The coelacanth, *Latimeria chalumnae*, the only living crossopterygian, was thought to be extinct until 1938. Coelacanths are descended from freshwater crossopterygians that returned to the sea. Prior to 1938, the last known coelacanth was from the late Cretaceous.
Vertebrates.

- Four extant groups of vertebrates.

1. **Agnatha** – jawless fish.

2. **Chondrichthyes** – sharks and rays (cartilaginous).

3. **Osteichthyes** – bony fish.

4. **Tetrapods** – amphibians, reptiles, birds, mammals.
   
a. Tetrapods evolved from a now extinct group of freshwater **lobefin fishes**.

b. Coelacanth, the only living lobefin, is secondarily marine.

c. Previously thought to have died out at end of Cretaceous.

Simplified vertebrate phylogeny. Red dots refer to presumptive change in habitat.

Top. A typical Devonian crossopterygian close to the ancestor of tetrapods. **Bottom.** The coelacanth, *Latimeria*, a deep water marine form and the only living representative of the group.
**Myllokunmingia**, a Cambrian jawless fish.
From Fish to Tetrapods.

• First vertebrates jawless.

1. Class **Agnatha**.

2. Principal fossil representatives belonged to the group called **ostracoderms** – external boney armor.

3. Living forms called cyclostomes (hagfish, lamprey)
   a. Lack bony skeletons.
   b. Special feeding structures for bottom scavenging (hagfish), and blood sucking (lamprey - right).
   c. Lampreys have a sessile “ammocete” larva that resembles *Amphioxus*.

**Above.** Ostracoderms. Note the armored heads. The paddles in *Hemicyclaspis* in back of the head shield evolved independently of the pectoral fins of modern fish. **Below.** Business end of a living lamprey.
Above. Cyclostome manifest a combination of primitive and derived features. Among the former is the absence of jaws and paired fins; among the latter, the complete lack of bone in the skeleton, predaceous (lampreys) or scavenging (hagfish) foraging and the tongue rasp, a structure that allows lampreys to burrow into the flesh of the creatures upon which they subsist, A. and B. hagfish; C. lamprey. Below. *Amphioxus*-like lamprey larva.
• Jaws.

1. Evolved from 3\textsuperscript{rd} pair of 
   \textit{gill arches} (bony gill supports).

2. 4\textsuperscript{th} gill arch became the 
   \textit{hyomandibular} – binds 
   jaws to cranium.

3. Third gill slit reduced to 
   small opening, called the 
   "spiracle".

4. Later,

   a. Mandible \textit{fused} to the 
      cranium.

   b. \textit{Stapes} (middle ear) and 
      \textit{hyoid} (supports tongue) 
      differentiated from hyo-
      mandibular bone.

\textbf{Above Right.} Conjectured evolution of the vertebrate jaw. The 
first two pairs of gill arches are lost. The 3\textsuperscript{rd} pair becomes the 
 jaws; the 4\textsuperscript{th} pair, the hyomandibular (H). Gill openings shaded. S 
– spiracle.
c. Jaws **first appeared in** placoderms – **now extinct.**

d. Some had **paired fins.** Include

  i. Giant **arthrodire** with parrot-like beaks;

  ii. “**Spiny sharks**” close to, but **off** – see previous lecture, the ancestry of modern fish.

e. **Antarchs** had **jointed flippers** – possibly used for **walking on** and/or **digging into** the substrate (burrows).

Reconstructed “spiny shark” with paired fins, well developed jaws and dermal armor unrelated to the skeletons of bony fish. The name derives from the asymmetrical tail fin reminiscent of living sharks. Tooth-like structures in the mouth were actually bony plates unrelated to teeth, which **disqualify** these animals as direct ancestors of modern fish.
Devonian placoderms. A. "Spiny shark" with paired pectoral and pelvic fins plus intervening fin-like spines that may have served a protective function. B. Predacious (~ 3m long) arthrodire. Related forms were up to 10 m in length. C. Antiarch with arthropod-like, jointed appendages that may have been used for burrowing and crawling. From Romer, A. S. 1964. *The Vertebrate Body.* W. B. Saunders. Philadelphia.
• Modern “fish” divided into

1. **Chondrichthyes** (cartilaginous fishes) - sharks and rays.

2. **Osteichthyes** (bony fishes) – everything else.

• Among bony fish, the basic split is between **actinopterygians** (ray-fin fishes) and **sarcopterygians** (lobe-fin fishes).

1. **Sarcopterygians** include

   a. **Crossopterygians**, which in turn include

      i. **Tetrapod ancestors**.

      ii. **Coelacanths** – marine offshoot of basal stock.

   b. **Lungfish**.

2. **Actinopterygians**.

   a. Descendants of marine placoderms that invaded fresh water.

   b. Re-invaded marine environments during the Mesozoic.

   c. May have contributed to ichthyosaur extinction.
Sarcopterygian fishes. **A.** Devonian species close to the ancestry of tetrapods. **B.** Living *Latimeria*, discovered in 1938 in deep water off the east coast of Africa. **C.** Devonian lungfish. **D.** Living Australian lungfish.
Bony fish (actinopterygians and sarcopterygians) evolution depicted as a "branching tree." The relationships among the various lobe finned fishes (crossopterygians, lungfish, coelacanths) and tetrapods differ from those deduced from molecular evidence.
• Lungs.

1. Ancestral actinopterygians may have resembled the living *Polypterus* where a bilobed, ventral lung connects to the pharynx thereby allowing for respiratory function.

2. In most living bony fish, this connection (if it existed) has been lost and what is now a swim bladder contains specialized tissue that secretes / re-absorbs gas.

Air bladders and lungs of fishes and tetrapods (schematic). **Top.** *Polypterus*, the "bichir" of central Africa, and possibly representative of the primitive state antecedent to all other lung and bladder types. **Bottom.** Tetrapod lung with complex internal structure. The swim bladders of most modern fishes are dorsal to the viscera and are generally unconnected to the throat.
3. Recent studies of living animals indicate air breathing via **dorsally situated spiracles** as well as the mouth (air gulping).

Sagittal and transverse magnetic resonance images of *P. palmas* showing the path (arrows) of air through the spiracles to the buccopharyngeal chamber and lungs. From Graham *et al.* (2014).

4. Dorsally situated spiracles also observed in fossil fish-amphibian intermediates such as *Tiktaalik* (next page).
• Limbs.

From fins to legs. Pectoral fin structure of recently discovered *Tiktaalik* is almost perfectly intermediate between that of lobe fin fishes and the legs of labyrinthodont amphibians. To the lobe fin humerus, radius and ulna, *Tiktaalik* added wrist elements. From R. Dalton (2006).
• **Crossopterygians.**

1. Retained the primitive ventral lung, which became the principal respiratory organ in the adult.

2. Paired fins evolved into legs in line leading to Amphibia.
   a. Involved
      i. Loss of dominance of central axis.
      ii. Differentiation of wrist and finger bones.
   b. Not observed in coelacanths and lungfish.

Crossopterygian fin anatomy. Only in the line leading to tetrapods (red) does the central bony axis differentiate into arm, wrist and finger bones. From left to right: living coelacanth (*Latimeria*) and lungfish (*Neoceratus*); extinct lungfish relative (*Glyptolepus*) and two taxa (*Sauripterus* and *Eustenopteron*) close to the ancestry of tetrapods. From D. C. Murphy. 2005. *Devonian Times.*
Completing the Water to Land Transition.

- **Amniotic egg** allows embryo to develop on land.

  1. **Porous shell** allows for gas exchange with environment.

  2. **Extra-embryonic membranes**.

     a. **Chorion** permits gas exchange; retains water.

     b. **Amnion** surrounds embryo $\Rightarrow$ an internal “pond”.

     c. **Yolk sac** encases food supply.

     d. **Allantois** stores metabolic waste.
• **Internal Fertilization** the complement.

• **Water Conservation.**

  1. **Fluid retention** by a water-impermeable **integument**.

  2. **Urine** concentration by the kidneys.\(^1\)

  3. **Water reabsorption** by the colon (and cloaca in birds and reptiles.)

  4. **Conversion of ammonia** (primary waste product of nitrogen metabolism) to less toxic compounds: **uric acid** (birds, reptiles) or **urea** (mammals).

    a. Permits concentrated urine / avoids **dehydration**.

    b. Likewise avoids **ammonia toxicity**.

    c. Requires **energy expenditure**.

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\(^1\) Only mammals and birds produce urine more concentrated than blood.
Toward More Active Life Styles.

- During Permian and Triassic, both archosaurs and synapsids evolved more active life styles.

1. **Posture.**
   a. Tucked the legs under the body.
   b. Synapsids quadrupedal; archosaurs, bipedal.
   c. Side to side wriggling replaced by **back and forth motion** of legs.
   d. Increased speed.

2. **Energy production.** Erect posture plus **broadening of anterior rib cage** => enhanced oxidative metabolism.
   a. Deeper chest => **larger lungs**.
   b. More air ⇒ **better oxygenation** of blood.
   c. More $O_2$ => greater **endurance**, *i.e.*, before muscles switch from **aerobic respiration to glycolysis**.
3. Respiration.

a. Breathing in mammals is **tidal**. Inspiratory volume enhanced by diaphragm, *i.e.*, lungs **expand**.

b. Avian dinosaurs (birds) use a **flow-through** system of **air sacs** and **non-expansive** lungs.

c. Some dinosaurs had air sacs. **When** did they evolve?

d. If air sacs a dinosaur synapomorphy, how does this bear on dinosaur endothermy / ectothermy?

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**Left.** In mammals, tidal breathing facilitated by the diaphragm. **Right** Belly breathing in crocodiles entails muscular contraction that pulls the liver backwards, thereby expanding the lungs. Recent studies suggest that crocodiles also have flow-through respiration (next page).
Avian respiration. Two inhalation-exhalation cycles are required to move air into, through and out of the animal. **Top left.** 1st cycle. Air moves into the posterior air sacs and then into the lungs. **Top right.** 2nd cycle, air moves from the lungs to the anterior air sacs and is then exhaled. **Right.** Air sacs in the living animal penetrate the hollow long bones. Flow-through respiration allows birds to sustain higher activity levels for longer periods than mammals and to survive at higher altitudes.
Air sacs in a non-avian theropod dinosaur (*Majungasaurus*) and a living bird compared. Some scientists speculate that air sacs evolved in dinosaur ancestors during the Permian when atmospheric concentrations of oxygen may have dropped to 10% (about half as much as current level of 21%).
4. Food processing / chewing.

a. Fenestration (holes) of skull independently acquired in both groups allows for larger / bulging jaw muscles.


c. Archosaurs: Gizzards.
5. In mammals, hypertrophy of the lower jaw resulted in a new skull-jaw *articulation* and the conversion of the reptilian elements into *inner ear ossicles*.

Evolution of mammalian jaw / middle ear. **Left.** Primitive mammal-like reptile. The *articular* (lower jaw) articulates with the *quadrat* (upper), and there is a single middle ear ossicle, the stapes. **Right.** Mammal. Hypertrophy of the dentary (coronoid process in particular) has resulted in the formation of a new jaw joint (*dentary-squamosal*). *Articular* and *quadrat* now the *malleus* and *incus*, while the angular bone has become the *tympanicum*, a boney ring that supports the tympanic membrane (eardrum). Also shown is increased tooth differentiation,
5. **Secondary bony palate in Synapsids.**

a. Crocodiles, but not most dinosaurs, also have them.

b. One explanation: Breathe while you chew.

c. Alternatively, secondary palates help resist the forces generated when the animal chews.

6. **Four chambered hearts.**

   a. Independently evolved in archosaurs and synapsids.

   b. Complete separation of oxygenated / deoxygenated blood.

7. **Birds / mammals endothermic.**

8. Regarding dinosaur endothermy, activity levels and intelligence, there is a **diversity of opinion** (see below).

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**Top Left.** In most fishes, the heart is a two-chambered pump. Deoxygenated blood is pumped forward from the ventricle to the gills where oxygen and CO₂ are exchanged. Oxygenated blood then passes to the tissues and eventually (now deoxygenated) returns to the heart via the single atrium. Birds and mammals. The heart has four chambers. Pulmonary and systemic circuits are entirely separate. Blood flows from the right ventricle to the lungs and returns to the left side of the heart from which it is pumped to the tissues, and finally returns to the right atrium.
9. High body temps. require heat generation + retention.
   a. Hair (mammals)
   b. Feathers (dinosaurs and birds) – later adapted for flight.
Warm Blood vs. Cold.

- The terms, warm- and cold-blooded, confound three different concepts.

1. **Source of heat**: ectothermy (external) vs. endothermy (internal).

2. **Metabolic rate** (MR): bradymetabolic (low rate) vs. tachymetabolic (high rate).

3. **Temperature regulation**: poikilothermy (unregulated) vs. homeothermy (regulated)

- Typical cold-blooded animal is an **ectothermic brady-metabolic poikilotherm**.

  1. Heat from the environment;

  2. Low MR / food intake.

  3. Internal temperature fluctuates with external.
     a. Become torpid when it’s cold.
     b. Behavioral temperature regulation in some – e.g., basking.
Before endothermy.
Typical “warm-blooded” animal is an endothermic tachy-metabolic homeotherm.

1. Generates heat internally.


3. Regulates internal temperature.

- Usually, but not always, correlated – e.g., hummingbirds go torpid on cold nights & can freeze to death.

Mammals and birds maintain roughly constant body temperatures over a wide range of ambient or environmental temperatures, $T_A$. **Top.** Within the so-called "thermo-neutral region" ($T_A$ bounded by lower and upper critical temperatures as shown in the figure), metabolic rate (MR) is constant ("basal MR"), and body temperature is regulated by increasing or decreasing heat loss through the skin via changing rates of peripheral blood flow. **Bottom.** Below the lower critical temperature, the animal produces metabolic heat (shivering) to compensate for increased heat loss to the environment. Above the critical temperature, the animal loses heat evaporatively (sweating or panting), which also increases metabolic rate. Maintenance of constant body temperature in the face of changing ambient conditions is an example of [homeostasis](#).
Mammals.

- Originate in the Triassic; coeval with 1st dinosaurs.
- 1st 2/3 of mammalian evolution before Chicxulub.
- Three living groups:
  1. Monotreme (prototheria) – lay eggs
  2. Marupsials (metatherians) – live birth, pouch
  3. Placental (eutherians) – extended gestation; no pouch.

Simplified summary of mammalian evolution.
Primates.

- Descended from tree-living Cretaceous insectivores.
  1. **Grasping** hands & feet\(^2\) **opposable** big toe; **nails**.
  2. Eyes directed forward; bino-ocular vision.
  3. Two main groups.

- **Prosimians:**
  1. Tree shrews, lemurs, *etc*.
  2. Nocturnal
  3. Most in Madagascar.

- **Anthropoids:**
  1. Tarsiers
  2. New world monkeys
    a. Arboreal;
    b. Many have prehensile tails;
    c. Rafted over from Africa.
  3. Old world monkeys – arboreal and terrestrial.
  4. Apes.
    a. Arms elongate;
    b. Brachiators and knuckle walkers.
  5. Hominins.

\(^2\) Hence the obsolete taxon, *Quadrumana*. 
**Hominins.**

- Diverged from Great Apes about 6 Mya.

- Early representatives include Australopithecines (Africa).
  1. Bipedal
  2. Robust, gracile species.

- Trends in hominid evolution:
  1. Arms shorten.
  2. Legs elongate.
  3. Face and jaws foreshortening; tooth size reduce.
  4. Body size, cranial capacity increase.
  5. Incr. protein consumption => larger brains. Facilitated by
     a. Manufacture of weapons.
     b. Adaptations for running including **hair loss / sweat gland proliferation**.
• Orthogenesis vs. Bushiness.

1. 19th century hominid fossils variously interpreted as

   a. Within the range of modern human variability (Huxley).

   b. Diseased humans – e.g., microcephalic idiots; representatives of “lower” modern races.

2. Large Neanderthal cranial capacity confusing – suggested that human brain had been larger in the past.

3. Only with discovery of Australopithecus, was it accepted that human ancestors bipedal, but small-brained.

4. Early reconstructions of hominid evolution suggested linear progress (orthogenesis) from ape to man. Reflected

   a. Paucity of fossils.

   b. Persistent ideas of directed (or self-directed) evolution.

5. Contemporary paleoanthropology emphasizes “bushiness” of human evolutionary tree.
Contemporary view of humanity’s evolutionary bush.
• Out of Africa.

1. As Darwin had predicted, Africa turned out to be man’s birth place.

2. Multiple migrations to other continents.


4. *H. erectus*.
   a. 1st known use of fire.
   b. Coexisted with and may have exterminated African Australopithecines.
   c. Replaced by *H. sapiens* about 200,000 y BP.

5. *H. s. neanderthalis* (European Ice Age Race) replaced by *H. s. sapiens* (Cro-Magnon man) 30-50,000 y BP.
6. Beginnings of culture. Agricultural revolution in the fertile crescent about 10,000 y BP – **self-domestication**.

7. Recent DNA analysis => **interbreeding** among multiple hominin species – see Lecture II.4.


“The secure age for Dmanisi’s first occupations reveals that Eurasia was probably occupied before *Homo erectus* appears in the East African fossil record.”

Cro-Magnon (*H. s. sapiens*) painting from Lascaux caves, France.
Questions.

1. *Tiktaalik* bridges the gap between fish and tetrapods by virtue of possessing which of the following?
   a. Humerus.
   b. Radius.
   c. Ulna.
   d. Wrist bones.

2. Morphologically, lungfish appear to be further from the ancestry of tetrapods than crossopterygians because they lack ________________.

3. Salmon spend one or more years (“parr” stage) in the river before going to sea. After additional time in the ocean, mature fish return to the river to spawn. **a.** From the viewpoint of natural selection, what are the advantages and disadvantages of such a life cycle? **b.** In some species, parr mature Pacific salmon life cycle. Atlantic salmon (different genus) can spawn more than once.
sexually and reproduce before going to sea. Generally, it is the males that do so and not the females. Why might selection have favored precocious reproduction in males and not females? (Requires outside reading)

4. Regarding the evolution of the mammalian jaw and middle ear: **a.** The articular bone in reptiles is to the quadrate as the _________ in mammals is to the _________. **b.** The reptile articular bone became the _________ in mammals; the quadrate, the _________.

5. On several occasions this semester, it has been observed that “reptiles” as traditionally defined (snakes, lizards, turtles, crocodiles) is a **paraphyletic** group. Yet in Figures 34-12 (4th edition) and 35.12 (5th edition), Reptilia is represented as a clade with “scales with hard keratin” given as the synapomorphies. What gives?

6. Synapsid lungs are expansive; avian lungs, not. Explain.

7. What was the Piltdown forgery? Who was responsible? (Requires outside reading. Be sure to cite sources.)
8. The Triassic witnessed the evolution of dinosaurs and mammals, the latter having descended from much larger, “mammal-like” reptiles that were the dominant tetrapods during the Permian. In short, species belonging to the lineage leading to mammals got smaller while archosaurs got larger. Discuss in terms of changing levels of atmospheric oxygen during the late Permian and early to mid-Triassic. (Requires outside reading. Be sure to cite sources.)

9. Modern human hunter gatherers hunt large mammals by pursuing (running / jogging / walking) their much faster prey until the latter collapse. Discuss in terms of temperature regulation by ungulates and man. (Requires outside reading. Be sure to cite sources.)