Chapter 25

Early Tetrapods and Modern Amphibians

Movement Onto Land

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

Early Evolution of Terrestrial Vertebrates

Devonian Origin of Tetrapods

- This period, 400 million years ago, was a time of mild temperatures, floods and droughts.
- The Devonian freshwater environment was unstable.
- As pools evaporated, water fouled and oxygen levels declined, only fish with some kind of lung could survive.
- More capillaries and arterial blood from the last aortic arch improved the air-filled cavity.
- Oxygenated blood returned directly to the heart by a pulmonary vein to form a double circulation.
- The bony elements of the fins of lobe-finned fishes resemble the limbs of amphibians.

Theories of Adaptation to Land

Seasonal drought hypothesis
- Amphibian ancestors developed legs from selection for migrating across land to new ponds.
- 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 underwater animal.

Theories of Adaptation to Land

- Lobe-finned fishes are therefore the sister group to tetrapods.
- Adaptations for life on land include skull, teeth, pectoral girdle and jointed limbs.
- 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.

Carboniferous Radiation of Tetrapods

- In contrast to the varied climate of the Devonian, the Carboniferous was uniformly warm and wet.
- Tetrapods radiated into the swampy moss and fern landscape.
- They ate insects, insect larvae and aquatic invertebrates.
- During the Carboniferous, amphibians developed additional adaptations for living in water.
  - Bodies became flatter for moving in water.
  - Early salamanders developed weaker legs and the tail became better developed.
  - Anurans developed webbing on hindlimbs for better swimming.
Fig. 25.3

Modern Amphibians

- Over 4200 living species are known in the three amphibian orders.
- The olfactory epithelium and the ear are redesigned to improve sensitivity to airborne sound.
- They remain tied to water; eggs are aquatic, and the larvae depend on gills for respiration.
- Some salamanders have retained aquatic morphology throughout life; and others lack the larval phase.
- Being ectothermic, their body temperature depends on the environment and restricts their range.
- Eggs easily desiccate and must be shed into water or kept moist; a few brood their young.

Brooding of Young

Caecilians: Order Gymnophiona (Apoda)

- About 160 living species of elongate, limbless, burrowing caecilians are known.
- They live in tropical forests in South America, Africa, and Southeast Asia.
- Their long bodies have many vertebrae, long ribs, no limbs, and a terminal anus.
- They eat primarily worms and small underground invertebrates.
- Fertilization is internal and the male has a protrusible copulatory organ.
- Eggs are deposited in moist ground near water.

- Larvae may be aquatic or undergo all larval development inside the egg.
  - In some species, eggs are guarded and develop in folds of the body.
  - In other species, viviparity allows embryos to obtain nourishment by eating the wall of the oviduct.

Salamanders: Order Caudata (Urodela)

- About 360 species of living salamanders are found mostly in northern temperate regions.
- Most are small, under 15 cm long, but the Japanese giant salamander is 1.5 m long.
- Usually their limbs are at right angles to the body; forelimbs and hindlimbs are about equal in length.
- Burrowing species and some aquatic forms may have lost their limbs.
- Salamanders are carnivorous as both larvae and adults, eating worms, small arthropods and molluscs.
- Their food is relatively rich in proteins; therefore they do not store much fat or glycogen.
- They are ectotherms with a low metabolic rate.

Breeding Behavior

- Some are aquatic throughout their life cycle; most have aquatic larvae and terrestrial adults.
- Most salamanders fertilize eggs internally.
- The female picks up a spermatophore that has been deposited on a leaf or stick.
- Aquatic species lay eggs in clusters or stringy masses.
- Completely terrestrial species deposit eggs in small, grape-like clusters under logs or in soft earth.
- Terrestrial species undergo direct development, hatching as miniature adults.
- Some North American newts have aquatic larvae that metamorphose into terrestrial juveniles that again metamorphose into secondarily aquatic, breeding adults.
- Some newt populations skip the terrestrial "red eft" stage and remain entirely aquatic.
Respiration

- Salamanders have a wide array of respiratory mechanisms.
- They have extensive vascular nets in their skin that exchange both oxygen and carbon dioxide.
- At various stages, they may also have external gills, lungs, both gills and lungs, or neither.
- Salamanders with an aquatic stage hatch with gills and lose them at metamorphosis.
- Where present, lungs are present from birth and become functional following metamorphosis.
  - Aquatic amphiumas lose their gills and respire by lungs, holding nostrils above the water surface.
  - Many species in the terrestrial family Plethodontidae lack lungs and use cutaneous respiration.
- Respiratory gases may also be exchanged across the vascularized lining of the mouth cavity.
- Lungless salamanders likely evolved in cold streams where lungs would have been too buoyant.

Paedomorphosis

- Paedomorphosis is the preservation of pre-adult features into adulthood.
- Eliminating ancestral adult morphology is a trend found in salamander evolution.
- Non-metamorphic species that retain gills, etc. are perennibranchiate.
  - Obligate perennibranchiates, like the mudpuppy, have never been observed to metamorphose.
  - Others reach sexual maturity with larval morphology but can change depending on the conditions.
  - In Mexico and the U.S., Ambystoma tigrinum may stay in a gilled stage as an axolotl.
    - When ponds dry up, they may metamorphose into a terrestrial form and migrate to a new pond.
    - Axolotls treated with thyroid hormone will metamorphose artificially; the pituitary gland appears to be the controlling factor in natural populations.
    - Paedomorphosis may be partial; the amphibian shifts to lungs but otherwise remains larval.
    - In another species, the larval appendages have been maintained to preserve a climbing ability.

Frogs and Toads: Order Anura

- Over 3450 species of frogs and toads compose the order Anura.
- This group is known from the Jurassic period, 150 million years ago.
- Tied to an aquatic mode of reproduction and a water-permeable skin, they must be near water.
- Ectothermy keeps anurans from inhabiting polar and subarctic habitats.
- All pass through a tailed larval stage to become tailless, jumping adults.
Eggs hatch into tadpoles with a long, finned tail, no legs, internal and external gills and specialized mouthparts for (usually) herbivorous feeding. Their internal anatomy is different and they look and act different from adult frogs. The perennibranchiate condition never occurs in frogs and toads. There are 21 families of frogs and toads. Anuran are declining worldwide and becoming patchy in distribution; the cause is not known. – Family Ranidae contains the common larger frogs in North America. – Family Hylidae includes the tree frogs. – Family Bufonidae contains toads with thicker skins and prominent warts.

Most larger frogs are solitary until breeding season. During the breeding season, males are especially noisy when trying to attract a female. They hold forelimbs near the body when swimming with their powerful hindlimbs. When they surface to breathe, only the head and foreparts are exposed. During winter in temperate climates, they hibernate in soft mud in the bottom of pools. During this hibernation period, the little energy they use is provided from stored glycogen and fat.

Frost-tolerant frogs prepare for freezing by accumulating glucose and glycerol in body fluids; this protects them from the otherwise damaging effects of ice-crystal formation. Many are easy prey; they defend themselves by aggression, concealment, and poison glands. Many species of amphibians have suffered from changes in the environment and climate brought about by human impact. Declines in population survival may be accompanied by an increased incidence of malformed individuals such as frogs with extra limbs. Climatic changes that reduce water depth at oviposition sites increases ultraviolet exposure of embryos and make them more susceptible to fungal infection. Decline of some amphibians may be caused by other amphibians such as *Bufo marinus*.

Frog skin is thin, moist and attached loosely to the body at a few points. The skin is composed of an outer stratified epidermis and an inner spongy dermis. Outer layer of epidermal cells is shed periodically; contains deposits of keratin. More terrestrial amphibians have heavier deposits of keratin; it remains soft. 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. Dendrobatid frogs of South America secrete highly toxic skin poisons.

Specialized pigment cells, chromatophores, produce skin color in frogs. Uppermost are xanthophores with yellow, orange or red pigments. The middle layer is composed of iridophores with a silvery light-reflecting pigment that acts like a mirror. Deeper are melanophores containing black or brown melanin. The green hue is an interaction of xanthophores containing yellow and underlying iridophores. Many frogs can adjust their color to blend with their background and thus camouflage themselves.
Skeletal and Muscular Systems

- A well-developed endoskeleton of bone and cartilage provides protection and muscle anchorage.
- Movement to land provided new mechanical stress problems.
- Anurans show dramatic changes in the musculoskeletal system for jumping and swimming.
- The vertebral column lost much of its flexibility in order to transmit force from limbs to the body.

Problems of Aquatic and Aerial Breathing

- Water and land are vastly different in their physical characteristics.
- Air contains about 20 times more oxygen than does water; fully saturated water contains 9 ml of oxygen per liter compared to 209 ml of oxygen per liter in air.
- Water is 800 times more dense and 50 times more viscous than air.
- Gas molecules diffuse about 10,000 times more rapidly in air than in water.
- Advanced fishes still must use up to 20% of their energy to extract oxygen from water.

Respiration

- Amphibians use three respiratory surfaces for gas exchange in air.
  - The skin provides cutaneous breathing.
  - The mouth provides buccal breathing.
  - Lungs are usually present in adults.
- Frogs and toads depend on lung breathing more than salamanders.
- The skin is critical during winter hibernation.
- The absorptive surface in a frog lung is 20 cm$^2$ per cc of air compared to 300 cm$^2$ for humans.

Problems of Aquatic and Aerial Breathing

- Mammals use only 1-2% of their resting metabolic energy to breathe.
- Respiratory surfaces must be thin and moist; this is not a problem for aquatic animals.
- Air breathers have respiratory surfaces invaginated, and pumping actions move air in and out.
- Evaginations of the body surface, such as gills, are used for aquatic respiration.
- Invaginations such as tracheae and lungs are used for air breathing.
Efficient Exchange in Water

- Gills may be simple external extensions of the body surface (e.g., dermal papulae of sea stars or branchial tufts of marine worms).
- Internal gills of fishes and arthropods are thin filamentous structures supplied with vessels.
- In gills, blood flow is opposite the flow of water to provide the maximum extraction of oxygen; this is countercurrent flow.
- Water is washed over the gills in a steady stream, pulled and pushed by an efficient, two-valved, branchial pump.
- The fish’s forward movement through water assists some gill ventilation.

Ventilation Through Gills

Lungs

- Despite the high oxygen levels in air, gills do not function in air because they dry out.
- Some invertebrates including snails, scorpions, some spiders, etc. have inefficient “lungs.”
- Terrestrial vertebrates generally have lungs that can be ventilated by muscle movements.

Positive Pressure Breathing

- A frog moves air into the lung by force.
- Rhythmic throat movements gulp air and force it backward.
- The rib cage does not expand to draw air into the lung, as is the case with amniotes.

Lungs

- Amphibian lungs vary from smooth-walled, bag-like salamander lungs to divided lungs of frogs.
- Reptiles lungs have greater surface area because they are subdivided further into air sacs.
- The mammalian lung has millions of small sacs, called alveoli.
- Human lungs have 1000 kilometers of capillaries and 50-90 square meters of surface area.
- However, in contrast to flow over a gill, the air does not continuously enter a lung.
- About one-sixth the air in human lungs is replenished each inspiration.

Vocalization

- Both male and female frogs have vocal cords; males have a better developed larynx.
- Air is passed back and forth over the vocal cords between the lungs to a large pair of vocal sacs.
- The song is unique and characteristic of the species.
Circulation

- Circulation is closed with a single pressure pump moving blood through the peripheral network.
- The main change in circuitry is the shift from gill to lung breathing.
- The elimination of gills reduced one obstacle to blood flow in the arterial circuit.
- Conversion of the sixth aortic arch into a pulmonary artery provided a blood circuit to the lungs.
- Separating the oxygenated blood from the deoxygenated blood circuit is not completed.

Frog Heart

- The frog heart has a single undivided ventricle and two separate atria.
- Blood from the body enters through the sinus venosus and right atrium.
- Blood from the lung enters the left atrium.
- When the ventricle contracts, blood moves to the lungs or body.

Circulation

- 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.
- Right and left atria contract asynchronously so that although the ventricle is undivided, blood remains mostly separated when it enters this chamber.
- Blood separation is aided by the spiral valve, which divides the systemic and pulmonary flows in the conus arteriosus, and by different blood pressure in the pulmonary and systemic blood vessels elaving the conus arteriosus.

Feeding and Digestion

- Most adult amphibians are carnivorous, feeding on insects, spiders, worms, slugs, etc.
- They catch prey with a tongue that is attached at the front of the mouth.
- The free end of the tongue is glandular; a sticky secretion adheres to prey.
- Any teeth that are present function to hold prey; they do not bite or chew.
- The short digestive tract produces enzymes for digesting fats, carbohydrates and proteins.
- Larval stages of tadpoles are usually herbivorous; their digestive tract is relatively long.

Nervous System

- The brain has three fundamental parts:
  - The forebrain or telencephalon interprets the sense of smell.
  - The midbrain or mesencephalon perceives vision.
  - The hindbrain or rhombencephalon perceives hearing and balance.
- The brain is gradually assuming more information processing ability independent of the spine.
- However, a headless frog still has highly coordinated behavior based on spinal cord alone.

Frog Brain

- The forebrain contains the olfactory center but the rest, the cerebrum, is of little function.
- Complex integrative activities are located in the midbrain optic lobes.
- The hindbrain is divided into an anterior cerebellum and a posterior medulla.
- A cerebellum that will be critical in movement coordination in other vertebrates is minor in frogs.
- The medulla is the enlarged anterior end of the spinal cord through which sensory neurons pass.
- The medulla has centers for auditory reflexes, respiration, swallowing and vasomotor control.
Special Senses

- The pressure-sensitive lateral line is only found in amphibian larvae and aquatic adults.
- The ear becomes specialized for detecting airborne sounds.
  - A large tympanic membrane or eardrum passes vibrations to the inner ear.
  - The inner ear has a utricle with three semicircular canals and a saccule with a lagena.
  - A lagena is covered with a tectorial membrane that is similar to the mammalian cochlea.
- Frogs are sensitive to low-frequency sound energy under 4000 Hz (cycles per second).

Vision

- Except for blind caecilians, vision is the dominant sense in many amphibians.
- Lachrymal glands and eyelids evolved to keep the eye moist, free of dust, and protected.
- At rest, the fish eye focuses on near objects and the frog eye focuses on distant objects.

Reproduction

- Frogs and toads are ectothermic; therefore they breed, feed and grow during the warm seasons.
- In the spring, males call to attract females.
- When the eggs are mature, females enter the water and the males clasp them in amplexus.
- As the female lays eggs, the male discharges sperm over them.
- The jelly layers absorb water and swell; the eggs are usually laid in large masses.

Development

- Begins immediately; a tadpole may hatch in 6-9 days.
- The tadpole head has horny jaws for feeding and a ventral adhesive disc for clinging to objects.
- Three pairs of external gills soon develop into internal gills covered with a flap of skin.
- On the right side of a tadpole, the operculum fuses with the body wall.
- On the left side, a spiracle remains; water enters the mouth to flow past gills and then out this same spiracle.

Metamorphosis

- Hindlegs are first to appear; the forelegs are temporarily hidden in folds of the operculum.
- The tail is resorbed.
- The intestine becomes shorter.
- The mouth transforms to the adult condition.
- Lungs develop and the gills are resorbed.
The End.