~ Chapter 3 ~

Early Vertebrates: Jawless Vertebrates & the Origin of Jawed Vertebrates

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New Vertebrate Features

1) Distinct head end

2) Tripartite brain

3) Cartilaginous cranium (skull)

4) Complex sense organs

5) Gills used for respiration instead of filter feeding, as in earlier chordates.

6) Active predators

7) External armor made of bone.

3.1 Reconstructing the Biology of the Earliest Vertebrates

Earliest Evidence of Vertebrates

1) Jawless vertebrates known as **ostracoderms**; they were fishes encased in bony armour (shell), 80 – 120 million years before whole-body vertebrate fossils appeared.

2) Other vertebrates appeared; small, fish-shaped, and about 3 cm long; with a cranium and W–shaped **myomeres**. No external bones but had a dorsal fin & ribbonlike ventral fins.

Figure 3-1: Some of the earliest vertebrates.

3) Next evidence of early vertebrates is from fossils belonging to armored, **torpedo-shaped** jawless fishes.

4) Evidence for **jawed fish** appeared in the fossils later than the ostracoderms.

Origin of Bone and Other Mineralized Tissues

1) Mineralized tissues composed of **hydroxyapatite** are a major new feature of vertebrates.
2) **Enamel** and **dentine** were first found associated with the dermal armor of ostracoderms.
3) Mineralized tissues **did not appear** at the start of vertebrate evolution & are lacking in extant jawless vertebrates. So the origin of bony tissues is not clear.
4) Basic units of mineralized tissue appear to be **odontodes** = little toothlike elements formed in the skin.
5) Odontodes occur in the skin of sharks, covered by a thin epidermis. These bony elements are formed **within the dermis** of the skin, not external to the skin.
6) **Bones** of primitive vertebrates lack cells. Cellular bone is found only in **gnathostomes**.
7) Bones evolved for protection and for storing calcium and phosphorous.
8) *New edition*:
    1. **Conodont elements** are microfossils spinelike or comblike structures similar to dentine which is uniquely vertebrate tissue & found widespread in **marine** deposits.
    2. Conodont elements are less than 1 mm long spinelike or comblike structures composed of **apatite** (a mineralized compound characteristic of vertebrate hard tissues).
    3. They are similar to dentine which is unique to vertebrate tissue.
    4. Conodont were considered to be the **toothlike** element of true vertebrates.
    5. Conodont animals (extinct) had conodont elements arranged within their pharynx (**Fig. 3-2**).
    6. Had **vertebrate** features such as the notochord, cranium, myomeres, and large eyes.

3.2 Extant Jawless Fishes

Hagfishes & Lampreys

Figure 3-4: Cladogram of vertebrates within the Chordata.

Hagfishes – Myxinoidea

1) **Adult** hagfishes are around 50 cm in length (**Fig. 3-5**).

2) Elongated, **scaleless**, and pinkish to purple in colour.

3) Deep-sea, cold-water marine animals; they are **scavengers**.

4) **Unique feature** of hagfishes is the large **mucus glands** that open through the body wall to the outside.

   - These **slime glands** secrete mucus & tightly coiled **proteinaceous threads** which straighten on contact with seawater to entrap the slimy mucus.
   - This slime deters **predators**. When danger has passed, the hagfish makes a knot in its body & scrapes off the mass of mucus, then **sneezes** to clear its nasal passage.

5) Hagfishes *lack vertebrae*, so they are considered a **sister group** of all other vertebrates.

6) **Internal anatomy** shows other primitive features **e.g.** simple kidneys, and there is only one semicircular canal on each side of the head.

7) Hagfishes have a single terminal **nasal opening** that connects with pharynx via a tube.

8) Eyes are **rudimentary** & covered with a thick skin.

Feeding

1) **Mouth** is surrounded by six tentacles that can be extended.

2) Two **horny plates** in the mouth (on each side of the tongue) bear toothlike structures. Tooth plates spread apart when **tongue** is protruded & fold together when it is retracted.

3) Hagfishes attack **dead** or **dying** vertebrate prey. Once attached to the flesh, they can tie a knot in their tail & make good grasp of their prey.

4) They attach and suck the **liquid** from the prey, or enter inside the prey's body (*new ed.*).

5) The food is then enfolded in a mucoid bag (membrane) which is permeable to digestive enzymes. Indigested matter is excreted while still enclosed in the mucoid bag.

Respiration

1) Hagfishes have **1–15** gill openings on each side.

2) Large blood sinuses & low **blood pressure**.

3) In contrast to all other vertebrates, hagfishes have **accessory hearts** in the liver & tail in addition to the **true heart** near the gills. The hearts are **aneural**.

4) Hagfishes resemble the primitive condition of amphioxus – although their blood does have **red blood cells** containing hemoglobin, & the true heart has **three chambers**.

Reproduction

1) Female hagfishes outnumber males.
2) Sexes are separate but some species are **hermaphroditic**.
3) Large amount of **yolk** is present in the eggs, which are encased in a tough covering that is secured to the sea bottom by hooks.
4) Development is **direct**, meaning that there is *no larval stage*.
5) Hagfish embryos possess neural crest like other vertebrates (*new edition*).
6) Fishermen suffer from hagfishes.

Lampreys – Petromyzontoidea

Figure 3-6: Lampreys

Lampreys are similar to hagfishes in size and shape, but they are **different** in certain respects:

1) Have many features lacking in hagfishes but shared with gnathostomes (vertebrates *n/e).*
2) Have cartilaginous vertebral structures (**arcualia**) resembling neural arches of gnathostomes.
3) Most lampreys are **parasitic** on other fishes.

Feeding

1) Some freshwater species have **non-feeding** adults. They attach tightly to the host using the **oral hood** and the tongue, both covered with spines.
2) **Tongue** is *not homologous* with the tongue of gnathostomes because it is innervated by a different cranial nerve.
3) An **oral gland** secretes an **anticoagulant** that prevents the prey's blood from clotting.
4) Digestive tract is straight and simple.
5) Lampreys do not kill their hosts. At sea, the hosts are whales, porpoises, and fishes.

Ventilation

1) Lampreys are unique among living vertebrates in having a single **nasal opening** (nostril in *new ed.*) combined with a duct leading to the **hypophysis** (pituitary) & known as a **nasohypophysial opening**.

2) Eyes of lampreys are large and well developed, as is the pineal body.

3) Have two **semicircular canals** on each side of the head, like the ostracoderms.

4) Heart is innervated by the parasympathetic nervous system (the **vagus nerve**, X).

5) Chloride cells in the gills & kidneys regulate **ions**, **water**, and **nitrogenous wastes**, allowing the lamprey to exist in a variety of salinities.

6) Lampreys have seven pairs of gill pouches that open to the outside just behind the head.

7) Water is both drawn in and expelled through the gill slits (**tidal ventilation**). In all other fishes, **flow-through ventilation** takes place.

8) Flap called **velum** prevents backflow of water into the mouth.

9) Mode of ventilation is not very efficient at **oxygen extraction**; however, it is a necessary compromise given their specialized parasitic mode of feeding.

10) Oxygen extraction from the water is *not efficient* because of the feeding mode (*new ed.*)

Reproduction

1) Nearly all lampreys are **anadromous** = live as adults in oceans & ascend rivers to breed.

2) Well-developed sense organs.

3) Female lampreys produce a large number of **eggs**, which have no covering.

4) Male & female lampreys construct a **nest** of small rocks, and water in the nest is **oxygenated** by vigorous movements of their bodies over the nest.

5) External fertilization.

6) Adult lampreys **die** after breeding once.

Larval Development

1) The **larvae** hatch in two weeks.

2) Larvae are radically different from their parents & were originally described as a distinct genus (**Ammocoetes**).

Figure 3-6 (c): Larval lamprey (ammocoete).

3) Ammocoetes are wormlike with a large oral **hood** & nonfunctional **eyes** covered by skin.

4) Ammocoetes burrow into the mud and spend 3-7 years as **sedentary filter feeders**. Food particles are trapped in mucus & carried to the esophagus.

5) **Metamorphosis** begins after several years when the larvae are about 10 cm in length, and produces a silver-grey **juvenile** ready to begin its life as a parasite. Adult life is no more than *two years*, and many lampreys return to spawn after *one year*.

6) There have been **anti-lamprey measures** to help recovering the jawed fish species from lamprey's attack (*new ed.*)

Importance of Extant Primitive Vertebrates in Understanding Ancient Ones

- Hagfishes & lampreys provide examples of **surviving** primitive vertebrates.
- Hagfishes **retain** more primitive features than lampreys or any known vertebrate.
- **Table 3.1** describes morphological features of **hagfishes** that are more primitive than those of lampreys and gnathostomes.

3.3 Jawless Vertebrates – "Ostracoderms"

1) Most ostracoderms are characterized by a covering of dermal bone, usually in the form of an extensive armored shell (**carapace**) or scales. *Some were not covered.*

2) More closely related to the **gnathostomes** (jawed vertebrates) – see **Fig. 3-3.**

3) More derived than extant agnathans. They had an **olfactory tract** connecting the olfactory bulb with the forebrain, & a **cerebellum** in the hindbrain.

4) Living **agnathans** lack a cerebellum, and their olfactory bulbs are incorporated within the rest of the forebrain.

5) Although they lacked jaws, some had various types of movable **mouth plates** that lack analogs (not similar to) in any living vertebrates.

6) Although most ostracoderms had midline dorsal fin, only the more derived forms had true **pectoral fins** with **pectoral girdle** & **endoskeleton fin support**. As in living jawless vertebrates, the notochord was the main axial support.

7) **Figure 3-7:** Ostracoderm diversity

3.4 Transition from Jawless to Jawed Vertebrates

Basic Gnathostome Design

- Difference between **gnathostomes** & **agnathans** is described as the possession of jaws that bear teeth & two sets of paired fins or limbs (**Fig. 3-8**).

- **Fig. 3-8:** Evolution of vertebrate jaw from anterior branchial arches

  Bony fishes and tetrapods have teeth embedded into the jawbones (*new ed.*).

- **Fig. 3-9:** Generalised jawed vertebrate (gnathostome) showing derived features compared to the jawless vertebrate (agnathan) condition.

- Gnathostomes are characterized by many other features:

  1) Improvement in **locomotion**

  2) Improvements in sensory & circulatory **systems**.

  3) Just as the transition from **nonvertebrate** chordate to **vertebrate** characterised by duplication of *Hox* gene complex, the transition from **jawless** to **jawed** vertebrates may have involved a second duplication event.

  4) Gene duplication resulted in more genetic material for building more complex animal.

  5) Ostracoderm taxa lie between living agnathans & gnathostomes (*new ed.*).

  6) Gnathostomes have **teeth** on their jaws but teeth evolved after the jaws.

  7) Cartilaginous fishes such as **sharks** & **rays** lack dermal bones, and their teeth form within the skin. This condition is primitive to gnathostomes.

  8) Adding jaws (new feature) & **hypobranchial muscles** (innervated by spinal nerves) allowed vertebrates to add powerful suction to their feeding mechanisms (**Fig 3-11 a**).

  9) Presence of two olfactory bulbs leading to two distinct nostrils.

  10) Cranium has been elongated compared to the **agnathan** condition.

  11) More complex vertebrae; **Fig. 3-11 b –** Central elements with attached ribs.

  12) Note that tetrapods have well developed centra (*new ed.*).

  13) Ribs are a new feature; located in connective tissue between segmental muscles.

14) In the inner **ear**, there is a third semicircular canal for improved balance.

15) New feature in nervous system: insulating sheaths of **myelin** on the nerve fibers that increase the speed of nerve impulses.

16) Heart has four chambers & an additional chamber called **conus arteriosus**.

17) Higher blood pressure.

Table 3.2: Derived Features of Gnathostomes

The Origin of Fins

1) Fins act as **hydrofoils** (= wing-like structures), applying pressure to the surrounding water.

2) Water is incompressible so force applied by a fin in one direction against the water produces a **thrust** (*reaction force*) in the opposite direction.

3) Caudal (**tail**) fin increases the area of the tail, giving more thrust during propulsion (*creating force for movement*).

4) Rapid adjustments of body position in water are important for active fishes.

5) Unpaired fins (dorsal & anal fins) control tendency of fish to **roll** or **yaw** (swing right/left).

Fig. 3-12: A primitive jawed fish shown...to illustrate pitch, yaw, and roll.

6) Paired fins (pectoral & pelvic fins):

- **a)** Control the **pitch** (tilt the fish up/down)
- **b)** Act as brakes
- **c)** Provide thrust.

7) Fins have non-locomotor functions as well: **Spiny fins** are used in defence, or to inject poison when combined with glandular secretions.

8) Colourful fins are used to send visual signals.

9) Even before the gnathostomes appeared, fish had **structures** that were functioning as fins. Ostracoderms had spines or enlarged scales that acted like immobile fins.

10) Most gnathostome fishes have a well developed **heterocercal** (notochord turns up or downwards) **caudal fin** for rapid acceleration during burst swimming.

The Transition from Jawless to Jawed Vertebrates (order/info from *new ed.*)

1) In Chapter 2 we saw how **branchial arches** (cartilage derived from neural crest) of vertebrate cranium provided support for the gills.

2) **Fig. 3-12** (*3-8 in old ed.*): Evolution of the vertebrate jaw from anterior branchial arches.

- Summarises differences in gill arches b/w jawed vertebrates & their jawless ancestor.
- If we think of the head as segments, then you can see the stages of the development.
- The mandibular arches (lower & upper jaws) formed from the second head segment and jaw supports are formed from the hyoid arch of the third head segment and the posterior branchial arches (3–7) are formed in the head segments 4–8.

3) See **Fig. 2-8** (*new ed.*):

- Non-living vertebrates had a pair of anterior gill supporting branchial arches.
- The early gill slit between arches 1 and 2 has disappeared in living jawless vertebrates, but in many cartilaginous fishes there is a small hole (**spiracle**) in this position which is used for water intake.

A Problem Posed by the Gills of Early Vertebrates (info from *new ed.*)

1) There's been much discussion about the different position of jaw support (branchial arches).

2) In extant jawless vertebrates, the gill arches lie **lateral** to the gill structure, while in the jawed vertebrates they lie **medially** (i.e. internal to the gills).

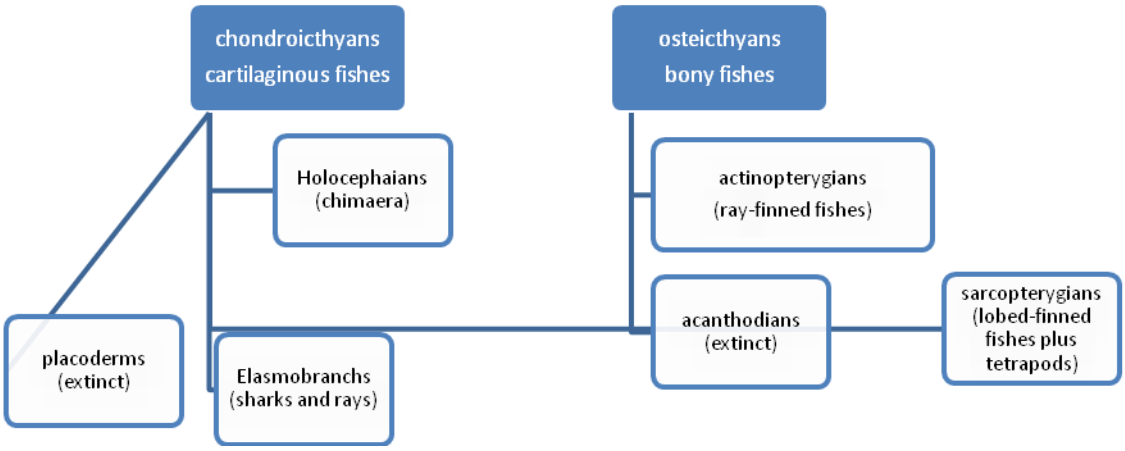
3) Also, jawless vertebrates have pouched gills with small, circular openings that are different from the flatter, more lens-shaped openings between the gills of the gnathostomes.

4) Scientists tried to explain the issue; noted that detailed structure of lamprey gills was more similar to the condition in sharks than condition in hagfishes (**Fig. 3-13**), and the different gill anatomy in hagfishes may represent a **highly specialized** rather than **primitive** condition.

5) Conclusion was that both hagfishes & lampreys have some evidence of internally placed **branchial velar cartilages**. The internal branchial arches in gnathostomes may be related to the more powerful mode of gill ventilation.

- **Derived anatomical features in gnathostomes:** true vertebrae, ribs and complete lateral line sensory system suggesting a sophisticated and powerful mode of locomotion and sensory feedback.
- Early radiation of jawed fishes included four major groups, two groups (**acanthodians** & **placoderms**) are extinct, and the two other groups – **chondrichthyans** (cartilaginous fishes) & **osteichthyans** (bony vertebrates) survive today. Osteichthyans were the form that gave rise to the tetrapods.

Fig. 3-15: Simplified cladogram of gnathostomes, showing living taxa & major extinct groups only.



Placoderms: armored fishes covered with thick bony shield (**Fig. 3-16 a** *new ed.*)

Ostracoderms: similar to placoderms but the placoderm bony shield was divided into head & trunk portions linked by a mobile joint that allowed the head to be lifted during feeding.

Acanthodians: fishes with stout spines, and well-developed dorsal, anal, and numerous paired fins (**Fig. 3-17**).

Self-Testing Questions (*not from textbook*)

True or False

1) Ostracoderms represent the earliest evidence of vertebrates.

2) The basic unit of mineralized tissues in vertebrates is odontodes.

3) Hagfishes have two nasal openings nathostomes is that the nerves are not covered by myelinated sheath.

4) Lampreys have cartilaginous vertebral structures.

5) Ammocoetes are separate species than the lampreys.

6) One of the derived features of the

Multiple Choice:

1) **The advantages of the evolution of the bony tissues:**

   a) Protection

   b) Insulation of electroreceptors

   c) Regulation of phosphorous

   d) Storing calcium and phosphrous

   e) All true

   f) None of the above

2) **What are the conodonts?**

   a) Small elements spinelike

   b) Animals that had vertebrate features

   c) Animals that had vertebrate features and conodonts within their pharynx.

   d) All of the above

Describe how the vertebrate jaw evolved? (use Fig. 3-12)