

## CHORDATA

**Michel Laurin**

*UMR 7207, CNRS/MNHN/UMPC, Muséum National d'Histoire Naturelle, Paris, France*

**Keywords:** Phylogeny, tunicates, cephalochordates, chordates, craniates, hagfishes, vertebrates, lampreys, gnathostomes, placoderms, chondrichthyans, acanthodians, osteichthyans, actinopterygians, sarcopterygians, tetrapods.

### Contents

1. Characteristics and Diversity of Chordates
  - 1.1. Introduction to Craniates
  - 1.2. Tunicata
  - 1.3. Cephalochordata
2. Origin of Craniates and Jawless Vertebrates
  - 2.1. Hypotheses about the Origin of Craniates and the Oldest Fossils
  - 2.2. Hagfishes
  - 2.3. Lampreys
  - 2.4. Euvertebrates
    - 2.4.1. Euvertebrate Phylogeny
    - 2.4.2. Pteraspidomorphs
    - 2.4.3. Anaspids
    - 2.4.4. Galeaspids
    - 2.4.5. Thelodonts
    - 2.4.6. Osteostracans
    - 2.4.7. Pituriaspids
    - 2.4.8. Histological Diversity of Euvertebrates
    - 2.4.9. Scientific Relevance of Euvertebrates
3. Evolution of gnathostomes
  - 3.1. Introduction to Gnathostomes
  - 3.2. Placoderms
  - 3.3. Chondrichthyans
  - 3.4. Acanthodians
4. Actinopterygians
  - 4.1. Origin and Early Evolution of Actinopterygians
  - 4.2. Teleosts
  - 4.3. Commercial Importance of Actinopterygians
5. Sarcopterygians
  - 5.1. Introduction to Sarcopterygians
  - 5.2. Actinistians
  - 5.3. Dipnomorphs
6. Limbed Vertebrates
  - 6.1. Introduction to Limbed Vertebrates
  - 6.2. Temnospondyls
  - 6.3. Embolomeres
  - 6.4. Seymouriamorphs

- 6.5. Lepospondyls
- 6.6. Lissamphibian Fossil Record
- 6.7. Diadectomorphs and Amniotes
- 6.8. Stegocephalian Phylogeny
- 6.9. Lissamphibian Phylogeny
- 7. Amniotes
  - 7.1. Introduction to Amniotes
  - 7.2. Mesosaurs
  - 7.3. Parareptiles
  - 7.4. Eureptiles
  - 7.5. Permo-Carboniferous Synapsids
  - 7.6. Therapsids
  - 7.7. Extant Therapsids: Mammals
- Acknowledgements
- Glossary
- Bibliography
- Biographical Sketch

## Summary

Chordates include urochordates, cephalochordates, and craniates. This taxon must have originated before the Cambrian because at that time, we already encounter fossils of cephalochordates and of vertebrates, and molecular studies suggest a pre-Cambrian origin of the main metazoan clades. This chapter summarizes our understanding of chordate phylogeny and evolution, both from a molecular and from a paleontological, morphological perspective. The evolution of relevant characters is discussed.

Ideas about basal chordate phylogeny have changed recently because several recent studies suggest that tunicates are most closely related to craniates than to cephalochordates. Basal craniate phylogeny is controversial, with most morphological studies suggesting that lampreys are closer to gnathostomes than to hagfishes, whereas most molecular studies suggest that hagfishes and lampreys form a clade (Cyclostomata) that excludes gnathostomes. Gnathostome phylogeny is also controversial, but placoderms may be the sister-group of crown-gnathostomes. Acanthodians may be closer to osteichthyans than to chondrichthyans.

Osteichthyans are comprised of actinopterygians and sarcopterygians. Polypteryforms are the sister-group of all other actinopterygians, but the affinities between acipenseriforms, amiiforms, lepisosteiforms, and teleosts are controversial. Morphological phylogenies suggest that amiiforms and lepisosteiforms are closer to teleosts than to acipenseriforms, whereas most molecular phylogenies suggest that teleosts are the sister-group of these three other taxa.

These lineages must have become individualized in the Carboniferous, according to molecular studies. Among extant sarcopterygians, actinistians represent the first lineage to have become individualized, and is the morphologically most conservative clade. Dipnoans appear in the fossil record in the Early Devonian, and fossils show that some members of this clade were able to estivate in the Early Permian. The limb with digits appeared in the Middle Permian, according to trace fossils, but limbed vertebrates are

known from skeletal remains from the Late Devonian onwards. The divergence between lissamphibians and amniotes probably dates from the Early Carboniferous. The origin of extant amphibians is controversial, but most authors consider that urodeles are closer to anurans than to gymnophionans. Among amniotes, the affinities of turtles remain controversial; they may be the sister-group of diapsids, or they may be diapsids that have lost the temporal fenestra. Mammal diversification started in the Triassic, according to molecular studies, even though the earliest fossil crown-mammals appear only in the Jurassic in the fossil record.

## 1. Characteristics and Diversity of Chordates

### 1.1. Introduction to Craniates

Chordates are deuterostomians characterized by the presence of a notochord (a stiff rod that represents the precursor of the vertebral column in vertebrates and that persists in the latter as the intervertebral disks). They also have pharyngeal slits, but this is apparently a synapomorphy of deuterostomians that was lost in extant echinoderms. In vertebrates, gills develop in these slits, but primitively in chordates, these slits were probably involved in feeding rather than breathing because that condition persists in cephalochordates and urochordates. In both taxa, ciliated cells in the pharynx create a current that ventilates these slits, and food particles are captured by mucus.

Chordates consist of three main taxa (craniates, cephalochordates, and urochordates or tunicates) whose phylogeny is still controversial. The most familiar of these are the craniates (because humans belong to that group), which include the hagfishes and vertebrates (lampreys and gnathostomes, the jawed vertebrates), of which more than 45 000 species are usually recognized (an exact count is difficult to obtain both because of gaps in our knowledge, and because of inherent limitations in rank-based nomenclature).

### 1.2. Tunicata

The Tunicata (the name that has priority) or Urochordata (a junior synonym) include more than 2500 species. Most are suspension feeders and sessile, benthic forms as adults (Figure 1), but a few (Appendicularia) are nectonic filter-feeders as adults, and a few species, such as *Megalodicopia hians*, are sessile predators. Tunicates are the only chordates with determinate cleavage, in which the fate of cells is determined early in ontogeny.

The larva of most Tunicates is much more similar to a vertebrate than the adult. The nectonic larva, which looks vaguely like a tadpole, uses its muscles and notochord to swim, and it apparently does not feed. It has a simple eye, the ocellus, a balancing organ, the statolith, and a simple cerebral ganglion.

Such a type of larva favors dispersal. In most tunicates, the late larva fixes itself to the substrate and metamorphoses into an adult devoid of a notochord. The pharynx expands and makes up most of the adult body, which consists in little more than a suspension feeding apparatus, while most sensory organs and the brain disappear. Most tunicates are hermaphrodites, and they are either solitary, social, or colonial.



Figure 1. The tunicate *Clavelina moluccensis*, the bluebell tunicate. Picture by Nhobgood published under the Creative Commons license. Downloaded from [http://en.wikipedia.org/wiki/File:Bluebell\\_tunicates\\_Nick\\_Hobgood.jpg](http://en.wikipedia.org/wiki/File:Bluebell_tunicates_Nick_Hobgood.jpg) on 18-8-2011.

Several recent molecular phylogenies suggest that Tunicates are more closely related to craniates than to cephalochordates, even though this seems counter-intuitive from a morphological point of view. Their phylogeny is likewise still in a state of flux, so the polarity of the evolution of several characters (like sociality) is difficult to assess. For instance, determining the polarity of metamorphosis in tunicates requires determining the position of the Appendicularia, which does not metamorphose.

Recent phylogenies (Figure 2) suggest that they are deeply nested among metamorphosing tunicates, so the absence of metamorphosis in Appendicularia is most likely a derived feature. However, support for the position of Appendicularia remains weak, so this conclusion remains tentative. They are known in the fossil record from the Early Cambrian (*Shankouclava shankouense*) to the present, with some Neoprotozoic (Ediacaran) potential representatives of debated affinities (*Ausia fenestrata* and *Yarnemia*).

### 1.3. Cephalochordata

The cephalochordates, which were long considered the closest extant relatives of craniates, retain the notochord throughout ontogeny. These include the amphioxus (*Branchiostoma*; 23 species) and *Epigonichthys* (7 species). They have about 180 pharyngeal slits and a post-anal tail (Figure 3A); the sexes are separate. These small animals (no more than 7 cm long) feed by filtering water through their pharyngeal slits; the necessary water current is created by ciliated cells. The larva is nectonic, but the adults normally live buried in the sand. Cephalochordates lack complex sensory organs (no eye, ear, etc.). They have a scanty fossil record, the oldest of which is the Early Cambrian *Yunnanozoon*. Cephalochordates are eaten in parts of Asia.

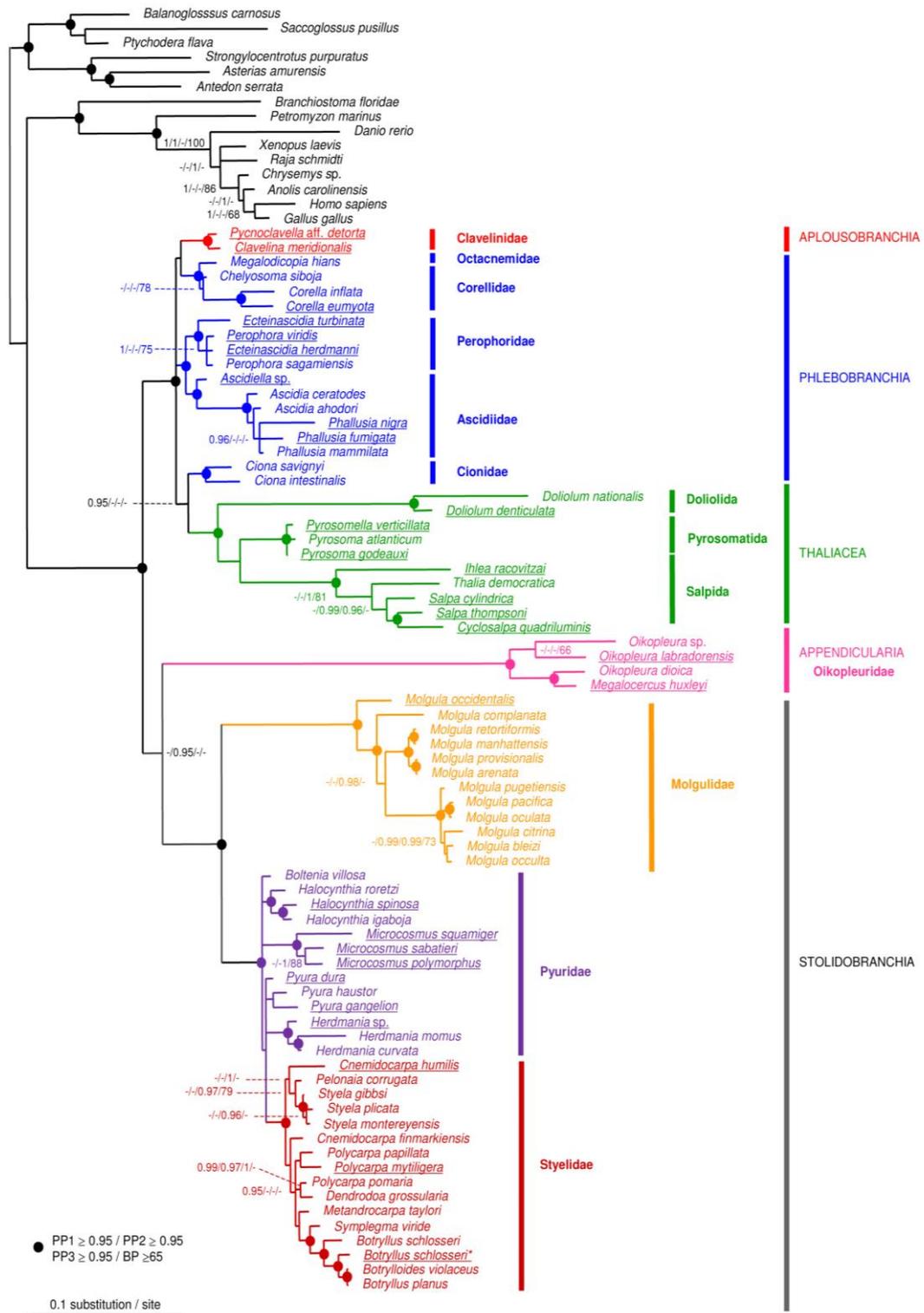


Figure 2. Tunicate phylogeny. Reproduced from Tsagkogeorga et al. (2009). Note that even though Tsagkogeorga et al. (2009) support close affinities between tunicates and craniates (in text), their phylogeny rather supports close affinities between cephalochordates (represented by Branchiostoma) and craniates.



Figure 3. Extant chordates. A, The cephalochordate *Branchiostoma lanceolatum* the amphioxus. Picture by Hans Hillewaert published under the Creative Commons license. Downloaded from [http:// en.wikipedia.org /wiki/ File:Branchiostoma\\_lanceolatum.jpg](http://en.wikipedia.org/wiki/File:Branchiostoma_lanceolatum.jpg) on 13-8-2011. B, The hagfish *Eptatretus polytrema*. Drawing by J. H. Richard downloaded from [http:// en.wikipedia.org/ wiki/ File:Eptatretus\\_polytrema.jpg](http://en.wikipedia.org/wiki/File:Eptatretus_polytrema.jpg) on 14-8-2011. C, The lamprey *Petromyzon marinus*, showing the buccal funnel and the horny denticles. In one individual, the eye and external gill slits of the right side are visible. Picture by “Drow male” taken in the *Sala Maremagnum* of *Aquarium Finisterrae*, in La Coruña, Galicia, Spain. Downloaded from [http:// en.wikipedia.org/ wiki/ File:Diversas\\_lampreas.1\\_-\\_Aquarium\\_Finisterrae.JPG](http://en.wikipedia.org/wiki/File:Diversas_lampreas.1_-_Aquarium_Finisterrae.JPG) on 14-8-2011.

The chordates clearly originated in the marine environment because all cephalochordates, all urochordates, and several craniates (all hagfishes, at least some ontogenetic stages of most lampreys, and most chondrichthyans) inhabit that environment.

## 2. Origin of Craniates and Jawless Vertebrates

### 2.1. Hypotheses about the Origin of Craniates and the Oldest Fossils

Several hypotheses compete to explain the origin of craniates. The tunicate specialists W. Garstang (1868–1949) and N. J. Berrill (1903–1996), and the paleontologist A. S. Romer (1894–1973) suggested that the ancestral craniate resembled vaguely urochordates and that through neoteny, the free larval stage with a notochord became the adult form. The recent molecular phylogenies are compatible with this hypothesis to the extent that they suggest that urochordates are closer to craniates than to cephalochordates. However, that hypothesis does not explain the origin of craniate characters. A more recent, alternative theory is that the ancestors of craniates were always motile and vermiform as adults, in this respect resembling more the cephalochordates and larval tunicates.

The oldest known craniate (*Myllokunmingia*; the simultaneously described *Haikouichthys* is apparently a synonym) lacked a mineralized skeleton. It was discovered in the Early Cambrian of China and looks vaguely like cephalochordates, but it displays more craniate characters. Thus, it has gills, fin rays, branchial cartilages, and some cranial cartilages (otic and nasal capsules, annular cartilage associated with the mouth, and a few more). The presence of the cranial cartilages linked to sense organs

suggests that *Myllokunmingia* is united to extant craniates by the presence of eye, inner ears (more involved in balance than in hearing), and an olfactory organ, all of which are much more elaborate, in extant craniates, than analogous structures found in tunicates (ocellus and statolith). It is more difficult to know if the gills were used in suspension feeding, as in tunicates and urochordates, or in breathing, as in extant craniates.

All known Ordovician, Silurian and Devonian vertebrates have a mineralized skeleton and thus form a clade (along with gnathostomes) called “euvertebrates”. The dermal skeleton of these forms is especially well developed and explains the name “ostracoderms” that was long given to this paraphyletic group. The first euvertebrates are mostly jawless forms, and they were formerly classified along the hagfishes and lampreys (the extant jawless craniates) in the taxon Agnatha, but that group is paraphyletic (it gave rise to gnathostomes) and thus should have no formal taxonomic status. The fossil record indicates that craniates, vertebrates, and euvertebrates originated in the seas; some euvertebrates moved into fresh water environments in the Devonian. No jawless euvertebrate survived beyond the Frasnian-Famennian (mid-Late Devonian) crisis.

## 2.2. Hagfishes

The extant hagfishes and lampreys were once thought to be derived from these early vertebrates through loss of the mineralized skeleton (Figure 4A), but recent phylogenies (Figure 4B) rather suggest that hagfishes and lampreys have more distant origins, that their ancestors never had a mineralized skeleton, and hence, they are not euvertebrates. Hagfishes and lampreys are sometimes classified into the clade Cyclostomata, and several molecular phylogenies support this classification.

However, many morphological characters instead suggest that lampreys are closer to gnathostomes than to hagfishes. These characters include a crystalline lens in the eye, at least two semi-circular canals (hagfishes have a single one), a closed circulatory system, the capacity to osmoregulate, electrosensory cells, neuromasts in the lateral-line organ, muscles inserting on the median fin endoskeleton, arcualia (neural arches, the first part of the vertebrae to appear), at least one dorsal fin, a reduction to fewer than 10 pairs of branchial arches (cephalochordates, tunicates, and some hagfishes have more), and calcified cartilage (long thought to be absent in lampreys). Because of this impressive (and non-exhaustive) list of synapomorphies, several morphologists distinguish Vertebrata, which includes lampreys, gnathostomes, and all other euvertebrates, and is characterized by the presence of vertebrae (represented only by the arcualia in lampreys) from Craniata, which also includes the hagfishes, which lack vertebrae, but possess a skull composed of several unmineralized cartilages.

Hagfishes (*Hyperotreti*) superficially resemble eels because of their long, slender body, but this similarity is of course convergent. Despite the absence of true jaws (i.e. homologous with those of gnathostomes), they can bite (but horizontally, rather than vertically as in gnathostomes), using a complex tongue made of cartilage and muscle (among other tissues) and covered with keratinous denticles. They prey or scavenge on teleosts. They have multiple venous hearts, lack muscle fibers in the caudal fin, and retain several other characters that presumably reflect the ancestral craniate condition. Extant hagfishes have only a caudal fin, but the Late Carboniferous hagfish *Myxini* has a

*siroka* had confluent dorsal, caudal, and anal fin; thus, extant hagfishes may have a reduced set of fins.

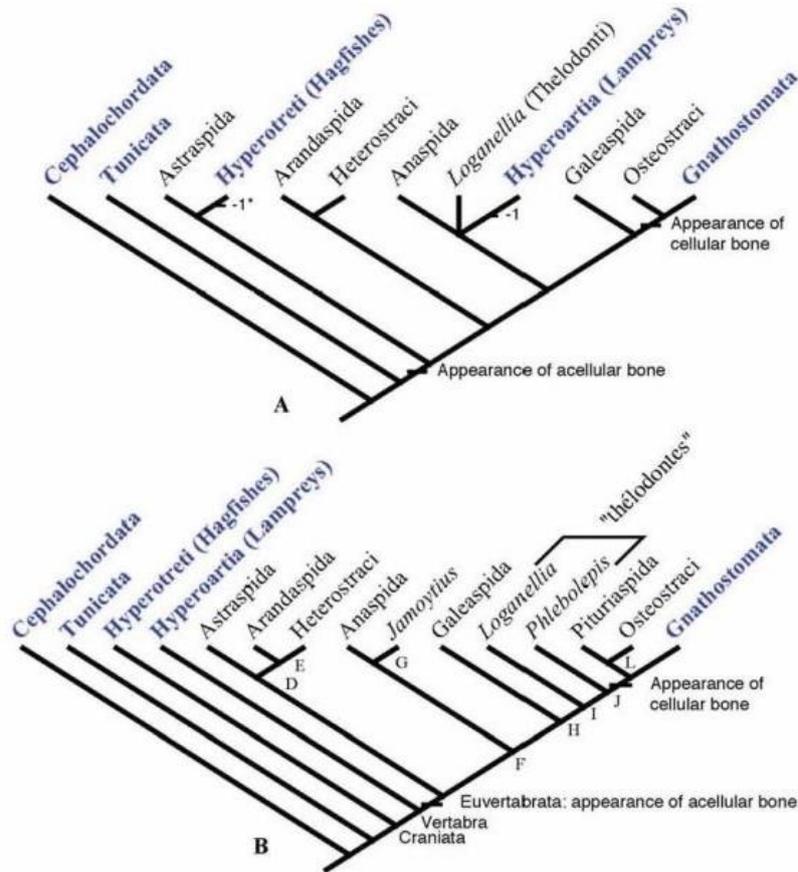


Figure 4. Chordate phylogeny emphasizing craniates. A, Hypothesis that prevailed in the late 1980s. B, Hypothesis published in 1996 and still widely accepted.

They have direct development (without a larval stage). Because of their extremely limited osmoregulation, they are strictly marine. They secrete copious amounts of slime (hence their popular name “slime eels”) that may have defensive properties (it may clog the gills of potential predators), which would explain that only birds and mammals are known to eat hagfishes. Their skin is extremely tough and is commercially sold under the inaccurate name of “eel skin”. Because of this, some species are endangered.

The fossil record of hagfishes is scanty, as can be expected in taxa lacking a mineralized skeleton. Close affinities between *Myllokunmingia* and hagfishes have been proposed, this is controversial. The oldest known undisputed hagfish dates from the Late Carboniferous. About 77 extant species and 5 extant genera (*Myxine*, *Neomyxine*, *Eptatretus*, *Nemamyxine*, and *Notomyxine*) are recognized. A molecular phylogeny of several species suggests that *Paramyxine* (a genus that most authors no longer recognize and consider synonymous with *Eptatretus*) is diphyletic and that *Eptatretus* is paraphyletic, but that *Myxine* is monophyletic (Figure 5).

The clade encompassing *Eptatretus* (and *Paramyxine* for the authors who still recognize it) is characterized by four to fourteen pairs of external gill openings, whereas the clade

that includes *Myxine*, *Notomyxine*, *Neomyxine*, and *Nemamyxine* has a single pair of external gill opening (there are several more gill slits, but these open into external branchial ducts that lead into a single paired external branchial opening).

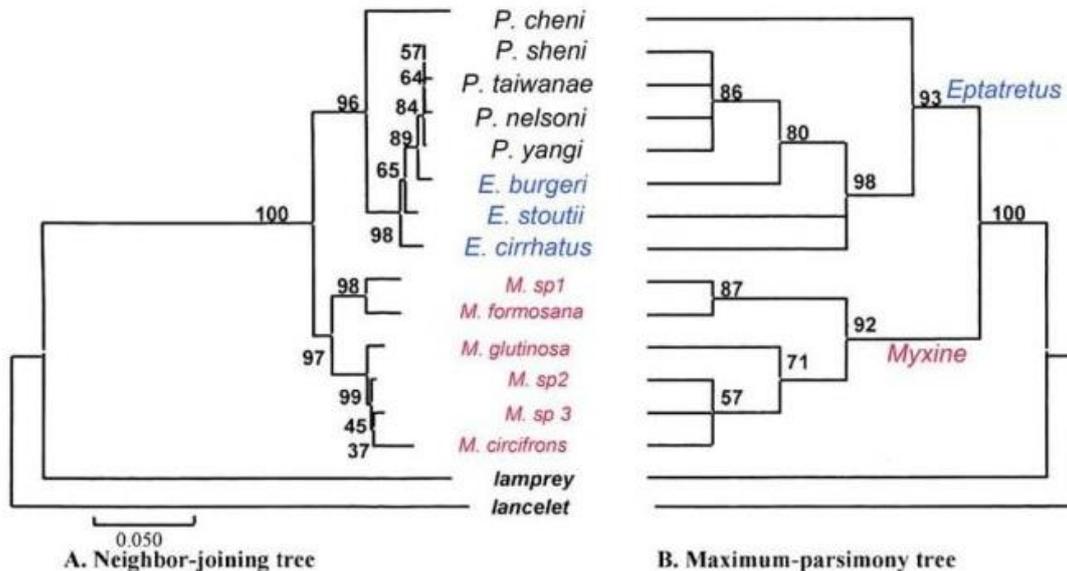


Figure 5. Hagfish phylogeny, redrawn from Kuo et al. (2003). Abbreviations: *E.*, *Eptatretus*; *M.*, *Myxine*; *P.*, *Paramyxine* (now considered a synonym of *Eptatretus*).

### 2.3. Lampreys

About 38 species of extant lampreys are currently recognized. All have blind larvae that burrow in sediment at the bottom of rivers and streams. These are suspension feeders that use ciliated cells in the pharynx to create a water current through the pharyngeal slits. This ammocoete larva is reminiscent of cephalochordates and appears to represent a striking case of recapitulation (the larva resembles a distant ancestor). These may metamorphose into non-feeding (non-parasitic) adults that stay in their natal habitat, breed and die within nine months at the most, or they may become feeding, parasitic adults that migrate to lakes or seas, depending on the taxon. Twenty species have non-feeding adults, which are smaller than their parasitic relatives; the 18 others are parasitic. Parasitic lampreys feed on gnathostomes, mostly teleosts, by attaching themselves to their body by their oral sucker, rasping the skin with their tongue (which is covered in horny denticles), and sucking the blood, eating the flesh, or both (depending on the taxa).

A molecular phylogeny of the lamprey *Lampreta* based on two genes (cytochrome b and NADH dehydrogenase subunit 3, or ND3 for short) has shown that non-parasitic lampreys have evolved several times from parasitic ancestors. Such evolutionary transitions seem to have occurred fairly recently, according to preliminary molecular dating, because some paired (closely related parasitic and non-parasitic) species could not be distinguished using cytochrome B and ND3, and may have diverged less than 70 000 years ago; some of these divergences may even have occurred in the last 10 000 years (after the end of the last ice age).

Other divergences within extant lampreys are far older; for instance, the genus *Lampreta* may have diverged from *Petromyzon* about 9 to 13 Ma (million years ago). Early lampreys had a hypocercal caudal fin, and this condition is retained in larvae of *Geotria australis*, but extant adults share a diphyccercal caudal fin. A phylogeny of lampreys based on 32 morphological characters shows that the Northern-hemisphere lampreys form a clade, but the monophyly of Southern-hemisphere lampreys could not be demonstrated (Figure 6). There are no tropical lampreys; they have an antitropical distribution.

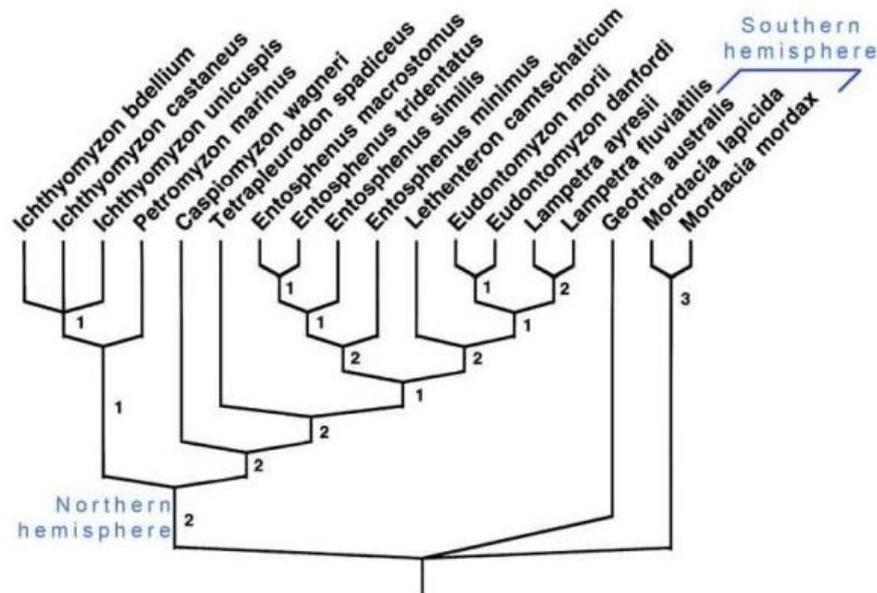


Figure 6. Phylogeny of extant parasitic lampreys, redrawn from Gill et al. (2003). Reproduced with permission from ASIH (American Society of Ichthyologists and Herpetologists).

Their fossil record goes back to the Late Devonian, but lampreys must be even older, given that they are the sister-group of gnathostomes. Lampreys have been eaten by humans at least since the Antiquity, in the Roman empire; in the Middle Ages, they were eaten throughout Europe by upper classes, and they are still eaten in several countries, notably in Spain, Portugal and France, where it is considered a delicacy (“lamproie bordelaise”, for instance), and also in Asia (South Korea). Because of this, several stocks have been overexploited.

## 2.4. Euvertebrates

### 2.4.1. Euvertebrate Phylogeny

Euvertebrates (Figure 4B, node C) share a few derived characters that suggest monophyly. The best is the presence of acellular dermal bone (bone lacking osteocyte lacunae), a type of bone often called “aspidine” that may be older than cellular bone. This view came to be accepted in the 1990s because earlier, hagfishes and lampreys were thought to both be derived from ancestors with a mineralized skeleton (Figure 4A).

This hypothesis still cannot be completely ruled out because several vertebrate taxa, including some jawless forms, have reduced their skeleton. Nevertheless, the phylogeny that is overwhelmingly accepted by paleontologists (Figure 4B) will form the basis of the following discussion. The only extant euvertebrates are gnathostomes. Thus, all other euvertebrates are stem-gnathostomes, even though most of them lacked jaws. Most jawless euvertebrates were demersal.

#### 2.4.2. Pteraspidomorphs

The oldest euvertebrates (vertebrates with a mineralized skeleton) are the pteraspidomorphs. They appear in the Ordovician. These taxa share the presence of a dorsal and a ventral shield (the rest of the body was covered by smaller scales) and dorsally located external branchial slits (Figure 7A, B). The largest group of pteraspidomorphs is the heterostracans, a taxon characterized by the presence of a single paired external branchial opening (but there were many more, perhaps about 15, pairs of gills).



Figure 7. Early jawless euvertebrates. A, The Devonian heterostracan *Drepanaspis gemuendina* (foreground) and the arthrodire placoderm *Tiaraspis* from the Early Devonian of Germany. B, The Ordovician pteraspidomorph *Arandaspis prionotolepis* from Australia. C, The Middle Silurian anaspid *Jaymoytius* with reduced ossification once considered closely related to lampreys. D, The galeaspids *Asiaspis expansa*, *Lungmenshenaspis kiangyouensis*, and *Bannhuanaspis vukhuci*, and a pair of *Yunnanolepis* antiarch placoderms, from the Early Devonian of China. E, The Early Devonian thelodont *Furcacauda heintzae*. F, The osteostracan *Cephalaspis*. From the top down, clockwise, *C. magnificans*, *C. poweriei*, *C. lyelli*, and *C. whitei*. G, The Middle Devonian *Pituriaspis dowlei* from Australia. Drawings by Stanton F. Fink, all of

which can be accessed through [http:// en.wikipedia.org/ wiki/ User:Apokryltaros](http://en.wikipedia.org/wiki/User:Apokryltaros), except for F, downloaded from [http:// en.wikipedia.org/ wiki/ Osteostraci](http://en.wikipedia.org/wiki/Osteostraci).

### 2.4.3. Anaspids

Closer to the gnathostomes, we find the anaspids (Figure 7C). Their body was covered by two rows of long, narrow scales of acellular bone arranged in a chevron pattern. The numerous branchial slits extend posteriorly and ventrally towards a large triangular scale. The tail is hypocercal (the vertebral axis extends into the ventral lobe of the caudal fin). The long paired ventrolateral fin has long been seen as a confirmation of the ventrolateral fin-fold theory of origin of the paired fins, but given the phylogenetic position of anaspids, this remains uncertain.

Anaspids possess a dorsal, median opening interpreted as a nasohypophyseal opening - a structure found in lampreys and thought to have occurred also in osteostracans (see below). Because of this, all three taxa were once thought to be closely related. *Jamoytius*, a jawless form resembling closely anaspids except in the absence of bone, raises the possibility that lampreys are closely related to anaspids (Figure 4A), although this is no longer the preferred, most parsimonious hypothesis (Figure 4B).

### 2.4.4. Galeaspids

Galeaspids (Figure 7D) appear to have been endemic to what is now China and Vietnam (North and South China continental blocks). The lateral-line organ was located deeply in the skeleton, resting partly at the interface between the dermal and endochondral bone. It was widely open to the exterior through rather long slits. A large opening on the dorsal surface of the cephalothorax led into the prenasal sinus, which communicated with the olfactoral organ and with the orobranchial chamber. Their dermal skeleton included acellular bone and enamel.

### 2.4.5. Thelodonts

Thelodonts form a group (possibly paraphyletic) of Paleozoic (mostly Devonian) jawless vertebrates characterized by a micromeric dermal skeleton (composed of small isolated scales). Their scales are sometimes fused near the gill openings and the orbit, thus rigidifying these regions. The scales often resemble vaguely teeth and are composed of odontodes (either a single odontode, when a single pulp cavity is present, as in *Thelodontida*, or an odontocomplex, when multiple pulp cavities are visible, as in *Phlebolepidida*). These scales are composed of dentin (meso- or metadentin; see below for definitions), which makes up the crown, and acellular bone, at the base that was attached to the skin. Because of their micromeric skeleton, the body shape is known in only a few taxa, but these possess a single paired pectoral fin (Figure 7E). Some authors have suggested thelodont monophyly based on the anchoring processes of the scales, but these do not occur in all thelodonts. Phylogenetic analyses suggest paraphyly (Figure 4B), and some authors suggest that thelodonts include stem-heterostracans, stem-galeaspids, stem-osteostracans, and even stem-gnathostomes. Some thelodonts have denticles in the pharynx (unlike other Paleozoic jawless euvertebrates), which is reminiscent of the teeth of gnathostomes, but given their systematic position, this may be a convergence. The tail was usually hypocercal, or more rarely, diphyrcal.

### 2.4.6. Osteostracans

Osteostracans possessed a paired pectoral fin (except in some forms, the tremataspids, which is interpreted as a loss in the most recent phylogeny), a nasohypophyseal opening (reminiscent of lampreys), and three enigmatic dorsal fields (a median and a paired one) of polygonal plates on the cephalothoracic shield (Figure 7F). The function of these fields is unknown, but the fact that they were linked to the labyrinth (inner ear) by branching canals suggests a sensory function. Their tail was usually heterocercal. They are the only jawless vertebrates to share with gnathostomes the presence of cellular bone (bone with osteocyte lacunae). Other synapomorphies with gnathostomes include sclerotic ossicles (forming a bony ring that protects the eye) and a dermal skeleton consisting of three layers: a basal layer of compact bone, a middle, spongy bone layer, and a superficial layer composed of dentin (Figure 8F). Even though most osteostracans had a massive cephalo-thoracic shield, the latest, Late Devonian forms, and some Middle Devonian forms appeared to have reduced their skeleton and had a micromeric dermal skeleton (Figure 8). Like all other euvvertebrate groups mentioned above, they appear to have become extinct in the Devonian.

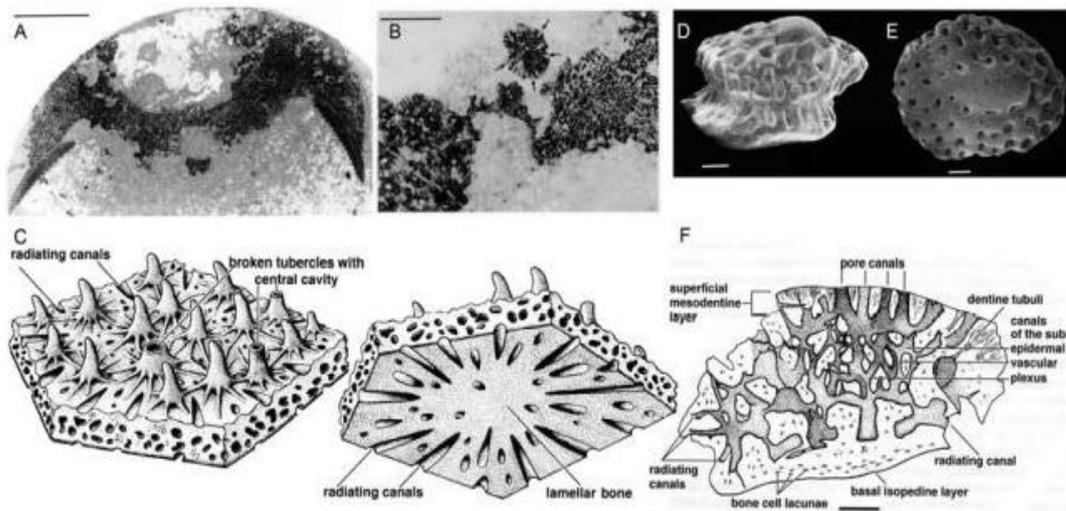


Figure 8. Osteostracan microanatomy and histology. Micromeric skeleton of the Middle Devonian osteostracan *Balticaspis latvica* (reproduced from Otto and Laurin, 2001). A, general view of the holotype, showing the characteristic shape of the cephalothoracic shield with the lateral cornua; B, enlarged view showing an isolated tessera. C, reconstruction of an isolated tessera in oblique superficial and deep view. D, E, picture and F, drawing of a histological section of a tessera of *Afannasiaspis porata*. Scale bar: A, 10 mm; B, 1 mm, D–F, 0.1 mm.

### 2.4.7. Pituriaspids

Pituriaspids (Figure 7G) are a small group (two genera) that resembles vaguely osteostracans, but they lack the fields of polygonal plates and the naso-hypophyseal opening. According to the most recent phylogenies osteostracans and pituriaspids are the closest relatives of gnathostomes. Therefore, the pectoral fin present in these taxa may be a synapomorphy, implying that the pelvic fin has a more recent origin.

#### 2.4.8. Histological Diversity of Euvertebrates

Paleohistology played an important role in taxonomic investigations of early vertebrates because their remains are often fragmentary, but also because early vertebrates exhibited a greater histological diversity than what is found in extant vertebrates. For instance, many people associate enamel with teeth because among mammals, that tissue is encountered only there, but enamel was present on much of the body surface (rather than in the mouth) in many early vertebrates. In extant vertebrates, enamel is produced by the ectoderm (whereas bone is mostly of mesodermal origin). In extinct taxa, its embryological origin cannot be assessed, but enamel (and enameloid, a similar tissue that may have a mesodermal origin) is recognizable because it is hypermineralized and always lacks osteocytes (found in bone), or extensions of the odontoblasts (Tome's fibers) that are found in most dentin types. The evolution of tissues appears to have been fast in early vertebrates because their distribution suggests a fair amount of convergence. Thus, enamel (or enameloid) was present in the pteraspidomorph *Astraspis*, in galeaspids, in osteostracans, and in most early gnathostomes, but it was absent in most pteraspifomorphs, anaspids, and thelodonts. Enamel may thus have appeared at least twice (once in *Astraspis*, and once in the clade that includes galeaspids, osteostracans, and gnathostomes).

Similarly, the taxonomic distribution of the various dentin types is phylogenetically informative. Thus, the pteraspidomorph *Eriptychius*, some "thelodonts" (such as *Phlebolepis*), and osteostracans had a peculiar type of dentin called "mesodentin" (Figure 9A), in which the odontocyte bodies were present in the dentin, whereas in meta- and orthodentin (Figure 9C, D), the odontocyte bodies are located in a pulp cavity, and only extension, Tome's fibers) extend into the dentin. Given its distribution, we could hypothesize that mesodentin appeared at least three times, but the organization of this tissue suggests the apparently incompatible hypothesis that it is primitive for euvertebrates and that the meta- and orthodentin found in many other euvertebrates is derived from mesodentin. In any case, meta- or orthodentin (Figure 9C, D) is found in heterostracans, some "thelodonts" (such as *Loganellia*), and in most gnathostomes, again suggesting three separate origins, although the similarities between these tissues argue against this. It is more likely that some form of histocompetence allowing differential expression of many of these tissue types arose fairly early in vertebrate evolution, allowing a fairly complex evolution. Many histological characters may thus be recurrent, *sensu* West-Eberhard (2003). In all jawless forms, dentin, like enamel, was found on the body surface, and is only occasionally (probably secondarily) associated with the mouth.

The conodonts (or more precisely, the euconodonts) have recently been suggested to be vertebrates, and this hypothesis has gained widespread acceptance in part of the scientific community and appears as a fact in some textbooks. However, the interpretation of most characters that have been invoked to justify vertebrate affinities is problematic. These characters include some soft anatomical ones, whose interpretation is difficult because it rests on poorly preserved soft tissues. Others rest on the mineralized tissues that compose the abundant, tiny conodont elements. Some authors have proposed that these tissues are homologous with vertebrate hard tissues, such as enamel, bone, and calcified cartilage. Thus, recent studies by several paleontologists (Blieck, Burrow, Schultze, and Turner, among others) raise serious doubts about the

interpretation of both sets of characters. Pending resolution of this controversy, conodonts will not be discussed further here.

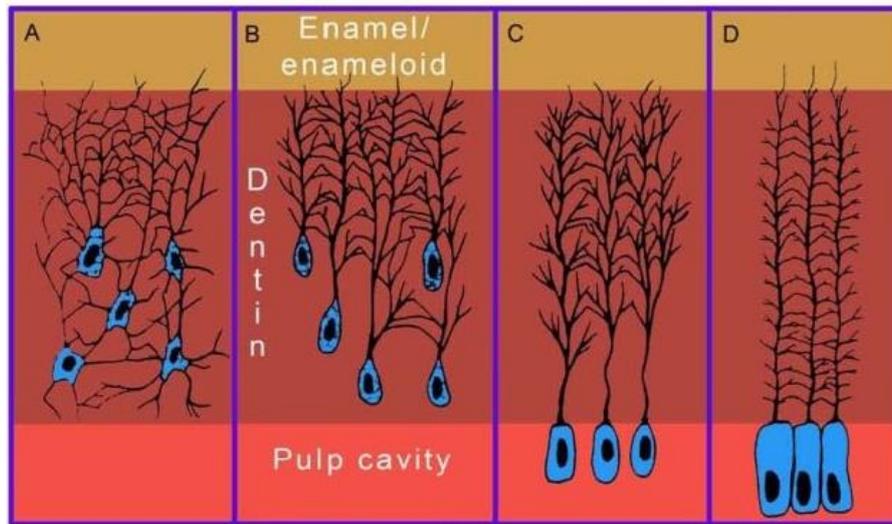


Figure 9. Dentin evolution, as proposed by the Russian paleontologist Ørvig in 1967. From the most primitive to the most recent types, we have mesodentin (A), semidentin (B), metadentin (C), and orthodentin (D). Modified from Smith and Hall (1993). © Springer, *Evolutionary Biology* 27: 387–448, fig. 5. Reproduced with kind permission from Springer Science+Business Media B. V.

#### 2.4.9. Scientific Relevance of Euvetebrates

Even though all jawless euvetebrates are now extinct, their fossil record documents the acquisition of many gnathostome characters. The abundance of fossils of some taxa, such as heterostracans and thelodonts, has even allowed the development of biostratigraphical scales that have proved especially useful in facies devoid of typical marine markers, such as conodonts, brachiopods, trilobites, and cephalopods.

### 3. Evolution of Gnathostomes

#### 3.1. Introduction to Gnathostomes

Gnathostomes are jawed vertebrates. In the extant fauna, they include the chondrichthyans (sharks, skates, rays, and chimeras) and osteichthyans (teleosts, tetrapods, lungfishes, etc.). They owe their name to a synapomorphy consisting of a jaw that closes vertically (by moving the lower jaw up). This jaw appears, from a structural and embryological point of view, to represent a specialized visceral arch that may be serially homologous with gill arches. However, no fossils ever proved that the mandibular arch, which forms the primitive jaw, is actually derived from an unspecialized gill arch of a jawless ancestor.

Gnathostomes appear in the fossil record in the Ordovician, time at which chondrichthyans are known (possible acanthodian remains have also been described). Their subsequent evolutionary radiation, modest in the Silurian, but spectacular in the

Devonian, coincides with the “predation revolution” because earlier, jawless euvertebrates are often thought to have been mud- or filter-feeders, although the predatory lifestyle of lampreys shows that the absence of true jaws does not necessarily preclude predation.

### 3.2. Placoderms

The phylogeny of ganthostomes remains controversial, but many authors consider placoderms to be the sister-group of all other gnathostomes. Placoderms are an extinct taxon known from the Silurian and mostly from the Devonian; they became extinct at the end of that period. So far, about one thousand species have been described. Placoderms lacked teeth, but their jaws were equipped with three pairs of gnathal plates (one on the mandible, and two on the upper jaw) with a sharp cutting edge. Placoderms are also characterized by a peculiar type of dentin called “semidentin” (Figure 9B), in which the odontocyte bodies is in the dentin, as in mesodentin, but in which the cytoplasmic processes are much more polarized (they extend towards the epidermis) than in mesodentin (in which processes extend in all directions). They are known mostly from the Devonian, although a few survived into the Carboniferous. Most had a heavy dermal skeleton consisting of large, tightly articulating plates covering the head and up to the pectoral region, and scales on the posterior part of the body; a few had a lighter dermal skeleton consisting of tesserae. The mandibular arch of placoderms was apparently lateral to the jaw adductor musculature, whereas it is medial to it in all other gnathostomes. Placoderms included some of the largest Devonian predators (up to 10 m long), such as *Dunkleosteus* (Figure 10A). Some authors have suggested that placoderms had a lung, but this appears to rest on overinterpretation of sedimentary infilling

### 3.3. Chondrichthyans

Chondrichthyans include about 1200 extant species. In the Paleozoic, several chondrichthyan taxa appeared, starting in the Ordovician and Silurian, in which few fossils have been found, and in the Devonian, in which their diversity increased rapidly. The affinities between most Paleozoic chondrichthyans and extant ones (Figure 10B–D) are poorly understood (Figure 11), except for the presence of stem-holocephalans in the Early Devonian (410 Ma).

The Devonian Cladoselachidae lack pelvic claspers, which are used in males during copulation; hence, cladoselachids may have retained a primitive external fertilization mode, contrary to extant chondrichthyans. Their paired fins had several unjointed radials that articulated directly with the girdles, contrary to extant chondrichthyans, in which no more than three radials, and especially the proximal metapterygial element, contact the girdle through a short articular region. They had cladodont teeth, a type of tooth that may be primitive for chondrichthyans but that does not occur in extant chondrichthyans. This type of tooth is characterized by several (three to five; three in the case of cladoselachids) long cusps in a row; the central cusp is always the longest.



Figure 10. Gnathostomes. A, The giant placoderm *Dunkleosteus*. Reconstruction by Nobu Tamura, downloaded from [http:// en.wikipedia.org/ wiki/ File:Dunkleosteus\\_BW.jpg](http://en.wikipedia.org/wiki/File:Dunkleosteus_BW.jpg). B, the extant holocephalan *Hydrolagus colliei*. Picture by Linda Snook, public domain, downloaded from [http:// en.wikipedia.org/ wiki/ File:Hydrolagus\\_colliei.jpg](http://en.wikipedia.org/wiki/File:Hydrolagus_colliei.jpg). C, the extant great white shark (*Carcharodon carcharias*), measuring about 3.5 m photographed by Terry Goss and downloaded from [http:// en.wikipedia.org/ wiki/ File:White\\_shark.jpg](http://en.wikipedia.org/wiki/File:White_shark.jpg). D, The extant ray *Manta birostris*. Picture by Jon Hanson downloaded from [http:// en.wikipedia.org/ wiki/ File:Manta\\_birostris-Thailand4.jpg](http://en.wikipedia.org/wiki/File:Manta_birostris-Thailand4.jpg). E, the Permo-Carboniferous eugeneodontid *Helicoprion*. Downloaded from [http:// en.wikipedia.org/ wiki/ File:Helicoprion\\_bessonovi1DB.jpg](http://en.wikipedia.org/wiki/File:Helicoprion_bessonovi1DB.jpg). F, the Early Carboniferous *Stethacanthus altonensis*. Drawing by Dmitry Bogdanov. Downloaded from [http:// en.wikipedia.org/ wiki/ File:Steth\\_pair1.jpg](http://en.wikipedia.org/wiki/File:Steth_pair1.jpg). G, the Permo-Carboniferous xenacanthid *Orthacanthus senkenbergianus*. Drawing by Nobu Tamura. Downloaded from [http:// en.wikipedia.org/ wiki/ File:Orthacanthus\\_BW.jpg](http://en.wikipedia.org/wiki/File:Orthacanthus_BW.jpg). H, the early Mesozoic *Hybodus*. Drawing by Nobu Tamura downloaded from [http:// en.wikipedia.org/ wiki/ File:Hybodus\\_NT.jpg](http://en.wikipedia.org/wiki/File:Hybodus_NT.jpg). A, C, and E-G are published under the GNU Free Documentation License; D is published under the Creative Commons Attribution-Share Alike 2.0 Generic license, and H, under version 3.0 of the same license.

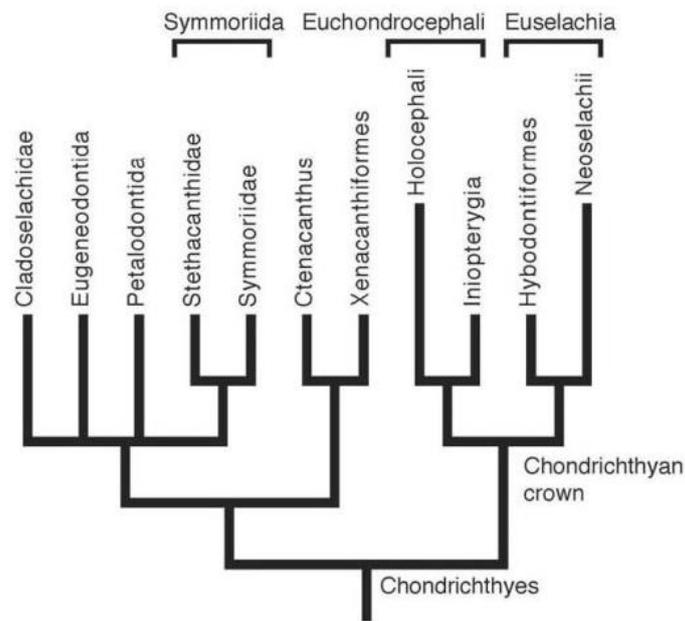


Figure 11. Chondrichthyan phylogeny. Most taxa shown here originated and became extinct in the Paleozoic; today, only Holocephali and Neoselachii (both drawn higher, for emphasis) survive. Redrawn from Janvier (1996: fig. 4.39) and Pradel et al. (2011).

Eugeneodontids (also called edestids) ranged from the Carboniferous to the Early Triassic. They possessed a median row of large, symphyseal teeth in the lower jaw. In *Helicoprion*, these were scrolled into a tooth whorl (Figure 10E). Most of their teeth consisted of several odontodes attached to a single base, although more simple scales with a single pulp cavity resembling more placoid scales are also known. The pectoral fins had a broad base, as in cladoselachids. Their body shape was variable, some looking like typical sharks, others like eels, and one (*Ornithoprion*) had a long rostrum on the lower jaw.

Petalodontids, known from the Carboniferous to the Permian, had teeth reminiscent of petals, hence their name. Their robust teeth, forming a sturdy bill, may have been used to eat coral. Their deep body form, reminiscent of some reef-dwelling teleosts, strengthens this interpretation.

The Late Devonian and Carboniferous Simmoriida had a very long metapterygial rod in the pectoral fin and a characteristic triangular endoskeletal support posterior to the dorsal fin. Claspers were present on the pelvic fin, suggesting internal fertilization. Contrary to most chondrichthyans, they had very few scales, located only over the head and fins. This group includes the Simmoriidae and the Stethacanthida. The latter had a strange dorsal “brush” or “club”, which probably represents modified anterior dorsal fins (Figure 10F). These are preceded by a large dermal spine, as in chondrichthyan dorsal fins, and are covered in large denticles. The dorsal “brush” or “club” may have been used in threat displays, to mimic a huge mouth. In some taxa, these strange structures occurred only in males suggesting the possibility that they were used in courtship behavior or in territorial display behavior, to intimidate other males. They had cladodont teeth. Their lateral-line canals were strengthened with small calcified rings, as

in holocephalans, which raises the possibility that these simmoriids were stem-holocephalans (although this is neither an established view, nor the hypothesis depicted in Figure 11).

The Xenacanthiformes, along with Ctenacanthiformes and Hybodontiformes, have long been thought to be related to Neoselachii, the extant sharks, skates and rays (Neoselachii includes about 1150 species). Together, these four taxa were classified into Elasmobranchii. However, some recent studies suggest that xenacanthiforms and ctenacanthiforms may be stem-chondrichthyans (Figure 11).

Xenacanthiforms have diplodont teeth (with two large, divergent cusps and a small, central cusp). The braincase had a long otico-occipital region, and their paired fins had a long metapterygial axis which had, in some taxa, postaxial radial giving the appearance of an archipterygium, as found in lungfishes. They had an anal fin, possibly a synapomorphy of elasmobranchs. Their dorsal fin was generally long (Figure 10G), in some members extending over the whole length of the back, up to the caudal fin. They extend from the Early Devonian to the Permian or Triassic. Some post-Devonian forms have long been considered to have inhabited freshwaters because they co-occur with limbed vertebrates (often inappropriately called “amphibians”; see below) in localities in which signs of marine influence were thought to have been absent. However, many of these localities have been re-interpreted as coastal, brackish to saltwater environments following more thorough paleoecological analyses.

Ctenacanthiformes may be paraphyletic and include a few clades of Devonian to Permian elasmobranchs. They had compound scales that grew by the addition of odontodes and cladodont teeth. Possible synapomorphies (if these are monophyletic) include a pectinate ornamentation of the dorsal fin spines and a broad otico-occipital region of the braincase.

Hybodontiformes lived from the Middle Devonian to the Late Cretaceous (Figure 10H). Their teeth had a long, low crown and numerous nutrient foramina in the low root. Their monophyly is suggested by a few characters, including calcified pleural ribs, two pairs of large, curved denticles on the head, smooth ridges of dentine on fin spines, and the low tooth crowns. However, some of these synapomorphies are not present in all taxa; some of the earliest had growing scales and high, cladodont teeth.

Neoselachian phylogeny is still in a state of flux. In the last two decades, some morphological phylogenies have suggested that batoids (skates and rays; Figure 10D) arose within Squalea, a group of sharks. However, more recent phylogenetic studies (both morphological and molecular) suggest instead that batoids are the sister-group of sharks, and that the latter comprise two main clades, Squalea and Galea (the most speciose clade of sharks). According to molecular dating and this hypothesis, batoids diverged from sharks in the Devonian (390 Ma); Squalea diverged from Galea in the Early Carboniferous (350 Ma). These dates are still poorly constrained because the fossil record of chondrichthyans is not the best, given that their endoskeleton is composed of calcified cartilage, which does not fossilize as well or as frequently as bone. Thus, many extinct chondrichthyans are known from teeth or fin spines only, which hampers assessing precisely their affinities. To exploit fully these fragmentary

remains, the enamel microstructure has been thoroughly studied in several taxa. However, the small teeth of several chondrichthyans were often neglected by paleontologists until at least the 1980s. Despite rapid progress being made in the last two decades, much remains to be done to better document the fossil record of chondrichthyans. Thus, it may not be surprising that the earliest neoselachian (crown-elasmobranch, or a closely related form) is reported from the Triassic, despite the fact that molecular phylogenies imply that these should appear in the Devonian (but the possibility that molecular estimates are too high cannot be dismissed either).

Holocephali (chimaeras, with over 50 extant species inhabiting mostly deep waters; Figure 10B) is known from the Devonian to the present. Molecular dating suggests that these Holocephali and Neoselachii diverged even earlier, possibly in the Ordovician (470 Ma). Some of the synapomorphies of crown-chondrichthyans include tribasal paired fins (with three basal cartilages that articulate with the girdles).

Chondrichthyans include several commercially important species, at least among elasmobranchs, which are consumed (rays, shark flesh, etc.). Unfortunately, the extremely wasteful practice of collecting the fins only to produce the “shark fin soup” is driving several species to extinction. Sharks have long been misunderstood by people, and movies such as “Jaws” have only exacerbated the problem by giving the impression that most sharks are very dangerous animals. In fact, sharks rarely attack humans, although a few species are indeed dangerous, but most attacks seem to result from errors on the part of the shark, who misidentified a human as a seal (part of the diet of some sharks), or on failure of divers to understand warning of a shark displaying territorial behavior. In any case, humans have proven far more dangerous to sharks than the reverse.

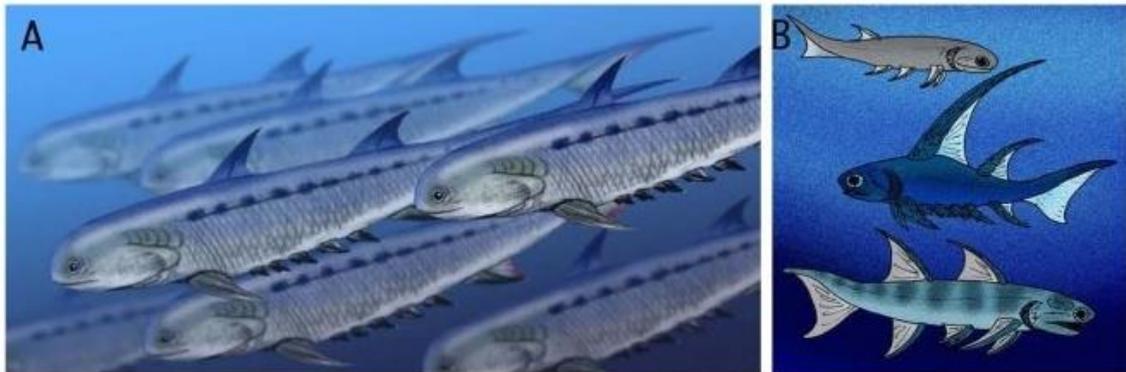


Figure 12. Acanthodians. A, The Devonian to Early Permian *Acanthodes*. B, *Mesacanthus*, *Parexus* (Early Devonian), and *Ischnacanthus* (Late Silurian to Early Devonian; from top to bottom). Drawings by Nobu Tamura (A) and Stanton F. Fink (B) published under the GNU Free Documentation License. Reproduced from Wikipedia ([http://en.wikipedia.org/wiki/File:Climatius\\_BW.jpg](http://en.wikipedia.org/wiki/File:Climatius_BW.jpg) for A and [http://en.wikipedia.org/wiki/File:Mesacanthus\\_Parexus\\_Ischnacanthus.JPG](http://en.wikipedia.org/wiki/File:Mesacanthus_Parexus_Ischnacanthus.JPG) for B).

-  
-  
-

TO ACCESS ALL THE 54 PAGES OF THIS CHAPTER,  
Visit: <http://www.eolss.net/Eolss-sampleAllChapter.aspx>

### Bibliography

Amson, E., Laurin, M. (2011). On the affinities of *Tetraceratops insignis*, an Early Permian synapsid, *Acta Palaeontologica Polonica* 56: 301–312. [Latest study of the oldest therapsid and phylogenetic study of the group]

Ballarin, L., Burighel, P. (2009). Tunicata and Cephalochordata. Biological Science Fundamentals and Systematics IV: (Minelli, A. and Contrafatto, G., Eds.), pp. 43–67. Ramsey, Isle of Man: Encyclopedia of Life Support System (EOLSS). [Survey of tunicate and cephalochordate general characteristics, development, and diversity]

Bardack, D. (1991). First fossil hagfish (Myxinoidea): a record from the Pennsylvanian of Illinois, *Science* 254: 701–703. [Description of a Late Carboniferous hagfish]

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Greyner, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A. (2007). The delayed rise of present-day mammals, *Nature* 446: 507–512. [Supertree-based, nearly exhaustive species-level dated molecular phylogeny of mammals]

Blieck, A. (2011). From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological approach, *Geologica Belgica* 14: 203–227. [Excellent review of the evolution of Paleozoic vertebrates, especially jawless forms, and of the geological and biological events that explain the paleobiodiversity patterns]

Blieck, A., Turner, S., Burrow, C.J., Schultze, H.-P., Rexroad, C.B., Bultynck, P. Nowlan, G.S. (2010). Fossils, histology, and phylogeny: Why conodonts are not vertebrates, *Episodes* 33: 234–241. [This paper reviews the recent controversy about the affinities of conodonts]

Botella, H., Blom, H., Korka, M., Ahlberg, P.E., Janvier, P. (2007). Jaws and teeth of the earliest bony fishes, *Nature* 448: 583–586. [Describes the stem-osteichthyans *Lophosteus* and *Andreolepis*, and provides a phylogeny of basal actinopterygians]

Botha, J., Abdala, F., Smith, R. (2007). The oldest cynodont: new clues on the origin and early diversification of the Cynodontia, *Zoological Journal of the Linnean Society* 2007: 477–492. [Description of the oldest known cynodont]

Currie, P.J. (1977). A new haptodontine sphenacodont (Reptilia: Pelycosauria) from the Upper Pennsylvanian of North America, *Journal of Paleontology* 51: 927–942. [Detailed anatomical description of a haptodontine]

Docker, M.F., Youson, J.H., Beamish, R.J., Devlin, R.H. (1999). Phylogeny of the lamprey genus *Lampetra* inferred from mitochondrial cytochrome b and ND3 gene sequences, *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2340–2349. [Molecular phylogeny of the lamprey taxon *Lampetra* with a review of the ontogeny and lifestyle of lampreys]

Dunn, C.W., Hejnal, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., Martin V. Sørensen, Haddock, S.H.D., Schmidt-Rhaesa, A., Okusu, A., Kristensen, R.M., Wheeler, W.C., Martindale, M.Q., Giribet, G. (2008). Broad phylogenomic sampling improves resolution of the animal tree of life, *Nature* 452: 745–749. [Recent molecular phylogeny of all metazoans discussing the phylogeny of chordates]

Friedman, M. (2007). *Styloichthys* as the oldest coelacanth: implications for early osteichthyan

interrelationships, *Journal of Systematic Palaeontology* 5: 289–343. [Thorough phylogenetic analysis of early sarcopterygians]

Gardiner, B.G., Schaeffer, B., Massarie, J.A. (2005). A review of the lower actinopterygian phylogeny, *Zoological Journal of the Linnean Society* 144: 511–525. [Recent morphology-based phylogenetic analysis of extant and extinct actinopterygians]

Gill, H.S., Renaud, C.B., Chapleau, F., Mayden, R.L., Potter, I.C. (2003). Phylogeny of living parasitic lampreys (Petromyzontiformes) based on morphological data, *Copeia* 2003: 687–703. [Morphological phylogeny of parasitic lampreys]

Goujet, D. (2011). “Lungs” in Placoderms, a persistent palaeobiological myth related to environmental preconceived interpretations, *Comptes rendus Palevol* 11: 323–329. [Critical review of the idea that placoderms had lungs]

Graham, J.B. (1997). *Air-Breathing Fishes—Evolution, Diversity and Adaptation*, 299 pp. London, Academic Press. [Good review of air-breathing adaptations in actinopterygians and dipnoans]

Heinicke, M.P., Naylor, G.J.P., Hedges, S.B. (2009). Cartilaginous fishes (Chondrichthyes). The Timetree of Life: (Hedges, S. B. and Kumar, S., Eds.), pp. 320–327. New York: Oxford University Press. [Recent large-scale molecular dating of chondrichthyan diversification]

Janvier, P. (1996a). *Early vertebrates*, 393 pp. Oxford, Oxford University Press. [Best review of all early vertebrates, from their origin, to the origin of limbed vertebrates in the Devonian]

Janvier, P. (1996b). The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies, *Palaeontology* 39: 259–287. [Most widely accepted phylogeny of early vertebrates, especially the jawless taxa]

Kuo, C.-H., Huang, S., Lee, S.-C. (2003). Phylogeny of hagfish based on the mitochondrial 16S rRNA gene, *Molecular Phylogenetics and Evolution* 28: 448–457. [Molecular phylogeny of hagfishes]

Lacalli, T.C. (2005). Protochordate body plan and the evolutionary role of larvae: old controversies resolved?, *Canadian Journal of Zoology* 83: 216–224. [Review of chordate anatomy, development, and scenarios on the origin of craniates]

Laurin, M. (1993). Anatomy and relationships of *Haptodus garnettensis*, a Pennsylvanian synapsid from Kansas, *Journal of Vertebrate Paleontology* 13: 200–229. [Detailed anatomical study of one of the oldest synapsids and phylogeny of haptodontines]

Laurin, M. (1998). New data on the cranial anatomy of *Lycaenops* (Synapsida, Gorgonopsidae), and reflections on the possible presence of streptostyly in gorgonopsians, *Journal of Vertebrate Paleontology* 18: 765–776. [Anatomical and functional study of the gorgonopsian skull]

Laurin, M. (2004). The evolution of body size, Cope's rule and the origin of amniotes, *Systematic Biology* 53: 594–622. [Study of body size evolution in Permo-Carboniferous stegocephalians]

Laurin, M. (2008). *Systématique, paléontologie et biologie évolutive moderne : l'exemple de la sortie des eaux des vertébrés*, 176 pp. Paris, Ellipses. [Review of how vertebrates became terrestrial and about basic principles of paleontology, paleobiology, phylogenetics, and biological nomenclature, in French]

Laurin, M. (2010). *How Vertebrates Left the Water*, xv + 199 pp. Berkeley, University of California Press. [Review of how vertebrates became terrestrial and about basic principles of paleontology, paleobiology, phylogenetics, and biological nomenclature; updated English translation of Laurin (2008)]

Laurin, M., Anderson, J.S. (2004). Meaning of the name Tetrapoda in the scientific literature: an exchange, *Systematic Biology* 53: 68–80. [Review of the nomenclature of limbed vertebrates]

Laurin, M., Reisz, R.R. (1995). A reevaluation of early amniote phylogeny, *Zoological Journal of the Linnean Society* 113: 165–223. [Phylogeny of early amniotes]

Laurin, M., Reisz, R.R. (1996). The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid, *Journal of Vertebrate Paleontology* 16: 95–102. [First detailed anatomical description of the oldest known therapsid]

Laurin, M., Soler-Gijón, R. (2001). The oldest stegocephalian from the Iberian Peninsula: evidence that temnospondyls were euryhaline, *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la*

*Life sciences* 324: 495-501. [Description of the temnospondyl *Iberospondylus schultzei*, along with a discussion of the habitat of temnospondyls]

Laurin, M., Soler-Gijón, R. (2010). Osmotic tolerance and habitat of early stegocephalians: indirect evidence from parsimony, taphonomy, paleobiogeography, physiology and morphology. *The Terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface* 339: (Vecoli, M. and Clément, G., Eds), pp. 151–179. London: The Geological Society of London. [Review of the paleoenvironment represented by several Permo-Carboniferous localities that have yielded fossil vertebrates, and the implications for the evolution of saltwater tolerance in limbed vertebrates]

Laurin, M., Everett, M.L., Parker, W. (2011). The cecal appendix: one more immune component with a function disturbed by post-industrial culture, *The Anatomical Record* 294: 567–579. [Review of the evolution of the appendix in mammals in an explicit phylogenetic context]

Müller, J. (2003). Early loss and multiple return of the lower temporal arcade in diapsid reptiles, *Naturwissenschaften* 90: 473-476. [Concise, legible basal diapsid phylogeny]

Orlov, Y.A. (1958). Primitive dinocephalians of the Isheeva fauna (Titanosuchi) 72: 1-113. [Review of a group of dinocephalian therapsids]

Otto, M., Laurin, M. (1999). Osteostracan tesseræ from the Baltic Middle Devonian: morphology and microanatomy, *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1999: 464-476. [Description of the isolated tesseræ of one of the geologically youngest osteostracan]

Otto, M., Laurin, M. (2001). Microanatomy of the dermal skeleton of *Balticaspis latvica* (Osteostraci, Middle Devonian), *Journal of Vertebrate Paleontology* 21: 186-189. [Description of the unfused tesseræ of one of the geologically youngest osteostracan, along with a discussion of the reduction of ossification found in the latest members of that clade]

Pradel, A., Tafforeau, P., Maisey, J.G., Janvier, P. (2011). A new Paleozoic Symmoriiformes (Chondrichthyes) from the Late Carboniferous of Kansas (USA) and cladistic analysis of early chondrichthyans, *PLoS ONE* 6: 1–22. [Description of a well-preserved Late Carboniferous chondrichthyan and one of the latest phylogenetic analyses of the main chondrichthyan clades]

Reisz, R.R., Laurin, M. (1991). *Owenetta* and the origin of turtles, *Nature* 349: 324–326. [Description of the parareptile *Owenetta* and of its synapomorphies with turtles]

Reisz, R.R., Laurin, M. (2004). A reevaluation of the enigmatic Permian synapsid *Watongia* and of its stratigraphic significance, *Canadian Journal of Earth Sciences* 41: 377-386. [Anatomical study of one of the latest and largest varanopid synapsids]

Romer, A.S., Price, L.I. (1940). *Review of the Pelycosauria*, 538 pp. New York, Arno Press. [Extremely thorough anatomical and taxonomic review of Permo-Carboniferous synapsids]

Schultze, H.-P. (2004). Mesozoic sarcopterygians. *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*: (Eds. Arratia, G. and Tintori, A.), pp. 463–492. München, Germany: Dr. Friedrich Pfeil. [Review of Mesozoic sarcopterygian phylogeny, diversity, and morphological evolution]

Schultze, H.-P. (2009). Interpretation of marine and freshwater paleoenvironments in Permo–Carboniferous deposits, *Palaeogeography, Palaeoclimatology, Palaeoecology* 281: 126–136. [Review of the paleoenvironment represented by several Permo-Carboniferous localities that have yielded fossil vertebrates]

Swartz, B.A. (2009). Devonian actinopterygian phylogeny and evolution based on a redescription of *Stegotrachelus finlayi*, *Zoological Journal of the Linnean Society* 156: 750–784. [Good review of actinopterygian phylogeny with emphasis on the relationships between Paleozoic and the main extant taxa, along with an original phylogenetic analysis]

Shu, D., Luo, H.-L., Conway Morris, S., Zhang, X.-L., Hu, S.-X., Chen, L., Han, J., Zhu, M., Li, Y., Chen, L.-Z. (1999). Lower Cambrian vertebrates from south China, *Nature* 402: 21-22. [This paper describes the oldest known craniate]

Smith, M.M., Hall, B.K. (1993). A developmental model for evolution of the vertebrate exoskeleton and teeth. *Evolutionary Biology* 27: (Ed. Hecht, M. K.), pp. 387-448. New York: Plenum Press. [Discussion of the evolution of dentin]

Tsagkogeorga, G., Turon, X., Hopcroft, R.R., Tilak, M.-K., Feldstein, T., Shenkar, N., Loya, Y., Huchon, D., Douzery, E.J.P., Delsuc, F. (2009). An updated 18S rRNA phylogeny of tunicates based on mixture and secondary structure models, *BMC Evolutionary Biology* 9: 187. doi:10.1186/1471-2148-9-187. [This includes the most recent phylogeny of urochordates]

Underwood, C.J. (2006). Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous, *Paleobiology* 32: 215–235. [Review of the elasmobranch fossil record in a phylogenetic context]

Venczel, M., Gardner, J.D. (2005). The geologically youngest albanerpetontid amphibian, from the Lower Pliocene of Hungary, *Palaeontology* 48: 1273-1300. [Description of albanerpetontid anatomy]

West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution*, xx+794 pp. New York, Oxford University Press. [Book that presents the concept of recurrent phenotypes, which may explain the distribution of many histological characters in vertebrates]

Zeng, L., Swalla, B.J. (2005). Molecular phylogeny of the protochordates: chordate evolution, *Canadian Journal of Zoology* 83: 24–33. [A good general review of chordates with emphasis on Tunicata]

Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T., Qu, Q. (2009). The oldest articulated osteichthyan reveals mosaic gnathostome characters, *Nature* 458: 469–474. [Description of the earliest, Silurian sarcopterygian and of the early evolution of that clad]

### Biographical Sketch

**Michel Laurin** received his PhD at the University of Toronto in 1994, and did a first postdoc at Berkeley (1994-1996). He then moved to Paris (1996-1997), where he worked as associate invited professor in the University Paris 7, where he lectured on paleontology, the evolution of animals, biological nomenclature, and other related topics. He then did a last postdoc in Berlin (1997-1998), in the Natural History museum. He was hired by the CNRS as a research scientist 1998. He has published several scientific papers, in addition to a book on paleontology and systematics in French and English. He has led the team “Squelette des vertébrés” for two years (2007–2008). He is a member of several scientific societies, and has served the *ISPN (International Society for Phylogenetic Nomenclature)* as both Secretary (two terms, including a current one) and President. He currently serves on nine editorial boards, including for the *Journal of Evolutionary Biology*. In January 2011, he has become Chief Editor of the *Comptes Rendus Palevol*. He has studied the evolution of vertebrates from the Cambrian to the present, and has covered most of their evolution, from early jawless vertebrates to extant mammals. His current interests include comparative methods and dating the tree of life, and he has tackled problems as diverse as the invasion of land by vertebrates, the appearance of the tympanum (ear drum), and origin of extant amphibians. He has introduced innovations in paleontology and paleobiology, notably in the form of computer programs, some of which can be used to perform paleontological dating of the tree of life or to analyze bone microanatomical data.