

Vertebrate origins and early radiations: jawless fishes and early gnathostomes

Read especially: Origin of Bone (49-50); Hagfish (pp. 51-55); Lampreys (pp. 55-58); Transition to Jawed Vertebrates (64-72)

- I. Earliest vertebrates and the origin of bone
 - A. Dates
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- II. Ostracoderms: ancient armored, jawless fishes
 - A. Dates
 - B. Systematics
 - C. Important characteristics of the ostracoderms gave them increased mobility, protection, and feeding/respiratory efficiency
 - D. Ostracoderms filled a variety of ecological niches
- III. Modern jawless fishes: hagfish and lampreys
 - A. Systematics
 - B. Hagfish
 - C. Lampreys
- IV. The transition to jawed vertebrates (origin of gnathostomes)
 - A. Jawed vertebrates are derived from an “ostracoderm” ancestor
 - B. Gnathostomes share a suite of derived characters related to increasing size, activity
 - C. Jaws arose from pharyngeal (“gill”) skeleton
 - D. Origin of paired fins
 - E. Placoderms - the early gnathostomes
 - F. Where does this leave us?
- I. Earliest vertebrates and the origin of bone
 - A. Some dates to set the stage:
 1. ~ 550 mya (early Cambrian): *Myllokumia*, *Haikouichthyes* from China = earliest vertebrate fossils:
 - a. small (~ 3mm), with cranium, W-shaped myomeres (muscle blocks along the body)
 - b. lacked bone or mineralized scales
 2. ~ 500 mya (late Cambrian): mineralized tissues, possibly from vertebrates, known from North American and Australia

3. ~ 480 mya (Ordovician): bone fragments, clearly vertebrate, known world-wide
4. ~445? mya (late Ordovician): some whole fossils of 12-35 mm armored, jawless fish
5. by 400 mya (late Silurian) whole body vertebrate fossils abundant, diverse, and widespread

B. Origin of bone and other mineralized tissues

1. Vertebrates have several types of mineralized tissues (= tissues to which hydroxyapatite is added to varying degrees) – main ones are
 - a. bone
 - b. dentine
 - c. enamel
2. Basic unit of mineralized tissues in most vertebrates (the “starting point” from which other tissues are derived evolutionarily) = **odontode**:
 - a. bony base
 - b. projection of dentine
 - c. enamel layer on top
3. The origin of bone remains a puzzle – we’re not sure when/why it arose
 - a. true vertebrate bone can’t be homologized with any kind of tissue from invertebrates – so we don’t have a histological “starting point”
 - b. fossil record “begins” with two very different, but very complex, forms of mineralized tissues – we don’t have any evidence of a simpler “precursor” to show the early evolutionary stages
 - (1) earliest fossils = **conodont elements** (see p. 49)
 - (a) small, complex spine- or comb-like structures < 1mm long
 - (b) widespread, diverse, and abundant from late Cambrian - Triassic
 - (c) histologically very similar to dentine and enamel
 - (d) now known to be part of pharynx of conodont animals:

- i) ~ 40 mm long with notochord, cranium, myomeres
 - ii) more derived than extant jawless fish, but apparently without living descendants – they’re still a real puzzle!
- (2) Scales of early jawless fishes showing “typical” complex bone structure also date to late Cambrian
- c. We also don’t know exactly what its earliest function might have been – some suggestions include:
- (1) electric insulation for electroreceptive organs
 - (a) structure of dentine in the head shield of early armored jawless fish suggest a sensory function
 - (b) problem = no other electroreceptive vertebrates use bone to insulate – why not?
 - (2) protection from predators
 - (a) early jawless fish had lots of big predators (e.g., eurypterids) – strong bony head shield would protect them
 - (b) problem: doesn’t explain how bone might have originated – small bits of bone wouldn’t serve protective function
 - (3) mineral storage
 - (a) phosphate is a rare element, especially in marine systems – individuals that could sequester it in a form that would allow storage and retrieval would be at an advantage
 - (b) bone is also an important site of calcium storage (calcium is actively deposited/removed from bone in extant vertebrates)
 - (c) this would explain how even small “bits” of bone would be advantageous
 - (4) “real answer” undoubtedly involves a combination of these: could have started as mineral storage, then been modified for sensory function, then

for protection (or some other sequence)

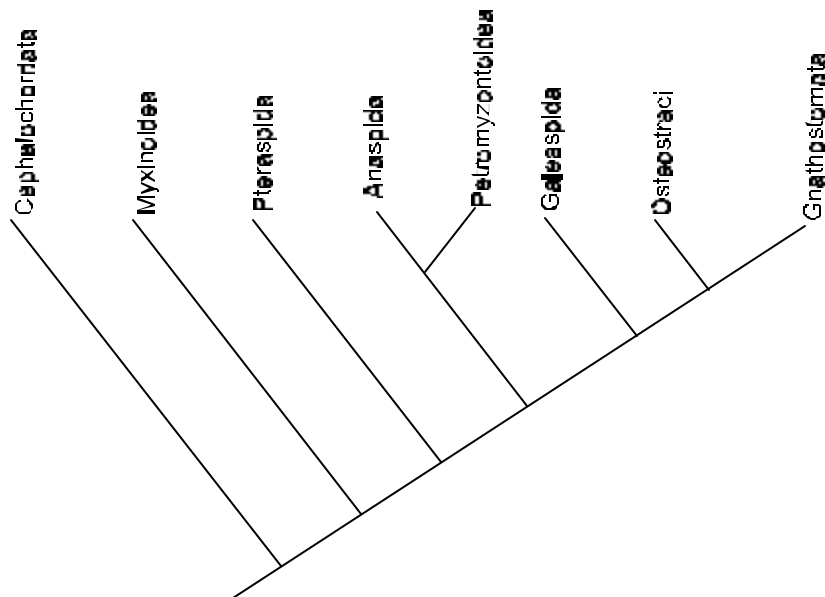
II. **Ostracoderms** – ancient armored, jawless fishes

A. Major dates

1. Earliest jawless fish originated in the late Cambrian/early Ordovician (they were the first vertebrates)
2. Jawed vertebrates arose very shortly after this; for most of their history, the two groups were contemporaries
3. We have a good fossil record of their radiation(s) from the Silurian to Devonian
4. Most lineages of jawless vertebrates were extinct by the end of the Devonian

B. Systematics

1. The evolutionary relationships among the various groups of jawless vertebrates are still being worked out; a conservative hypothesis is:



2. The term “ostracoderm” is generally applied to Pteraspida, Anaspida, Galeaspida, Osteostraci:

- a. clearly, this is a paraphyletic group: doesn't include all descendants from single ancestor
 - b. group is often subdivided into two subgroups:
 - (1) **Pteraspida = Heterostraci** (monophyletic group)
 - (2) others combined into **Cephalaspida**: this is also not a monophyletic group
 - c. for our purposes, we'll recognize "ostracoderms" as a "catch-all" term referring to any of the diverse assemblage of extinct, armored, jawless forms
- C. Important characteristics of the ostracoderms gave them increased mobility, protection, and feeding/respiratory efficiency (compared to non-vert chordate ancestors)
1. size ranged from 10cm to 3m – making them fairly large compared to many of the inverts in their environments
 2. gills used for gas exchange (instead of or in addition to filter feeding, which was original function)
 3. pharyngeal muscles:
 - a. sucked water into mouth (more efficient than ciliary action; can be used for feeding and for gas exchange)
 - b. pumped under pressure across gills (more efficient gas exchange)
 4. external "armor" = covering of dermal bone
 - a. variously arranged as a series of plates of various sizes over body
 - b. in some forms, plates were able to grow over the lifetime of the animal; in others, they were of fixed size
 - c. for at least the former, bony plates were covered with skin
 5. internal skeleton was probably fairly simple, made of cartilage and including:
 - a. gill supports
 - b. notochord stabilized body during lateral muscle contraction

- c. cranium incorporating anterior part of notochord, surrounding brain & anterior sensory capsules
 - d. no jaws – but some had moveable mouthplates
 - 6. more derived forms had anterior paired fins, possibly with internal skeletal support; some have evidence of pectoral limb girdle
 - a. primitively, pectoral limb girdle = ring of bones attached to back of skull (so not considered “internal”)
 - 7. Well-developed cranial sense organs, possibly including electroreception
 - 8. Mobile tail of various shapes
 - D. Given the range of body sizes, body conformations, positions of the mouth, etc., can conclude that these animals filled a range of ecological niches
 - 1. some filter feeders
 - 2. some probably predatory (via suction feeding)
- III. Modern jawless fishes: hagfish and lampreys
- A. Systematics: historically, hagfish and lampreys were classified together in the Class Agnatha, Order Cyclostomata
 - 1. this classification, though, was based on characteristics that are either
 - a. primitive (e.g., lack of jaws, lack of fins) or
 - b. superficially similar due to convergence (long, slender bodies)
 - 2. We now understand that the two are not closely related at all; based on current understanding, neither “Class Agnatha” and “Order Cyclostomata” are good monophyletic groups
 - 3. We’ll continue to use traditional “Agnatha” to refer to extant jawless fish – although it’s not a monophyletic group, it’s a good descriptive term
 - B. **Hagfish = Myxinoidea** (myx = slime, mucus)
 - 1. The relationship of the hagfish to other vertebrates remains somewhat unclear.
 - a. A key problem with clarifying hagfish relationships is that many features

seem to be either

- (1) primitive for all vertebrates – so don't tell us who closest relatives are; or
- (2) unique derived traits related to burrowing, scavenging niche

- b. Current consensus is that hagfish are actually very primitive vertebrates (or vertebrate relatives), probably remnants of a lineage that pre-dates the ostracoderms (see cladogram above)
 - (1) primary reason (as noted earlier) is lack of vertebrae and cartilagenous braincase
 - (2) but this interpretation is complicated by fact that their burrowing/scavenging ecology is commonly correlated with reductions in many organ systems – so some of the apparent “primitive” features may actually be derived
- 2. Diversity and distribution of modern hagfish:
 - a. ~ 60 spp in 2 genera currently recognized
 - b. Nearly worldwide distribution; habitats are
 - (1) entirely marine
 - (2) primarily continental shelves; often very deep
- 3. General ecology not well known
 - a. burrowers; some colonial
 - b. feed on polychaete worms, scavenge fish carcasses
 - c. virtually nothing known about life history, except that
 - (1) most species have strongly female-biased sex ratio (100:1); reason unclear
 - (2) young have direct development (no larval stage) and
 - (3) at least some species are hermaphroditic
- 4. Some general characteristics:
 - a. size generally < 1m in length

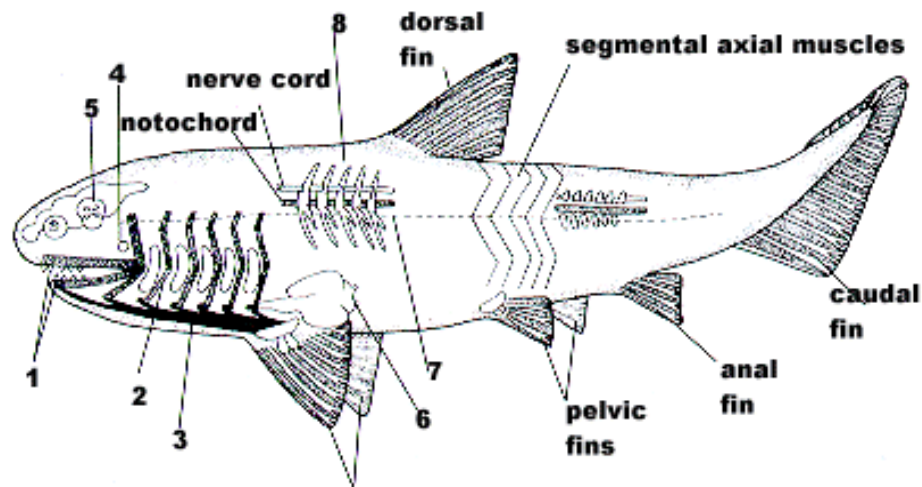
- b. scaleless, smooth skin
 - c. feeding apparatus seems to be well adapted for worm diet
 - d. eyes are degenerate or rudimentary, but have good tactile sense
 - e. lack jaws, fins
 - f. apparently lack strong osmoregulatory systems – maintain body fluids ~ isotonic to seawater (which explains why they're exclusively marine)
5. Some peculiar characteristics:
- a. large mucus glands secrete combination of large amounts of mucus, proteinaceous threads
 - (1) threads “hold” mucus close to body
 - (2) used as defense mechanism
 - (3) to get rid of slime, tie knot in tail & pass along body to scrape it off.
 - b. once food is swallowed, it's enfolded in a mucoïd bag secreted by gut wall
 - (1) bag is permeable to digestive enzymes & digestate
 - (2) secreted as wrapper around feces
 - c. have unique circulatory system:
 - (1) venous return blood drains into large, open sinuses (basically, an open circulatory system, as opposed to the closed system in all other vertebrates)
 - (2) this means that venous return blood is under extremely low pressure, so use “accessory hearts” around gills and in caudal region to drive venous return blood to heart
 - (3) hearts aneural - pumping rhythm is intrinsic, not regulated by nervous input from CNS
6. Conservation status
- a. Since 1970's, hagfish have had increasing economic impact on fishing industry by scavenging fish caught in stationary gear (e.g., gill nets)

- b. More recently, specialty leather industry has begun using hagfish to make “eelskin” products – very thin, soft, supple leather
 - c. Result has been significant overfishing and eradication of commercially harvestable hagfish populations (fisheries) in some parts of Asia, North America.
 - d. Problem is that we don’t know enough about biology to manage them properly (assuming we’d do so if we had sufficient knowledge)
 - (1) however, we do know that they have relatively large eggs and direct development
 - (2) size of eggs/offspring is often correlated with reproductive rate – large eggs usually means
 - (a) a late age at first reproduction
 - (b) long interval between reproductive episodes and
 - (c) relatively few offspring produced during each episode
 - (3) together suggests that proper management would require more careful limitation on take than might apply to other kinds of fish
 - e. Doubtful that this will cause much outcry – think about why not
- C. **Lampreys = Petromyzontoidea** (petro- = rock; myzo = suck – lampreys suck rocks??? -- read text to see where this name comes from)
- 1. Comparisons with fossil species supports lampreys as close relatives of the Anaspida (one of the cephalaspid lineages of ostracoderms) (see cladogram above).
 - 2. Distribution and diversity:
 - a. 40-50 species in 2 genera
 - b. distributed worldwide except for high polar and tropical regions
 - c. occupy variety of marine and freshwater habitats
 - 3. Ecology varies among species, but some general points:

- a. life history includes distinctive larval stage (Ammocoetes larva) that was originally considered a separate species (didn't know it was a larva)
 - b. adults are generally parasitic; in some species, adults don't feed at all, just live long enough to breed
 - c. Many (most?) species are **anadromous** – individuals live adult lives in oceans or large lakes, and ascend rivers/streams to breed
 - d. larvae spend 3-7 years as burrowing filter-feeders living in quiet stretches of rivers and streams
4. Some general characteristics:
- a. like hagfish, lack jaws and fins
 - b. unlike hagfish, eyes are well-developed
 - c. osmoregulatory systems associated with gills, kidneys allow precise regulation of body fluids (which permits anadromous life history!)
 - d. oral apparatus in adults highly adapted to parasitism: allows adults to
 - (1) attach to fish via suction
 - (2) rasp away integument; oral gland produces anticoagulant
 - (3) suction feed on body fluids
5. Interaction with humans: best known for invasion of Great Lakes and impact on commercial/sports fisheries (see website)
- a. Species in question = sea lamprey, *Petromyzon marinus*
 - b. Indigenous to Lake Ontario, but Niagra Falls (between Lake Erie and Lake Ontario) prevented colonization of upper Great Lakes
 - c. Welland canal provided access to upper Great Lakes in 1829
 - d. Lake Erie not very good lamprey habitat, but by 1920's lampreys made it past Erie to rest of Great Lakes
 - e. What mechanisms are being used to control them? See text and web site for more info.

IV. The transition to jawed vertebrates (the origin of the **Gnathostomata**)

- A. According to our best current information, jawed vertebrates arose from a common ancestor with osteostracans – i.e., they're derived from an "ostracoderm" ancestor
1. fragmentary evidence of jawed vertebrates date to late Ordovician
 2. extensive fossil record of jawed vertebrates from Silurian, with radiations throughout the Devonian and beyond – their major radiations gave rise to the rest of the vertebrates we'll be studying
- B. Gnathostomes share a large suite of derived characteristics related to increasing size, activity:



1. historically, considered **jaws** and **paired fins** to be key shared, derived traits
Now recognize that paired fins may be primitive for gnathostomata
2. Major novel traits associated with increased development of locomotor, sensory, and circulatory systems, in response to selection favoring larger, more active animals: some examples include (see fig 3-10 & accompanying text):
 - a. additions to internal skeleton provide sites of attachment for stronger, more active muscles:

- (1) jaws for respiration, later feeding (#1)
- (2) jointed **branchial arches** = gill supports for attachment of new muscles, greater pharyngeal mobility for suction inhalation, feeding (#2, 3)
- (3) more complete **vertebrae** begin to replace notochord, supporting action of strong locomotor muscles (#8)
- (4) **ribs** also support action of stronger locomotor muscles
- (5) **pectoral girdle** = u-shaped ring of bones providing internal support and muscle attachment for paired fins – strong, mobile pectoral fins

b. soft tissue structures indicate greater mobility

- (1) **3rd semicircular canal** in inner ear → improved orientation, maintenance of body position while moving (#5)
- (2) **additional chamber of heart** to accommodate higher-pressure blood flow (improved circulatory system delivers oxygen, nutrients, more efficiently) (#6)
- (3) numerous other changes, especially to nervous, reproductive systems

C. Jaws arose from pharyngeal (“gill”) skeleton

1. We’ve long known from embryology that jaws are derived (developmentally and evolutionarily) from the same material that makes up the branchial arches (b.a. = cartilaginous rod that supports gill filaments)
2. What might transitional stages in evolution of jaws “looked like” – i.e., what might be the original “protojaw” function, and might this have been different from the functions of jaws now (feeding, etc.)? Mallatt proposes that original function and current function not the same; suggests four basic stages, driven by selection for increasing activity (= selection for more efficient gas exchange; feeding efficiency):
 - a. Time frame: changes happening ~ rapidly, ~ 450 mypb
 - b. Basic scenario:

- (1) ancestral, unjointed branchial basket used in conjunction with relatively weak ventilation; low overall activity levels
 - (2) selection favored increase in ventilatory efficiency associated with increase in activity levels
 - (3) consequently, selection favored evolution of new ventilatory muscles & stronger, jointed branchial arches to support them
 - (a) jointed b.a.'s provide enhanced range of motion for powerful muscles compared to unjointed
 - (4) most powerful muscles were those associated with opening & closing mouth; these attached to first branchial arch – advantages are
 - (a) prevent leakage of HOH during expiration by strong mouth closing
 - (b) increase “suction” by being able to open mouth wide, quickly
 - (c) improves ventilation
 - (d) also allows powerful suction feeding (larger, more active prey “sucked in” with HOH)
 - (5) Selection favors biting jaws to help hold larger, more active prey in place before swallowing
- c. So envisions four basic stages in evolution of jaws from branchial arche (see diagram at end of notes:
- (1) Ancestral vertebrate: unjointed branchial basket
 - (2) Early pre-gnathostome: jointed internal arches support stronger ventilation muscles; gives stronger inspiration & expiration
 - (3) Late pre-gnathostome: mouth-closing, ‘ventilatory’ jaw permits more forceful expiration of water across gills
 - (4) Early gnathostome: feeding jaws
 - (5) note positions of first (**mandibular**) and second (**hyoid**) arches
3. Later stages:

- a. as jaws get larger, stronger, incorporate element of hyoid arch
(**hyomandibular**) to brace, suspend jaw – THIS IS IMPORTANT!
 - b. Note also terms used for upper, lower jaws of cartilaginous fish:
palatoquadrate, Meckel's cartilage
 - c. During early evolution of Osteichthyes (bony fish), bone replaces cartilage as major structural element of jaws:
 - (1) Palatoquadrate reduced to small posterior bone = **quadrate**
 - (2) Meckel's cartilage reduced to small posterior bone = **articular** (quadrate + articular is the jaw joint)
 - (3) Anterior portions of jaw made up of a number of small bones (names don't matter)
 4. Significance of jaws: not only enhanced respiration and feeding, but also permit manipulation of the environment in ways not previously possible – Romer was right!
- D. Paired fins
1. Origin of paired pelvic and pectoral fins uncertain – no good fossil intermediates, and no one satisfactory hypothesis
 2. Structure includes not only external appendages, but internal skeletal support for muscles that control orientation, position, movement
 3. Functional significance clear: precise control of body position, especially during rapid locomotion, is impossible in HOH without this kind of structure
 4. read text (p. 69) for additional functions
- E. Placoderms - early gnathostomes?
1. extinct group of armored, jawed vertebrates
 - a. had arisen by Middle Ordovician
 - b. by Devonian had diversified into at least four major groups – they were the most diverse vertebrates of that time
 - c. like ostracoderms, had external "armor" covering of dermal bone

- d. like ostracoderms, underwent major extinction during late Devonian mass extinction
 2. one lineage = acanthodians shared a common ancestor with modern Chondrichthyes, Osteichthyes
- F. Where and when does all this leave us?
1. By Devonian, both jawless and jawed fish were diverse and abundant; both groups experienced radiations throughout this period.
 2. Both groups also experienced significant extinctions, especially toward end of Devonian.
 3. By the end of the Devonian, "ostracoderms" were extinct; only jawless forms persisting were the ancestors of today's hagfish and lampreys
 4. Jawed fish continued to radiate, ultimately giving rise to terrestrial vertebrates.

Special reference:

Mallatt, Jon. 1996. Ventilation and the origin of jawed vertebrates: a new mouth.
Zoological Journal of the Linnean Society, 117:329-404.

Stages in the evolution of jaws, from Mallatt (1996)

