CHAPTER 17 TETRAPOD & MODERN AMPHIBIANS STUDY GUIDE

17.1 Vertebrate Landfall

- **A.** Evolutionary transition from water to land took millions of years.
- **B.** At that time, there was no competition from other terrestrial vertebrates, unlike today.
- **C.** Only living vertebrate group that has a transition from water to land in both their ontogeny and phylogeny.
- **D.** Even today, few amphibians are completely adapted to a terrestrial existence.
- **E.** These animals form a monophletic group known as **tetrapods.**
- **F.** Amphibians and amniotes (birds, reptiles, mammals) represent the two major branches of tetrapod phylogeny.

17.2 Movement Onto Land

A. Adaptations

1. Animal composition is mostly water; land represents a **relatively dangerous habitat.**
2. Vascular plants, pulmonate snails and tracheate arthropods all made the transition earlier.
3. Amphibians most clearly represent this vertebrate transitional stage.
4. Accommodations address oxygen content, density, temperature regulation and habitat diversity.
   - a. Oxygen is 20 times more abundant in air and diffuses much more rapidly through air.
   - b. Air is 1000 times less dense and provides less buoyancy than water; limbs and the skeleton must therefore support more weight.
   - c. Air fluctuates in temperature more rapidly than does water; animals must adjust to these extremes.
   - d. The variety of terrestrial habitats allows dramatically greater opportunities for adaptation.

B. Physical Accommodations

1. Even earliest forms had to deal with important physical difference between aquatic and terrestrial environments.
   - a. oxygen content
   - b. density
   - c. temperature regulation
   - d. habitat diversity

17.3 Early Evolution of Terrestrial Vertebrates

A. Devonian Origin of Tetrapods

1. This period, **400 million years ago**, was a time of mild temperatures, floods and droughts.
2. The Devonian freshwater environment was unstable; lungs and limbs evolved.
3. As pools evaporated, water fouled and oxygen levels declined, only fish with some kind of **lung** could survive.
4. Gill filaments collapse and dry when exposed to air.
5. Lobe-finned fishes and lung fishes developed lungs as outgrowths of the pharynx.
6. More capillaries and arterial blood from the last aortic arch improved the air-filled cavity.
7. Oxygenated blood returned directly to the heart by a pulmonary vein to form a **double circulation**.
8. The bony elements of the fins of lobe-finned fishes resemble the limbs of amphibians.
   - a. *Eusthenopteron* was able to crawl along on the bottom mud; it had both lungs and "walking" fins.
   - b. Its humerus, radius and ulna were homologous with tetrapod wrist bones.
   - c. *Acanthostega* had clearly formed digits on both fore and hind limbs; its body still dragged on the ground (Figure 17.1).
   - d. *Ichthyostega* had bulkier limb muscles to walk onto land, although not with great efficiency.
   - e. Newly discovered fossils of Devonian tetrapods show more than five fingers and toes.
9. **Theories of Adaptation to Land**
   - a. **Seasonal drought hypothesis**: amphibian ancestors developed legs from selection for migrating across land to new ponds.
   - b. Recent fossil finds show *Acanthostega* with tetrapod legs to be otherwise **fully aquatic**; this suggests that legs completely developed while the animal remained a fully aquatic animal.
10. **Lobe-finned fishes** are therefore the sister group to tetrapods (Figure 17.2).
11. Adaptations for life on land include skull, teeth, pectoral girdle and jointed limbs.
12. Tetrapods also selected for stronger backbone, muscles to support the body in air, muscles to elevate the head, stronger shoulder and hip girdles, a more protective rib cage, ear structure and longer snout.
13. *Ichthyostega* still retained aquatic features including fin rays and opercular bones.

B. Carboniferous Radiation of Tetrapods

1. In contrast to the varied climate of the Devonian, the Carboniferous was uniformly warm and wet.

2. Tetrapods radiated into the swampy moss and fern landscape.
3. They ate insects, insect larvae and aquatic invertebrates.
4. Several extinct lineages, plus the **Lissamphibia,** with modern amphibians formed the **temnospondyls.**
5. Temnospondyls generally had four rather than five digits on the forelimb.
6. During the Carboniferous, amphibians developed additional adaptations for living in water.
   a. Bodies became flatter for moving in water.
   b. Early salamanders developed weak legs and the tail became better developed.
   c. Anurans developed webbing on hind-limbs for better swimming.
   d. Swampy forests encouraged the use of porous skin as an accessory breathing organ.
7. **Lissamphibians** diversified during the Carboniferous to produce ancestors of the three major groups of amphibians:
   a. **Anura (Salientia) – frogs**
   b. **Caudata (Urodela) – salamanders**
   c. **Apoda (Gymnophiona) - caecilians**

17.4 Modern Amphibians (See BOX, page 340)

A. Diversity

1. Over 4200 living species are known in the three amphibian orders (Figure 17.3).
2. The olfactory epithelium and the ear are redesigned to improve sensitivity to airborne sound.
3. They remain tied to water; eggs are aquatic, and the larvae depend on gills for respiration.
4. Some salamanders have retained aquatic morphology throughout life; and others lack the larval phase.
5. Generally, gills are lost and lungs are activated when salamanders breathe air.
6. Respiration also occurs across the skin especially in terrestrial salamanders.
7. The thin skin loses water rapidly; this restricts even terrestrial forms to moist habitats.
8. Being ectothermic, their body temperature depends on the environment and restricts their range.
9. Eggs easily desiccate and must be shed into water or kept moist; a few brood their young.

B. Caecilians: Order Gymnophiona (Apoda)

1. About 160 living species of elongate, **secondarily limbless**, burrowing caecilians are known.
2. They live in tropical forests in South America, Africa and Southeast Asia.
3. Their long bodies have many vertebrae, long ribs, no limbs, and a terminal anus.
4. They eat primarily worms and small underground invertebrates.
5. Fertilization is internal and the male has a protrusible copulatory organ.
6. Eggs are deposited in moist ground near water.
7. In some species, eggs are guarded and develop in folds of the body (Figure 17.4).
8. In other species, viviparity allows embryos to obtain nourishment by eating the wall of the oviduct.
9. Unlike adults, hatchling have a tail fin, open gill slit, and external gills in some species.

C. Salamanders: Order Caudata (Urodela)

1. About 500 species of living salamanders are found mostly in northern temperate regions.
2. Most are small, under 15 centimeters long, but the Japanese giant salamander is 1.5 meters long.
3. Usually their limbs are at right angles to the body; forelimbs and hind-limbs are about equal in length.
4. Burrowing species and some aquatic forms may have secondarily lost their limbs.
5. Salamanders are carnivorous as both larvae and adults, eating worms, small arthropods and molluscs.
6. They are ectotherms with a low metabolic rate.
7. **Breeding Behavior**
   a. Some are aquatic throughout their life cycle; most have aquatic larvae and terrestrial adults.
   b. Most salamanders fertilize eggs internally.
   c. The female picks up a **spermatophore** that has been deposited on a leaf or stick (Figure 17.5).
   d. Aquatic species lay eggs in clusters or stringy masses that hatch into larvae with external gills and a finlike tail.
   e. Completely terrestrial species deposit eggs in small, grape-like clusters under logs or in soft earth (Figure 17.6).
   f. Terrestrial species undergo direct development, hatching as miniature adults.
   g. Some North American newts have aquatic larvae that metamorphose into terrestrial juveniles that again metamorphose into secondarily aquatic, breeding adults (Figure 17.7).
8. **Respiration**
   a. Salamanders have a wide array of respiratory mechanisms.
   b. They have extensive **vascular nets** in their skin that exchange both oxygen and carbon dioxide.

c. At various stages, they may also have external gills, lungs, both gills and lungs, or neither.
d. Salamanders with an aquatic stage hatch with gills and lose them at metamorphosis.
e. Several diverse lineages fail to undergo metamorphosis and retain gills and a fin-like tail (Figure 17.8).
f. Where present, lungs are present from birth and become functional following metamorphosis.
g. Aquatic amphiumas lose their gills and respire by lungs, holding nostrils above the water surface.
h. Many species in the terrestrial family **Plethodontidae** lack lungs and use cutaneous respiration (Figure 17.9)
i. Cutaneous respiration is increased by epidermal capillaries or thinning of the epidermis over dermal capillaries.
i. Respiratory gases may also be exchanged across the vascularized lining of the mouth cavity.
j. Lungless salamanders likely evolved in cold streams where lungs would have been too buoyant.

9. **Paedomorphosis**
   a. Paedomorphosis is the preservation of pre-adult features into adulthood (i.e., they reach sexual maturity while retaining their gills, aquatic lifestyle, and other larval characteristics).
   b. Eliminating ancestral adult morphology is a trend found in salamander evolution.
   c. There are non-metamorphic species that retain gills, like the **mudpuppy,** *Necturus* (Figure 17.8A).
   d. Others reach sexual maturity with larval morphology but can change depending on the conditions.
   f. When ponds dry up, *Ambystoma tigrinum* may metamorphose into a terrestrial form and migrate to a new pond.

D. Frogs and Toads: Order Anura (Salientia)

1. Over 4840 species of frogs and toads compose the order Anura.
2. This group is known from the Jurassic period, 150 million years ago.
3. Tied to an aquatic mode of reproduction and a water-permeable skin, they must be near water.
4. Lack of endothermy keeps anurans from inhabiting polar and subarctic habitats.
5. All pass through a tailed larval stage to become tailless, jumping adults.
6. Eggs hatch into **tadpoles** with a long, finned tail, no legs, internal and external gills and specialized mouthparts for (usually) herbivorous feeding.
7. They look and act different from adult frogs; permanent gills never occur in frogs and toads.
8. There are 21 families of frogs and toads.
   a. Family Ranidae contains the common larger frogs in North America (Figure 17.10A).
   b. Family Hylidae includes the tree frogs (Figure 17.10B).
   c. Family Bufonidae contains toads with thicker skins and prominent warts (Figure 17.11).
   d. The West African *Conraua goliath* may weigh 3.3 kg (7.5 pounds) (Figure 17.12).
   e. The Cuban *Phyllobates limbatus* is 1 cm long, the smallest frog recorded.
9. **Habitats and Distribution**
   a. The 260 species of the genus *Rana* are common in temperate and tropical regions.
   b. *Rana sylvatica*, the wood frog, spends most of its time on damp forest floors, returning to pools for breeding.
   c. Bullfrogs and green frogs are found in or near permanent water and swamps.
   d. The leopard frog is widespread and commonly studied in laboratories.
   e. The pickerel frog is restricted to certain localities.
10. **Life Cycle**
   a. Most larger frogs are solitary until breeding season.
   b. During the breeding season, males are especially noisy when trying to attract a female.
   c. They hold forelimbs near the body when swimming with their powerful hind-limbs.
   d. When they surface to breathe, only the head and foreparts are exposed.
   e. During winter in temperate climates, they hibernate in soft mud in the bottom of pools.
   f. During hibernation, the little energy they use is provided from stored glycogen and fat.
   g. Frost-tolerant frogs prepare for freezing by accumulating glucose and glycerol in body fluids; this protects them from the otherwise damaging effects of intracellular ice-crystal formation.
   h. Many are easy prey; they defend themselves by aggression, concealment, and poison glands.
   i. Populations of many species have fallen dramatically (see Inset, page 335).
   j. The African clawed frog, *Xenopus laevis* (Figure 17.13) is a voracious, aggressive, primarily aquatic frog introduced into North America in the 1940s that is rapidly displacing native frogs and fish from several waterways in southern California.
11. **Integument and Coloration (in Instructor's Guide only; no text counterpart).**

a. Frog skin is thin, moist and attached loosely to the body at a few points.
b. The skin is composed of an outer **stratified epidermis and an inner spongy dermis**.
c. The outer layer of epidermal cells is shed periodically; it contains deposits of **keratin**.
d. More terrestrial amphibians have heavier deposits of keratin; it remains soft.
e. The inner layer of epidermis has two types of integumentary glands: **mucous glands** secrete protective waterproofing and large serous glands produce a whitish, watery poison.
f. **Dendrobatid frogs** of South America secrete highly toxic skin poisons.
g. Specialized pigment cells, **chromatophores**, produce skin color in frogs.
h. Uppermost are xanthophores with yellow, orange or red pigments.
i. The middle layer is composed of **iridophores** with a silvery light-reflecting pigment that acts like a mirror.
j. Deeper are **melanophores** containing black or brown melanin.
k. The green hue is an interaction of xanthophores containing yellow and underlying iridophores.
l. Many frogs can adjust their color to blend with their background and thus camouflage themselves.

12. **Skeletal and Muscular Systems (in Instructor's Guide only; no text counterpart).**
    a. A well-developed **endoskeleton of bone and cartilage** provides protection and muscle anchorage.
    b. Movement to land provided new mechanical stress problems.
    c. Anurans show dramatic changes in the **musculoskeletal system** for jumping and swimming.
    d. The vertebral column lost much of its flexibility in order to transmit force from limbs to the body.
    e. Anurans have an extremely shortened body; they have only nine trunk vertebrae and an urostyle.
    f. Caecilians have not moved toward tetrapod locomotion and have as many as 285 vertebrae.
    g. The front of the frog skull, containing the brain, eyes, and nose is lightweight and flattened; the back of the skull, which contained the gill apparatus in fishes, is reduced.
    h. The posterior limbs have three main joints: hip, knee and ankle.
    i. The foot generally has **five rays** and the hand is four-rayed; both have several joints in the digits.
    j. This system is derived from the **pattern in rhipidistian lobe-finned fish**.
    k. Limb musculature is in two groups: an anterior, ventral group pulls the limb forward and toward the midline, and the posterior, dorsal group draws the limb backward and away from the body.
    l. The myomeres have been highly modified to support the head and brace the vertebral column.
13. **Respiration and Vocalization (in Instructor's Guide only; no text counterpart).**
    a. Amphibians use three respiratory surfaces for gas exchange in air.
        1) The skin provides **cutaneous breathing.**
        2) The mouth provides **buccal breathing**.
        3) Lungs are usually present in adults.
    b. Frogs and toads depend on lung breathing more than salamanders.
    c. The skin is critical during winter hibernation
    d. Carbon dioxide is mostly lost across the skin while oxygen is absorbed across the lungs.
    e. Lungs are supplied by pulmonary arteries and these return directly to the left atrium.
    f. Frog lungs are ovoid, elastic sacs; the inner surfaces divide into a network of smaller chambers.
    g. The absorptive surface in a frog lung is 20 cm^2 per cc of air compared to 300 cm^2 for humans.
    h. **Positive Pressure Breathing**.
        1) A frog moves air into the lung by force.
        2) **Rhythmic throat movements** gulp air and force it backward.
        3) The rib cage does not expand to draw air into the lung, as is the case with amniotes.
    i. Both male and female frogs have vocal cords; males have a better developed larynx.
        1) Air is passed back and forth over the vocal cords between the lungs to a large pair of vocal sacs.
        2) The song is unique and characteristic of the species.
14. **Circulation (in Instructor's Guide only; no text counterpart).**
    a. Circulation is closed with a single pressure pump moving blood through the peripheral network.
    b. The main change in circuitry is the shift from gill to lung breathing.
    c. The elimination of gills reduced one obstacle to blood flow in the arterial circuit.
    d. Conversion of the sixth aortic arch into a pulmonary artery provided a blood circuit to the lungs.
    e. Separating the oxygenated blood from the deoxygenated blood circuit is not completed.
    f. Frog Heart.
        1) The frog heart has a **single undivided ventricle** and **two separate atria.**

    2) Blood from the body enters through the sinus venosus and right atrium.
    3) Blood from the lung enters the left atrium.
    4) Both atria contract at the same time, driving blood into the ventricle.
    5) When the ventricle contracts, blood moves to the lungs or body.
    6) Although there is no septum, deoxygenated blood goes primarily to the lungs and oxygenated blood goes mostly to the body due to separation by a spiral valve in the conus arteriosus.

15. **Feeding and Digestion (in Instructor's Guide only; no text counterpart).**
    a. Most adult amphibians are carnivorous, feeding on insects, spiders, worms, slugs, etc.
    b. They catch prey with a tongue that is attached at the front of the mouth.
    c. The free end of the tongue is glandular; a sticky secretion adheres to prey.
    d. Any teeth that are present function to hold prey; they do not bite or chew.
    e. The short digestive tract produces enzymes for digesting fats, carbohydrates and proteins.
    f. Larval stages or tadpoles are usually herbivorous; their digestive tract is relatively long.
16. **Nervous System and Special Senses (in Instructor's Guide only; no text counterpart).**
    a. The brain has three fundamental parts.
        1) The **forebrain or telencephalon** interprets the sense of smell.
        2) The **midbrain or mesencephalon** perceives vision.
        3) The **hindbrain or rhombencephalon** perceives hearing and balance.
    b. The brain is gradually assuming more information processing ability independent of the spine.
    c. However, a headless frog still has highly coordinated behavior based on spinal cord alone.
    d. The forebrain contains the olfactory center but the rest, the cerebrum, is of little function.
    e. Complex integrative activities are located in the midbrain optic lobes.
    f. The hindbrain is divided into an anterior cerebellum and a posterior medulla.
    g. A cerebellum that will be critical in movement coordination in other vertebrates is minor in frogs.
    h. The medulla is the enlarged anterior end of the spinal cord through which sensory neurons pass.
    i. The medulla has centers for auditory reflexes, respiration, swallowing and vasomotor control.
    j. The pressure-sensitive lateral line is only found in amphibian larvae and aquatic adults.
    k. The ear becomes specialized for detecting airborne sounds.
        1) A large tympanic membrane or eardrum passes vibrations to the inner ear via the columella.
        2) The inner ear has a utricle with three semicircular canals and a saccule with a lagena.
        3) A lagena is covered with a tectorial membrane that is similar to the mammalian cochlea.
    l. Frogs are sensitive to low-frequency sound energy under 4000 Hz (cycles per second).
    m. Except for blind caecilians, vision is the dominant sense in many amphibians.
    n. **Lachrymal glands and eyelids** evolved to keep the eye moist, free of dust, and protected.
    o. The cornea and the lens bend light rays to focus an image on the retina.
    p. At rest, the fish eye focuses on near objects and the frog eye focuses on distant objects.
    q. The amphibian retina contains both **rods and cones**; the cones provide frogs with **color vision.**
    r. The iris can rapidly change aperture to adjust to light levels.
    s. The upper eyelid is fixed; the lower is folded into a transparent nictitating membrane.
    t. Other sensory receptors include chemical receptors in skin, taste buds on the tongue and olfactory epithelium in the nasal cavity.
17. **Reproduction and Development** (Figures 17.14, 17.15, 17.16)
    a. Frogs and toads are ectothermic; therefore they breed, feed and grow during the warm seasons.
    b. In the spring, males call to attract females.
    c. When the eggs are mature, females enter the water and the males clasp them in **amplexus** (Figure 17.14).
    d. As the female lays eggs, the male discharges sperm over them (Figure 17.15).
    e. The jelly layers absorb water and swell; the eggs are usually laid in large masses.
    f. Development begins immediately and within a few days embryos hatch into tadpoles.
        1) The tadpole head has **horny jaws** for feeding and a ventral adhesive disc for clinging to objects.
        2) Two deep pits in front of the mouth become nostrils.
        3) Swellings on each side of the head become external gills.
        4) The three pairs of external gills soon develop into internal gills covered with a flap of skin.
        5) On the right side of a tadpole, the **operculum** fuses with the body wall.
        6) On the left side, a **spiracle** remains; water enters the mouth to flow past gills and then out this same spiracle.
    g. **Metamorphosis** (Figure 17.15)

1) Hind legs are first to appear; the forelegs are temporarily hidden in folds of the operculum.
2) The tail is resorbed.
3) The intestine becomes shorter.
4) The mouth transforms to the adult condition.
5) Lungs develop and the gills are resorbed.

h. There is a great variety of unique anuran reproductive strategies (Figure 17.16 A, B, C, D).
1) Eggs may float on surface foam masses or be deposited on leaves overhanging the ponds.
2) Some lay eggs in burrows, tree cavities, on in water-filled chambers on plants.
3) Most frogs abandon their eggs but some tend their eggs and carry tadpoles on their backs.
4) Marsupial frogs carry eggs in a dorsal pouch.
5) Many tropical frogs have direct development.

17.5 Classification

Class Amphibia
- Order Gymnophiona
- Order Urodela
- Order Anura