

BIOLOGY 524
ADVANCED VERTEBRATE MORPHOLOGY
-OSTEOLOGY-

POSTCRANIAL SKELETON – I
AXIAL SKELETON

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INTRODUCTION

The axial skeleton is generally considered one of the hallmark features of vertebrates; it is after all, the namesake of the group. However, the idea that the group was defined by having vertebrae or a vertebral column turns out to be an oversimplification.

NOTOCHORD

In fact, the beginnings of the axial skeleton of vertebrates, both embryologically and phylogenetically is not about the vertebral column. Rather it is about the notochord. The notochord:

- Derived from mesoderm
- A trans-segmental structure immediately ventral to the dorsal hollow nerve cord.
- A laterally flexible, but incompressible rod, that prevents telescoping of the body in primitive vertebrates, as well as embryos.
- It does not become the vertebral column, but is replaced in varying degrees by structures of the sklerotome of the somite.

VERTEBRAL COLUMN AND ASSOCIATED STRUCTURES

Most of the story of the axial skeleton is about the vertebral column (backbone; spinal column, spine). However, associated ribs in gnathostomes, as well as sternal structures in birds and mammals are also significant. Through the evolution of the vertebral column, we will track the following significant trends:

- Eventual replacement of the notochord (in whole or in part) by vertebrae.
- Reorganization of sklerotomal materials to facilitate terrestrial biomechanics.

- Differing trajectories of emphasis on different structures depending on whether tetrapods remain aquatic or become more terrestrially adapted.
- Development and consolidation of the atlas-axis complex.
- In mammals and birds, the development of regionally specialized sections of the vertebral column.

AXIAL STRUCTURE IN PRIMITIVE VERTEBRATES

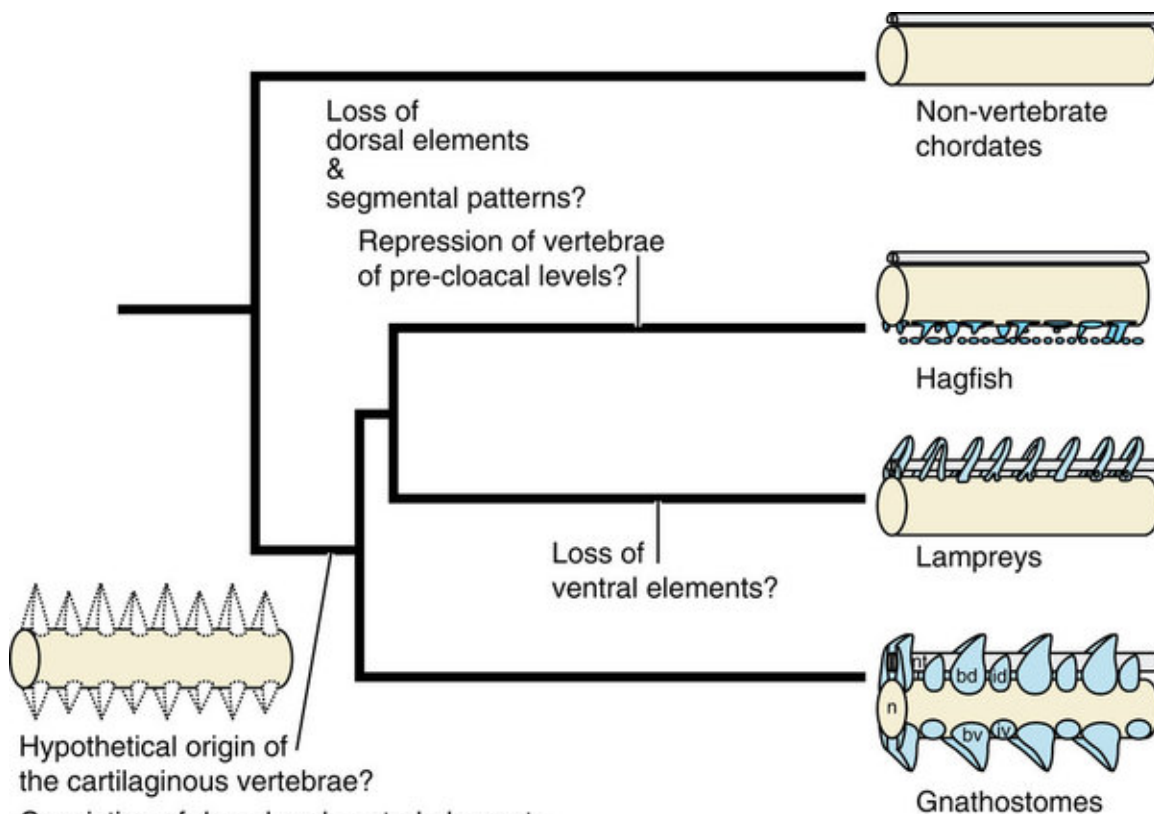
The subphylum Vertebrata is defined by the presence of ectodermal placodes and neural crest tissue and structures that develop from them. The reason the “Vertebrata is not defined by vertebrae” is because the most basal of vertebrates do not in fact have a true vertebral column.

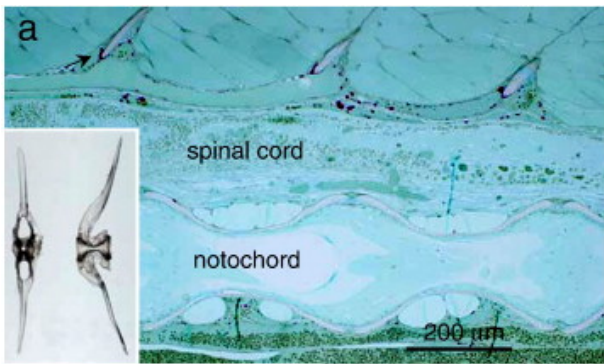
(This is where someone is supposed to say, “Ironic, isn’t it?)

Agnathans and even primitive gnathostomes do not have a fully ossified vertebral column. Fossil agnathans show little or no evidence of an ossified vertebral column. With such highly developed dermal armor, it may not have been necessary.

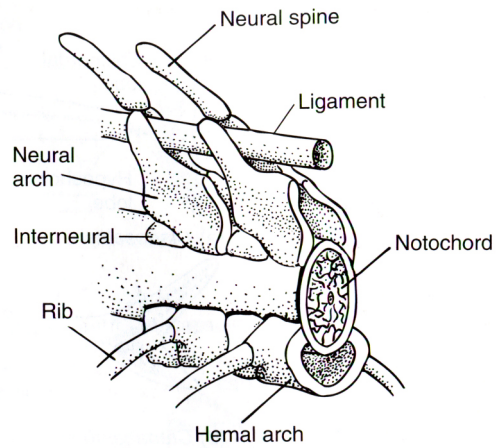
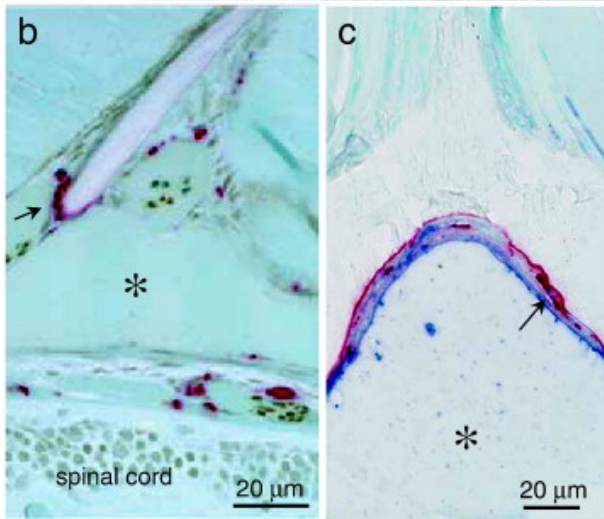
Living agnathans do not have much in the way of vertebral structures either.

- Hagfish: small, poorly developed haemal arches.
- Lampreys: small, poorly developed neural arches.





Even primitive living gnathostomes only have structures dorsally and ventrally, with the notochord remaining the majority of the mass of the axial skeleton. Not the primitive bony fish condition below.

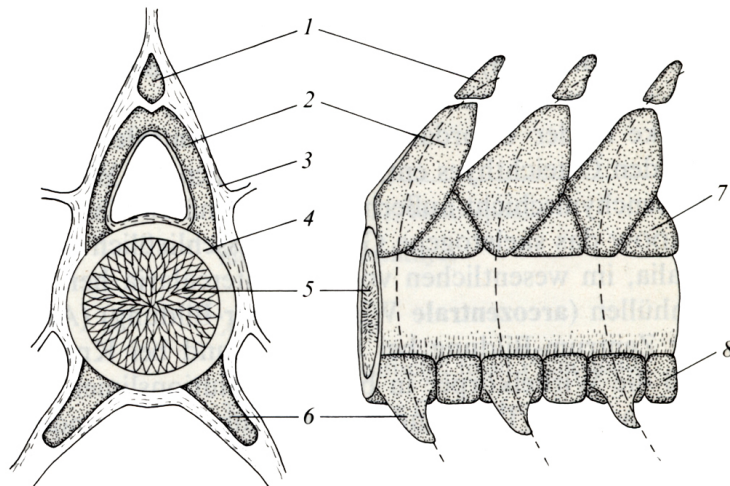


Where dorsal structures rest on the top of the notochord, and ventral structures attach to the underside of the notochord, there are often supporting

plugs of material that are dense, and occasionally even become calcified cartilage.

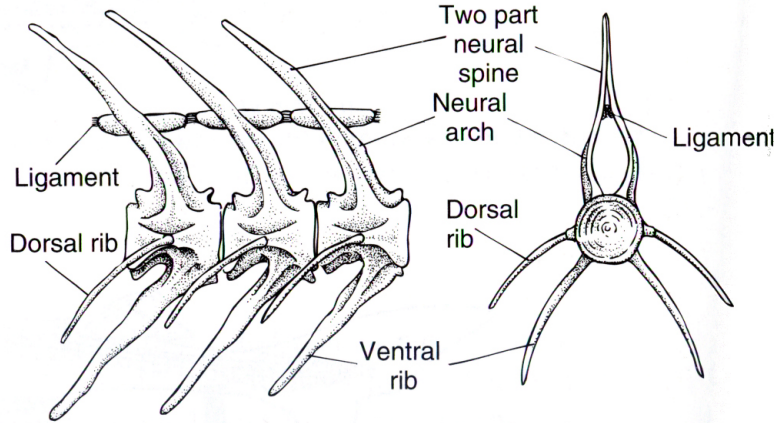
These are known as **ARCH BASES**.

- 1 Spinale
- 2 Basidorsale
- 3 Bindegewebige Umhüllung
- 4 Chordascheiden
- 5 Chorda dorsalis
- 6 Basiventrals
- 7 Interdorsale
- 8 Interventrals



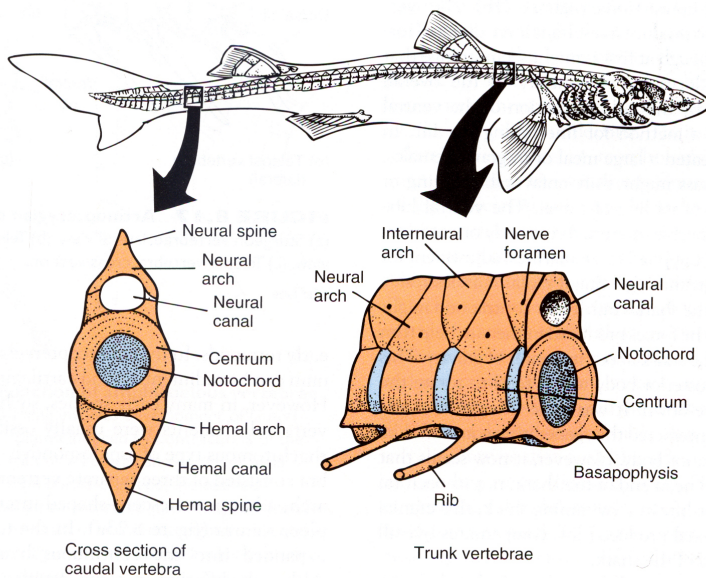
AXIAL SKELETON IN MORE DERIVED FISHES

In more derived fishes the structures that reinforce the notochord and eventually come to replace part of the notochord develop.



- The **CENTRUM** or vertebral body is present as an externally cylindrical structure that replaces the notochord in part.
- The centrum is surmounted by the **NEURAL ARCH**, the right and left side of which unite to become the neural spine dorsally.
- Often two sets of ribs are present, plunging into the mass of the axial musculature. These are **DORSAL RIBS** and **VENTRAL RIBS**.

VERTEBRAL STRUCTURE IN CHONDRICHTHYES

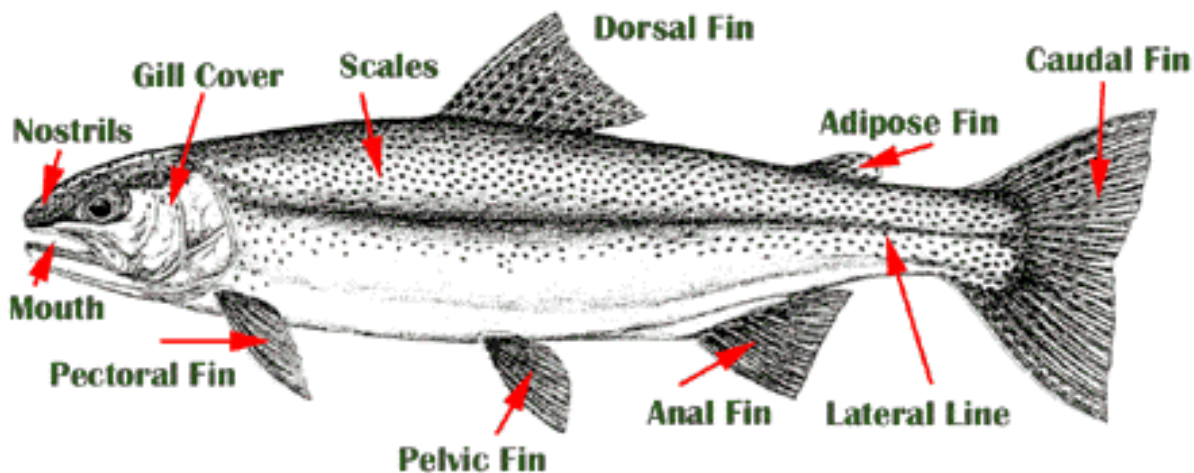
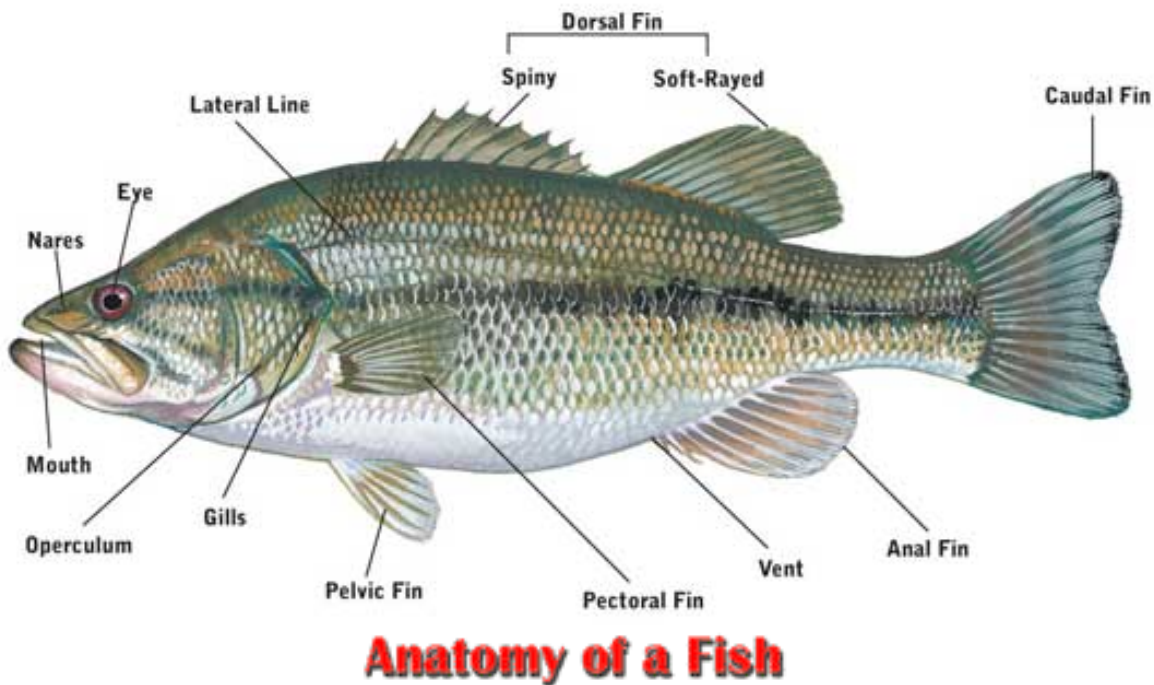


Sharks and their relatives have fully developed vertebral central, as well as neural arches. In the tail region, HAEMAL ARCHES combine to protect the caudal extension of the dorsal aorta.

In the trunk region, the neural arches are triangular in outline laterally. This would leave a series of triangular spaces between each neural arch. But in sharks these spaces are plugged by structures known as INTERCALARY PLACES, or interneural plates.

Vertebral central are NOTOCHORDAL, with the notochord persisting and running through the center of each centrum.

MEDIAN FINS OF FISHES



Fishes have midline structures that are most properly considered with the axial skeleton, especially as they are usually supported by midline extensions away from the vertebral column. **UNPAIRED MEDIAN FINS include:**
 One or more dorsal fins.

In salmonid fishes, the second of the dorsal fins is fleshy with no bony support, and called an **ADIPOSE FIN**.

An **ANAL FIN**, sometimes called a ventral fin.

The **TAIL FIN**.

Tail fins take on many different morphologies, particularly in terms of their internal, supporting endoskeleton. The varieties of tail fin morphologies include:

HOMOCERCAL – tail that looks externally symmetrical, but may not be internally. (There are many ways to build a homocercal tail.)

HETEROCERCAL - tail in which longer lobe is dorsal, usually with vertebral column continuing into it.

HYPOCERCAL – tail in which longer lobe is ventral, usually with vertebral column continuing into it.

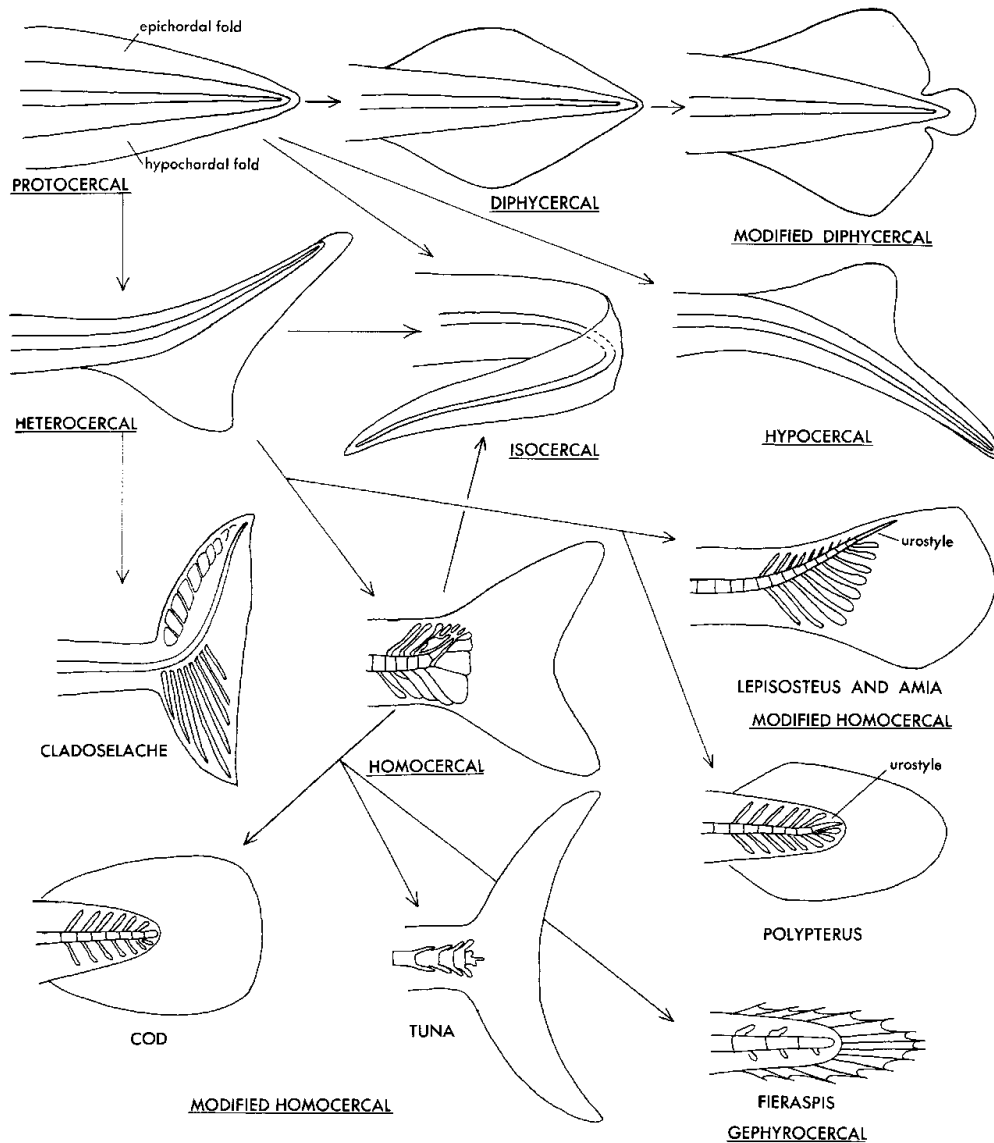
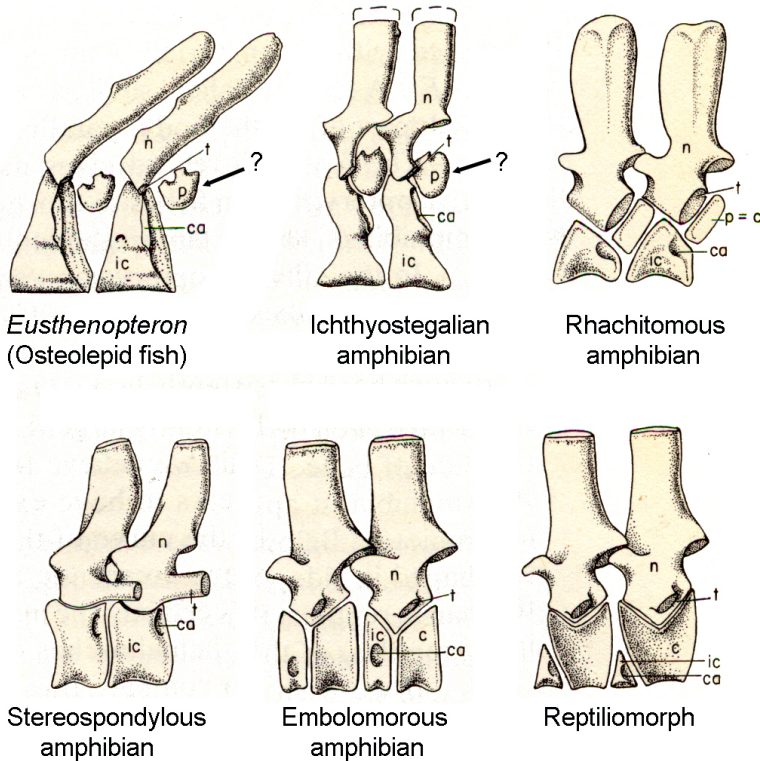


Figure 6-42. Evolution of tail fins in fishes.

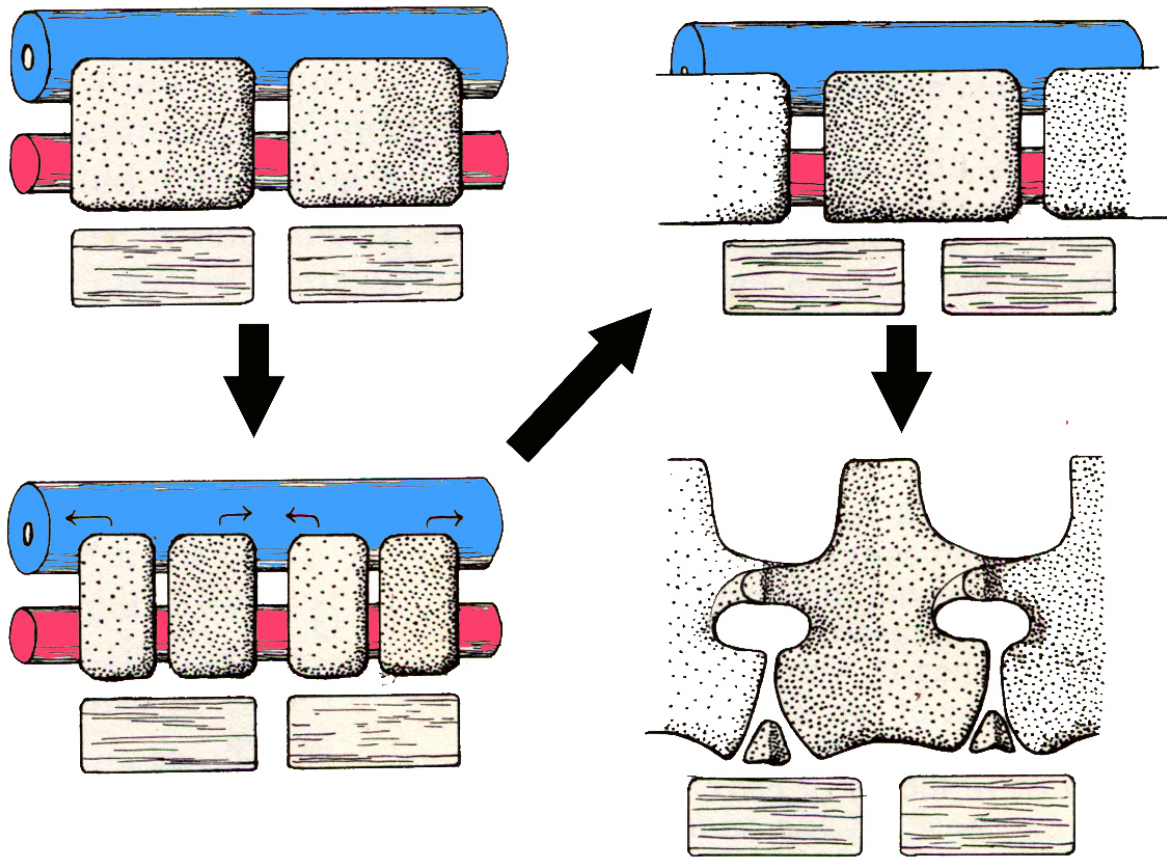
VERTEBRAL STRUCTURE FROM CROSSOPTERYGIAN FISHES TO THE EARLIEST TETRAPODS



- Vertebral centra of crossopterygians are wedge-shaped, and triangular in outline in lateral view. Small accessory structures sometimes called pleurocentra (singular = pleurocentrum) may actually be intercalary plates.
- Neural arches become somewhat more erect.
- And although the earliest tetrapods appear to have remained largely aquatic, they must have had to deal with gravity and the needs for support at least on occasion, as they do demonstrate the development of zygapophyses.
- **ZYGAPOPHYSES** are structures for articulation between successive vertebral structures so that each vertebra rests partially on the vertebra immediately caudal to it. This helps resist ventral-ward collapse of the column in tetrapods.

In the above diagrams you will notice that the vertebral bodies/centra are multipartite, labeled “IC” and “PC”, which stand for **INTERCENTRUM** and **PLEUROCENTRUM** respectively.

To understand the difference between the two, the early embryology of the vertebra must be understood. To understand that, recall that the segmental somites are subdivided into dermatome, myotome, and sklerotome. Key here is the sklerotome that will give rise to vertebral structures, and the myotome which gives rise to the musculature that attaches to that skeletal structure.



- Note that the developing sklerotome (above) and myotome are initially in line with one another.
- This is not an advantageous means of attachment if the muscle is to act across a joint.
- Each sklerotome SPLITS into a cranial half and a caudal half, which then migrate away from one another.
- This causes the cranial half of one sklerotome and the caudal half of that immediate forward of it to move toward one another.
- When they touch the like tissues fuse, giving rise to a vertebral structure that is built from caudal and cranial halves of adjacent sklerotomes.
- This results in myotomes/muscle blocks now spanning intervertebral joints, generating a condition more useful for stabilizing the vertebral column and RESISTING SAGGING DUE TO GRAVITY.
- This is clearly an adaptation for terrestrial conditions.
- This reorganized vertebra type is a PLEUROCENTRUM.
- A vertebra that does not go through this reorganization is known as an INTERCENTRUM. Notably, even when much of the vertebra resegments, sometimes small parts of the original sklerotome does not. This is the intercentrum.

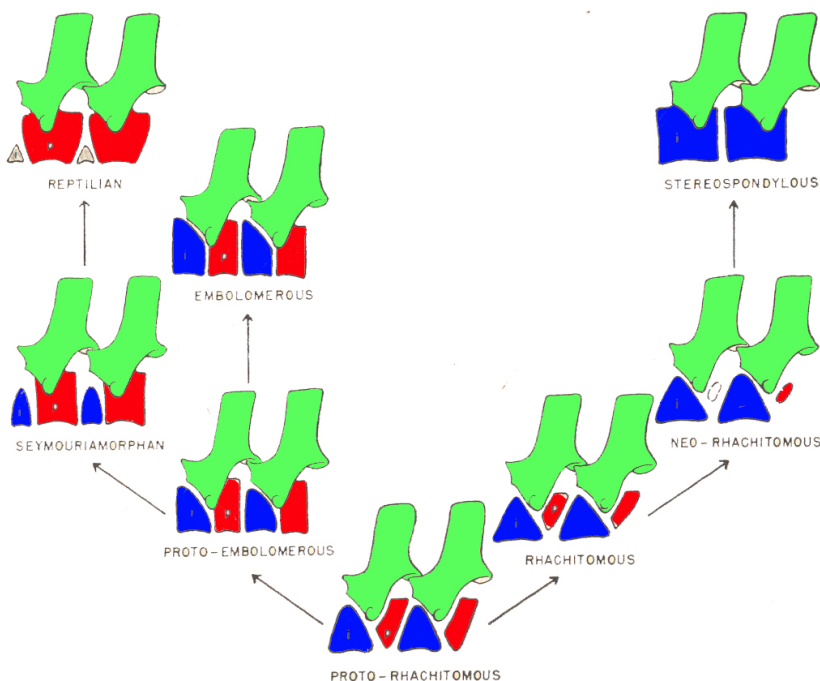
NOTE! The original condition — i.e. the fish condition, the aquatic condition – is NOT to resegment. To remains as an intercentrum.

What we will see is that those lineages of tetrapods that come to be more and more terrestrially adapted will come to emphasize the pleurocentrum more and more. This will included the lineage leading to Amniota.

Conversely, some early tetrapod lineages never truly left the water, and some became obligate aquatic organisms. In other words, they continued to mostly swim. Those groups came to continue the emphasis on the intercentrum.

Below we can see two main lineages of basal tetrapods. One lineage, that leading from crossopterygian fishes has a small pleurocentrum for a bit but eventually it is abandoned and the intercentrum is the only component of the vertebral body. (In this case color-coded blue).

On the other hand, the lineage that lead toward more completely terrestrial amniotes emphasized the pleurocentrum, (In this case color-coded red.) and the intercentrum became smaller and smaller.



How can you tell an intercentrum from a pleurocentrum in a fossil with no development to watch? Note that from fishes on, the ribs articulate with the neural arch and the **intercentrum**.

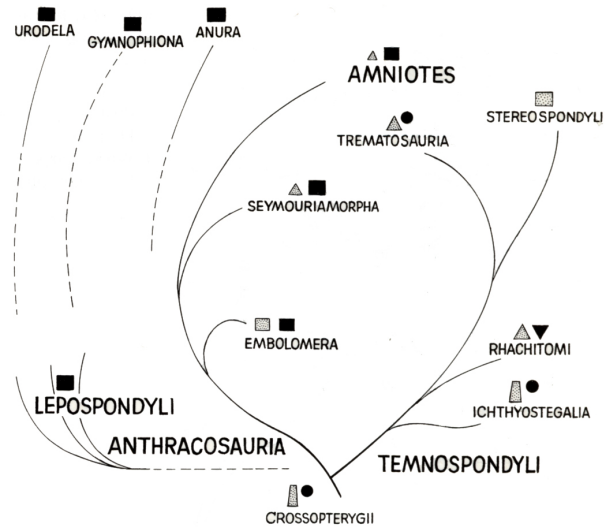
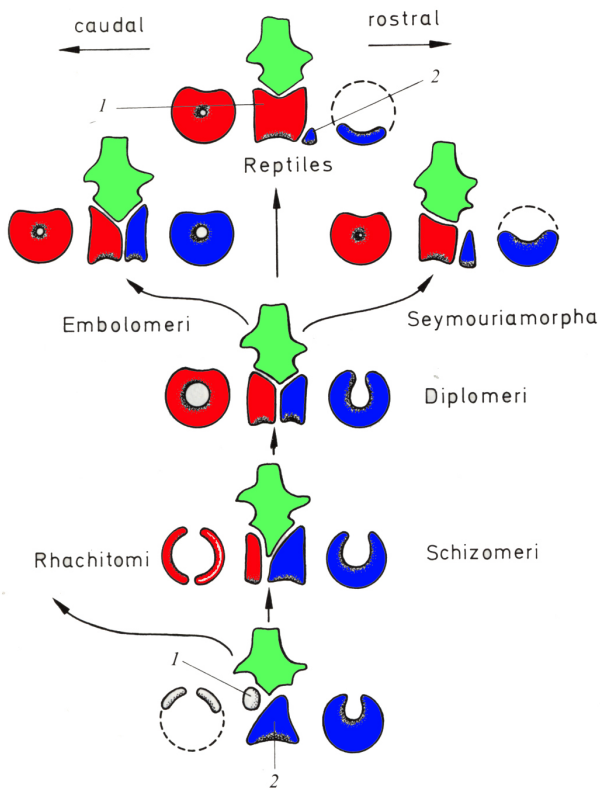
The names of the large groups of Paleozoic tetrapods are generally given based on their vertebral structure:

- The Rhachitomi have a “rachitomous” condition of alternating wedges intercentra and pleurocentra.
- The “stereospondylous” condition of the Stereospondyli is that of a single cylindrical intercentrum and no pleurocentrum.

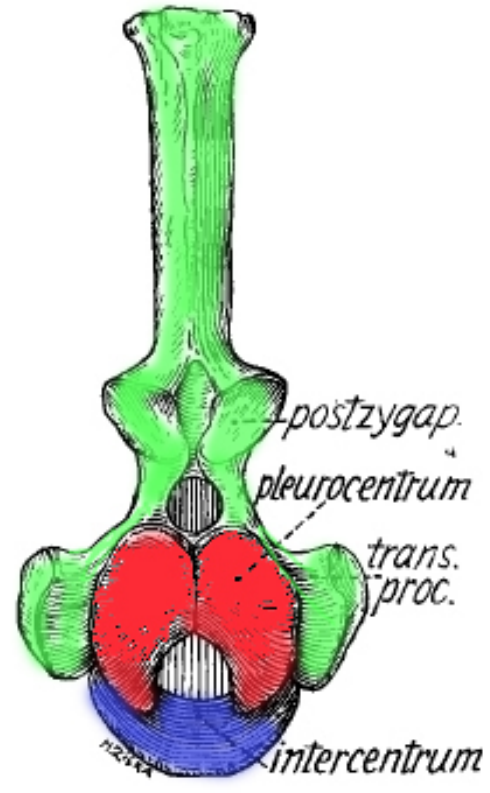
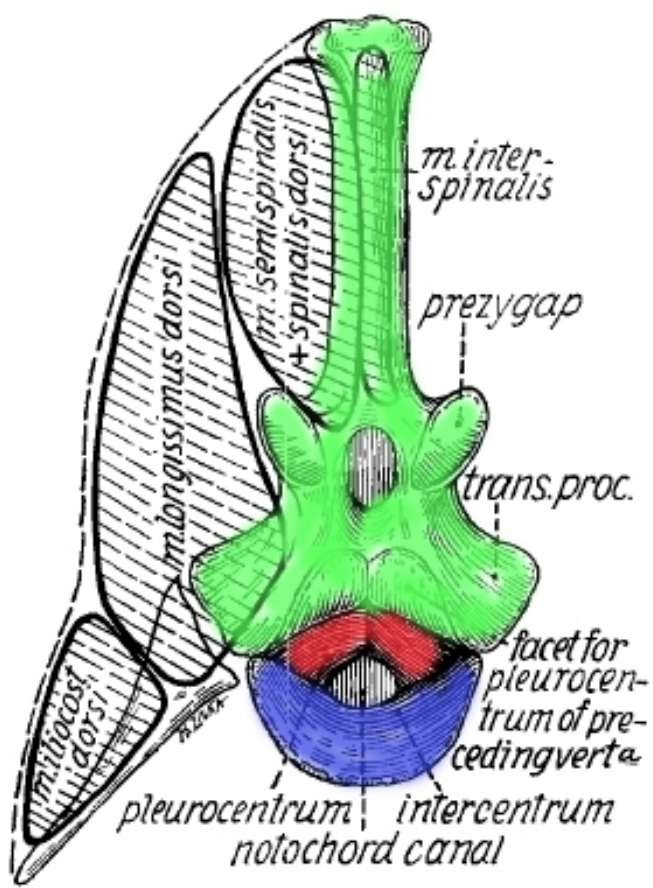
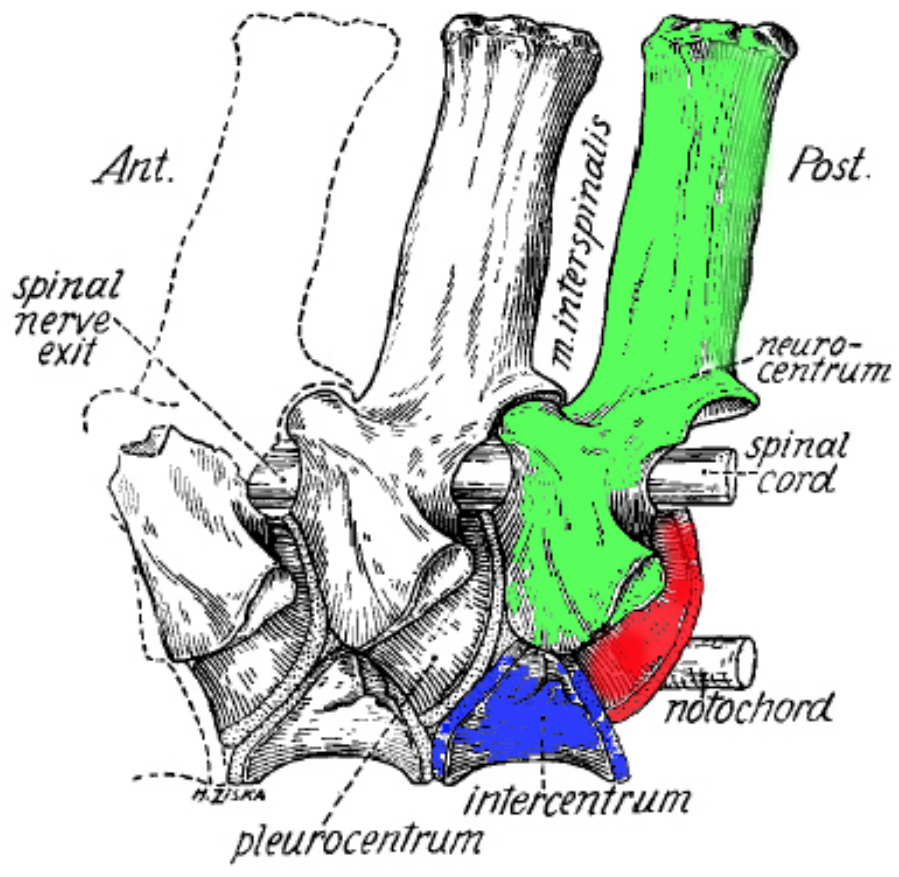
On the lineage leading to Amniota:

- Embolomeri with the “embolomerous” condition have centra made of two distinct disc-like structures, one the interentrum, the other the pleurocentrum.
- Seymouriamorpha have a dominant pleurocentrum and smaller intercentrum. The intercentrum must have been continued dorsally as cartilage, but the pleurocentrum is clearly becoming dominant.
- Amniota has a large pleurocentrum, and only tiny intercentrum though it is present and does accept the costal articulation.

Following are two more ways of visualizing the major vertebral types.

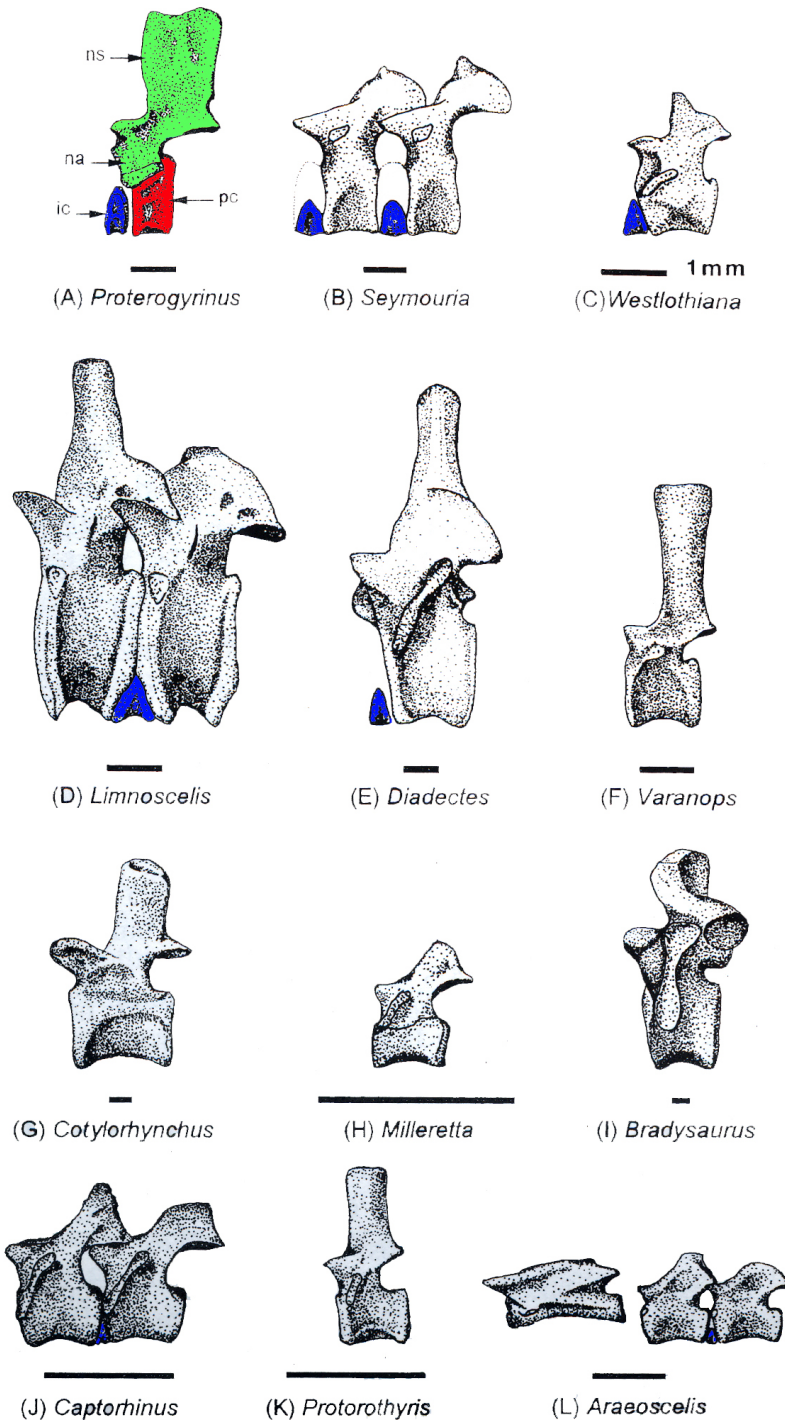


Following is an illustration of the Early Permian tetrapod/amphibian *Eryops*. It is color coded to match the schemes in above diagrams.



VERTEBRAL STRUCTURE IN AMNIOTA

Following is a survey of vertebrae of various vertebrate genera, most of which are amniote or close relatives.



After the example of the very terrestrially adapted amphibians *Proterogyrinus*, only the intercentra are color-coded for reference.

Note that in some cases two successive vertebrae are illustrated. This is because in many Late Paleozoic tetrapods, there was an alternation in structure of the neural spines between tall, cylindrical, robust spines, and those with low, narrow or non-existent spines.

This phenomenon was probably to give interspinous musculature a greater potential range of contraction.

Limnoscelis and *Diadectes* belong to a group known as DIALECTOMORPHA. They are very amniote-like, and may well have been amniotes for all we know

The remainder of taxa illustrated are either basal reptiles or basal synapsids.

ATLAS-AXIS COMPLEX

Tetrapods also begin to develop specialized modifications of the first two vertebrae to facilitate support and movement of the large head.

Amniotes and those closely related to them show a particularly diagnostic condition. See the situation in the diadectomorph *Diadectes* below.

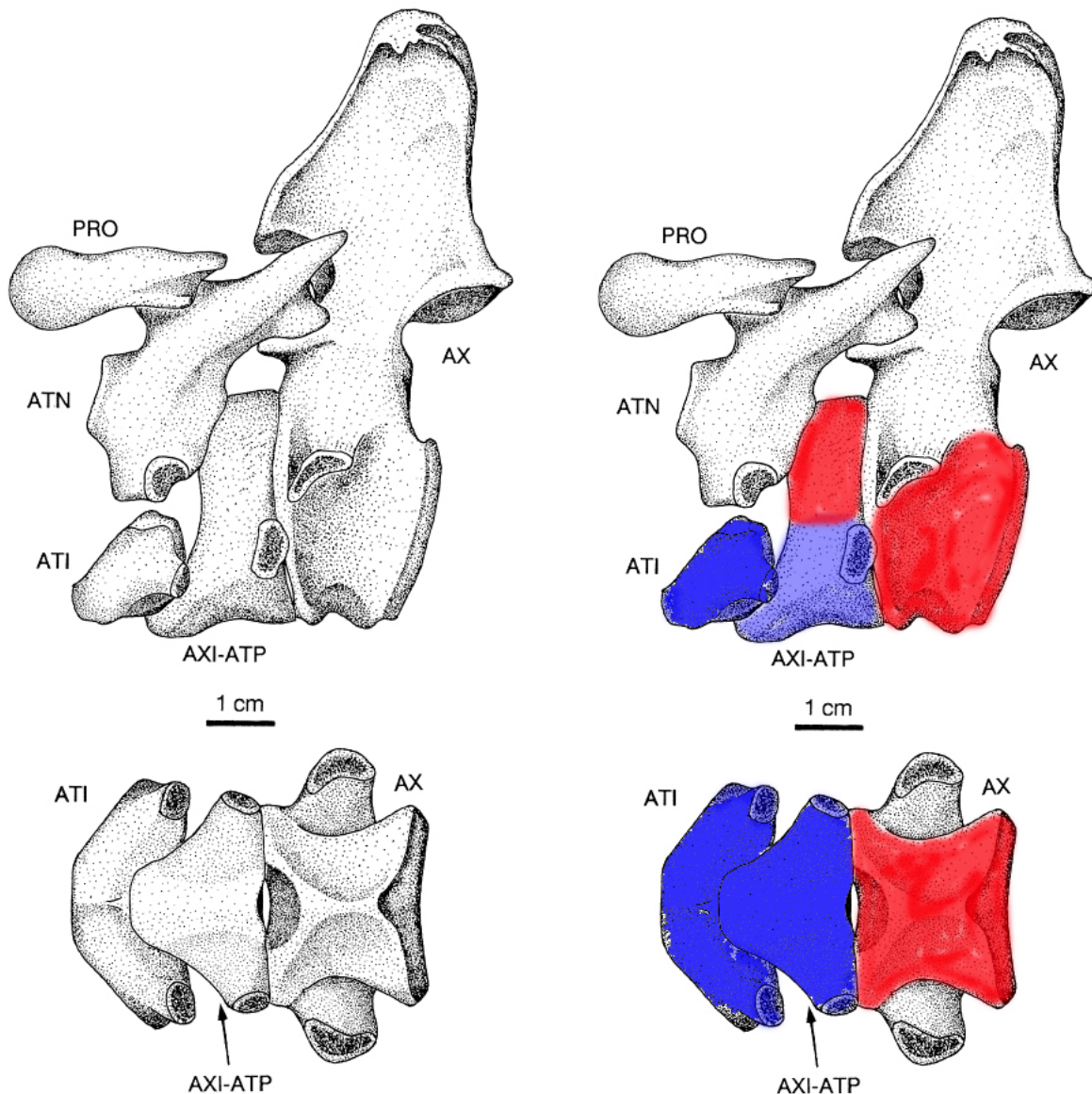
Atlantal intercentrum is an independent structure.

Right and left **atlantal neural arches** are independent structures, and do not fuse in the dorsal midline.

The **axial intercentrum** comes to underlie the **atlantal pleurocentrum** – excluding the axial pleurocentrum from ventral exposure on the underside of the vertebral column.

A small right and left **proatlas** provide articulation for the atlantal neural arches with the occipital region of the skull

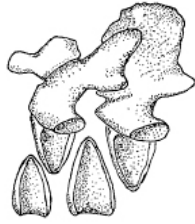
The **axis** is very robust, as is the very large neural spine.



Following is a survey of atlas-axis complex structure in amniotes and their near relatives. Note the similarities.



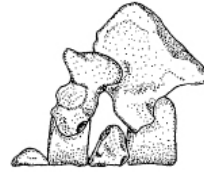
Eryops



Greererpeton



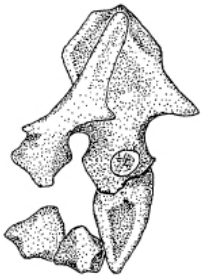
Archeria



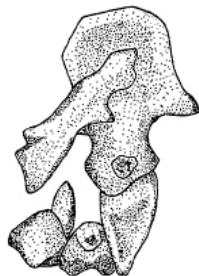
Gephyrostegus



Proterogyrinus



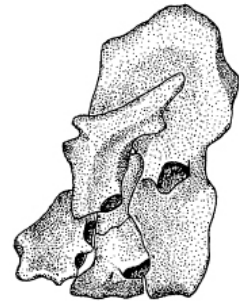
*Seymouria
sanjuanensis*



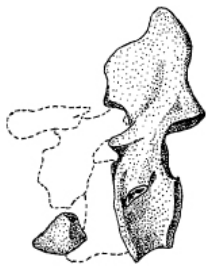
*Seymouria
baylorensis*



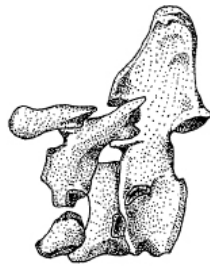
Tseajaia



Limnoscelis



Diasparactus



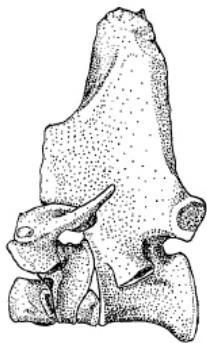
Diadectes



Cotylorhynchus



Ophiacodon



Dimetrodon



Captorhinus



Paleothyris

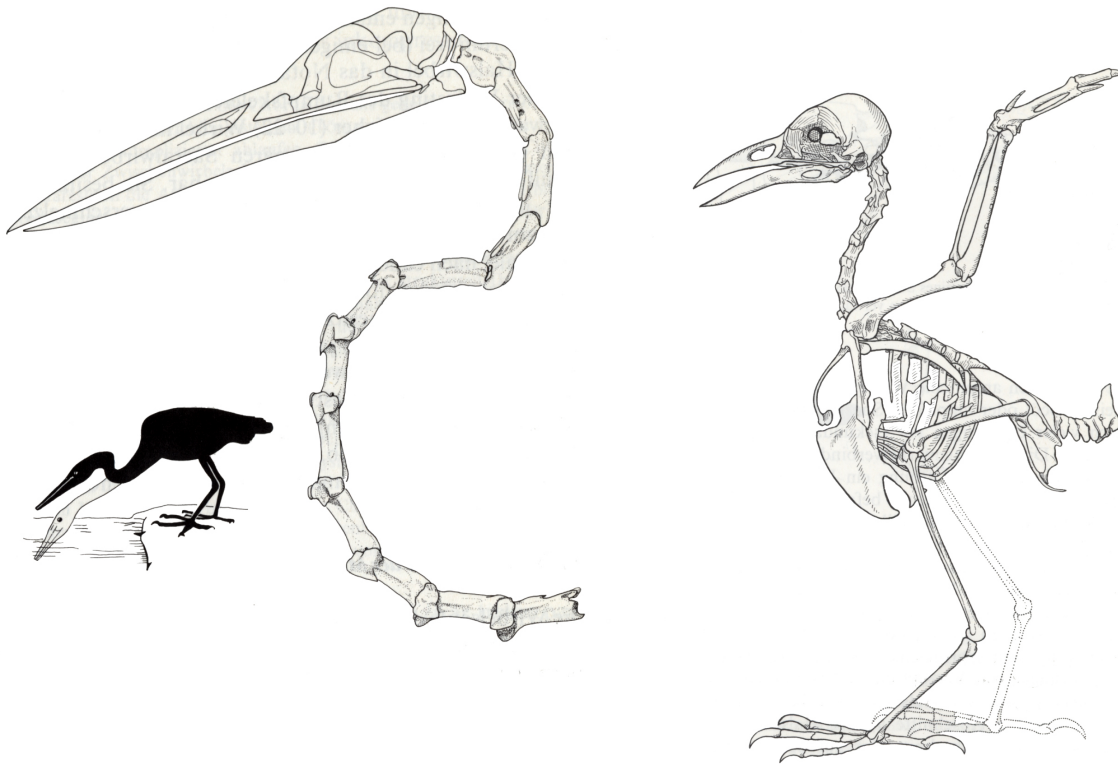


Petrolacosaurus

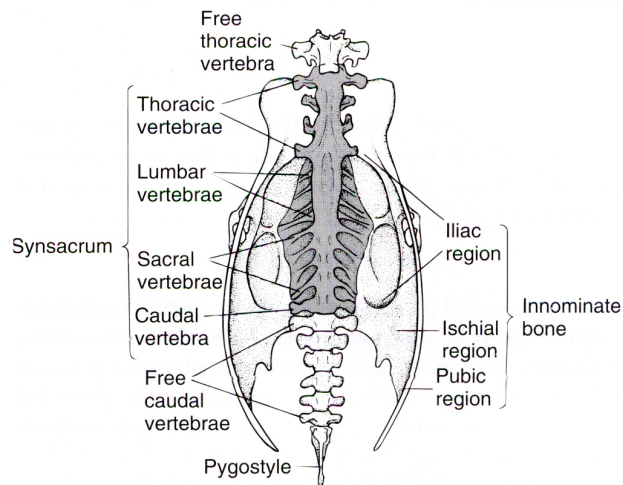
VERTEBRAL COLUMN IN BIRDS

As birds are descended from theropod dinosaurs they inherit an essentially reptilian condition. However, extant avian vertebral structures are part of the air-sac system and there are very light and thin walled.

Neck vertebrae in birds remain mobile; in fact highly mobile, in many cases with extreme curvature in neck vertebrae.

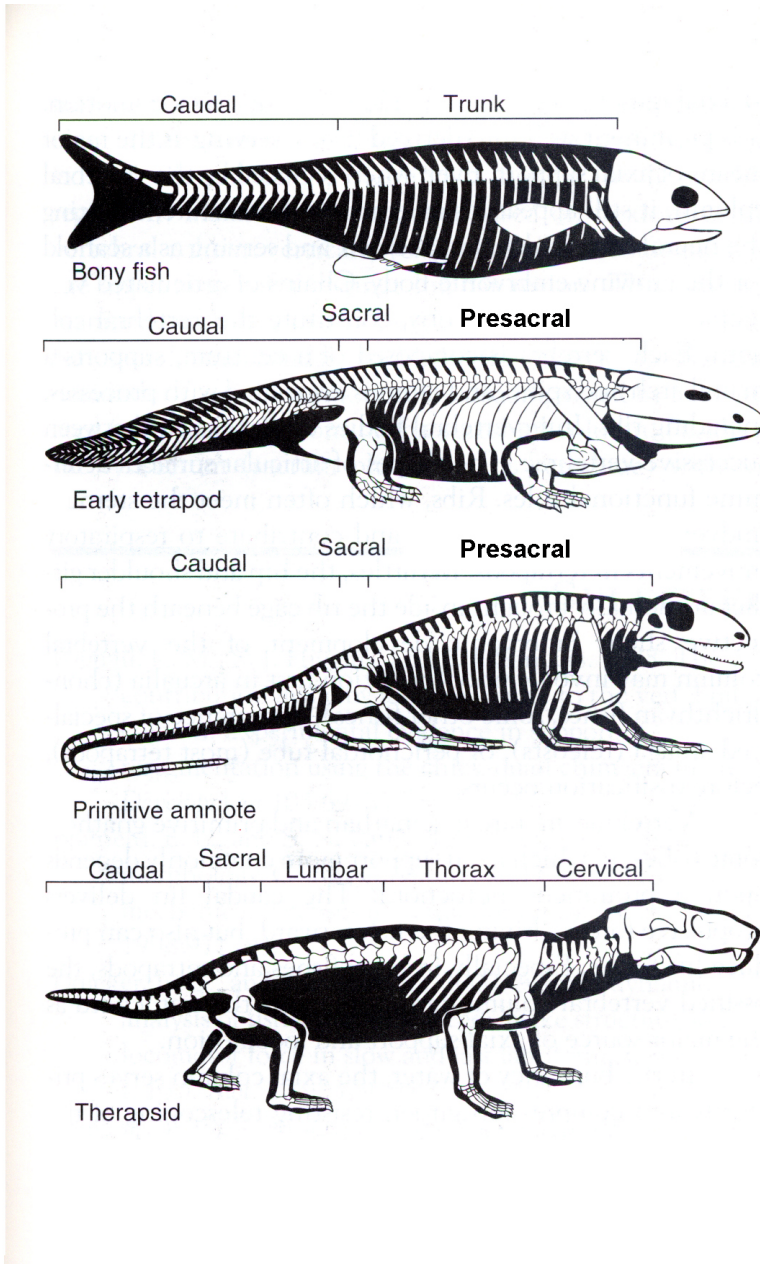


Birds usually fuse all but a couple trunk vertebrae to a stiff, median **SYNSACRUM**.



VERTEBRAL STRUCTURES IN MAMMALS

The hallmarks of mammals are the development of regional differentiation of the backbone into cervical, thoracic, lumbar, and sacral regions; as well as the loss or fusion of ribs, leaving the thoracics as the region with mobile ribs.



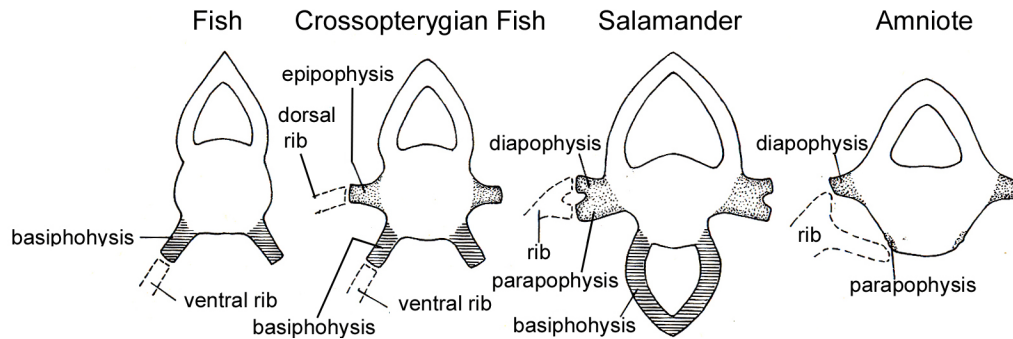
In general, the **CERVICAL** region, which includes the atlas-axis complex, are defined by the presence of the transverse foramen on either side.

THORACIC vertebrae retain mobile ribs.

Developing ribs fuse to the transverse processes of the **LUMBAR** region.

The **SACRUM** is the fusion of two or more segments to provide anchorage for the ilium of the pelvic limb.

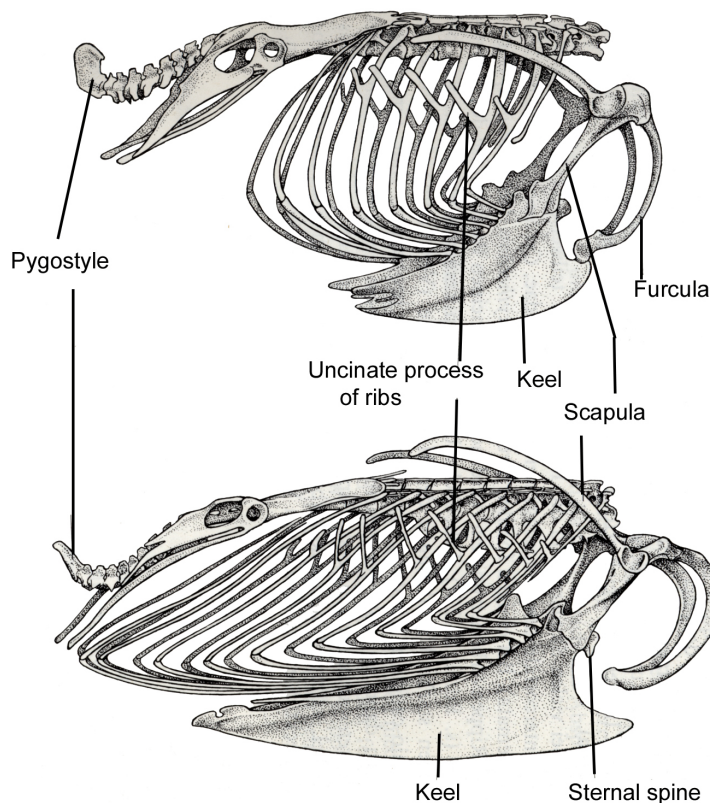
OTHER AXIAL STRUCTURES: RIBS



Agnathans do not show rib development, but otherwise, gnathostomes have a rib for every vertebral segment, including the atlas-axis complex in tetrapods.

As mentioned earlier, fishes have two distinct sets of ribs, **DORSAL RIBS** and **VENTRAL RIBS** – which articulate at the **EPIPOPHYSES** and **BASIPOPHYSES** respectively.

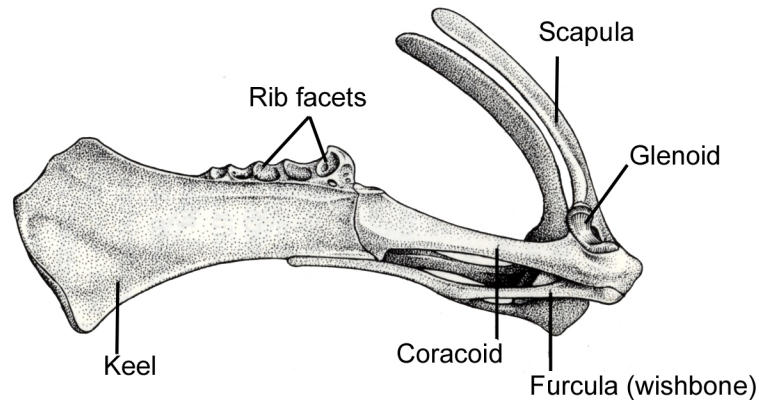
In tetrapods, ribs are generally double-headed, articulating with the **DIAPOPHYSIS** of the neural arch and the **PARAPOPHYSIS** of the intercentrum.



OTHER AXIAL STRUCTURES: STERNUM

In birds and mammals, the STERNUM provides a ventral articulation for the more cranial of the ribs.

In birds it is elaborated into the robust **KEEL** or **KARINA**. It has a deep ventral keel providing extensive surface area for the supracoracoideus (wing elevator muscle) and pectoralis (wing depressor muscle).



The STERNUM in mammals is a segmental structure, derived originally from multiple STERNEBRAE.

Generally the mammalian sternum is subdivided into a **MANUBRIUM** cranially, **BODY**, and **XIPHOID PROCESS** most caudally.

