

CHAPTER 34

VERTEBRATE EVOLUTION AND DIVERSITY

OUTLINE

- I. Invertebrate Chordates and the Origin of Vertebrates
 - A. Four anatomical features characterize phylum Chordata
 - B. Invertebrate chordates provide clues to the origin of vertebrates
- II. Introduction to the Vertebrates
 - A. Neural crest, cephalization, a vertebral column, and a closed circulatory system characterize subphylum Vertebrata
 - B. Overview of vertebrate diversity
- III. Superclass Agnatha: Jawless Vertebrates
 - A. Lampreys and hagfishes are the only extant agnathans
- IV. Superclass Gnathostomata I: The Fishes
 - A. Vertebrate jaws evolved from skeletal supports of the pharyngeal slits
 - B. A cartilaginous endoskeleton reinforced by calcified granules is diagnostic of class Chondrichthyes
 - C. A bony endoskeleton, operculum, and swim bladder are hallmarks of class Osteichthyes
- V. Superclass Gnathostomata II: The Tetrapods
 - A. Amphibians are the oldest class of tetrapods
 - B. Evolution of the amniotic egg expanded the success of vertebrates on land
 - C. A reptilian heritage is evident in all amniotes
 - D. Birds began as flying reptiles
 - E. Mammals diversified extensively in the wake of the Cretaceous extinctions
- VI. Primates and the Phylogeny of *Homo sapiens*
 - A. Primate evolution provides a context for understanding human origins
 - B. Humanity is one very young twig on the vertebrate tree

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Describe the four unique characteristics of chordates.
2. Distinguish between the three subphyla of the phylum Chordata and give examples of each.
3. Describe the specialized characteristics found in the subphylum Vertebrata and explain how each is beneficial to survival.
4. Compare and contrast members of Agnatha, Placadermi, and Chondrichthyes.

5. Explain how members of the class Osteichthyes have become so diversified.
6. Summarize the evidence supporting the fact that amphibians evolved from crossopterygians.
7. Distinguish between the three orders of living amphibians.
8. List the distinguishing characteristics of members of the class Reptilia and explain any special adaptations to the terrestrial environment.
9. Explain how environmental changes during the Cretaceous Period may have affected the dinosaurs.
10. List the distinguishing characteristics of members of the class Aves and explain any special adaptations for flight.
11. Summarize the evidence supporting the fact that birds evolved from reptilian ancestors.
12. Explain why mammals underwent an adaptive radiation during the Cenozoic.
13. Distinguish between monotreme, marsupial, and placental mammals.
14. Explain how convergent evolution produced marsupial and placental ecological counterparts on different continents.
15. Compare and contrast the four main evolutionary lines of placental mammals.
16. Describe the characteristics found in early primates which indicate an arboreal existence.
17. Appraise the significance of the three most prominent misconceptions about human evolution.
18. Diagram an evolutionary tree for humans.
19. Explain how humans have influenced the extinction rates of other organisms.

KEY TERMS

vertebrates	Superclass	lungfishes	Chelonia
chordates	Gnathostomata	Subclass Sarcopterygii	Squamata
notochord	placoderms	Class Amphibia	Crocodylia
urochordates	Class Chondrichthyes	urodeles	Class Aves
tunicates	spiral valve	anurans	ratites
lancelets	lateral line system	apodans	carinates
cephalochordates	oviparous	extraembryonic membranes	Class Mammalia
somites	ovoviviparous	Class Reptilia	placenta
paedogenesis	viviparous	ectotherms	therapsids
neural crest	cloaca	synapsids	monotremes
tetrapods	Class Osteichthyes	sauropods	eutherian mammals
amniotic egg	operculum	anapsids	prosimians
amniotes	swim bladder	diapsids	anthropoids
Superclass Agnatha	ray-finned fishes	therapsids	paleoanthropology
ostracoderms	lobe-finned fishes	endothermic	mosaic evolution
passeriforms			

LECTURE NOTES

I. Invertebrate Chordates and the Origin of Vertebrates

The phylum Chordata includes three subphyla: two invertebrate subphyla, Urochordata, Cephalochordata; and the subphylum Vertebrata.

A. Four anatomical features characterize phylum Chordata

Chordates are deuterostomes with four unique characteristics which appear at some time during the animal's life. These characteristics are the notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a muscular postanal tail (see Campbell, Figure 34.1).

1. Notochord

Notochord = A longitudinal, flexible rod located between the gut and nerve cord

- Present in all chordate embryos
- Composed of large, fluid-filled cells encased in a stiff, fibrous tissue
- Extends through most of the length of the animal as a simple skeleton

In some invertebrate chordates and primitive vertebrates it persists to support the adult.

In most vertebrates, a more complex, jointed skeleton develops and the notochord is retained in adults as the gelatinous material of the discs between the vertebrae.

2. Dorsal, hollow nerve cord

Develops in the embryo from a plate of dorsal ectoderm that rolls into a tube located dorsal to the notochord.

Unique to chordates; other animal phyla have solid, usually ventral, nerve cords.

The brain and spinal cord (central nervous system) develops from this nerve cord.

3. Pharyngeal slits

Chordates have a complete digestive system (mouth and anus). The pharynx is the region just posterior to the mouth and it opens to the outside through several pairs of slits.

- The presence of these pharyngeal slits permits water entering the mouth to exit without passing through the entire digestive system.
- These pharyngeal gill slits function for suspension-feeding in invertebrate chordates.
- They have become modified for gas exchange and other functions during the evolution of vertebrates.

4. Muscular postanal tail

A tail extending beyond the anus, it is found in most chordates and contains skeletal elements and muscles.

- Provides much of the propulsive force in many aquatic species.

The digestive tract in most nonchordates extends nearly the whole length of the body.

II. Invertebrate Chordates Provide Clues to the Origin of Vertebrates**A. Subphylum Urochordata**

Species in the subphylum Urochordata (*urochordates*) are commonly called *tunicates*.

Entire animal is cloaked in a tunic made of a celluloselike carbohydrate.

Most are sessile marine animals that adhere to rocks, docks, and boats (see Campbell, Figure 34.2a).

Some species are planktonic, while others are colonial.

The tunicates are filter feeders.

- Seawater enters through an incurrent siphon, passes through the slits of the pharynx into a chamber called the atrium, and exits via an excurrent siphon, the atriopore (see Campbell, Figure 34.2b).
- Food filtered from the water by a mucus net of the pharynx is moved by cilia into the intestine.

- The anus empties into the excurrent siphon.
- When disturbed, tunicates eject a jet of water through the excurrent siphon, so they are commonly called sea squirts.

Adult tunicates bear little resemblance to other chordates.

- They lack a notochord, a nerve cord and tail.
- They possess only pharyngeal slits.

Larval tunicates are free swimmers and possess all four chordate characteristics (see Campbell, Figure 34.2c).

- Larva attach by the head on a surface and undergo metamorphosis to adult form.
- In some species, if the *Manx* gene (named after the tailless cat) is turned off during development, the larvae will be tailless. *Manx* expression also is required for notochord and nerve cord development.
- These observations remind us that a relatively small number of genes that regulate development may influence the evolution of some basic aspect of an animal body plan.

B. Subphylum Cephalochordata

Animals in the subphylum Cephalochordata (*cephalochordates*) are known as *lancelets* due to their bladelike shape (see Campbell, Figure 34.3). Chordate characteristics are prominent and persist in the adult. These include:

- Notochord
- Dorsal nerve cord
- Numerous gill slits
- Postanal tail

Cephalochordates are marine filter feeders.

- They burrow tail first into the sand with only the anterior exposed.
- Water is drawn into mouth by ciliary action and food is trapped on a mucous net secreted across the pharyngeal slits.
- Water exits through the slits and trapped food passes down the digestive tube.

Cephalochordates are feeble swimmers with fishlike motions.

- Frequently move to new locations
- Muscle segments are serially arranged in chevronlike rows, and coordinated contraction flexes the notochord from side to side in a sinusoidal pattern.
- Muscle segments develop from blocks of mesoderm called *somites* that are arranged along each side of the notochord in the embryo.
- The serial musculature is evidence of the lancelet's segmentation (see Campbell, Figure 34.4).

⇒ Whether segmentation evolved independently in annelids, arthropods, and chordates, or from a common ancestor of all bilateral animals, is currently under debate.

C. Relationship of invertebrate chordates to the vertebrates

Vertebrates first appeared in the fossil records in Cambrian rocks.

- Fossilized invertebrates (about 550 million years old) resembling cephalochordates were found in Burgess Shale of British Columbia.
- This is about 50 million years older than the oldest known vertebrates.

Most zoologists feel the vertebrate ancestors possessed all four chordate characteristics and were suspension-feeders.

- They may have resembled lancelets but were less specialized.
- Information provided by molecular systematics supports the idea that cephalochordates are the closest relatives of vertebrates.

Cephalochordates and vertebrates may have evolved from a sessile ancestor by paedogenesis.

Paedogenesis = Precocious attainment of sexual maturity in a larva

- Cephalochordates more closely resemble urochordate larvae than adult urochordates.
- Changes in the developmental control genes can alter the timing of developmental events (e.g., gonad maturation).
- Zoologists postulate that some early urochordatelike larval forms became sexually mature and reproduced before undergoing metamorphosis.
- If reproducing larvae were successful, natural selection may have reinforced the absence of metamorphosis and a vertebrate life cycle may have evolved.

The divergence of cephalochordates from vertebrates occurred about 500 million years ago.

- The differences between the two groups can be viewed as vertebrate adaptations to larger size and a more mobile life style.

III. Introduction to the Vertebrates

Vertebrates have retained the primitive chordate features while adding other specializations. These synapomorphies distinguish the vertebrates from urochordates and cephalochordates.

A. Neural crest, pronounced cephalization, a vertebral column, and a closed circulatory system characterize subphylum Vertebrata

The unique vertebrate structures probably evolved in association with increased size and more active foraging for food. The unique vertebrate adaptations include:

- The *neural crest*, a group of embryonic cells found only in vertebrates, contributes to the formation of certain skeletal components and many other structures distinguishing vertebrates from other chordates.
 - ⇒ The dorsal, hollow nerve cord develops from an infolding of the edges of an ectodermal plate on the surface of the embryo.
 - ⇒ The neural crest forms near the dorsal margins of the tube resulting from this infolding (see Campbell, Figure 34.5).
 - ⇒ Cells from the neural crest then migrate to various specific areas of the embryo and help form a variety of structures including some of the bones and cartilage of the cranium.
- Vertebrates show a much greater degree of *cephalization* than cephalochordates.
 - ⇒ The brain and sense organs are located at the anterior end which is the portion of the body which is in contact with the most environmental stimuli.
- A skeleton including a cranium and vertebral column is the main axis of the body, replacing the notochord as the basic skeleton.
 - ⇒ The cranium protects the brain.
 - ⇒ The vertebral column provides support and a strong, jointed anchor that provides leverage to the segmental swimming muscles.
 - ⇒ The axial skeleton made larger size and stronger, faster movement possible.
 - ⇒ Most vertebrates also have ribs (anchor muscles and protect internal organs) and an appendicular skeleton supporting two pairs of appendages.

- The vertebrate skeleton may be composed of bone, cartilage, or a combination of the two.
 - ⇒ A majority of the skeleton is a non-living matrix which is secreted and maintained by living skeletal cells.
 - ⇒ The living vertebrate endoskeleton can grow with the animal unlike the exoskeleton of arthropods.

Some anatomical adaptations also support the greater metabolic demands of increased activity.

- The generation of ATP by cellular respiration, to replace the energy used by vertebrates in obtaining food or escaping predators, consumes oxygen.
 - ⇒ The respiratory and circulatory systems of vertebrates show adaptations which support the mitochondria of muscles and other active tissues.
- Vertebrates have a closed circulatory system composed of a ventral chambered (two to four) heart, arteries, capillaries, and veins.
 - ⇒ The heart pumps the blood through the system.
 - ⇒ The blood becomes oxygenated as it passes through the capillaries of the gills or lungs.
- The more active the lifestyle, the larger the amounts of organic molecules necessary to produce energy.
 - ⇒ Vertebrates have several adaptations for feeding, digestion and nutrient absorption.
 - ⇒ For example, muscles in the walls of the digestive tract move food from organ to organ along the tract.

B. Overview of Vertebrate Diversity

The vertebrates are divided into two major groups, or superclasses: Superclass Agnatha, whose members lack jaws, and Superclass Gnathostomata, whose members possess jaws (see Campbell, Table 34.1)

The gnathostomes are divided into six classes: Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia. The last four classes are collectively known as the tetrapod vertebrates.

- *Tetrapod* = An animal possessing two pairs of limbs that support it on land

In addition to being tetrapods, the reptiles, birds and mammals have other adaptations for a terrestrial lifestyle which are not found in the amphibians.

- The *amniotic egg* (a shelled, water resistant egg) allows completion of the life cycle on land.
- Most mammals do not lay eggs but retain other features of the amniotic condition, consequently, they are also considered *amniotes* along with the birds and reptiles.

Review Figure 34.6 to establish the relationships among the classes of the subphylum Vertebrata.

IV. Superclass Agnatha: Jawless Vertebrates

Vertebrates probably arose in the late Precambrian and early Cambrian. The oldest fossils of vertebrates are of jawless animals found in rock strata 400 to 500 million years old.

Early agnathans were small, less than 50 cm in length.

- They were jawless with oval or slitlike mouths; most lacked paired fins and were bottom-dwellers.

- Some were active and had paired fins.
- Were probably bottom- or suspension-feeders that trapped organic debris in their gill slits.

Ostracoderms and most other agnathans declined and disappeared during the Devonian.

A. Lampreys and hagfishes are the only extant agnathans

Extant forms include about 60 species of lampreys and hagfishes which lack paired appendages and external armor (see Campbell, Figure 34.7).

Lampreys are eel-shaped and feed by clamping their round mouths onto live fish.

- Once attached, they use a rasping tongue to penetrate the skin and feed on the prey's blood.
- Sea lampreys spend their larval development in freshwater streams and migrate to the sea or lakes as they mature.
- Larva are suspension-feeders that resemble lancelets (cephalochordates).
- Some lamprey species feed only as larvae. Once they mature and reproduce, they die within a few days.

Hagfishes superficially resemble lampreys.

- They are scavengers without rasping mouthparts.
- Some species will feed on sick or dead fish while others feed on marine worms.
- Lack a larval stage and are entirely marine (Physiologically, they are the only extant vertebrate that is a true osmoconformer; all other vertebrates are osmoregulators).

V. Superclass Gnathostomata I: The Fishes

The agnathans were gradually replaced by vertebrates with jaws (Superclass Gnathostomata) during the late Silurian and early Devonian. Early gnathostomes included ancestors of class Chondrichthyes and class Osteichthyes and a now extinct group of armored fishes called *placoderms* appeared.

Most placoderms were less than 1 m in length, but some were up to 10 m long.

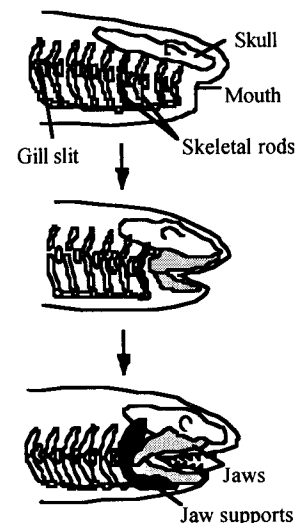
- Differed from agnathans in that they possessed paired fins and hinged jaws.
- Paired fins enhanced swimming ability and hinged jaws allowed more varied feeding habits including predation.

A. Vertebrate jaws evolved from skeletal supports of the pharyngeal slits

Hinged jaws evolved as modifications of the skeletal rods which previously supported the anterior pharyngeal (gill) slits (see Campbell, Figure 34.8).

- Remaining gill slits retained function as major gas exchange sites.
- Hinged jaws of vertebrates work in an up and down direction; those in arthropods work from side to side.

Placoderms and another group of jawed fishes, the acanthodians, radiated during the Devonian period (the Age of Fishes) and many new forms evolved in fresh and salt waters.



- Placoderms and acanthodians disappeared by the start of the Carboniferous period (350 million years ago).
- Ancestors of the placoderms and acanthodians also gave rise to early sharks (class Chondrichthyes) and bony fishes (class Osteichthyes).

B. A cartilaginous endoskeleton reinforced by calcified granules is diagnostic of class Chondrichthyes

The class Chondrichthyes contains about 750 extant species of cartilaginous fishes (e.g., sharks, skates, rays) (see Campbell, Figure 34.9).

Species in the class Chondrichthyes have flexible skeletons composed of cartilage, well-developed jaws and paired fins.

- The ancestors of members of this class had bony skeletons.
- The characteristic cartilaginous skeleton is thus a derived characteristic, having evolved secondarily.
- The developmental sequence in cartilaginous fishes differs from other vertebrates in that the initial (first) cartilaginous skeleton does not become ossified.
- In most species, however, parts of the skeleton are strengthened by calcified granules
- The cartilaginous skeleton is more elastic and lighter than a bone skeleton.

Sharks have streamlined bodies and are swift swimmers.

- The tail provides propulsion.
- The dorsal fins serve as stabilizers.
- Pectoral and pelvic fins produce lift.
- Some buoyancy is provided by large amounts of oil stored in liver, but most must swim continuously to remain in the water column.
 - ⇒ Continual swimming also produces water flow through mouth and over gills for gas exchange.
 - ⇒ Some sharks are known to rest on the sea floor and in caves; they use jaw and pharynx muscles to pump water over their gills while resting.

Most sharks are carnivorous, although the largest sharks and rays are suspension-feeders.

- Prey may be swallowed whole or pieces may be torn from large prey.
- Teeth evolved as modified scales.
- The digestive tract is proportionately shorter than in other vertebrates.
 - ⇒ A *spiral valve*, which increases surface area and slows food movement, is present in the intestine.

Sharks possess sharp vision (cannot distinguish color) and olfactory senses that are adaptations to their lifestyle.

- Electric sensory regions that detect muscle contractions of prey are located on the head.
- A *lateral line system* is present along the flanks.
 - ⇒ It is composed of rows of microscopic organs sensitive to water pressure changes and detects vibrations.
- A pair of auditory organs also detect sound waves passing through the water.

Sharks reproduce sexually with internal fertilization.

- A pair of claspers on the pelvic fins of males transfers sperm into the female reproductive tract.
- Some species are *oviparous*, some are *ovoviviparous*, and a few are *viviparous*.

- A *cloaca* (common chamber for reproductive, digestive and excretory systems) is present.

Rays are adapted to a bottom-dwelling lifestyle.

- They have dorsoventrally flattened bodies.
- Their jaws are used to crush mollusks and crustaceans.
- Enlarged pectoral fins provide propulsion for swimming.
- The tail in many species is whiplike and, in some, bears venomous barbs.

C. A bony endoskeleton, operculum, and a swim bladder are hallmarks of class Osteichthyes

The class Osteichthyes contains the bony fishes, which are represented by more than 30,000 extant species.

- Abundant in marine and fresh waters (see Campbell, Figure 34.10)
- Range from 1 cm to 6 m in length
- Skeleton is bony, reinforced with a matrix of calcium phosphate
- Skin is covered with flattened bony scales
- Skin glands produce mucus that reduces drag when swimming
- A lateral line system is present as a row of tiny pits in the skin on both sides of the body (see Campbell, Figure 34.11).

Gas exchange occurs by drawing water over the four or five pairs of gills located in chambers covered by an operculum.

- Water is drawn into the mouth, through the pharynx and out between the gills by movement of the operculum and contraction of muscles within the gill chambers.

⇒ Allows bony fishes to breath while stationary.

A *swim bladder*, located dorsal to the digestive tract, provides buoyancy.

- Transfer of gases between blood and swim bladder varies bladder inflation and adjusts the density of the fish.

Bony fishes are very maneuverable swimmers. The flexible fins provide better steering and propulsion than the stiff fins of sharks.

- The fastest bony fish can swim to 80 km per hour in short bursts.
 - A fusiform body shape is common to all fast fishes and aquatic mammals.
- ⇒ This body shape reduces drag produced by the density of water (convergent evolution).

Most bony fish are oviparous and utilize external fertilization.

- Some are ovoviviparous or viviparous and utilize internal fertilization.
- Some display complex mating behavior.

The cartilaginous and bony fishes diversified during the Devonian and Carboniferous periods.

- Sharks arose in the sea, bony fishes probably originated in fresh water.
- The swim bladder was modified from lungs of ancestral fishes which supplemented the gills for gas exchange in stagnant waters.

The two extant subclasses of bony fishes had diverged by the end of the Devonian: Subclass Actinopterygii (ray-finned fishes) and Subclass Sarcopterygii

The *subclass Actinopterygii* includes fish with fins supported mainly by flexible rays.

- These are the most familiar fishes.

- They spread from fresh water to the seas and many returned to fresh water during evolution of the taxon.
- Some bony fish (e.g., salmon and sea-run trout) reproduce in fresh water and mature in the sea.

The *subclass Sarcopterygii* includes lobe-finned fishes (coelocanths and rhipidistians) and lungfishes that evolved in fresh water. The ancestors of these fishes continued to use their lungs to aid the gills in gas exchange.

Coelocanths and rhipidistians are referred to as lobe-finned fishes.

- Their fins were fleshy, muscular, and supported by extensions of the bony skeleton.
- Many were large, bottom-dwelling forms that used their paired fins to walk on the substratum.
- The only extant species, the coelocanth, is marine and lungless. It belongs to a lineage that became marine at some point in its evolution.
- All rhipidistians are extinct.

Three genera of lungfishes exist in the Southern Hemisphere.

- They live in stagnant ponds and swamps where they surface to gulp air into lungs connected to the pharynx.
- When ponds dry, lungfishes burrow in the mud and aestivate.

Lobe-finned fishes of the Devonian were numerous and important in vertebrate genealogy because they probably gave rise to amphibians (see Campbell, Figure 34.13).

VI. Superclass Gnathostomata II: The Tetrapods

A. Amphibians are the oldest class of tetrapods

The first vertebrates to move onto land were members of *Class Amphibia*.

Today there are about 4000 extant species of frogs, salamanders, and caecilians.

1. Early amphibians

Some scientists suggest that early amphibians evolved from lobe-finned fishes that adapted to environmental variations (drought and flooding) of the Devonian.

- The skeletal structure of the lobed fins suggest they could have assisted in movement on land.
- Fossil lobe-fins, such as the rhipidistian *Eusthenopteron*, exhibited many anatomical similarities to early amphibians (see Campbell, Figure, 34.14a)

Recent molecular and other data, however, suggest that amphibians are more closely related to lungfishes than they are to lobe-fin fishes.

The oldest amphibian fossils are from the late Devonian (365 million years ago) (see Campbell, Figure 34.14b).

- Early amphibians probably were mostly aquatic and periodically came on land to eat insects and other invertebrates that had moved previously onto land.
- Amphibians were the only vertebrates on land in the late Devonian and early Carboniferous.

Radiation of forms occurred during the early Carboniferous period.

- Some forms reached 4 m in length and some resembled reptiles.
- Amphibians began to decline during the late Carboniferous. At the beginning of the Triassic period (245 million years ago), most of the survivors resembled modern species.

2. Modern amphibians

There are three extant orders of amphibians: Urodela (salamanders), Anura (frogs and toads) and Apoda (caecilians) (see Campbell, Figure 34.15).

The order Urodela (urodeles; e.g., salamanders) contains about 400 species.

- Some are aquatic and some are terrestrial.
- Terrestrial forms walk with a side-to-side bending of the body. Aquatic forms swim sinusoidally or walk along the bottom of streams or ponds.

The order Anura (*anurans*; e.g., frogs and toads) contains about 3500 species, which are better adapted to the terrestrial habitat than urodeles.

- Enlarged hindlegs provide better movement (hopping) than in urodeles.
- They capture prey by flicking the sticky tongue which is attached anteriorly.
- Predator avoidance is aided by camouflage color patterns and distasteful or poisonous mucus secreted by skin glands.
⇒ Bright coloration is common in poisonous species.

The order Apoda (*apodans*; e.g., caecilians) contains about 150 species.

- They are legless and almost blind.
- Most species burrow in moist tropical soils; a few species inhabit freshwater ponds and streams.

Many frogs exhibit a metamorphosis from the larval to adult stage (see Campbell, Figure 34.16):

- The tadpole (larval stage) is usually an aquatic herbivore. It possesses internal gills, a lateral line system, and a long, finned tail.
- The tadpole lacks legs and swims by undulating the tail.
- During metamorphosis, legs develop and the gills and lateral line system disappear.
- A young frog is tetrapod. It has air-breathing lungs, a pair of external eardrums, and a digestive system that can digest animal protein.
- The adult is usually terrestrial or semiaquatic and a predator.

Many amphibians, including some frogs, do not have a tadpole stage.

- Some species in each order are strictly aquatic while others are strictly terrestrial.
- Urodeles and apodans have larva that more closely resemble adults and both larva and adults are carnivorous.
- Paedogenesis is common in some groups of urodeles.

Most amphibians maintain close ties with water and are most abundant in damp habitats.

- Terrestrial forms in arid habitats spend much of their time in burrows where humidity is high.
- Gas exchange is primarily cutaneous and terrestrial forms must keep the skin moist.
⇒ Lungs can aid in gas exchange although most are small and inefficient. Some forms lack lungs.
⇒ Many species also exchange gases across moist surfaces of the mouth.

Amphibians are dioecious.

- They reproduce sexually usually with external fertilization in water (e.g., ponds, streams, temporary pools).

- In frogs, the male grasps the female and sperm are released as the female sheds her eggs (see Campbell, Figure 34.16a)
- Eggs are unshelled and produced in large numbers by most species.

Some species exhibit parental behavior and produce small numbers of eggs.

- Males or females (species dependent) incubate eggs on their back, in the mouth or in the stomach.
- Some tropical species lay eggs in a moist foamy nest that prevents drying.
- Some species are ovoviviparous and a few are viviparous with the eggs developing in the female's reproductive tract.

Amphibians exhibit complex and diverse social behavior especially during breeding season (e.g., vocalization by male anurans, migrations, navigation or chemical signaling).

B. Evolution of the amniotic egg expanded the success of vertebrates on land

Many specialized adaptations for living in a terrestrial habitat were necessary for reptiles to evolve from their amphibian ancestor.

- The amniotic egg was important. Its development broke the last ties with the aquatic environment by allowing life cycles to be completed on land.
 - ⇒ The shell of the amniotic egg helps prevent desiccation, therefore, it can be laid in a dry place.
 - ⇒ Most mammals have dispensed with the shell, instead, the embryo implants in the wall of the uterus and obtains its nutrients from the mother.
- The *extraembryonic membranes* within the egg develop from tissue layers that grow out from the embryo.
 - ⇒ These specialized membranes function in gas exchange, transfer of stored nutrients to the embryo, and waste storage.
 - ⇒ One of these membranes, the amnion, encloses a compartment filled with amniotic fluid that bathes the embryo and provides a cushion against shocks (see Campbell, Figure 34.17).

Reptiles, birds, and mammals make up a monophyletic group, the amniotes.

C. A reptilian heritage is evident in all amniotes

The class *Reptilia* is a diverse group with about 7000 extant species and a wide array of extinct forms.

- This grouping is based on the apparent similarity of the tetrapods (lizards, snakes, turtles, and crocodilians), but cladistic analysis indicates that grouping these vertebrates in a class that does not include birds is inconsistent with phylogeny.
- Birds appear to be more closely related to crocodiles than are turtles.
- Class *Reptilia* can only be defined by the absence of features that distinguish birds (feathers) and mammals (hair and mammary glands)

1. Reptilian characteristics

Reptiles possess several adaptations for terrestrial living not found in amphibians.

- Scales contain the protein keratin which helps prevent dehydration.
- Gas exchange occurs via lungs although many turtles also use moist cloacal surfaces.
- They are dioecious with sexual reproduction and internal fertilization.
 - ⇒ Most are oviparous and produce an amniotic egg (see Campbell, Figure 34.18).

- ⇒ Some species of snakes and lizards are viviparous with the young obtaining nutrients from the mother across a “placenta” which forms from the extraembryonic membranes.

Reptiles are ectotherms and use behavioral adaptations to regulate their body temperature.

- *Ectotherm* = An animal that uses behavioral adaptations to absorb solar energy and regulate its body temperature.
- Due to ectothermy, reptiles can survive on less than 10% of the calories required by mammals of comparable size.

Reptiles were abundant and diverse in the Mesozoic era.

2. The Age of Reptiles

a. Origin and early evolutionary radiation of reptiles

The oldest reptilian fossils are found in late Carboniferous rock (300 million years old).

- Ancestors were probably Devonian amphibians.
- Two waves of adaptive radiation resulted in reptiles being the dominant terrestrial vertebrates for 200 million years.

The first reptilian radiation was in the early Permian period and gave rise to two main evolutionary branches: the synapsids and sauropsids (see Campbell, Figure 34.19).

- Synapsids were terrestrial predators and gave rise to the therapsid lineage which were mammal-like reptiles.
 - ⇒ Therapsids were large, dog-sized predators from which mammals are believed to have evolved.
- Sauropsids gave rise to the modern amniote groups other than mammals. They split into two lineages early in their history: the anapsids and the diapsids.
 - ⇒ The anapsids are presently represented only by the turtles.
 - ⇒ The extant diapsids are represented by the lizards, snakes, and crocodylians; dinosaurs and some other extinct groups were also diapsids. Cladistic analysis suggests that birds are the closest living relatives of extinct dinosaurs.

b. Dinosaurs and pterosaurs

The second reptilian radiation began in the late Triassic (about 200 million years ago) and several lineages evolved during this event.

- Two groups are most important: the dinosaurs and pterosaurs (flying reptiles).
- Dinosaurs varied in body shape, size, and habitat.
 - ⇒ Some fossilized forms measure 45 meters in length.
- Pterosaurs had wings formed from skin stretched from the body wall, along the forelimb to the tip of an elongate finger and supported by stiff fibers.

Evidence indicates that dinosaurs were agile, fast moving, and social, some may have even exhibited parental care of the young (see Campbell, Figure 34.20).

There is also some anatomical evidence supporting the hypothesis that dinosaurs were endothermic.

- *Endothermy* = The ability to keep the body warm through an animal's own metabolism

- Skeptics of this hypothesis feel that the Mesozoic climate was warm and consistent, and that basking may have been sufficient for maintaining body temperature.
- Low surface-to-volume ratios of large forms reduced fluctuations of body temperature vs. air temperature; thus, dinosaurs may not have been endothermic.

c. The Cretaceous crisis

In the Cretaceous (last period of the Mesozoic), the climate became cooler and more variable, and mass extinctions occurred.

A few dinosaurs survived into the early Cenozoic, but all these reptiles were gone by the end of the Cretaceous (65 million years ago).

3. Modern reptiles

The largest and most diverse extant orders are the: *Chelonia* (turtles), *Squamata* (lizards and snakes), and *Crocodylia* (alligators and crocodiles).

Turtles of the order Chelonia evolved from anapsids during the Mesozoic.

- They show little change from the earliest forms (see Campbell, Figure 34.21a).
- They are protected from predators by a hard shell.
- All turtles, even aquatic species, lay their eggs on land.

Lizards and snakes are classified in the order Squamata.

Lizards are the most numerous and diverse group of extant reptiles (see Campbell, Figure 34.21b).

- They evolved from the diapsid lineage.
- Most are small.
- Many nest in crevices and decrease activity during cold periods.

Snakes probably descended from burrowing lizards (see Campbell, Figure 34.21c).

- They are limbless and most live above ground.
- Vestigial pelvic and limb bones present in primitive snakes (boas) are evidence of a limbed ancestor.
- Snakes are carnivorous and have a number of adaptations for hunting prey.
 - They have acute chemical sensors.
 - They are sensitive to ground vibrations (although lacking eardrums).
 - Pit vipers have sensitive heat-detecting organs between their eyes and nostrils.
 - Flicking tongue helps transmit odors toward olfactory organs on roof of mouth.
 - Poisonous snakes inject a toxin through a pair of sharp, hollow teeth and loosely articulated jaws allow them to swallow large prey.

Crocodiles and alligators are among the largest living reptiles (see Campbell, Figure 34.21d).

- Crocodylians also evolved from the diapsid lineage.
- They spend most of their time in the water, breathing air through upturned nostrils.
- They are confined to warm regions of Africa, China, Indonesia, India, Australia, South America, and the southeastern United States.
- They are the living reptiles most closely related to dinosaurs.

D. Birds began as flying reptiles

The *class Aves* (birds) evolved during the great reptilian radiation of the Mesozoic era (see Campbell, Figure 34.19).

- They possess distinct reptilian characteristics such as the amniotic egg and scales on the legs, but modern birds also look quite different because of their feathers and other flight equipment.

1. Characteristics of birds

Each part of the bird's anatomy is modified in some way that enhances flight.

- The bones have a honeycombed internal structure that provides strength while reducing weight (see Campbell, Figure 34.22).
- Some organ systems are reduced (only one ovary in females).
- Birds have no teeth (reduces weight) and food is ground in the gizzard.
⇒ The beak is made of keratin and evolution has produced many shapes in relation to the bird's diet.

Flying requires much energy production from an active metabolism.

- Birds are endothermic with insulation provided by feathers and a fat layer.
- Birds have efficient circulatory system with a four-chambered heart that segregates oxygenated blood from unoxygenated blood.
- They have efficient lungs with tubes connecting to elastic air sacs that help dissipate heat and reduce the body density.

Birds also have a very well developed nervous system.

- Acute vision and well-developed visual and coordinating areas of the brain aid in flying.
- They show complex behavior especially during breeding season when elaborate courtship rituals are performed.

Birds are dioecious with sexual reproduction and internal fertilization.

- Sperm are transferred from the cloaca of the male to the cloaca of the female (males of most species lack a penis) during copulation.
- Eggs are laid and must be kept warm through brooding by the female, male or both depending on the species.

Wings are airfoils, formed by the shape and arrangement of the feathers, that illustrate the same aerodynamic principles as airplane wings (see Campbell, Figure 34.23).

- Power is supplied to the wings by contraction of the large pectoral (breast) muscles which are anchored to a keel on the sternum (breastbone).
- Some birds have wings adapted for soaring (hawks) while others must beat their wings continuously to stay aloft (hummingbirds).

Feathers are made of keratin and are extremely light and strong.

- Feathers evolved from the scales of reptiles and may have first functioned as insulation.
- Feathers also function to control air movements around the wing.

Radical alteration of body form was necessary for evolution of flight, but flight provides many benefits.

- Allows aerial reconnaissance that enhances hunting and scavenging.
- Birds can exploit flying insects as an abundant, highly nutritious food resource.
- Flight provides an escape mechanism from land-bound predators.

- Flight also allows migration to utilize different food resources and seasonal breeding areas.

2. The origin of birds

Birds shared a common ancestor with *Archaeopteryx lithographica*.

- Fossils of *Archaeopteryx* have been recovered from limestone dating to the Jurassic period (150 million years ago).
- *Archaeopteryx* had clawed forelimbs, teeth, a long tail containing vertebrae and feathers (see Campbell, Figure 34.24).
- *Archaeopteryx* is not considered the ancestor to modern birds, but a side branch of the avian lineage.
 - ⇒ The skeleton indicates a weak flyer that may have been a tree-dwelling glider.

Cladistic analysis suggests that birds arose from a theropod dinosaur. Some researchers, however, believe that birds arose from early Mesozoic reptiles (theconodonts), a group that also was ancestral to the dinosaurs.

E. Modern birds

There are about 8600 extant species in 28 orders. Most birds can fly but several are flightless (ostrich, kiwi, and emu) (see Campbell, Figure 34.25a).

- Flightless birds are called *ratites* because the breastbone lacks a keel and large breast muscles used for flying are absent.
- Flying birds are referred to as *carinates* due to the presence of a sternal keel (carina) that supports the large breast muscles used in flying.
- Carinate birds exhibit a variety of feather colors, beak and foot shape, behavior and flight ability (see Campbell, Figure 34.25 b and c).
 - ⇒ Penguins are carinate birds that do not fly, but use powerful breast muscles in swimming.
- Almost 60% of extant species belong to one order of carinate birds (the *passeriforms*, or perching birds), which includes the jays, swallows, sparrows, warblers and many others (see Campbell, Figure 34.25d).

F. Mammals diversified extensively in the wake of the Cretaceous extinctions

There are about 4500 species of extant mammals.

Extinction of the dinosaurs and the fragmentation of continents opened new adaptive zones at the end of the Mesozoic era.

Mammals underwent a massive radiation to fill these vacant zones.

1. Mammalian characteristics

Species in *class Mammalia* have the following characteristics:

- Hair that is composed of keratin, but is not believed to have evolved from reptilian scales; it provides insulation
- Endothermic with an active metabolism
 - ⇒ An efficient respiratory system that utilizes a diaphragm for ventilation supports the metabolism.
 - ⇒ A four-chambered heart segregates oxygenated from unoxygenated blood.
- Mammary glands that produce milk to nourish the young
- Teeth that are differentiated into various sizes and shapes, which are adapted to chewing many types of food.

⇒ The jaw apparatus of the ancestral reptiles was also modified during evolution with two of the jaw bones becoming incorporated into the middle ear.

Mammals are dioecious with sexual reproduction and internal fertilization.

- Most are viviparous with the developing embryo receiving nutrients from the female across the *placenta*.
- A few are oviparous.

Mammals have large brains in comparison to other vertebrate groups and are capable of learning.

- Parental care of long duration helps young learn from the parents.

2. The evolution of mammals

Mammals evolved from therapsid ancestors (part of the synapsid branch) during the Triassic period.

- The oldest fossil mammals are dated to 220 million years ago.
- Early mammals coexisted with dinosaurs throughout the Mesozoic era.
- Most Mesozoic mammals were small, probably insectivorous and nocturnal.

Mammals continued to diversify during the Cenozoic.

- During the Cretaceous period (last of the Mesozoic), mass extinctions and mass radiations transformed the flora and fauna of Earth.
- By the beginning of the Cenozoic, mammals were undergoing an adaptive radiation, and their diversity is represented today by three major groups: monotremes, marsupials, and eutherian (placental) mammals.

3. Monotremes

The *monotremes* include the platypuses and echidnas, which are characterized by:

- Oviparity
 - A reptilian-like egg with large amounts of yolk that nourishes the developing embryos (see Campbell, Figure 34.27a)
 - Hair
 - Milk production from specialized glands on the belly of females
- ⇒ After hatching, young suck milk from the fur of the mother who lacks nipples.

The mixture of ancestral reptilian and derived mammalian traits suggests that monotremes descended from an early branch of the mammalian lineage.

- Extant monotremes are found in Australia and New Guinea.

4. Marsupials

The *marsupials* include opossums, kangaroos, koalas, and other mammals that complete their development in a marsupium (maternal pouch).

Marsupial eggs contain a moderate amount of yolk that nourishes the embryo during early development in the mother's reproductive tract.

- Young are born in an early stage of development and are small (about the size of a honeybee in kangaroos).
- The hindlegs are simple buds, but the forelimbs are strong enough for the young to climb from the female reproductive tract exit to the marsupium.
- In the marsupium, the young attaches to a teat and completes its development while nursing.

Convergent evolution in Australian marsupials has produced a diversity of forms which resemble eutherian (placental) counterparts in all ecological roles (see Campbell, Figure 34.28).

- Opossums are the only extant marsupials outside of the Australian region.
- South America had an extensive marsupial fauna during the Tertiary period, as seen in the fossil record.

Plate tectonics and continental drift provide a mechanism which explains the distribution of fossil and modern marsupials.

- Fossil evidence indicates marsupials probably originated in what is now North America and spread southward while the land masses were joined.
- The breakup of Pangaea produced two island continents: South America and Australia.
 - ⇒ With isolation, their marsupial faunas diversified away from the placental mammals that began adaptive radiation on the northern continents.
- Australia has remained isolated from other continents for about 65 million years, thus isolating its developing fauna.
- When North and South America joined at the isthmus of Panama, extensive migrations took place over the land bridge in both directions.
 - ⇒ The most important migrations occurred about 12 million years ago and again about 3 million years ago.

5. Eutherian (placental) mammals

In placental mammals, embryonic development is completed within the uterus where the embryo is joined to the mother by the placenta.

Adaptive radiation during the late Cretaceous and early Tertiary periods (about 70 to 45 million years ago) produced the orders of extant placental mammals (see Campbell, Table 34.2)

- Fossil evidence indicates that placentals and marsupials diverged from a common ancestor about 80 to 100 million years ago; thus, they are more closely related than either is to the monotremes.

Most mammalogists favor a genealogy that recognizes at least four main evolutionary lines of placental mammals.

- One lineage consists of the orders Chiroptera (bats) and Insectivora (shrews) which resemble early mammals.
 - ⇒ The modified forelimbs which serve as wings in bats probably evolved from insectivores that fed on flying insects.
 - ⇒ Some bats feed on fruits while others bite mammals and lap the blood.
 - ⇒ Most bats are nocturnal.
- A second lineage consists of medium-sized herbivores that underwent a massive adaptive radiation during the Tertiary period.
 - ⇒ This led to such modern orders as the Lagomorpha (rabbits), Perissodactyla (odd-toed ungulates), Artiodactyla (even-toed ungulates), Sirenia (sea cows), Proboscidea (elephants) and Cetacea (whales, porpoises).
- The third evolutionary lineage produced the order Carnivora which probably first appeared during the Cenozoic.
 - ⇒ Included in this order are the cats, dogs, raccoons, skunks, and pinnipeds (seals, sea lions, walruses).
 - ⇒ Seals and their relatives evolved from middle Cenozoic carnivores that became adapted for swimming.
- The fourth lineage had the greatest adaptive radiation and produced the primate-rodent complex.

⇒ Includes the orders Rodentia (rats, squirrels, beavers) and Primates (monkeys, apes, humans).

VII. Primates and the Phylogeny of *Homo sapiens*

A. Primate evolution provides a context for understanding human origins

The first primates were small arboreal mammals.

- Dental structure suggests they descended from insectivores in the late Cretaceous.
- *Purgatorius unio*, found in Montana, is considered to be the oldest primate.

Primates have been present for 65 million years (end of Mesozoic era) and are defined by characteristics shaped by natural selection for living in trees. These characteristics include:

- Limber shoulder joints which make it possible to *brachiate* (swing from one hold to the next).
- Dexterous hands for hanging on branches and manipulating food.
- Sensitive fingers with nails, not claws.
- Eyes are close together on the front of the face, giving overlapping fields of vision for enhanced depth perception (necessary for brachiating).
- Excellent eye-hand coordination.
- Parental care with usually single births and long nurturing of offspring.

B. Modern primates

Modern primates are divided into two suborders: Prosimii (premonkeys) and Anthropoidea (monkeys, apes, humans).

- Prosimians (lemurs, lorises, pottos, tarsiers) probably resemble early arboreal primates (see Campbell, Figure 34.29).

There is a question as to which early *prosimian* lineage is ancestral to the *anthropoids*.

- Two groups of prosimian fossils are recognized by paleontologists.
 - ⇒ One ancestral to the tarsiers, the other to lemurs, lorises, and pottos (see Campbell, Figure 34.30).
- The divergence of these two groups occurred at least 50 million years ago and it has been debated as to which of these two groups was also ancestral to the anthropoids.
- Recently discovered fossils raise another possibility.
 - ⇒ Fossils found in Asia and Africa, which date at least 50 million years ago, appear to be more similar to anthropoids than to either groups of prosimian fossils.
 - ⇒ These fossils indicate an early divergence of prosimians into three lineages with the third being ancestral to the anthropoids.

Fossils of monkeylike primates indicate anthropoids were established in Africa and Asia by 40 million years ago in Africa or Asia (South America and Africa had already separated).

- Ancestors of New World monkeys may have reached South America by rafting from Africa or migration southward from North America.

New World monkeys and Old World monkeys have evolved along separate pathways for many millions of years (see Campbell, Figure 34.31)

- All New World monkeys are arboreal.
- Old World monkeys include arboreal and ground-dwelling forms.

- Most monkeys, both New and Old World, are diurnal and usually live in social bands.

There are also four genera of apes included in the anthropoid suborder: *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas) and *Pan* (chimpanzees) (see Campbell, Figure 34.32).

- Apes are confined to the tropical regions of the Old World.
- They are larger than monkeys (except the gibbons) with relatively long legs, short arms, and no tails.
- Only gibbons and orangutans are primarily arboreal although all are capable of brachiation.
- Social organization varies with the gorillas and chimpanzees being highly social.
- Apes have larger brains than monkeys and thus exhibit more adaptable behavior.

C. Humanity is one very young twig on the vertebrate tree

Paleoanthropology concentrates on the small span of geological time during which humans and chimpanzees diverged from a common ancestor.

Paleoanthropology = The study of human origins and evolution

Competition between researchers has often clouded the field of paleoanthropology.

- Researchers gave new names to fossil forms which were actually the same species recovered by others. (This practice ended about 20 years ago.)
- Theories were proposed on insufficient evidence; often a few teeth or a jawbone fragment.
- Such actions resulted in many persistent misconceptions about human evolution even though fossil discoveries have disproved many of the myths.

1. Some common misconceptions

Our ancestors were chimpanzees or other modern apes.

Humans and chimpanzees represent two divergent branches of the anthropoid lineage which evolved from a common, less specialized ancestor.

Human evolution represents a ladder with a series of steps leading directly from an ancestral anthropoid to *Homo sapiens*.

- This progression is usually shown as a line of fossil hominids becoming progressively more modern.
- Human evolution included many branches which led to dead ends with several different human species coexisting at times (see Campbell, Figure 34.33).
- If punctuated equilibrium applies to humans, most evolutionary change occurred with the appearance of new hominid species, not phyletic (anagenic) change in an unbranched lineage.

Various human characteristics like upright posture and an enlarged brain evolved in unison.

- *Mosaic evolution* occurred with different features evolving at different times.
- Some ancestral forms walked upright but had small brains.

Present understanding of our ancestry remains unclear even after dismissing many of these myths.

2. Early anthropoids

The oldest known fossils of apes are of *Aegyptopithecus*, the "dawn ape," which was a cat-sized tree-dweller from about 35 million years ago.

About 23 million years ago (during the Miocene epoch), descendants of the first apes diversified and spread to Eurasia.

About 20 million years ago, the Indian plate collided with Asia and the Himalayan range formed.

- The climate became drier and the African and Asian forests contracted.
⇒ This isolated these regions of anthropoid evolution from each other.

Most anthropologists believe that humans and apes diverged from a common African anthropoid ancestor 6 to 8 million years ago.

- Evidence from the fossil record and DNA comparisons between humans and chimpanzees supports this conclusion.

3. The first humans

Australopithecus africanus was discovered by Raymond Dart in 1924.

- Additional fossils proved that *Australopithecus* was a hominid that walked fully erect and had humanlike teeth and hands.
- The brain was about one-third the size of modern humans.
- Various species of *Australopithecus* began appearing about 4 million years ago and existed for over 3 million years.

"Lucy", an *Australopithecus* skeleton, was discovered in 1974 in the Afar region of Ethiopia by paleoanthropologists.

- Lucy is 3.2 million years old.
- The skeleton was 40% complete and small, about one meter tall with a head the size of a softball.
- The structure indicates an upright posture.
- It was different enough to be placed in a different species, *Australopithecus afarensis*.
- Similar fossils have been discovered which indicate the species existed for about one million years.

Since 1994, other hominid bone fragments have been recovered in east Africa areas near the site of Lucy's discovery. These fragments are so different from *A. afarensis* that new hominid species have been named:

- *Australopithecus anamensis*, from about 4 million years ago
- *Australopithecus ramidus*, from about 4.4 million years ago

A. ramidus, which represents the oldest known hominid, exhibited some interesting characteristics.

- Skull fragments indicated the head balanced on top of the spinal column—evidence of the early evolution of upright posture.
- The skeletons of forest-dwelling animals were found among the bones—this challenges the view that bipedalism evolved when humans began living on the savanna.

The discovery of *A. ramidus* and *A. afarensis* has raised several questions.

- Is *A. ramidus* the ancestor of *A. afarensis* or an extinct evolutionary branch?
- Is *A. afarensis* ancestral to other hominids or did it share a common ancestor with *Homo*?
 - *A. afarensis* underwent little change during its one million year span.
 - Several new hominid species resulted from an adaptive radiation which began about 3 million years ago.

- The new species included *A. africanus*, several heavy-boned species of *Australopithecus*, and *Homo habilis* (appeared about 2.5 million years ago).

While the phylogeny of early hominids is uncertain, one fact is clear: hominids walked upright for two million years without a substantial increase in brain size.

- This posture may have freed the hands for other things such as gathering food or caring for infants.

4. *Homo habilis*

Enlargement of the human brain is first evident in fossils dating to about 2.5 million years ago.

- Skulls with brain capacities of about 650 cubic centimeters have been found compared with the 500 cc capacity of *A. africanus*.
- Simple stone tools have been found at times with the larger-brained fossils.
- Most paleoanthropologists believe these advances warrant placing the larger-brained fossils in the genus *Homo* and naming them *Homo habilis*.
- It is clear from the fossil record that after walking upright for more than two million years, hominids began to use their brains and hands to fashion tools.

Homo habilis and other new hominids were a part of a larger speciation event among African mammals.

- About 2.5 million years ago, Africa's climate began to become drier and savannas started to replace forests.
- The fauna began to adapt to these new conditions.
- *Homo habilis* coexisted with the smaller-brained *Australopithecus* for nearly one million years.
- One hypothesis is that *Australopithecus africanus* (and other australopithecines) and *Homo habilis* were two distinct lines of hominids.
⇒ *Australopithecus africanus* was an evolutionary dead end, while *Homo habilis* may have been on the line to modern humans, leading first to *Homo erectus* which later gave rise to *Homo sapiens*.

5. *Homo erectus* and descendants

Homo erectus was the first hominid to migrate out of Africa into Europe and Asia.

- Fossils known as Java Man and Beijing Man are examples of *H. erectus*.

Homo erectus lived from about 1.8 million years ago until 250,000 years ago.

- Fossils found in Africa cover the entire span of *H. erectus*' existence.
- These populations existed during the same period as *H. erectus* populations on other continents.
- The spread to new continents may have resulted from a gradual range expansion associated with a shift in diet to include a larger portion of meat.
⇒ In general, carnivores need a larger range than herbivores.

Homo erectus was taller and had a larger brain than *H. habilis*.

- The *H. erectus* brain capacity increased to as large as 1200 cc during the 1.5 million years of its existence.
⇒ This overlaps the normal range of modern humans.

The intelligence that evolved in *H. habilis* allowed early humans to survive in the colder climates to which they migrated.

- *Homo erectus* lived in huts or caves, built fires, wore clothes of skins, and designed more refined stone tools than *H. habilis*.

- *Homo erectus* was poorly equipped in a physical sense to live outside of the tropics but made up for the deficiencies with intelligence and social cooperation.

Some descendants of *H. erectus* developed larger brain capacities and exhibited regional diversity in populations.

- The Neanderthals are the best known descendants of *H. erectus*.
- Neanderthals lived in Europe, the Middle East, and Asia from 130,000 to 35,000 years ago.
- They had heavier brows, less pronounced chins, and slightly larger brain capacities than modern man.
- They were skilled tool makers who participated in burials and other rituals requiring abstract thought.

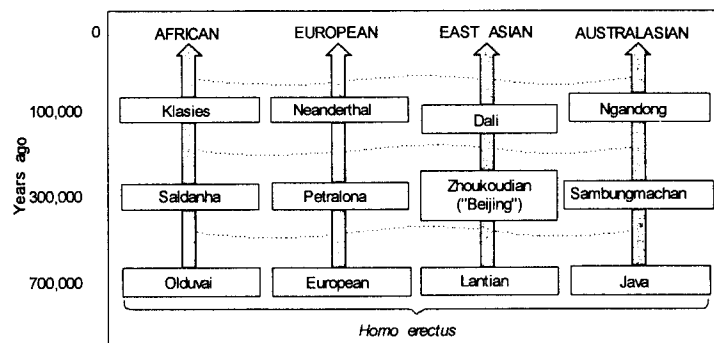
Many paleoanthropologists group the African post-*Homo erectus* fossils with Neanderthals and other descendants from Asia and Australasia. They believe these fossils represent the earliest forms of *Homo sapiens*.

- Some post-*H. erectus* fossils date to 300,000 years ago.

6. The emergence of *Homo sapiens*: Out of Africa...but when? *science as a Process*

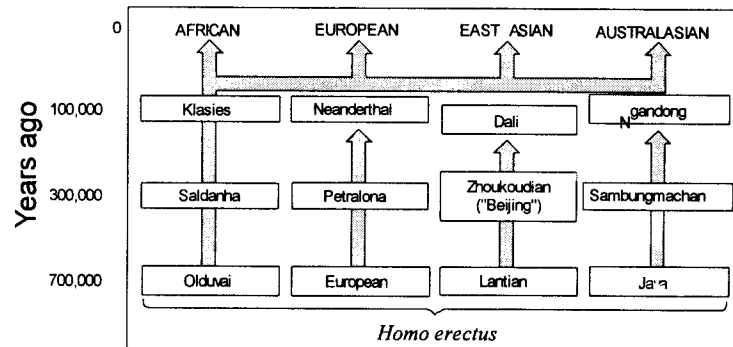
The debate over the origin of modern humans continues unabated with two widely divergent models currently being discussed. These are the multiregional model and the monogenesis model.

The *multiregional model* proposes: 1) Neanderthals and other post-*Homo erectus* hominids were ancestors to modern humans; and 2) modern humans evolved along the same lines in different parts of the world (see also, Campbell, Figure 34.35a).



- If this model is correct, the geographic diversity of humans originated between one and two million years ago when *Homo erectus* spread from Africa to other continents.
- Supporters feel that interbreeding among neighboring populations provided opportunities for gene flow over the entire range and resulted in the genetic similarity of modern humans.

During the 1980s, some paleoanthropologists who interpreted the fossil record in a different way began to develop an alternative to the multiregional model. This alternative became known as the “Out of Africa” or *monogenesis model*.



The *monogenesis model* proposes: 1) *Homo erectus* was the ancestor to modern humans who evolved in Africa; and 2) modern humans dispersed from Africa, displacing the Neanderthals and other post-*H. erectus* hominids (see also Campbell, Figure 34.35b).

- If this model is correct, the diversity of modern humans has developed from geographic diversification within the last 100,000 years.
- To supporters of this model, an exclusively African genesis for modern humans is strongly indicated by the fact that the complete transition from archaic *Homo sapiens* to modern humans is found only in African fossils.
- The focus of their interpretations is on the relationship between Neanderthals and modern humans in Europe and the Middle East.
- The oldest fossils of modern *Homo sapiens* are about 100,000 years old. These were found in Africa and similar fossils have been recovered from caves in Israel.
- The fossils from Israel were found in caves near other caves containing Neanderthal-like fossils which date from 120,000 to 60,000 years ago—overlapping *H. sapiens* by about 40,000 years.
- Supporters of the monogenesis model interpret this information to mean that no interbreeding occurred during the time of coexistence since the two types of hominids persisted as distinct forms.
- This interpretation means the Neanderthals were not ancestors of modern humans since they coexisted and were probably evolutionary dead ends along with other dispersed post-*H. erectus* hominids.

Modern molecular techniques are being used to examine the question of human origins.

- In the late 1980s, a group of geneticists compared the mitochondrial DNA (mtDNA) from a multiethnic group of more than 100 people from four different continents.
- The premise for this analysis is that the greater the differences in the mtDNA of two people, the longer the time of divergence from a common source.
- Analysis of the mtDNA comparisons resulted in the tracing of the source of all human mtDNA back to Africa with the divergence from that common source beginning about 200,000 years ago.

- These results appeared to support the monogenesis model in that the divergence from the common source was too late to represent dispersal of *Homo erectus*, but supported a later dispersal of modern humans.

Several researchers have challenged the interpretation of the mtDNA study, especially the methods used to construct evolutionary trees from this type of data and the reliability of mtDNA as a biological clock.

- This criticism has encouraged advocates of the multiregional model to argue that the fossil evidence supports the multiregional evolution of humans more strongly than African monogenesis.
- These scientists also consider certain fossils from different geographical regions to be links between that region's archaic *Homo sapiens* and the modern humans currently on that continent.

New evidence from comparisons of nuclear DNA and new methods for using the mtDNA data to trace the relationships of populations are stimulating further debate.

- This new information strengthens the monogenesis model.
- Greater genetic diversity is found in African populations south of the Sahara than in other parts of the world.
 - ⇒ If modern humans evolved in southern Africa, these populations would have the longest history of genetic diversification.
 - ⇒ If populations of humans in other parts of the world resulted from migrations out of Africa, the smaller genetic diversity could be the result of the founder effect and genetic drift.

Debate continues about whether the multiregional model or the monogenesis model is more accurate.

- New evidence obtained by attempts to extract DNA from fossilized Neanderthal and other archaic *Homo sapiens* skulls may shed new light on this question.

7. Cultural evolution: a new force in the history of life

Erect stance was a very radical anatomical change in our evolution and required major changes in the foot, pelvis and vertebral column.

Enlargement of the brain was a secondary alteration made possible by prolonging the growth period of the skull and its contents.

The brains of nonprimate mammalian fetuses grow rapidly, but growth slows and stops soon after birth.

- The brains of primates continue to grow after birth and the period is longer for a human than other primates.
- Parental care is lengthened due to this extended development and this contributes to the child's learning.

Learning from the experiences of earlier generations is the basis of culture (transmission of accumulated knowledge over generations); the transmission is by written and spoken language.

A cultural evolution is a continuum, but three stages are recognized:

1. Nomads of the African grasslands made tools, organized communal activities and divided labors about 2 million years ago.
2. The development of agriculture in Africa, Eurasia, and the Americas about 10,000 to 15,000 years ago encouraged permanent settlements.
3. The Industrial Revolution began in the eighteenth century. Since then, new technology and the human population have escalated exponentially.

No significant biological change in humans has occurred from the beginning to now.

Evolution of the human brain may have been anatomically simpler than acquiring an upright stance, but the consequences of cerebral growth have been enormous.

- Cultural evolution resulted in *Homo sapiens* becoming a species that could change the environment to meet its needs and not have to adapt to an environment through natural selection.
 - ⇒ Humans are the most numerous and widespread of large animals.
- Cultural evolution outpaces biological evolution and we may be changing the world faster than many species can adapt.
 - ⇒ The rate of extinctions this century is 50 times greater than the average for the past 100,000 years.
 - ⇒ The overwhelming rate of extinction is due primarily to habitat destruction and chemical pollution, both functions of human cultural changes and overpopulation.
 - ⇒ Global temperature increase and alteration of world climates are a result of escalating fossil fuel consumption.
 - ⇒ Destruction of tropical rain forests, which play a role in maintenance of atmospheric gas balance and moderating global weather, is startling.

The effect of *Homo sapiens* is the latest and may be the most devastating crisis in the history of life.

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