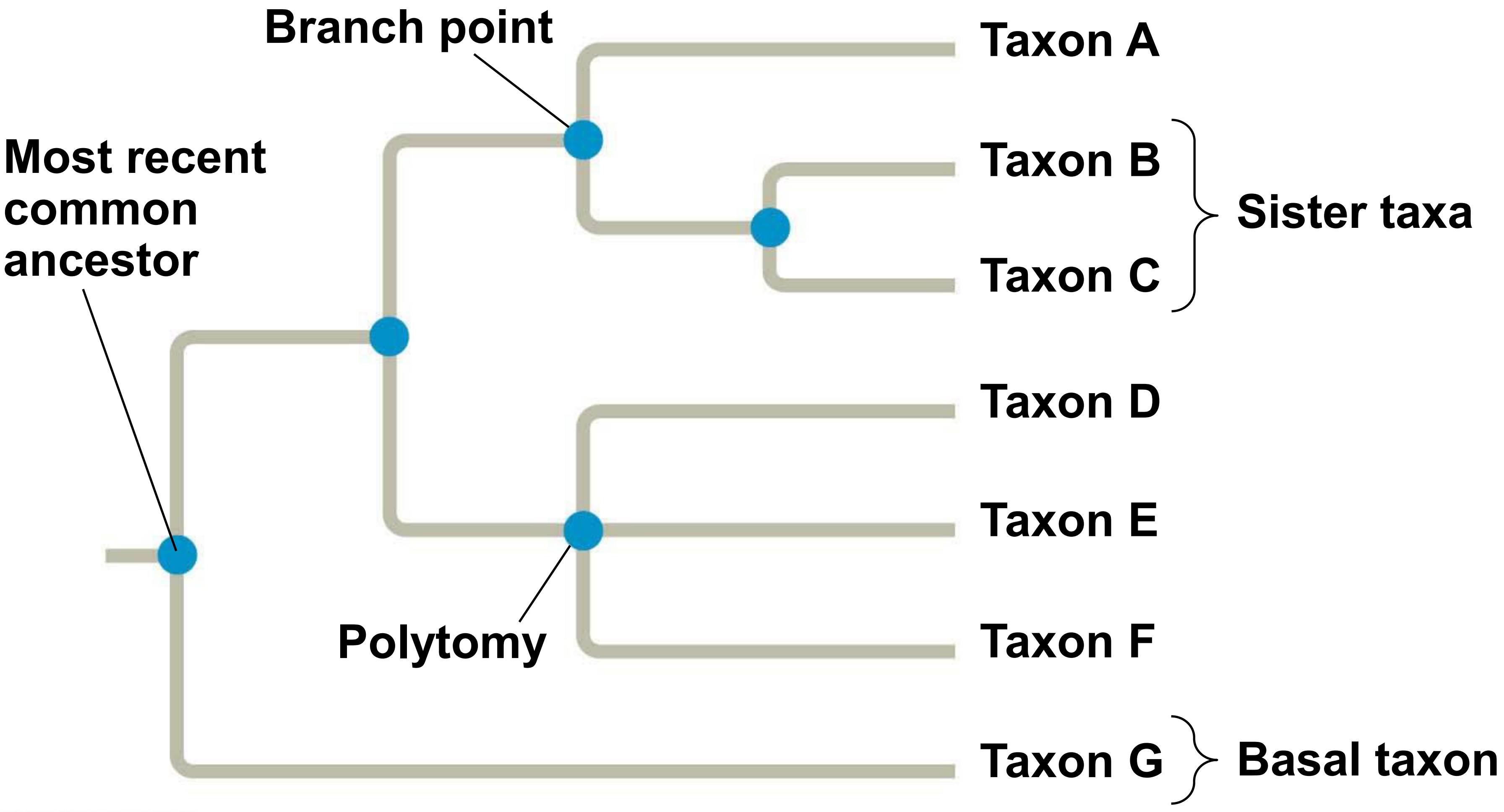


Figure 20.UN05

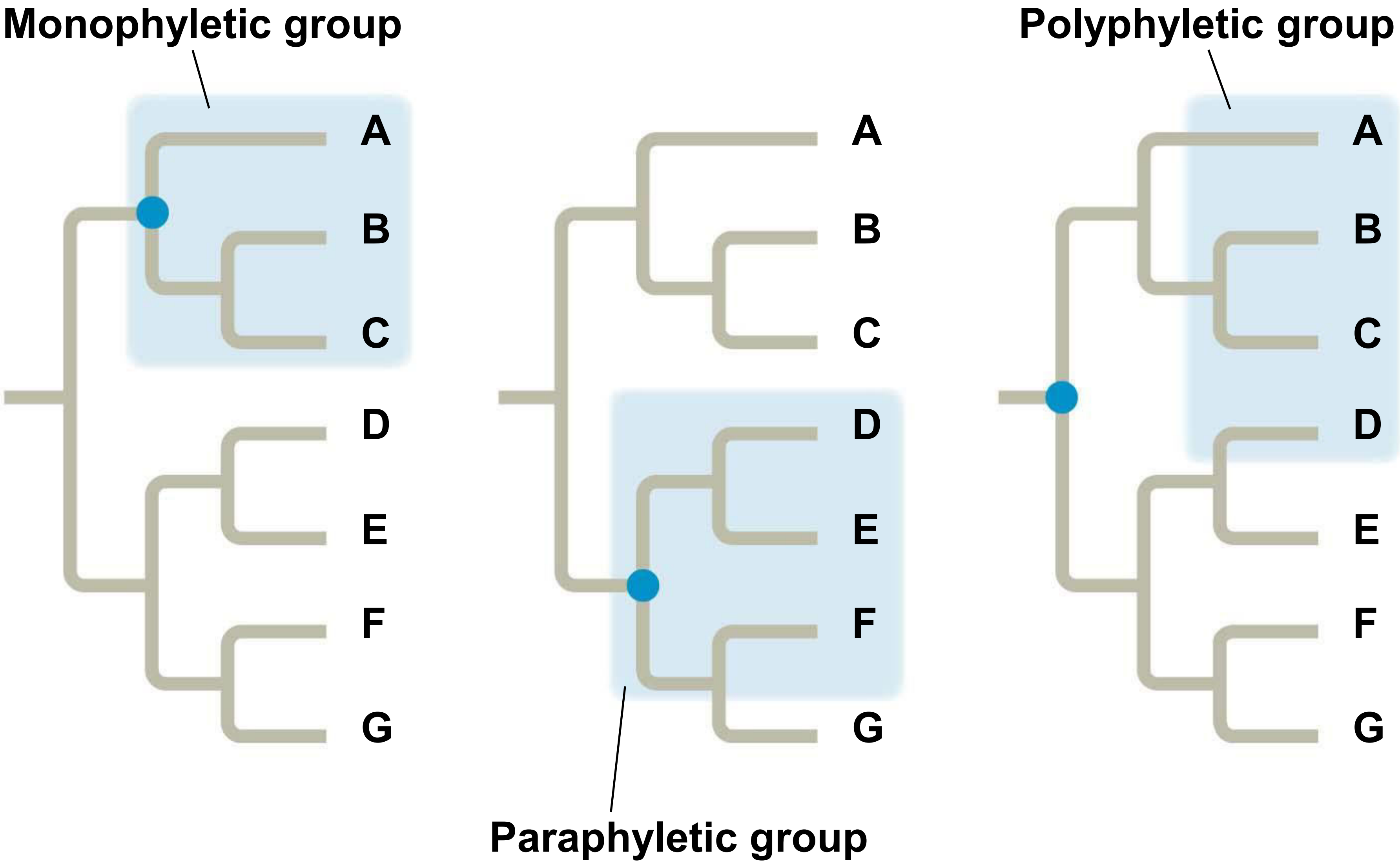


Figure 20.UN06

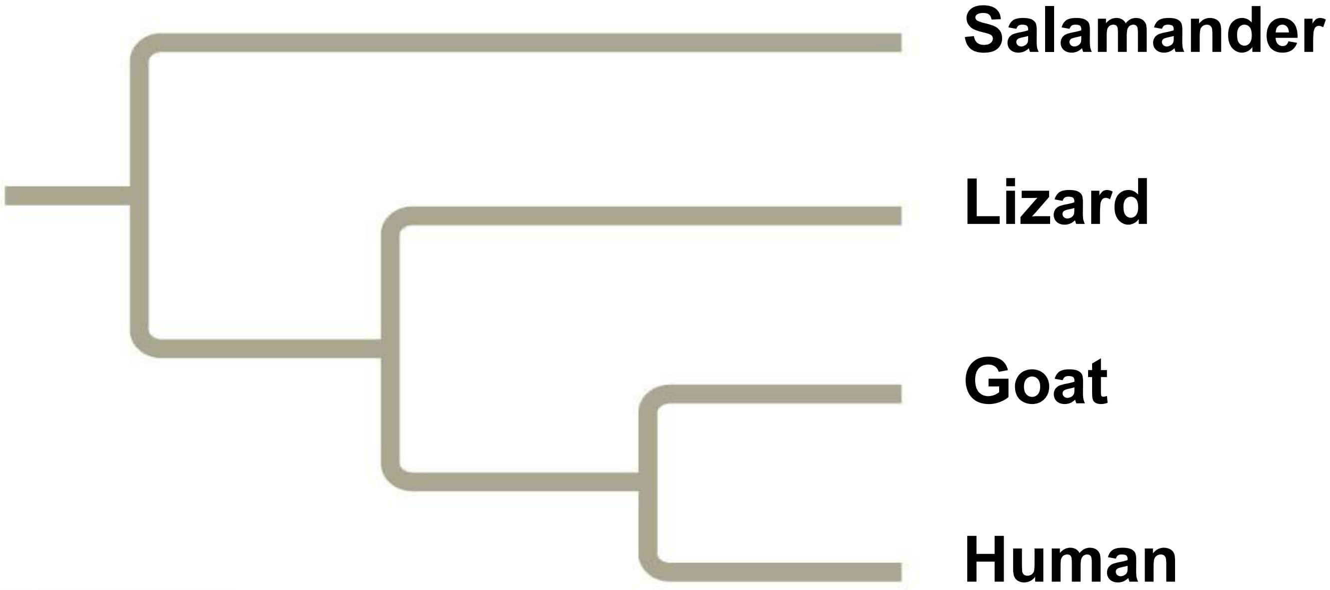


Figure 20.UN07

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.

Figure 20.UN08