FOSSIL FISHES

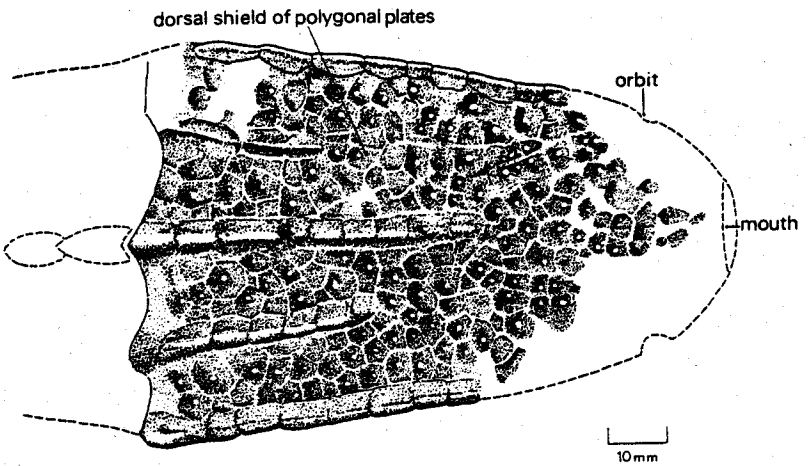
FISH/ZOOL 311

The primary purpose of this handout is to familiarize you with the diversity, form, and taxonomy of **extinct fishes**. One problem facing a researcher in this field is the paucity of whole or nearly whole specimens, as well as the poor condition of the fossil record of the Paleozoic, especially the early Paleozoic. As groups have evolved, and the fossils are of lesser antiquity, the record becomes considerably more clear and the condition of the fossils improves greatly. Still, however, we often have inadequate information to answer convincingly even the simpliest questions about how early fishes (and therefore vertebrates) evolved. Relationships have to be deduced from similarities in morphology that can often lead to erroneous conclusions because of **evolutionary convergence**. Similar selective pressures impacting on vertebrates occupying similar aquatic environments can, and often do, lead to remarkable examples of morphological convergence (e.g., pelagic sharks, ichthyosaurs, and porpoises). Convergence of another type is seen in the recurrent trends of increased size, lose of dermal armor, and apparent accompanying increase in locomotory ability as a group radiates from relatively small, generalized, heavily armored stem groups.

The first recognizable fish fossils appear in deposits laid down in late **Cambrian** or very early **Ordovician** (about 500 mybp). Because their structure is complex even at this early date–many taxa appearing highly specialized–the ancestors of these forms date back considerably farther, but just how far back is completely unknown. Why these more ancient ancestors are missing from the fossil record is puzzling. We have numerous invertebrate fossils from early Cambrian and even Precambrian times, and they are not limited to those of animals encased in hard shells: algal formed stromatolites are common at the earlier period; in the Cambrian, arthropodan trilobites fossilized in tremendous numbers, as did brachiopods. The latter had hard shells made of the same form of crystalline calcium phosphate as vertebrate bone. The lack of fish fossils from this period is therefore a mysterious and unfortunate circumstance.

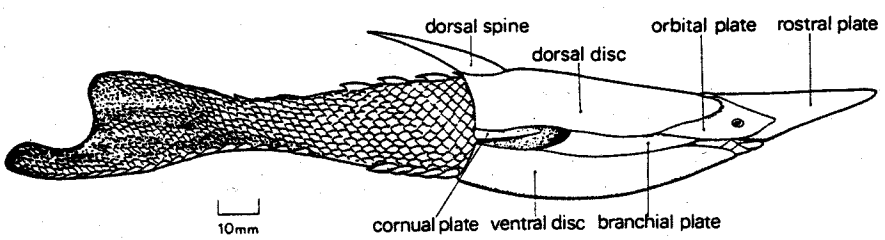
Fossils of hypothetical chordate relatives of the first fishes are well known. Among postulated groups are such non-vertebrate chordates as the **graptolites**–small, lophophorate colonial polyps. Another possible relative is the conodont-bearing animal (**Conodonta**) that had a body not unlike amphioxus and a rather remarkable chewing apparatus.

Some of the earliest known vertebrate fossils (500-490 mybp) are from the Ordovician of the Baltic Region and the Harding Formation of Colorado–broken bits and pieces that are probably mineralized dermal armor of **pteraspidomorph** (**heterostracan**) agnaths, such as genus ***Astrapsis,*** known only from such fragments. Here is the head shield of *Astrapsis* in dorsal view, showing the tesselate structure of the armor.



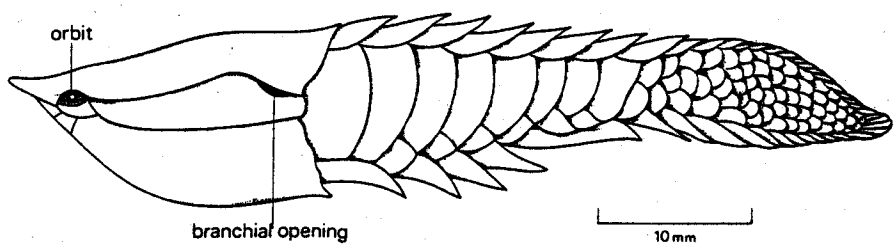
Astraspis desiderata. Restoration of head in dorsal view.

Pteraspidomorphs (Heterostracans) flourished in the **Silurian** and **Devonian** (430-380 mybp). These were characterized most strikingly by having a multi-pieced head shield and a hypocercal tail. ***Pteraspis,*** a Lower Devonian form, is known from reconstruction of numerous fragments, a diagram of which is shown below.

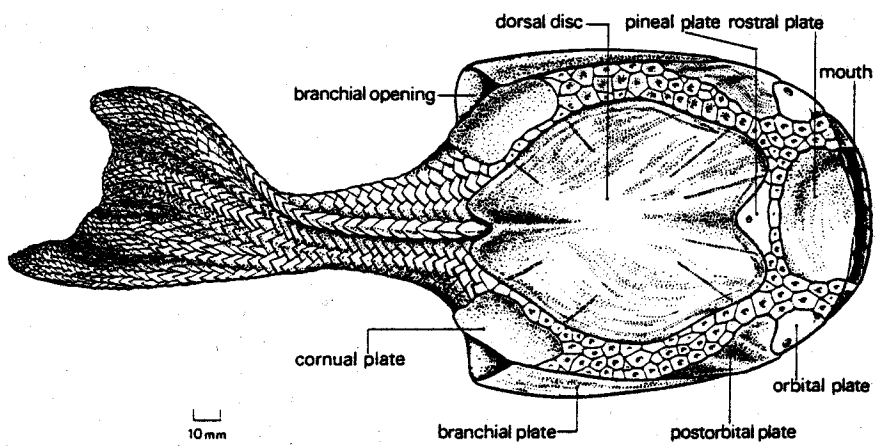


Pteraspis rostrata. Restoration in lateral view.

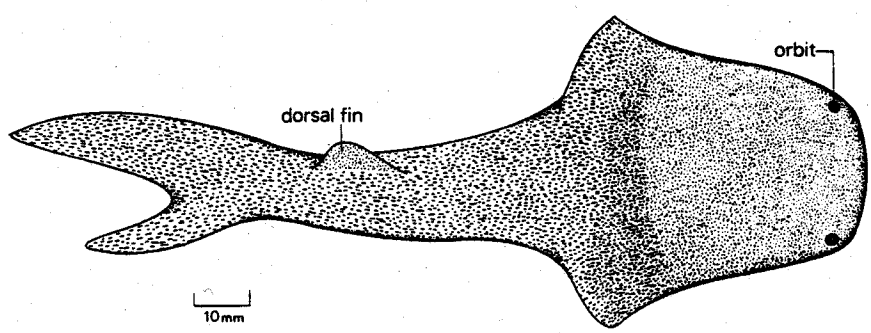
Considerably more bizarre forms of this group include members of the genera ***Anglaspis, Drepanaspis, Longania, Doryaspis,*** and ***Pycnosteus***, shown below.



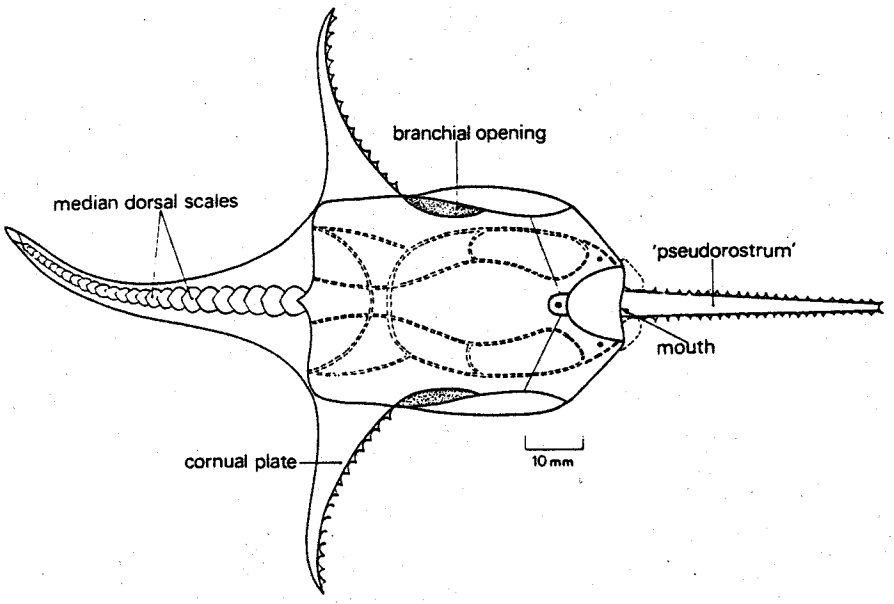
Anglaspis heintzi. Restoration in lateral view.



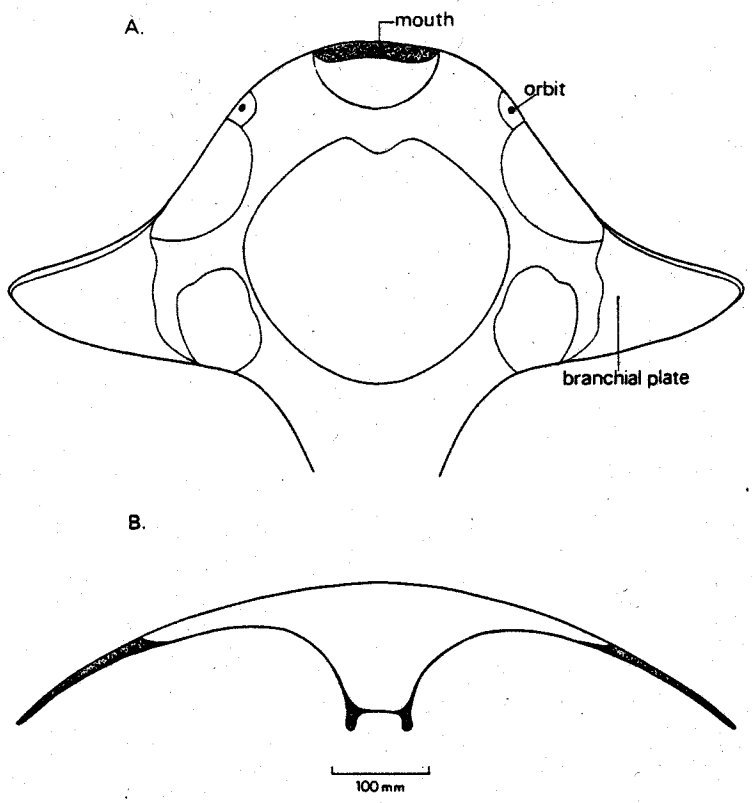
Drepanaspis gemuendenensis. Restoration in dorsal view.



Longania scotica. Restoration in dorsal view.

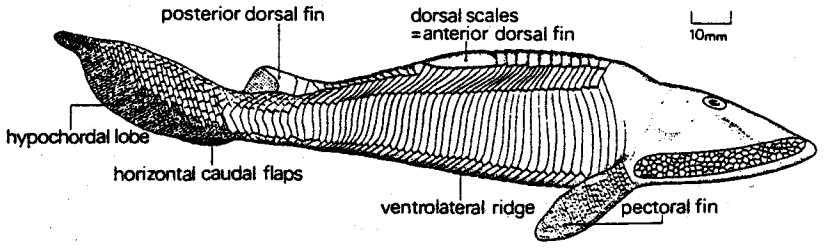


Doryaspis sp. Restoration in dorsal view.



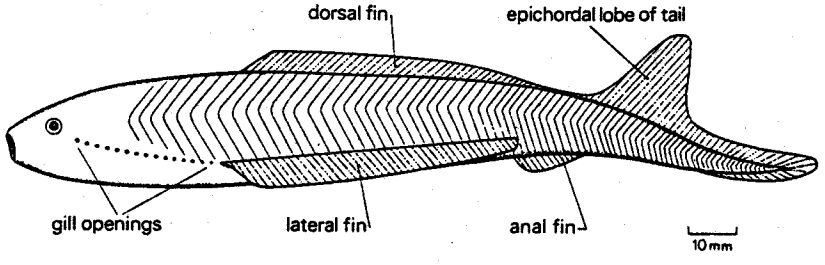
Pycnosteus tuberculatus. Restoration of head in dorsal view (A), with thick section through branchial plates (B).

Another major subgroup of jawless fishes is the **Cephalaspidomorpha**, first found in mid-Ordovician deposits (about 460 mybp). The best known are members of the order **Cephalaspidiformes**, such as the genus ***Hemicyclaspis,*** which is sufficiently abundant and available in complete intact specimens to allow detailed reconstruction of its cranial neuroanatomy. With a little stretch of the imagination, a parallel can be drawn between forms like Hemicyclaspis and similar, modern-day benthic stream fishes, such as loricariid catfishes.

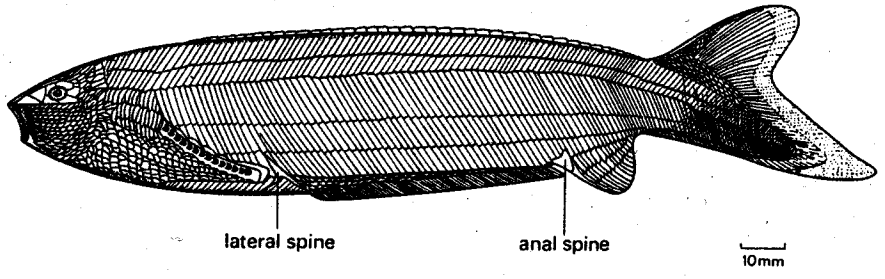


Hemicyclaspis murchisoni. Restoration in lateral view.

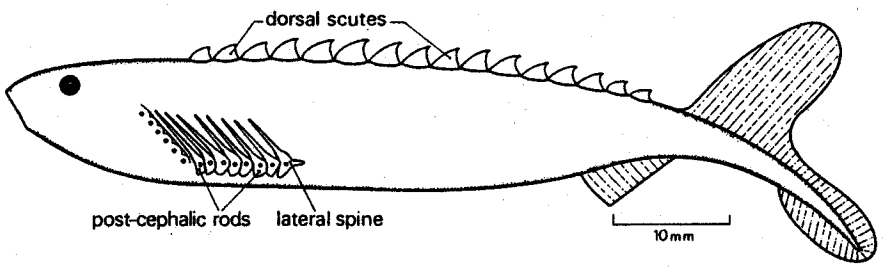
Members of the cephalaspidomorph order **Anaspidiformes**, which appear to be more closely related to the group that gave rise to extant lampreys, like quite different. Here are examples of the genera ***Jamoytius, Pharyngolepis***, and ***Lasanius.***



Jamoytius kerwoodi. Restoration in lateral view.



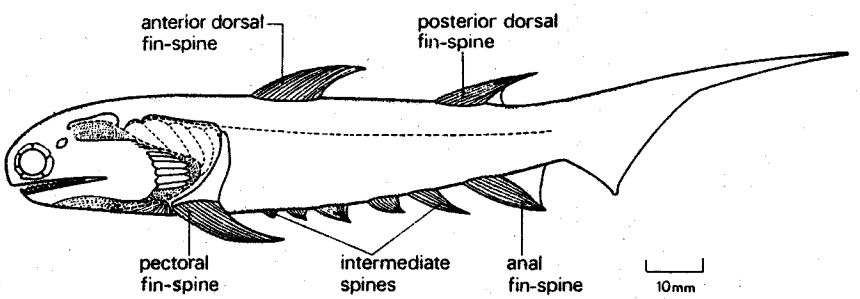
Pharyngolepis oblongus. Restoration in lateral view.



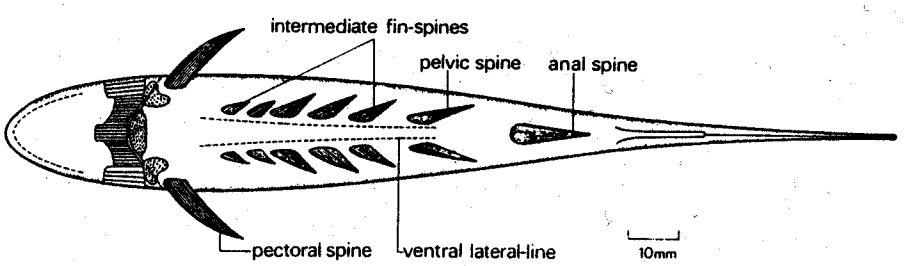
Lasanius problematicus. Restoration in lateral view.

Both the **pteraspidomorphs** and **cephalaspidomorphs** were heavily armored with thick plates of **dermal bone**. It has been hypothesized that this dermal armor functioned to protect these fishes from predation by great "scorpions" known as **eurypterids**.

Evolving along with the jawless fishes were the earliest **jawed vertebrates**, the **Acanthodii**, also known as the **spiny sharks**. The earliest known acanthodians date back to early Silurian times (about 440 mybp). Highly specialized, freshwater forms, these fishes were characterized by having a series of paired fins along their ventral margin (see **Euthacanthus** below), each supported by a stout spine. Probably the best known acanthodian is ***Climatius*** shown here.

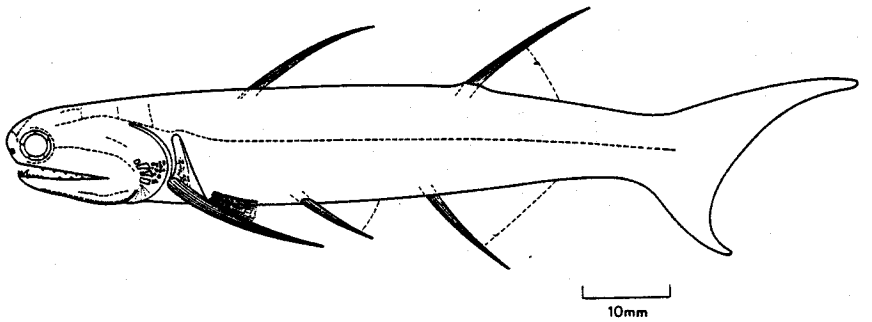


Climatius reticulatus. Restoration in lateral view.

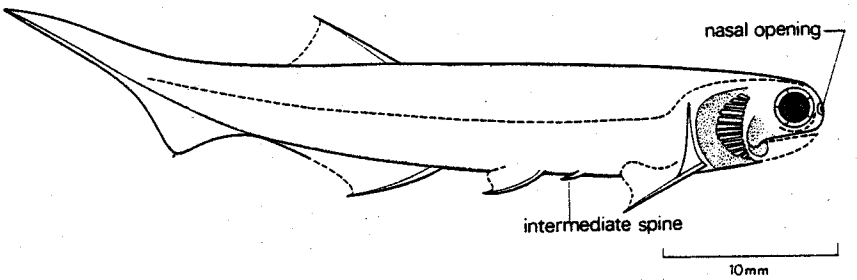


Euthacanthus macnicoli. Restoration in ventral view.

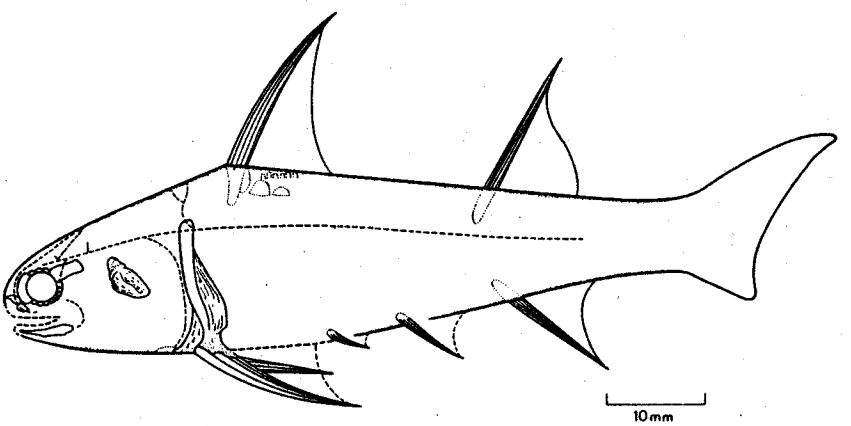
Other interesting but lesser known acanthodians include such genera as **Ischnacanthus**, **Triazeugacanthus**, and , **Diplacanthus**.



Ischnacanthus gracilis. Restoration in lateral view.

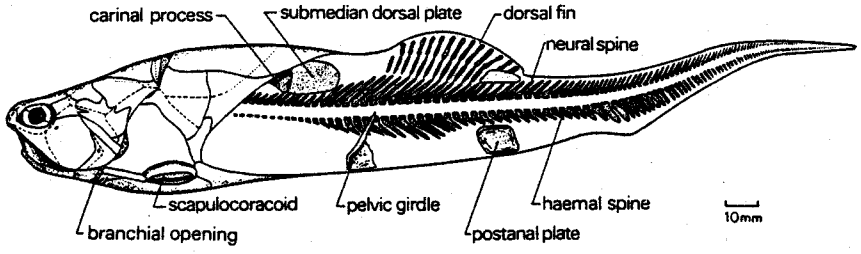


Triazeugacanthus affinis. Restoration in lateral view.



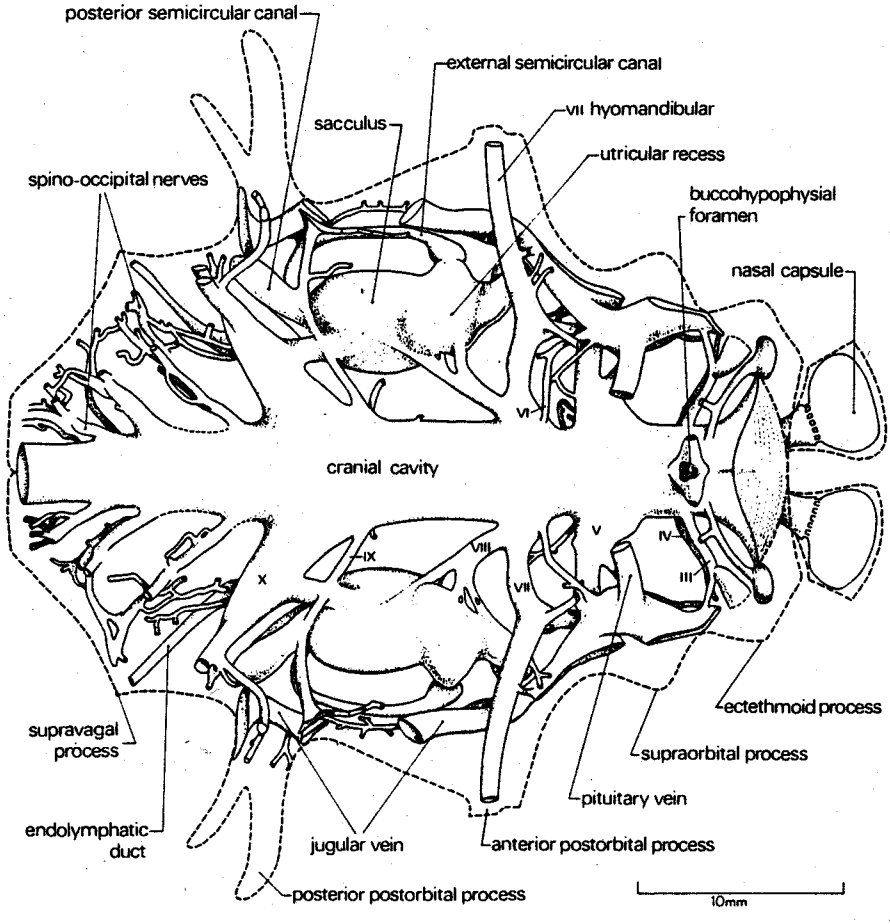
Diplacanthus striatus. Restoration in lateral view.

A second major group of early-jawed vertebrate is the **Placodermi,** which arose during the **Silurian** (about 420 mybp), dominated in marine habitats of the **Devonian** (350 mybp), but became extinct in early **Carboniferous** times (about 325 mybp). These fishes are noted for several peculiar features, perhaps most unusual being the ball-and-socket joints between the head and shoulder region (the **cranio-vertebral joints** perhaps best demonstrated by the genus **Coccosteus**, shown below). All members of this group possessed true paired fins and a plated armor covering that became reduced in the more derived representatives.



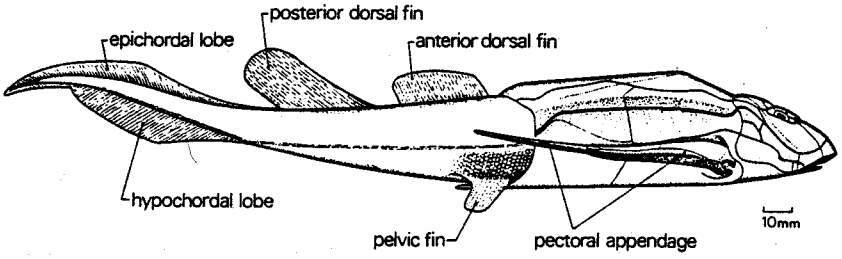
Coccosteus cuspidatus. Restoration in lateral view.

Many **placoderms** (as well as other extinct paleozoic fishes) are so well preserved that it is possible to make detailed and accurate reconstructions of internal anatomy, for example, the brain cavity, including cranial nerves, blood vessels, skeletal elements, and various canals, as shown here in **Kujdanowiaspis.**

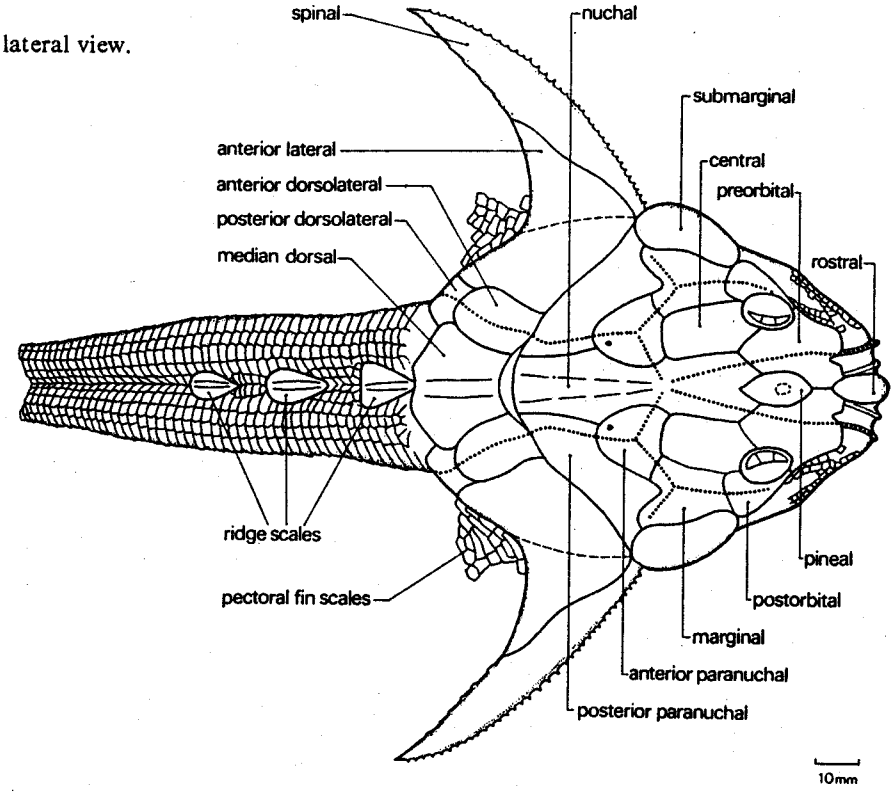


'Kujdanowiaspis' sp. Restoration of brain cavity and canals in neurocranium, in ventral view.

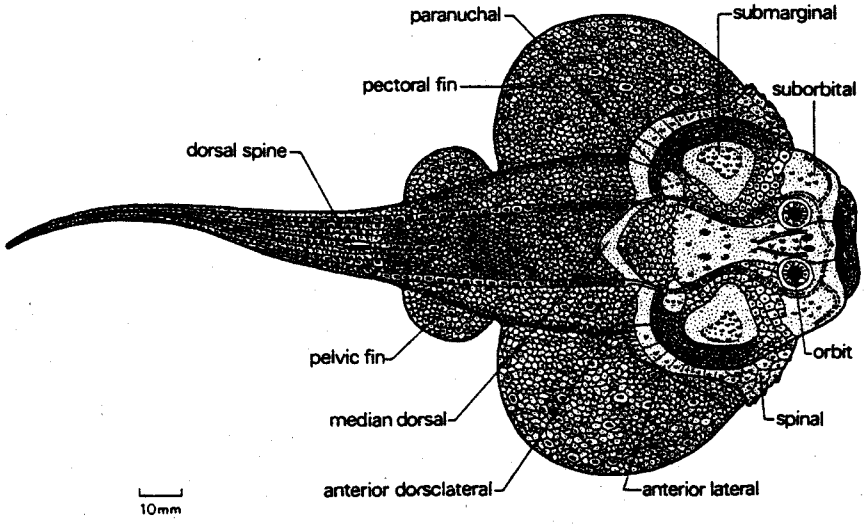
Other **placoderms** of interest include ***Bothriolepis, Lunaspis,*** and, ***Gemuendina.***



Bothriolepis canadensis. Restoration in lateral view.

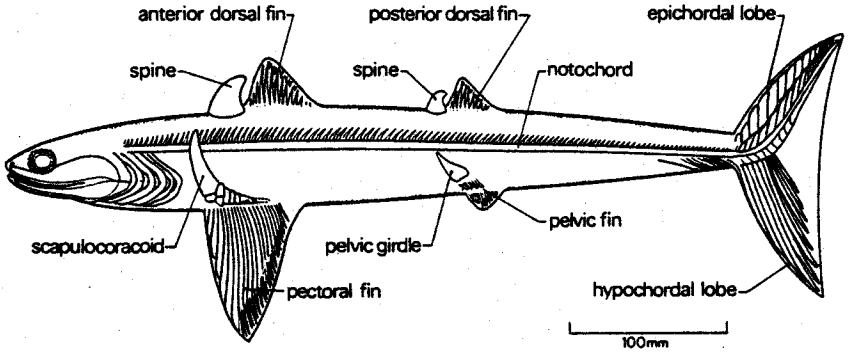


Lunaspis broilii. Restoration in dorsal view.



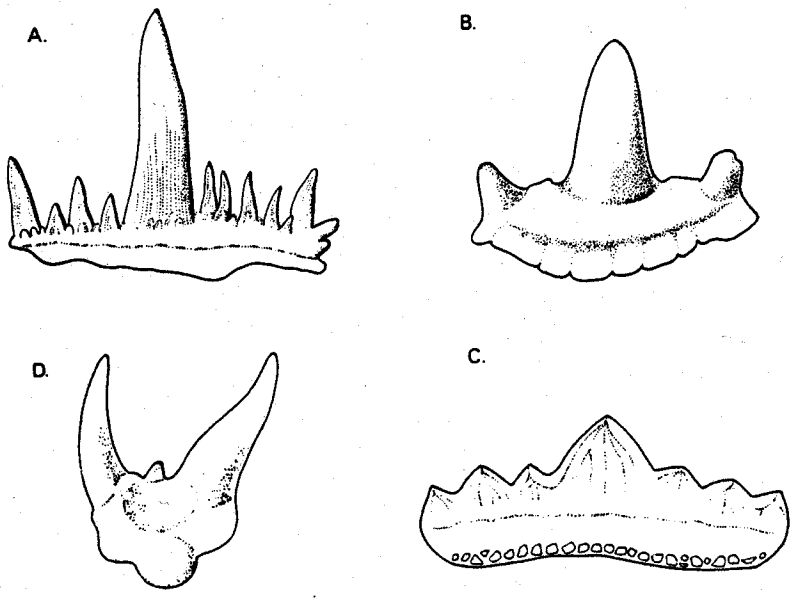
Gemuendina stuertzi. Restoration in dorsal view.

The earliest traces of **Chondrichthyan** fishes, the sharks, rays, and chimaeras, are isolated spines, teeth, dermal denticles, and calcified jaw cartilages that date from the mid Devonian (about 370 mybp). The earliest representatives were they **cladodonts**, of which the genus **Cladoselache** is probably the best known.



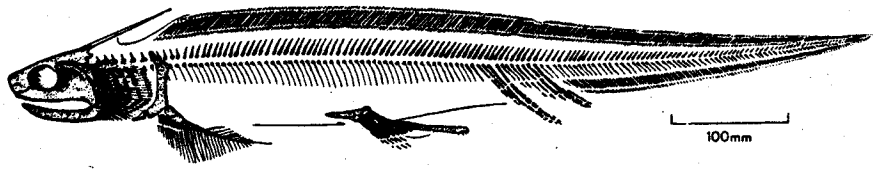
Cladoselache fyleri. Restoration in lateral view.

Identification as well as studies of evolutionary relationships of extinct sharks (and for that matter living elasmobranchs as well) rely largely on the morphology of **teeth** and scales or their evolutionary derivatives. Thus, these ancient cladodonts are best defined by having **Cladodont-type teeth:** teeth with one tall central cusp and one or more pairs of lateral cusps all situated on a broad base. Although **claspers**, intermittent organs used by males to pass sperm to females, are present in all living chondrichthyan fishes, they are absent in many cladodonts.



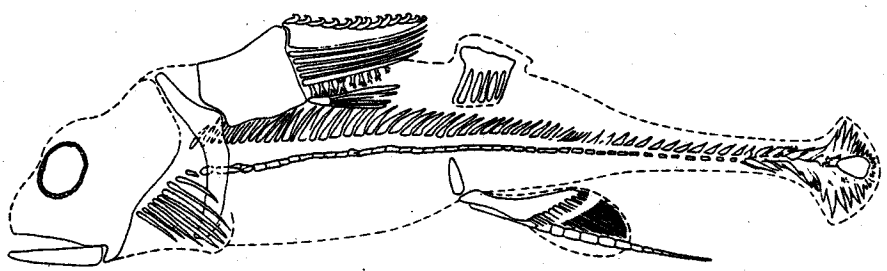
Teeth of cladodont-level sharks. (After Schaeffer.); A. 'Cladodus' sp.; B. 'Cladodus' sp.; C. *Protacrodus vetustus*.; D. *Xenacanthus* sp.

Another group of now extinct Devonian sharks is the superorder **Xenacanthimorpha**, containing a single order, the **Xenacanthiformes**, and a single family **Xenacanthidae**. These are defined by having **Pleuracanth-type teeth**: teeth with three cusps of variable size, usually two prominent lateral cusps, and a smaller median one (see figure D. on page 10). **Claspers** were present in the males of all known taxa.

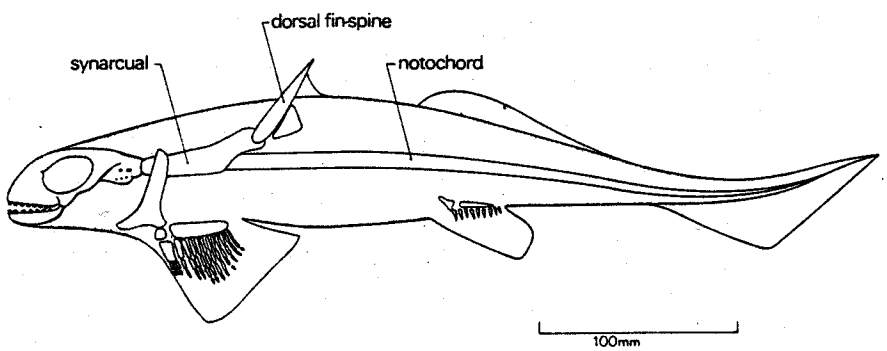


Xenacanthus sessilis. Restoration in lateral view.

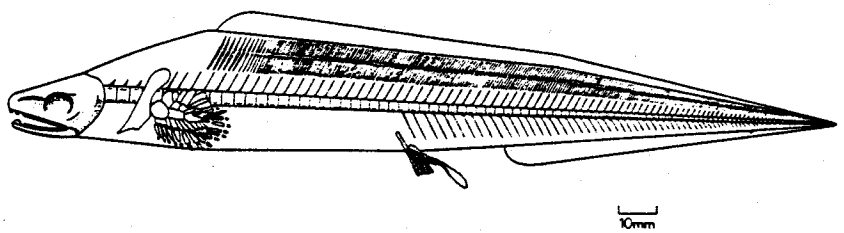
Paleozoic **batiomorphs** (rays) and **holocephalans** (chimaeras) are poorly known relative to sharks. Among the latter, there are at least eight extinct orders, and a ninth order that contains several extinct suborders, in addition to all the living **Chimaeroidei**. But many of these orders are only provisionally placed within **Holocephali** and some are represented only by bits and pieces, e.g., in some cases, only by teeth. The extinct holocephalan order **Iniopterygiformes** is interesting because it contain forms that appear intermediate between sharks and chimaeras. Other notable extinct holocephalans include the genera ***Helodus, Chondrenchelys***, and the poorly known ***Menaspis.***



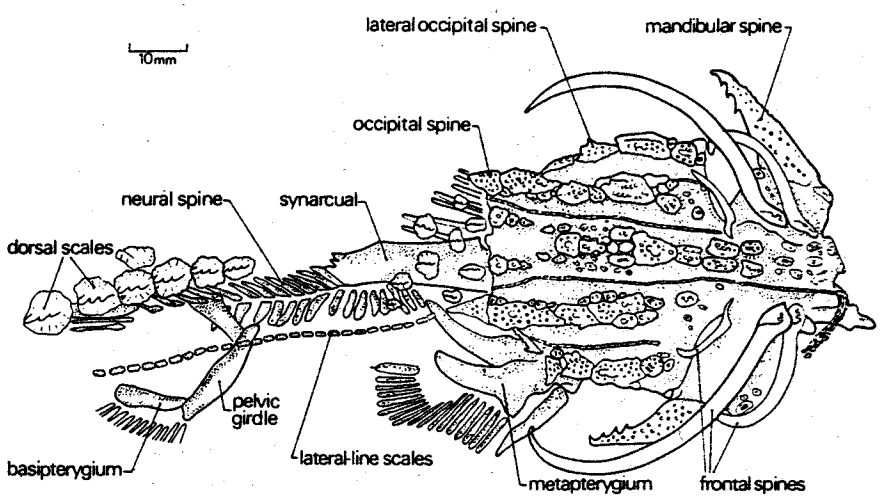
Iniopteryx, one of a group of Carboniferous fishes which may have been closely related to the holocephalians.



Helodus simplex. Restoration in lateral view.

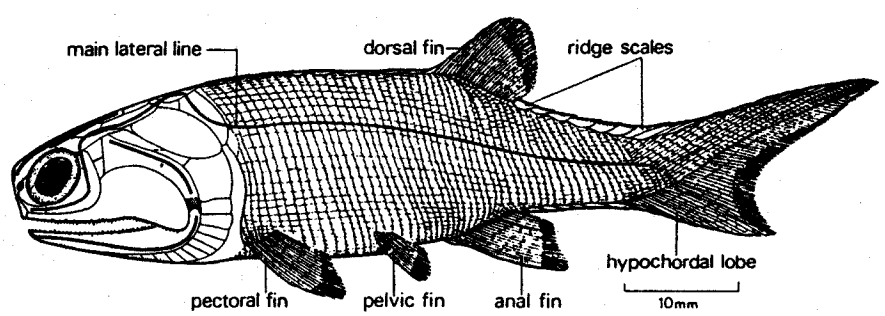


Chondrenchelys problematica. Restoration in lateral view.

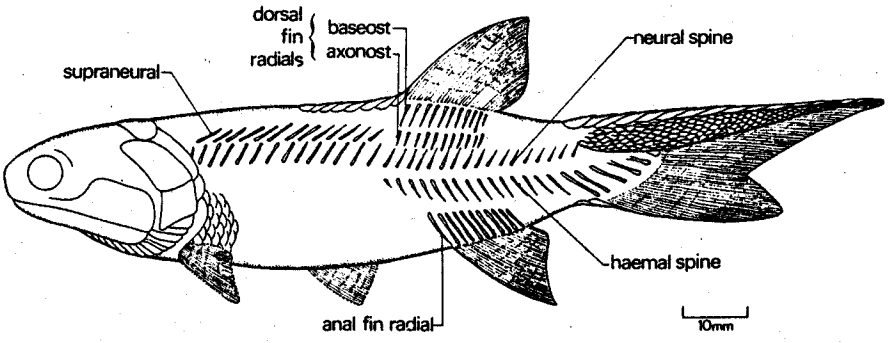


Menaspis armata. In dorsal view.

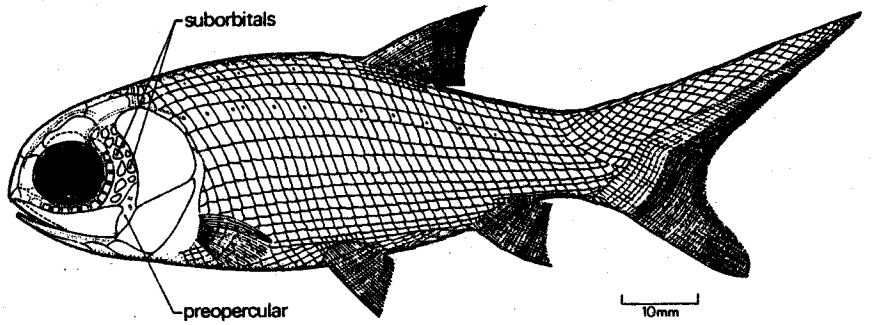
Actinopterygian fishes arose in late Silurian or early Devonian times about 390 MYBP. The earliest representatives are the **paleoniscoid fishes**, named for the type genus ***Paleoniscus.*** The group is considered by most to be directly ancestral to the living but highly specialized chondrosteans, the **sturgeons** and **paddlefishes**. The origin of the paleoniscoids along with all other bony fishes remains unknown because of the lack of well preserved Silurian and Devonian material. Most paleoniscoids looked similar to ***Moythomasia, Phanerosteon,*** and ***Aeduella.*** But others appear quite aberrant, including some strange deep-bodied forms (see pictures below).



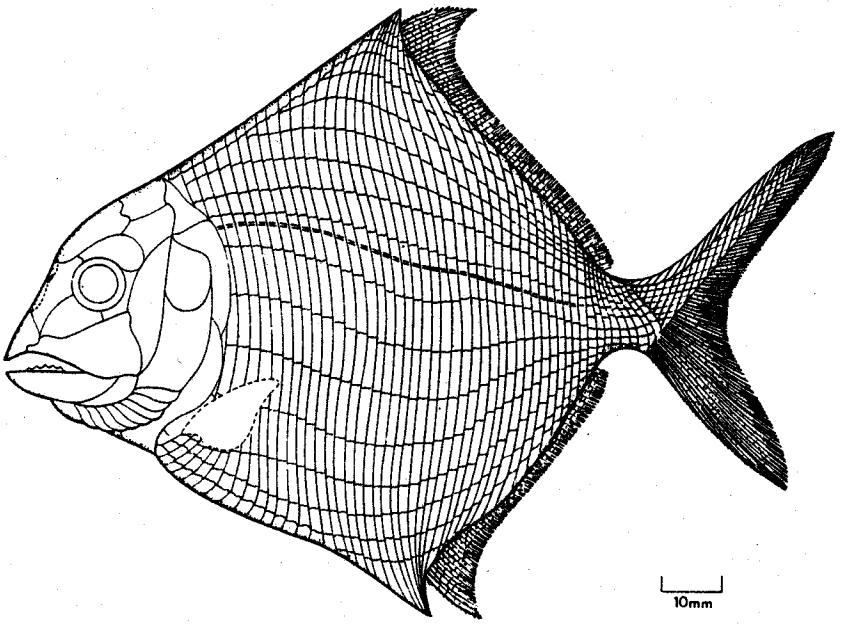
Moythomasia nitida. Restoration in lateral view.



Phanerosteon mirabile. Restoration in lateral view.

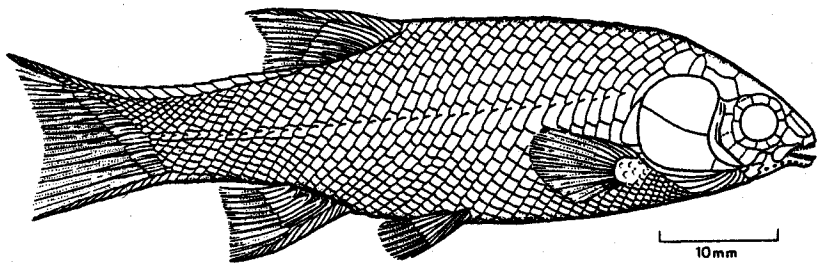


Aeduella blainvillei. Restoration in lateral view.



Chirodus granulosus. Restoration in lateral view.

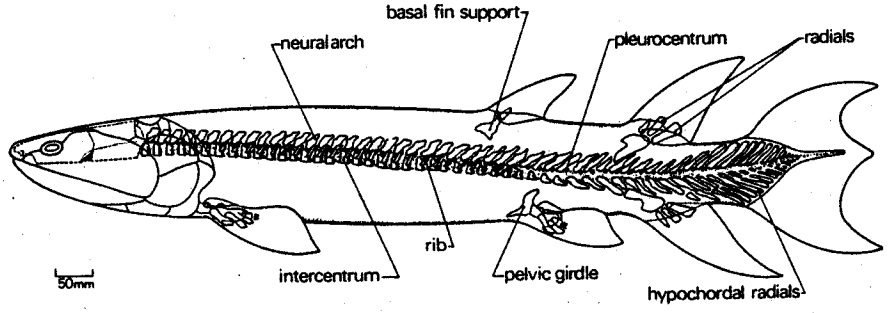
The fossil record of the **Mesozoic** is understandably better than that of the Paleozoic. Well preserved remains demonstrate strikingly how structures and fishes have changed little in 150 million years. Early **neopterygian** fishes are well represented by fossils that date back to the Permian, approximately 225 MYBP. The neopterygian order **Semionotiformes** contains a number of extinct families, of which the genus ***Acentrophorus*** is probably the best known, but also the living **bowfin**, genus ***Amia***, and the **gars**, genus ***Lepisosteus***.



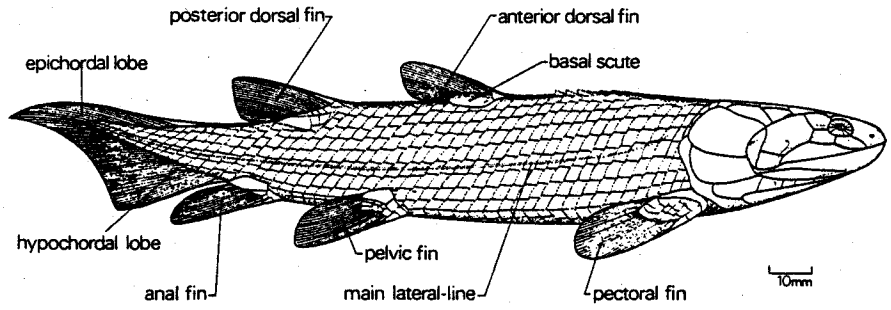
Acentrophorus varians. Restoration in lateral view.

By the late **Cretaceous**, about 65 MYBP, fishes essentially identical to derived extant forms had evolved. The fossils from this time period are also stunningly complete. Some examples, especially those of early **teleosts** are so well preserved that radii of the scales, the growth lines of the opercular bones, and the pores of the acoustico-lateralis system can be

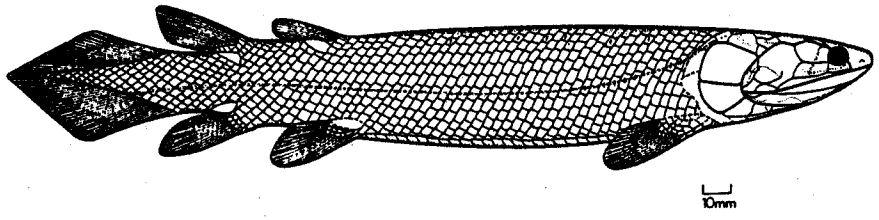
To view **sarcopterygian** fossils we have to jump back to the Paleozoic, where the earliest remains of these fishes date to Devonian times, approximately 380 MYBP. The **Rhipidistia**, also known as the **Osteolepimorpha**, contains the famous genus **Eusthenopteron**, probably the best known of all fossil fishes. Also of interest are the rhipidistian genera ***Osteolepis*** and ***Gyroptychius***. Note the strikingly different caudal fin structure of these three taxa.



Eusthenopteron foordi. Restoration in lateral view, with scales omitted to show postcranial skeleton.

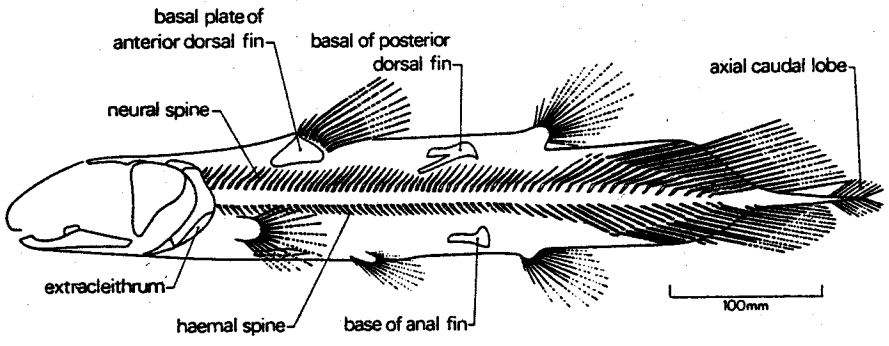


Osteolepis macrolepidotus. Restoration in lateral view.

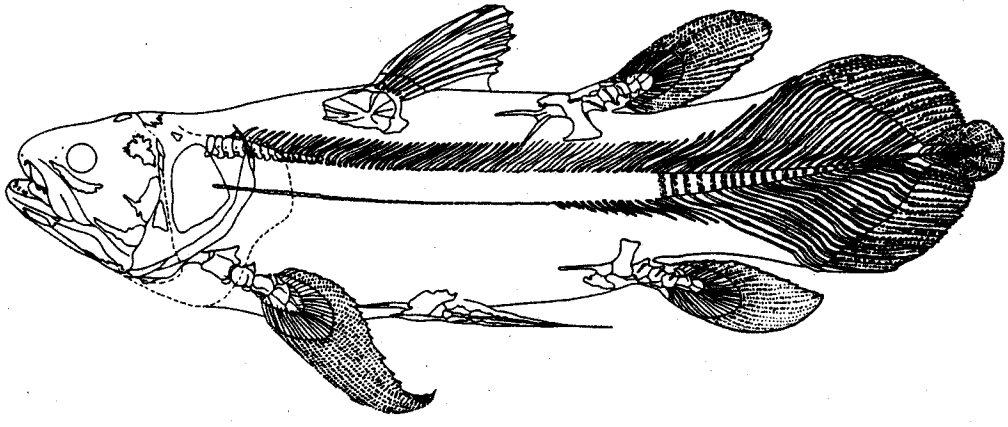


Gyroptychius agassizi. Restoration in lateral view.

The **Actinistia**, also known as the **Coelacanthimorpha**, is very well represented in the fossil record of the late Devonian and Cretaceous. It contains at least four extinct families as well as a fifth, family **Coelacanthidae**, that includes a single living species, ***Latimeria chalumnae***. Compare below a reconstruction of ***Coelacanthus***, one of the best known Devonian actinistians, with the the extant ***Latimeria***.

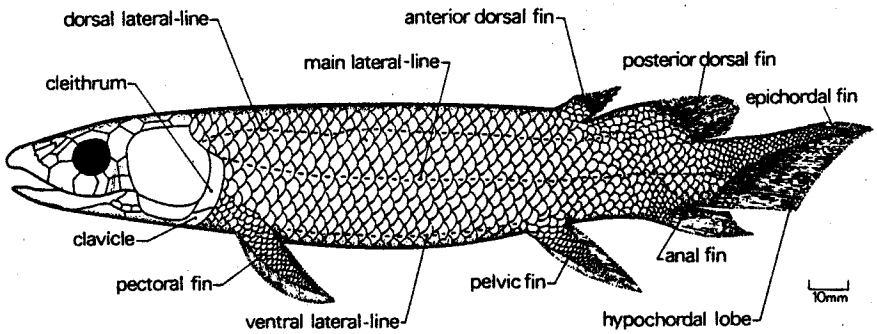


Coelacanthus granulatus. Restoration in lateral view.

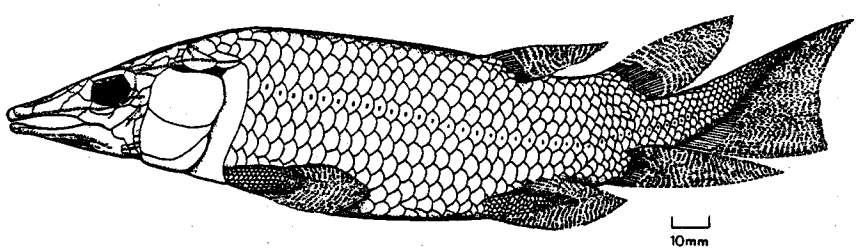


The modern coelacanth *Latimeria chalumnae*, showing the anatomy of the skeleton. (From Millot and Anthony.)

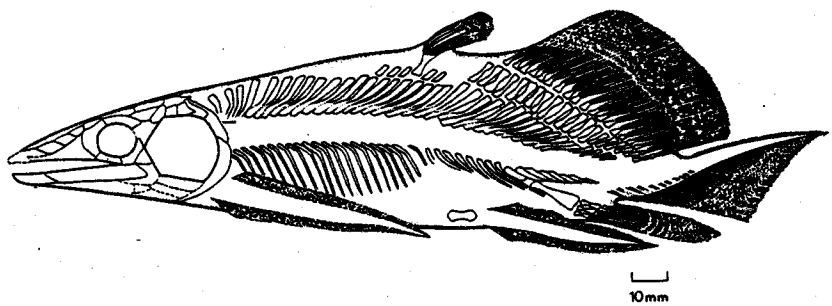
The **lungfishes**, infraclass **Dipnoi** (= Dipneusti), were remarkably diverse during the Devonian, first appearing in deposits laid down about 380 MYBP. The earliest member of this group were heavily armored types, with well-ossified internal skeletons and large double-lobbed tails. Modern descendants of the Dipnoi, however, have lost the external armor, their skeletons are mostly cartilaginous, and their tail has been drastically reduced. These trends can be seen here in the following reconstructions of Devonian, Carboniferous, and Permian representatives.



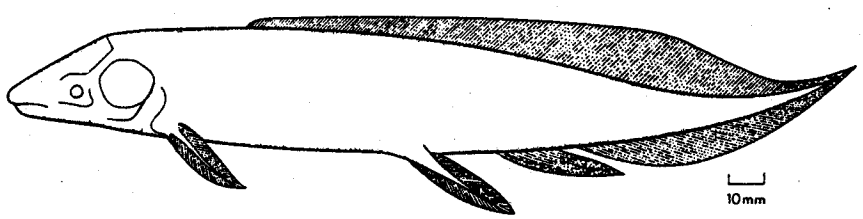
Dipterus valenciennesi. Restoration in lateral view.



Griphognathus sculpta. Restoration in lateral view.



Fleurantia denticulata. Restoration in lateral view.



Phaneropleuron andersoni. Restoration in lateral view.