Natural History of Vertebrates
Lecture Notes
Chapter 6 - Major Radiation of Fishes

These notes are provided to help direct your study from the textbook. They are not designed to explain all aspects of the material in great detail; they are a supplement to the discussion in class and the textbook. If you were to study **only** these notes, you would not learn enough to do well in the course.

Be sure to study the List of Terms

There are several important advances the bony fishes made that eventually allowed them to become the most speciose group of vertebrates living today.

Gills and Swim Bladders

One of these is the evolution of an efficient mechanism for extracting oxygen from the water. The structure where gas exchange takes place is the **gills**. Water comes in through the mouth, passes through the **buccal cavity**, across the gills in the gill pouch, and out beneath the **operculum**. In general, water is pumped across the gills via a buccal pump (figure 4-1). When swimming some fishes allow the forward motion of the fish's body to push water into the mouth and then across the gills; this is called ram ventilation.

Coming off the **gill arch** are numerous **gill filaments**. The gill filaments are then divided into **secondary lamellae**, which have extensive capillary beds for gas exchange (figure 4-1). Each gill arch has two arteries that branch into each gill filament. The **afferent artery** carriers blood from the gill arch to the tip of the gill filament (it carries unoxygenated blood). The **efferent artery** carries blood from the tip of the gill filament back to the gill arch and then to the body (it carries oxygenated blood) (figure 4-1). The blood flow through the secondary lamellae is in the opposite direction of the water flow. This creates a countercurrent flow, in which the fish is able to extract the maximum amount of oxygen from the water (figure 4-2).

In addition to gills, many fish can also exchange gases across membranes in the mouth or pharynx, stomach or intestinal lining, or lips. However, the most common accessory organ for gas exchange is some variation on a **vascularized swim bladder** that works similar to a lung. In fact, the presence of a swim bladder that serves as an accessory respiratory organ is a primitive condition for all bony fishes.

These early swim bladders probably served as floats to help maintain neutral buoyancy and this feature is still important to modern bony fishes. Fish that have a **pneumatic duct** (a connection between the gut and the swim bladder) can gulp air at the surface to fill the swim bladder and burp air out to empty the bladder (**physostomous swim bladder**, figure 4-3). Fish that lack a pneumatic duct must rely on a **gas gland** to fill the bladder (**physoclistic swim bladder**, figure 4-3), though both physostomous and physoclistous fishes have a gas gland. This is a highly vascularized **rete mirabile** that can push oxygen into the gland even against some very high pressures. To release gas from the swim bladder, the fish opens a set of constrictor muscles that allows the gas to pass into the **ovale**, from here the gas diffuses into the blood stream. (study pages 81 through 83)

Locomotion

When we studied sharks and the origin of fins, we discussed yaw, pitch, and roll (figure 6-14). Bony fishes have basically the same sets of fins to solve these problems of control. However, because bony fishes are a much more diverse group, they have developed a number of different locomotor adaptations for providing thrust or forward movement. In general, fish fall on a continuum from anguillaform (eel-like), through carangiform (trout-like), to ostraciform (boxfish-like), with a few other types also named.

Anguillaform is eel-like in which the entire body undulates in a sine-wave. Thrust results as the successive loops of the body move back along the axis of the body and push against the water (figures 6-13 and 6-15). Eels are generally slow swimmers because the length of the body increases drag, which acts counter to thrust. To increase swimming speed the fish increases the frequency or the undulations but not the amplitude of the undulations.

Carangiform is tuna-like propulsion in that the anterior two-thirds to three-fourths of the body does not bend and all of the force is applied by flexing the posterior third or fourth of the body (figures 6-13 and 6-15). This generates maximum thrust with a minimum of drag and thus tunas and related fishes are some of the fastest. Trout and similarly shaped fishes (bass) have a modified carangiform swimming motion (subcarangiform)that is intermediate between that of an eel and a tuna, with more of the anterior portion of the body involved.

Ostraciiform is boxfish-like in which the body is completely rigid and the caudal fin can only move at the **caudal peduncle**. Because of the shape of these fish, they generate a lot of drag and as such are slow swimmers (figure 6-15).

Ballistiform is a type of movement in which thrust comes from undulatingboth the dorsal and anal (median) fins (figure 6-15). This type of locomotion is named for the family of triggerfishes. **Amiiform** is undulation of only the dorsal fin. This type of locomotion is named for the family of bowfin. **Gymnotiform** is undulation of only the anal fin. This type of locomotion is named for the family of knife fishes.

Labriform is a type of movement in which thrust comes from rowing the pectoral and pelvic (paired) fins. This type of locomotion is named for the family of parrot fishes.

Fishes have to fight against **drag** and the faster one swims the greater the drag that is generated. There are two kinds of drag.

Viscous drag is caused by friction between the body surface and the water. Long thin bodies will generate a lot of viscous drag (for example an eel). Viscous drag is also influenced by the surface of the body. Having small scales or being scaleless reduces viscous drag.

Inertial drag is caused by the displacement of water as the fish's body moves through the water.

A box, for example, would have high inertial drag. Streamlining, which reduces the cross-sectional area presented to the water, reduces inertial drag.

The compromise between these two types of drag is a body shape that is roughly like that of a football or blimp (fusiform, an elliptical spheroid with a width to length ratio of 0.25, figure 6-16). In addition, the shape of the tail plays a large role in the generation of thrust and drag. This is reflected in the **aspect ratio** of the caudal fin (dorsal-ventral length divided by anterior-posterior width). Fast but continuous swimming fish have a high aspect ratio which generates much less drag. These fish (for example tunas) are slow to get going. A low aspect ratio is associated with fish that have very quick starts but do not swim at high speed for long periods of time (for example, bass).

Sensory Systems

Bony fish have basically the same sensory modalities that we discussed for sharks. Chemoreception is via receptors in the mouth, nasal cavity, on the head, and on the fins. The **lateral-line system** bears another look. It consists of a series of canals over the head and body that communicate with the external environment via a series of pores (figure 4-4). The primary sense organ is the **neuromast organ**. This consists of a number of pairs of hair cells. Each hair cell has a **kinocilium** embedded among several **microvilli**. Movement of the kinocilium causes the microvilli to move and changes the rate of discharge from the two **afferent nerves** (one from each hair cell). The pair of hair cells is embedded in a **cupula**. Any deformation of the cupula causes a change in the rate of discharge from the pair of afferent nerves. By comparing the change in rate between the two afferent nerves, the brain can interpret the direction of the force that deformed the cupula. Fish can detect currents on the order of 0.025 mm/sec. (which works out to be about 0.00006 miles/hour). The neuromast organs arranged over the head and body of the fish provide it with information about the type of currents or turbulence coming from each area around the fish. The fish gets a very accurate picture of events in the water near it just from the lateral-line system (study pages 80-81).

Electric discharge

Electric discharge is produced from modified muscle cells (**electrocytes**) that no longer contract but instead produce an electrical potential. At rest, each cell is about 100 millivolts more negative on the inside relative to the outside. This is due to the active pumping of sodium and potassium ions across the cell membrane. When stimulated each cell reverses the net charge on one side of the cell, which results in an electrical flow from one side of the cell to the other. Each cell is linked in series with the cells adjacent to it so that the voltage adds across the cells (figure 4-6). 100 millivolts summed over thousands of cells produces hundreds of volts. For example, the South American electric eel can produce a total of 600 volts. Some fish are strongly electric and can use the electricity for defense or predation. Others are weakly electric and can only use the electricity for communication (courtship) or navigation. The skin of these fishes contain sense organs (**ampullary organs** or **tuberous organs**) that can detect changes in the electric field by objects in the field (figure 4-7). It appears that primitive vertebrates had the ability to detect electric fields. This ability was lost in the lineage that gave rise to the Teleostei, but several lineages reevolved the ability to detect electric fields, making the ability to detect electric fields a **homoplasic** condition with the Teleostei (study pages 86 through 90).

Evolution of bony fishes

Acanthodians

- The sister taxon to the Osteichthyes (figure 3-14)
- Earliest jawed fishes in the fossil record dating from the Early Silurian, but disappeared by the Early Permian.
- Had stout spines anterior to the dorsal, anal, and many paired fins (figure 3-16)
- 20 cm in length
- teeth lacked enamel
- few enlarged scales, though some lacked scales
- three semicircular canals
- cranium composed of cartilage
- neural and haemal arches but no vertebral centra are known
- shared several characteristics that aligns this taxon with the Osteichthyes and places them in the group the Teleostomi (presence of an ossified dermal **operculum**, mechanism of opening the mouth via the **hyoid apparatus** transmitting motion to the lower jaw, **branchiostegal rays**).

The two basic groups of osteichtyians (the **Actinopterygii** and the **Sarcopterygii**) are abundant by the Middle Devonian (table 6-1, figure 6-2). Shared derived characters for the Osteichthyes are:

- lateral-line canals
- similar opercular and pectoral-girdle elements
- fin webs supported by bony dermal rays
- endochondral bone

Among the Actinopterygii, there are a number of lineages that share a variety of primitive characters, and some members of these lineages are extant today (sturgeon, paddlefishes, bichir). However, by the end of the Paleozoic, we see several new morphological forms that give rise to the bulk of the modern bony fishes (**Neopterygii**).
In the Neopterygii, we see:

- an increase in locomotor ability, which is accompanied by a reduction in bony armor (size and thickness of scales).
- an increase in the sucking ability of the jaw. This is accomplished by an increase in the suction generated when the mouth opens.
- an increase in the size of the gape and making the opening of the mouth more circular
- an increase the force of contraction when closing the mouth

These improvements were accomplished by loosening the attachment of the **maxilla**, such that it can rotate downward from its point of attachment at the **premaxilla** (figures 6-6 and 6-7). This also has the effect of making the gape more round and in closing off the sides of the mouth so that prey cannot escape out the sides of the mouth. The gap between the dermal bones covering the sides of the head was increased. This allows the adductor muscle to increase in size and this increases the force of closing the mouth. In addition, several lineages of Neopterygii developed protrusible jaws by allowing the premaxilla to slide forward via a variety of attachments. This also allows the mouth to be shut while the **orobranchial cavity** is still greatly expanded, which helps to retain prey as the mouth is shut. Thus the feeding efficiency of the fish was much greater.

We also see the appearance of **pharyngeal jaws**. These begin as dermal tooth plates in the pharynx. Then we see a trend toward fusion of these plates to the gill arches, and eventually the development of the ability to grind food between these plates and bony plates on the skull. These fish can chew plant material, which is an important trophic level (for example minnows).

We also see several changes in the fins. The caudal fin becomes more symmetrical (**homocercal** tail) which, in theory, generates thrust without tending to raise or lower the fish in the water column. This is thought to have freed the paired fins from the need to keep the fish at the same depth and thus the paired fins could take on different roles.

The Ostariophysi developed an interesting adaptation called a **Weberian apparatus**. This is a series of small bones that allows sound that vibrates the swim bladder to be transmitted to the inner ear and thus increases the ability of the fish to hear. These fish can hear a much broader range of frequencies than can fish that lack a Weberian apparatus (figure 6-11). The sequence of sound transmission is
swim bladder ---->tripus ---->intercalarium ---->scaphum ---->claustrum ---->labrinyth of the inner ear

Sex in fish

Most fish are either male or female throughout their life, however this is not always so in that some fish change sex during their lifetime. Few teleosts have sex chromosomes and thus the potential exists for sex to be determined by the environment of the individual. In some cases (for example, silversides), the temperature at which the eggs incubate determines sex. Eggs laid early in the breeding season when temperatures are cooler will be females. These fish have a long growing season are thus larger and will produce numerous eggs. Eggs laid late in the summer, when temperatures are warmer become males. These fish have a short growing season and are smaller. They produce sperm because sperm are cheap and they can produce a lot of them, while they would only be able to produce a few eggs.

A very few fish are simultaneously functional **hermaphrodites** in that they are functionally male (producing sperm) and functionally female (producing eggs) at the same time. However, a fish cannot fertilize its own eggs and must mate with another fish for fertilization to occur. An example is *Rivulus*, the little fish that is sometimes found in muddy pools in the Bahamas.

The more common form of hermaphrodism is **sequential hermaphroditism**, in which a sex change occurs at some point in the life of the fish.

Protandrous hermaphroditism is male first, then female. This occurs in several different species, for example sea bream. In this situation, the selective force is gamete production. As sperm are relatively cheap a small individual can produce a lot of sperm, enough sperm that the individual could fertilize all the eggs that any female could produce. Thus as small adults the fish are males. As they get larger and can thus put more effort into reproduction, they switch to producing the more costly gamete (eggs). Thus at a certain body size a sex change occurs and the fish becomes female.

Protogynous hermaphroditism is female first, then male. This occurs in several species of wrasses. The mating system is harem-based polygyny, in which one large male controls a group of females for mating. In this case, only a few large males are capable of having a harem, thus if one is small, it is better off being female and a member of a harem. However, if the male dies, then the largest female (the one most able to control the harem) begins to change sex and within a week will switch from egg production to sperm production. This new male then takes over the harem.

Deep-See Fishes

The oceans can be divided into three zones:

- Epipelagic is that part of the ocean in which photosynthesis can occur and generally no deeper than the continental shelf.
- Mesopelagic is that part of the ocean through which light penetrates.
- Bathypelagic is the aphotic zone of the ocean (below 1000 meters).

As one goes deeper into the ocean the availability of food energy decreases rapidly (figure 6-18). Generally, food comes into the lower regions as dead or decomposing material from above (except around black smokers (hydrothermal vents)). Mesopelagic fishes often migrate vertically on a circadian cycle, rising to shallow water during the night and descending to depth during the day. Thus they can take advantage of the more abundant food supply near the surface, but avoid predators at lower depth and reduce metabolic needs.

Bathypelagic fishes are too deep to migrate vertically. They must be adapted to very low food supplies, constant cold near freezing (4 C), and perpetual darkness. Adaptation include:

- Reduced muscle mass and limited locomotion
- Reduced skeletal material and reduced ossification (figure 6-20)
- Increased sensitivity of the eyes to blue pigment
- Development of photophores to produce bioluminescent light
- Enormous jaws and teeth relative to body size
- Highly distensible stomach for holding a meal larger than they are
- Bioluminescent lures to attract prey or mates
- may also rely on scent trails of pheromones to find mates

Anglerfish have a unique mating system in which the males, as adults, are parasites on the much larger female. Mating is monogamous as a female only has one mate and for life (figure 6-21).

Sarcopterygii (lobe-finned fishes)

This is the group that will give rise to the tetrapods and though there are very few living today, it is best that we do this group just before starting the tetrapods. The Sarcopterygii, as defined as a monophyletic clade (table 6.1), include all of the tetrapods as these are also descendants of the common ancestor for this clade, however, in practice only 4 living non-tetrapod genera are include in the Sarcopterygii, and these are divided into two groups, the **Actinistia** (1 extant genus) and the **Dipnoi** (3 extant genera).

Actinistia (coelocanths, figure 6-4)

- first appear in the Middle Devonian
- well-developed, fleshy lobed fins, even the median fins have lobes.
- Fossil actinistians are known from the Devonian through the Late Cretaceous, however no fossils are known since the Cretaceous and thus they were thought extinct until 1938.
- lack a maxilla
- predaceous on fish and cephalopods
- internal fertilization as the females give birth to live young (by holding eggs in the oviduct until birth), however males have no copulatory organs.
- The fish does not use its paired, lobed fins to walk on the substrate, but when it swims it moves the fins in the same sequence that tetrapods move theirs when walking on land.

Dipnoi (lungfishes, figure 6-3)

- The earliest forms from the Devonian were marine and modern forms are not too different from the forms that were common in the Late Devonian.
- long, eel-like body
- crushing teeth on the palate (eats **durophagus** foods)
- no tooth bearing maxilla and premaxilla
- fusion of the palatoquadrate to the cranium
- a fusion of the median fins (dorsal and anal) with the caudal fin and the development of a symmetrical (homocercal) tail.
- There has been a reduction in number of small bones that make up the skull and the loss of the sheet of cosmine that covered the skull.
- some have external gills as larvae
- Modern forms are all freshwater and the three genera are found on three separate continents.
- The Australian lungfish is more aquatic in that its gills are sufficient to meet the oxygen demand of its body and uses its lung only rarely. The paired, lobed-fins are better developed and are used for locomotion. It can also use the paired fins as walking appendages.
- The South American and Africa genera are much more eel-like and the paired fins are very thin but highly mobile. The gills are not sufficient to meet the oxygen demand of the body and they are obligate air-breathers.
- The African genera have the habitat of estivating in the mud at the bottom of a pool during the dry season, when the pools dry up. They can stay encased in mud at the bottom of the pool for several months, however if the rains do not come in time, they will die. This behavior as led to the production of many fossils of these fishes from the Carboniferous and Permian.
- sister taxon to the tetrapods

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