Vertebrates

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
      |--Jamoytiiformes
      |--Hyperoartia (= Petromyzontiformes)
      `--+--Conodonta
         `--+--Anaspida
            `--+--Pteraspidomorphi
               `--+==Thelodonti
                  `--+==Cephalaspidomorphi
                     `--Gnathostomata
```

Contents

The Vertebrates

Generally mention the word "animal" and most people think of a vertebrate animal -- and more particularly a higher vertebrate, especially a mammal. Vertebrates are large enough for people to relate to, and most like us in appearance and structure. Hence they are distinguished from all other members of the animal kingdom, which are considered "bugs", "worms", etc. Not surprisingly, when Linnaeus was formulating his systematisation of nature, four of his six classes of the animal kingdom -- mammals, birds, amphibia (including reptiles) and fish -- were vertebrates.

Vertebrates are animals with a backbone. They differ from other Chordata in that they possess at least some rudiments of a vertebral column or backbone instead of (or in addition to) a notochord. There is a well developed head, with the brain encased in a skull or cranium. Most vertebrates have an elaborate internal skeleton that acts as a support for muscles and organs. The advantage of an internal skeleton is that it allows the animal to grow much larger than is the case with the arthropod-type exoskeleton.

All vertebrates have a single heart and closed circulatory system. They also possess ductless endocrine glands that play a critical role in regulating the body metabolism. In their circulatory, excretory, and endocrine functions, vertebrates differ markedly from other animals.

The vertebrate body plan has proved extraordinarily successful. Since their first humble beginnings in Furongian seas, the Vertebrates have conquered the land, sea, and air. Thre are some 45,000 living species, and who knows how many extinct forms that have lived and died in past ages. MAK010430.

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checked ATW031116, revised MAK111027

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Craniata

Hagfishes and Haikouichthys

Abbreviated Dendrogram

```
Chordata
|
o Craniata
|--Myllokunmingia
|--Haikouichthys
`--+--Zhongjianichthys
   |--Myxinoidea
   `--Vertebrata
      |--Jamoytiiformes
      `--+--Hyperoartia (= Petromyzontiformes)
         `--+--Conodonta
            `--+--Anaspida
               `--+--Pteraspidomorphi
                  `--+==Thelodonti
                     `--+==Cephalaspidomorphi
                        `--Gnathostomata
```

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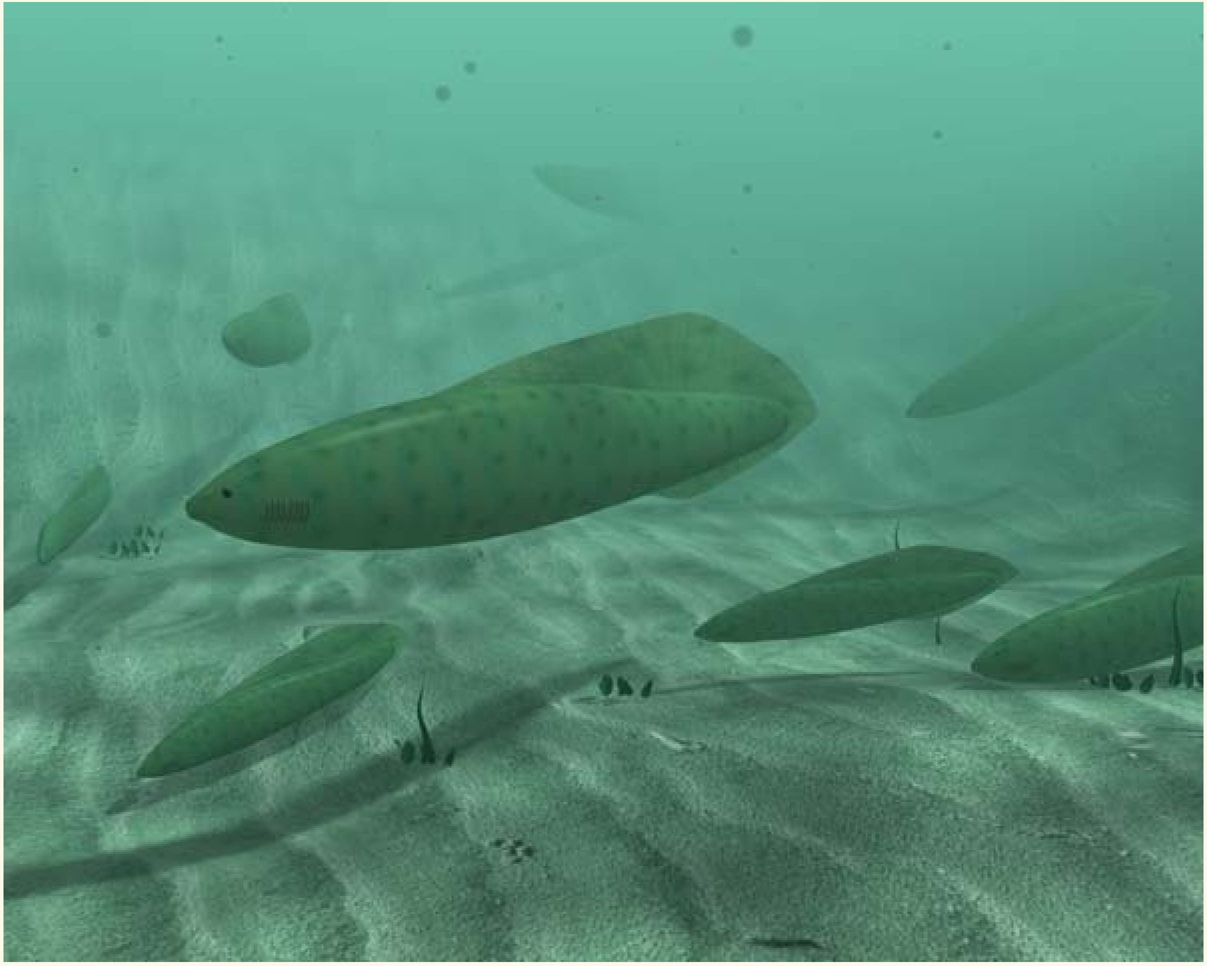
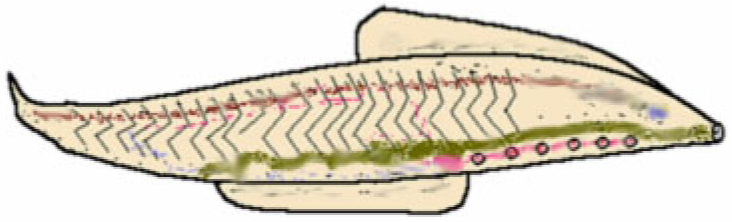
2. *Haikouichthys*
3. Myllokunmingia
4. Myxinoidea
5. Zhongjianichthys



Life reconstruction of the basal craniate or vertebrate Haikouichthys ercaicunensis. Length: 2.5 cm. All vertebrate animnals descended from a humble ancestor such as this. Artwork by Talifero, Wikipedia, Creative Commons Attribution-Share Alike 3.0 Unported license.

Here we enter a strange and poorly known area of phylospace, one in which both timing and phylogeny are poorly understood. Somewhere between 750 and 550 million years ago, a new line ofchordates evolved. These were characterised by a relatively concentrated set of sensory neurons at the anterior end and a particularly pronounced notochord extending beyond the anterior and posterior ends of the torso. In other words, they had the beginnings of a head and a tail. In addition, probably as a later development, the myomeres, the charcateristic bands of muscle along the torso, were reorganized in dorsal and ventral halves, separated by a septum, and acquired a distinctive 'V'- or 'W'-shape. These folks were our ancestors among chordate-kind.

The last common ancestor of hagfish and you, with all of its descendants, is referred to as Craniata. Craniates are animals with well-developed heads and a skull of sorts. A very early craniate, *Myllokunmingia* from the Cambrian of China, is badly illustrated in the figure at right. A rather better illustration of a possibly related and similar form is shown here. Since there is no really good reason to suppose that *Haikouella* belonged to this clade, we treat as a sort of "craniatomorph," but not a craniate.



***Myllokunmingia fengjiaoa*: attempted life reconstruction based on Shu etal. (1999)**

From the first craniates evolved a bewildering variety of creatures. At least they have bewildered systematists for over a century. The first step seems relatively clear. The most primitive craniates we know are the living Myxinoidea (hagfishes): eel-like, rather assymmetric creatures with a strong propensity to flood their immediate neighborhood with slime at the slightest provocation. All other known craniates are Vertebrates. ATW020417.

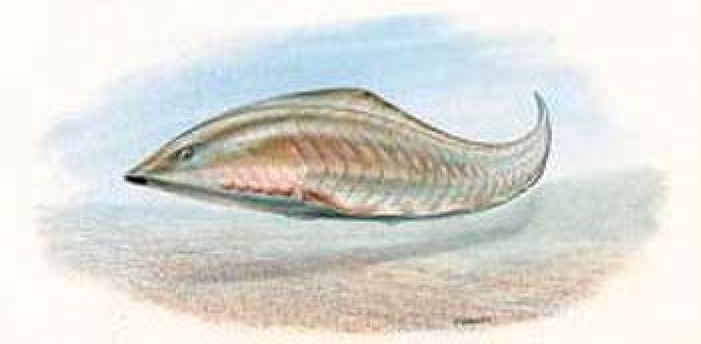
Descriptions

Craniata: *Myllokunmingia*, ?*Haikouichthys*

Range: From the Tommotian

Phylogeny: Chordata::: *Haikouella* + *: Myxinoidea + Vertebrata.

Characters: Neural crest cells, somites, gills with cartilagenous or bone supports (absent in *Myllokunmingia*?), tripartite brain and paired cranial sense organs, cranium with anterior notochord, semi-circular canal(s), 1 heart, kidneys.



The ancestral craniate *Myllokunmingia fengjiaoa*, as it may have appeared in life. Note that this illustration is highly speculative; it is not known for example if Myllokunmingia had eyes, although it is usually drawn that way, perhaps for anthropomorphic or anthropocentric reasons. See also reconstruction of the very similar *Haikouichthys*. Original url

Note: The description by Shu et al. (1999) of *Myllokunmingia* from the Lower Cambrian of South China is generally what one might have expected of a very primitive craniate. The surprising exception is the probable presence of paired fin folds, as well as a definite dorsal fin. None of the fins have detectable radials. The state of preservation is also insufficient to state whether *Myllokunmingia* had eyes, a single heart, an anterior notochord, or even a brain, so that the exact position of this fossil is uncertain. Shu describes it as a vertebrate, but the evidence is unclear. Perhaps it is better treated as a pre-vertebrate craniate since, as Shu states, it is not part of the crown group vertebrates, defined as the LCA of lampreys and gnathostomes.

Links: Waking Up to the Dawn of Vertebrates, Science News Online (11/6/99); BBC News | Sci/Tech | Oldest fossil fish caught. ; Craniata; UW-Green Bay Cofrin Arboretum Center for Biodiversity - - ...; Craniata.

References: Janvier (1999); Shu et al. (1999); Zimmer (2000). APW040314.

Myllokunmingia fengjiaoa Shu, Zhang & Han

Range: Early Cambrian Maotianshan shales of China (Yunnan Province, Chengjiang County).

Phylogeny: Basal Craniate/ basal Vertebrate

Size: around 28 mm long and 6 mm high

Comments: appears to have a skull and skeletal structures made of cartilage. There is no sign of mineralization of the skeletal elements (biomineralization). The holotype was found in the Yuanshan member of the Qiongzhusi Formation in the Eoredlichia Zone near Haikou at Ercaicun, Kunming City, Yunnan, China. The animal has a distinct head and trunk with a forward sail-like (1.5 mm) dorsal fin and a ventral fin fold (probably paired) further back. The head has five or six gill pouches with hemibranchs. There are 25 segments (myomeres) with rearward chevrons in the trunk. There is a notochord, a pharynx and digestive tract that may run all the way to the rear tip of the animal. The mouth cannot be clearly identified. There may be a pericardic cavity. There are no fin radials. There is only one specimen which has the tip of the tail buried in sediment. A similar creature from these shales is known as *Haikouichthys*. Other suspected chordates (primitive hemichordates) are also known from these deposits. BILL 061113, HAJ090202.

Haikouichthys ercaicunensis Luo et al., 1999

Range: Early Cambrian Maotianshan shales of China.

Phylogeny: Basal Craniate/ basal vertebrate

Characters: gills supported by gill bars, a more advanced ararngement than the contemporary *Myllokunmingia fengjiaoa* (BBC Sci/Tech); small lobate extension to the head, with eyes and possible nasal sacs and otic capsules. Notochord with separate vertebral elements. (Shu et al 2003)

Size: about 2.5 cm long

Comments: a fish from Haikou, China, not verse from Japan. APW040314. Cladistic analysis indicates that the animal is probably a primitive agnathan fish most closely related to the lampreys. It is narrower than *Myllokunmingia*, another primitive fish that comes from the same beds. The holotype was found in the Yuansshan member of the Qiongzhusi Formation in the Eoredlichia Zone near Haikou at Ercaicun, Kunming City, Yunnan, China. The animal has a distinct head and trunk. The head has at least six and perhaps nine probable gills. There are a number of segments (myomeres) with rear directed Vs in the trunk. There is probably a notochord although only a short segment is preserved in the single known specimen. The tail end of the animal is apparently missing. There is a prominent dorsal fin with fin radials. The fin radials seem to angle "forward" toward the end thought on the basis of internal structures to be the head. This happens with a few modern fish but is an uncommon arrangement. There is a ventral fin fold. There are 13 circular structures along the bottom that may be gonads, slime organs, or something else entirely. There is no sign of mineralization of the skeletal elements. BILL 061113 Previously considered a possible basal lamprey, new analysis by Sansom et al now places it as a basal craniate MAK111022. The holotype was found in the Yuansshan member of the Qiongzhusi Formation in the 'Eoredlichia' Zone near Haikou at Ercaicun, Kunming City, Yunnan, China (Wikipedia). Phylogenetic analysis indicate that this species lies within the stem-group craniates. Although *Haikouichthys* resembles the ammocoete larva of modern lampreys, this is likely a symplesiomorphy (shared primitive feature). (Shu et al 2003). Cladistic analysis places *Haikouichthys* either as more derived (advanced) than hagfish Shu et al 2003) or in an unresolved polytomy or more basal than them (Sansom et al 2010). We have followed Shu 2003 and Janvier, 2003 in considering these stem vertebrates more basal. MAK111027

Links: BBC News Sci/Tech Walking with Wiki

Zhongjianichthys rostratus

Range: Early Cambrian Maotianshan shales of China.

Phylogeny: Basal vertebrate

Characters: Eyes are located behind the antero-dorsal lobe (an advanced feature, in *Jamoytius* the eyes are forward-positioned); absence of myotome impressions, indicating thicker epidermis, consisting of multiple layers of cells, as in living lower craniates (lamprey and hagfish). (Shu 2003)

Comments: Another of the tiny enigamtic proto-vertebrates whose fossil remains have been discovered in China. Similar to but more advanced than the contemporary *Haikouichthys* and *Myokunmingia*. It may be a vertebrate proper, or simply independently aqcuired these features, just as a number of lineages of amphibians during the Carboniderous were independently evolving to the reptilian condition. An eel-like, elongated form; Its reduced fins suggest that it did not swim frequently, if at all.

Reference: Shu 2003

Links: Deviant Art

Myxinoidea: Hagfish (*Myxine*, *Neomyxine*, *Paramyxine*, *Eptatretus*).

Range: from the Late Carboniferous

Phylogeny: Craniata: Vertebrata + *.

Characters: Anterior nasal opening; "taste" per unique neural and sensory system; mouth surrounded by ring of tentacles; rasping tongue with keratinous teeth; velum; water inhaled through separate nasopharyngeal opening; cartilagenous braincase and branchial basket; poorly developed eyes, with no lenses; gills asymmetric; no vertebrae, finrays absent; no muscles in caudal web fin; scales absent; numerous dermal mucous glands; no lateral line neuromasts; primitive kidney; aneural heart & accessory hearts; isomolal body fluid; benthic and nektobenthonic; marine (deep shelf); ties itself into slip knot to remove food; scavengers; very low metabolism.

Links: link: UC Berkeley; OceanLink: OceanInfo - The Hagfish Page; Hyperotreti; Agnatha.Head.pdf; Hagfish At Home; Pirålar. APW040314.

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Vertebrata

Abbreviated Dendrogram

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Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
       |--Jamoytiiformes
       |--Hyperoartia (= Petromyzontiformes)
       `--+--Conodonta
          `--+--Anaspida
             `--+--Pteraspidomorphi
                `--+==Thelodonti
                   `--+==Cephalaspidomorphi
                      `--Gnathostomata
```

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1. Vertebrata

Representative vertebrates. Clockwise, starting from top left: 1. Fire Salamander (*Salamandra salamandra*) 2. Saltwater Crocodile (*Crocodylus porosus*) 3. Southern Cassowary (*Casusarius casuarius*) 4. Black-and-rufus Giant Elephant Shrew (*Rhynchocyon petersi*) 5. Ocean Sunfish (*Mola mola*). Wikipedia, Creative Commons Attribution-Share Alike 3.0 Unported license.

Some Early Vertebrate Systematics

The most basal group of vertebrates are the Hyperoartia (lampreys) which survive as disgusting, but rather interesting, blood-sucking parasites on fish. In addition, the vertebrates produced the Euconodonta, the Pteraspidomorphi, and a vague, perhaps polyphyletic group referred to for the time being as "Thelodonti". These will be discussed in more detail in other sections.

Work on what is now the vertebrates section of **Palaeos** began less than five years ago [*ed. note* - this was written in 2001 - MAK111022]. At that time, the consensus view of early vertebrate evolution was not far from the cladogram reflected when the predecessor to this site first went on line. The standard texts generally reflected craniates evolving sometime in the Ordovician, with vertebrates arising somewhat thereafter, perhaps during an apparent secondary "explosion" in the Silurian. Eventually, the Osteostraci emerged, and some Osteostracan or a closely related forms developed jaws and paired pectoral limbs -- all at about the same time -- resulting in another quick radiation of gnathostome forms during, perhaps, the Late Silurian. At that time, conodonts were not considered chordates -- much less vertebrates -- and the thelodonts were considered as little as possible, since they made no phylogenetic sense. For that matter, the thelodonts *still* make very little sense.

Nonetheless, things have changed a good deal, and -- although there is probably not yet a new consensus – it has been necessary to change the very backbone of the vertebrate cladogram (to introduce a serious redundancy). After a recent series of significant revisions, the story unfolds at a much more leisurely pace.

The origin of chordates now seems to date back to Pre-Cambrian times, perhaps 600 My. *Haikouella* was described by from the Early Cambrian (about 530 My) of South China in 1999. It is a derived chordate, just short of being a crown group craniate. *Myllokunmingia*, from about the same time and location, probably *is* a crown group craniate. Shu et al. (1999). Crown group vertebrates, i.e., the last common ancestor of lampreys and gnathostomes, can scarcely have been much later. In fact *Haikouichthys*, also described in Shu's paper, may well be a very primitive hyperoartian (lamprey cousin).

By Furongian times, at 500 My, vertebrates had evolved a variety of forms, including the extraordinarily strange and successful euconodonts. Conodonts have been known for almost as long as there has been paleontology, but their peculiar dentition was all that was known of the group. Since conodont remains are very common, they were much-studied as stratigraphic markers but otherwise little understood. As Donoghue et al. (2000) state in their recent study: "Just a year before the first conodont fossil with preserved soft tissues was found, Müller (1981) compiled a list of groups to which conodonts had been attributed; his list includes at least three kingdoms and almost every major animal phylum." *Id.* at 192.

It now seems fairly well accepted that conodonts are chordates. The Donoghue group's own detailed cladistic study places them within the vertebrates, just above the Hyperoartia. Interestingly, the authors state that the earliest (Pre-Cambrian to Early Cambrian) conodonts, known as the Protoconodonta, are probably unrelated. They assert that the Early to Late Cambrian Paraconodontida *are* related, but do not include them in their analysis because there are no known soft tissue remains. Thus their analysis is based only on the relatively derived Euconodonta. If paraconodont soft tissue remains are ever found, the picture may be different.

The exact placement of this group is of some interest because the inclusion of conodonts has other strange effects on the vertebrate cladogram. Donoghue et al.'s final result looks like this:

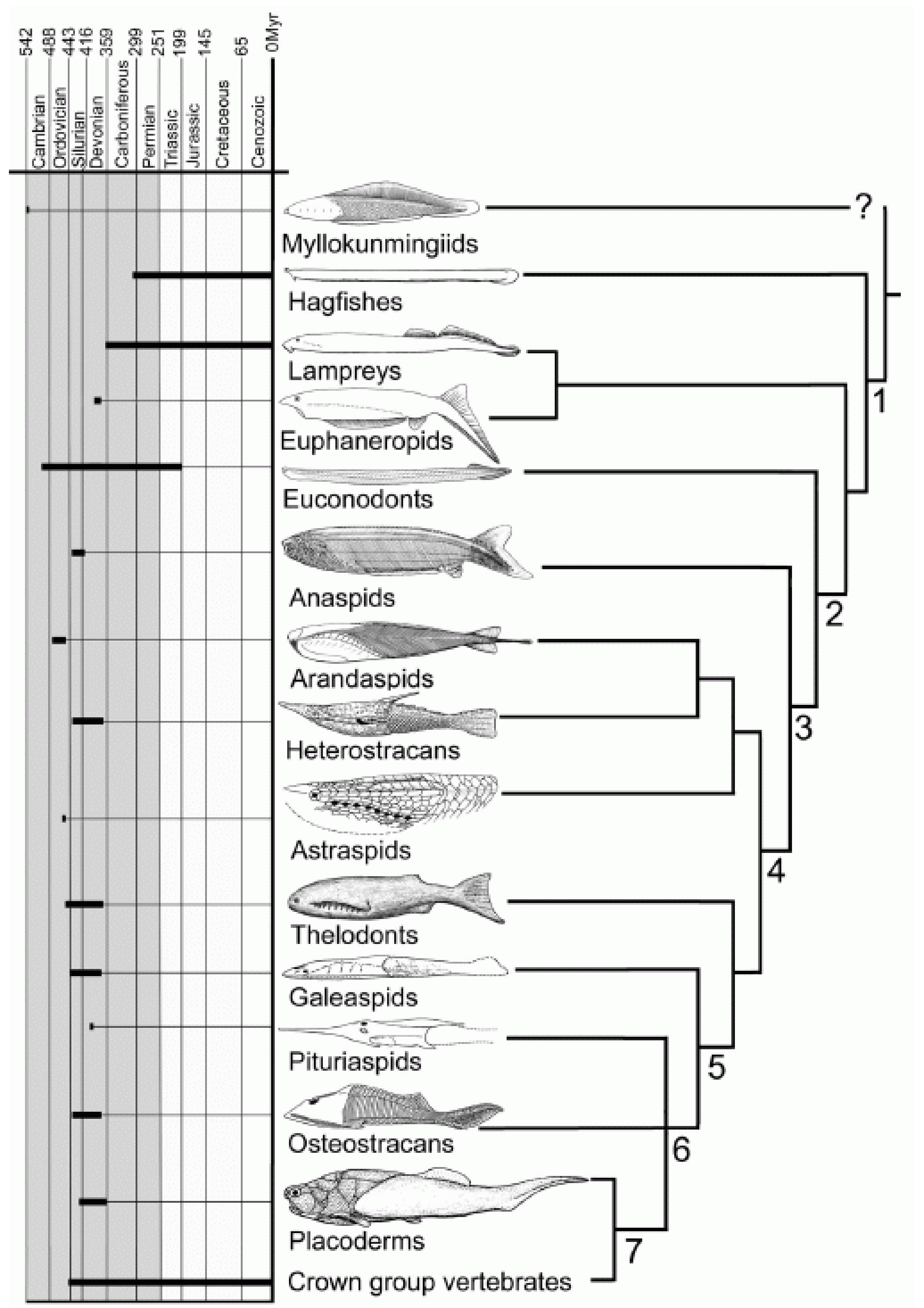
```
Chordata
|--Tunicata (i.e. Urochordata)
`--+--Cephalochordata
   `--+--Petromyzontiformes (= Petromyzonida = Hyperoartia)
      `--+--"Conodonta" (i.e. Euconodonta?)
         `--+--+--Astraspis
            |  `--+--Heterostraci
            |     `--Arandaspida
            `--+--+--Anaspida
               |  `--+--Jamoytius (a lamprey-like anaspid)
               |     `--Euphanerops (similar to Jamoytius)
               `--+--Loganellia (a thelodont)
                  `--+--+--Eriptychius (an Ordovician form known only from fragments)
                     |  `--Gnathostomata
                     `--+--Osteostraci
                        |--Pituriaspida
                        `--Galeaspida
```

Note that the headshield forms (osteostracans and their close relatives) are now monophyletic -- no longer gnathostome ancestors. This is odd, but appealing. The Osteostraci have never been satisfactory gnathostome ancestors because they are very highly derived forms. The general direction of osteostracan evolution seems to have been toward a *loss* of fins and an ever-more benthic existence. Only the most basal forms, like *Ateleaspis*, really suggest a gnathostome relationship. The separation of anaspids from lampreys is less congenial. Janvier (1996) shows a rather neat series between the anaspids and lampreys which can be seen below. However, this separation does seem to be required by the current data.

Somewhat similar results were obtained by Wilson & Caldwell (1998) in their study of the "fork-tailed" thelodonts, the Furcacaudiformes. The thelodonts, like conodonts, are another old group of misfits. They come in a great variety of forms: some resembling anaspids, osteostracans, and gnathostomes. Thelodonts appear to be united only by lacking large dermal plates and having very small scales somewhat similar to those of primitive sharks, and have been widely believed to be para- or polyphyletic. See, e.g. Thelodonti. Some appear to have paired fins (located *over* the gill slits) and other advanced features, including a well-developed anal fin and possible fin spines. Unfortunately, since thelodonts lack large dermal plates or massive cartilaginous headshields, they are rarely found as articulated specimens. Wilson & Caldwell, however, used their new data on the aberrant furcacaudiforms to try to anchor the group. Although some of their conclusions are too difficult to accept at the moment, they, like Donoghue et al., also conclude that *Loganellia* and other thelodonts (e.g. *Turinia*) are close to the gnathostome base and that that the osteostracans are several steps removed.

Given these results, it may now be possible to advance seriously the hypothesis that the thelodonts are the main stem of vertebrate evolution, and that the other groups are only branches. Consequently, we have taken the liberty of temporarily promoting the thelodonts to "Thelodonti" to include anaspids, gnathostomes, furcacaudiforms, and the headshield forms. This solution is only slightly radical and finds comfortable homes for both of the perennial orphans of early vertebrate paleontology: the conodonts and thelodonts. No doubt these are only foster homes, and some new and different arrangement will be necessary in a few more years, particularly for the conodonts. However this hypothesis surely makes more sense than relegating to footnotes the conodonts, who make up 65% of all non-gnathostome chordate species, and thelodonts, our closest known relatives among jawless fish. ATW 010126

Update: While vertebrate systematics, like science in general, is likely always to remain in a state of flux, a consensus is emerging regarding the relationships of some of the primitive jawless forms (e.g. Janvier 2007a, Janvier 2007b, Sansom et al 2010). The following dendrogram is from Janvier 2008 fig 1, Sansom et al 2010's tree differs in some respects.



Dendrogram showing the distribution of the taxa through time. Stratigraphic range is indicated by bold lines in the time scale to the left, phylogeny by the tree on the right. Major synapomorphies as follows: 1, neural crests, epidermal placodes, fin radials; 2, dermoskeleton in mouth and pharynx; 3, extensive dermoskeleton over the entire body; 4, extensive lateral-line system enclosed in grooves and canals, vertical semicircular canals forming loops, cerebellum; 5, endoskeleton lined with calcified cartilage or perichondral bone; 6, pectoral fins in postbranchial position; 7, jaws. Illustrations of respective taxa after Janvier, 2007b. Diagram and caption Janvier 2008, fig.1, p.1047.

The main difference with earlier phylogenies is that primitive forms like *Euphanerops* and *Jamoytius* are now considered more basal than the Anaspida proper. There is also some uncertainty whether these early types belong on the lamprey stem (diagram here) or are a seperate clade of early vertebrate evoluution (Sansom et al 2010a). The dendrogram given in Janvier 2007 p.30 differs slightly from the above, by placing hagfish, lampreys, Euphaneropids, possibly conodonts, and higher vertebrates in an unresolved polytomy. The status of the thelodonts is ambigious, they are variously placed above (Janvier 2007, Janvier 2008 fig 1) or below (Sansom et al 2010a) the Anaspida and Pteraspidomorphs. These latter two groups meanwhile have also played musical chairs, the Anaspida, previously more derived than the Pteraspidomorphi (Benton 2005 p.41) are now shown below them. However, whilst molecular phylogeny mostly argues for cyclostome monophyly (lampreys and hagfish sharing a distinct common ancestor separate from all other extant vertebrates - Delabre et al 2002 Kuraku et al 2009a, Kuraku et al 2009b, Heimberg et al 2010; with a few exceptions in older papers e.g. Gürsoy 2000) there is no morphological and paleontological evidence for such. Interestingly, Janvier, previously opposed this interpretation (Janvier 2008) now has come around in support of it (Janvier 2010). We will have more to say on this subject later (pending time constraints). For now we would tend to interprate unusual molecular phylogenies of this sort as methodological artifacts rather than empirical evidence of actual deep time phylogeny (similar instances include turtles as crown group archosaurs, and the monophyly of monotremes and marsupials against eutheria). This is yet another example of the need for a total evidence approach, rather then relying - as specialists inevitably tend to - on a single methodology to the exclusion of all others.

For now we have decided, rather unimaginitively, to go with the consensus approach of gnathostomes emerging from Cephalaspidomorphi, while retaining the thelodonts as a paraphyletic and possibily polyphyletic grouping of unarmoured agnaths on the way to the vertebrate condition (and sometimes evolving parallel to it) MAK111027

Vertebrata: Used here as crown group, i.e. LCA lampreys + gnathostomes.

Range: from the Lower Cambrian

Phylogeny: Craniata: Myxinoidea + *: Conodonta + (Hyperoartia + (Anaspida + (Pteraspidomorphi + Thelodonti))).

Characters: Well-developed eyes; extrinsic eye muscles attached to the eyeball and orbital wall; 2-3 semi-circular canals; muscular, perforated pharynx; endoskeleton with at least cranium, visceral arches, limb girdles, and 2 pairs of appendages; repeating endoskeletal elements flanking the spinal cord, primitively two pairs in each metamere (interdorsals and basidorsals); radial muscles in fins; integument with two layers, epidermis and dermis; lateral line canals with true neuromasts; atrium and ventricle of heart closely-set; nervous regulation of heart by vagus nerve; blood with (a) red blood cells (erythrocytes) containing hemoglobin, and leukocytes; mesodermal muscle fibers in gut; *hox* gene duplications; neural crest cells (arguably the basis for most other important vertebrate characters); sensory placodes (neuroectoderm discs giving rise to nose, lens of eye, ears and lateral line system).

Links: Vertebrata; Subphylum Vertebrata; Introduction to Vertebrates; Vertebrata -- The Dinosauricon; LAB 13 71.125; Phylum Chordata Overview; Subphylum Vertebrata; Chordata: Subphylum Vertebrata; Chordata: Subphylum Vertebrata; À la recherche du premier vertébré; PNAS -- Cameron et al. 97 (9): 4469; Subphylum Vertebrata; Basal Vertebrata.

References: Cameron *et al*. (2000). APW040314.

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Hyperoartia

Lampreys and their relatives

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
      |--Jamoytiiformes
      |  |-- Jamoytius
      |  `-- Euphanerops
      |--Hyperoartia (= Petromyzontiformes)
      |  |- Hardistiella montanensis Janvier &
Lund, 1983 [paraphyletic Mayomyzoninae]
      |  `--+-- Mayomyzon pieckoensis Bardack &
Zangerl, 1962;  [paraphyletic Mayomyzoninae]
      |     `--+- Pipiscius zangerli Bardack &
Richardson, 1977 [paraphyletic Mayomyzoninae]
      |        `--+-- Priscomyzon riniensis
Gess, Coates & Rubidge, 2006;
      |           `--+-- Mesomyzon mengae Chang,
Zhang & Miao, 2006;
      |              `-- Petromyzontidae
      `--+--Conodonta
         `--+--Anaspida
            `--+--Pteraspidomorphi
               `--+==Thelodonti
                  `--+==Cephalaspidomorphi
                     `--Gnathostomata
```

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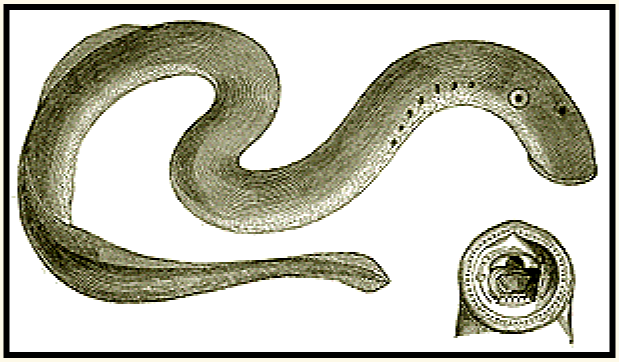
2. Hyperoartia
3. *Mayomyzon pieckoensis* X
4. *Mesomyzon mengae* X
5. Petromyzontidae
6. Petromyzontiformes
7. *Pipiscius zangerli* X
8. *Priscomyzon riniensis* X

Hyperoartia, also known as the Petromyzontiformes, include the modern lampreys (sometimes incorrectly called "eels", because of their superficial appaearnce, they are unrelated and far more primitive) and their fossil relatives, The discovery of the fossil *Priscomyzon riniensis*, pushed back the oldest known occurence of true lampreys to the Late Devonian, and showing that these parasitic jawless fish that have barely changed since the mid Palaeozoic. The evidence of phylogeny, however, suggests that the lamprey lineage diverged much earlier from other vertebrates, rather than arising from ostracoderm fishes. The origin of Hyperoartia may therefore extend back to the early Paleozoic, if not earlier. Although other early jawless fish such as Endeiolepis and Euphanerops are included in this group, new research (Sansom et al) shows them to be a distinct group further up the fish family tree. BILL 061113, HAJ100314, MAK111022

Descriptions



Hyperoartia: Lampreys and their ancestors. *Hardistiella, Mayomyzon, Pipiscius*. (= Petromyzontiformes)

Range: Early Carboniferous to Recent

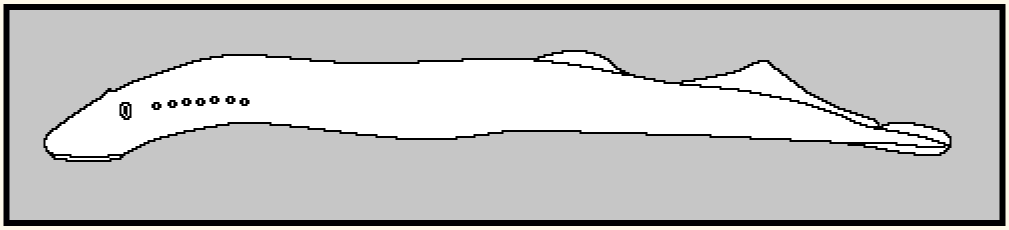
Phylogeny: Vertebrata:: (Anaspida + (Pteraspidomorphi + Thelodonti)) + *: *Euphanerops* (Janvier) + Petromyzontiformes.

Characters: Eel-shaped aspect; oral sucker with keratinous "teeth"; sucker reinforced by annular cartilage; sucker with the pumping velum; piston cartilage in lingual apparatus with pectinate keratinous "teeth" which rotate on the tip of the retractable piston cartilage; eyes relatively large, with lens, but no intrinsic muscles; extrinsic eye muscles almost same as gnathostomes; **$** single median dorsal nasohypophysial opening for both the olfactory organ and a blind hypophysial tube including the hypophysis (hypophysial tube may be remnant of primitive nasopharyngeal duct, *but see* The Basisphenoid); translucent pineal spot; true cartilagenous braincase plus cranial cartilage plates and bars; labyrinth with two vertical semicircular canals; seven gill openings; gill pouches large and posteriorly placed; spine-shaped process on gill arches; unjointed "branchial basket" for gills; arches external to gill pouches and branchial circulation; small cartilaginous dorsal arcualia (basidorsals and interdorsals) on notochord; loss or absence of anal fin; dorsal and caudal fins with thin cartilaginous radials associated with radial muscles; tail slightly hypocercal; loss or absence of mineralized exoskeleton; no scales; large neuromasts present; *ammocete* larva and extensive larval stage; anadromous; genome probably has undergone one round of duplication from ancestral chordate.

Comment: Relationships of *Euphanerops* (previously known as *Endeiolepis*) with lampreys are proposed by Janvier 1996 and elsewhere but disputed by in view of new study by Sansom et al, is transferred to the new vertebrate clade Jamoytiiformes, which would mean that Petromyzontiformes and Hyperoartia are synonymised. For now we keep the possibility of either thesis open MAK111026

Links: Hyperoartia; Introduction to the Petromyzontiformes; Hyperoartia; Neuroethology: Swimming in the Lamprey; Evolution der Fische (German); Phylogénomique.

References: Janvier (1999); Shu et al. (1999).



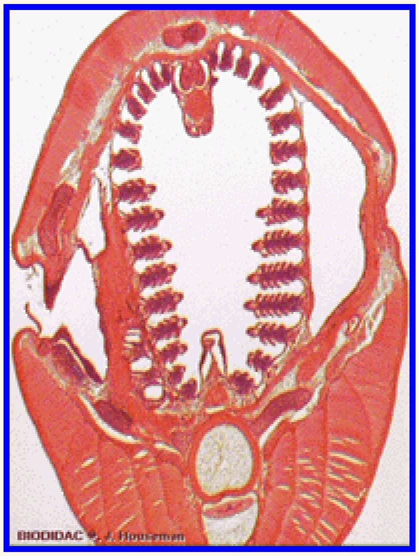
Petromyzontiformes: Lampreys and their ancestors. *Hardistiella, Mayomyzon, Pipiscius*.

Range: Late Devonian to Recent

Phylogeny: Vertebrata ::: *Euphanerops*(?) + * ::: Petromyzontidae

Characters: : Body anguilliform; round, suckerlike jawless subterminal mouth filled with rows of keratinous "teeth";

rasplike "tongue"; internal ring of cartilage supports rim of mouth; 1 median dorsal nasal opening; 2 semicircular canals; 7 gills similar to anaspids arranged behind the orbit; vertebrae present; 2 dorsal fins; no bone; often anadromous; *ammocoete* larvae 3-7 yrs as sedentary filter feeders filtering particles from mucous secretions; short-lived, parasitic adult form.



Links:: Introduction to the Petromyzontiformes; Svenska fiskar: havsnejonöga (Swedish); Geol 437 jawless fishes (NOT \AGNATHA\), Fall, 1995; Lampreys (Petromyzontiformes); Petromyzontiformes (mtDNA equence data); Petromyzontiform.

Image credits: top, from John Pojeta, Jr.; Right: unidentified lamprey from Fishbase. Left: Cross-section of an ammocete larva at the level of the gills from BIODIDAC. Note the external gill supports that have become a key issue in Mallat's theory of the origin of jaws. The (even more significant) *internal* gill supports are not readily identifiable in this image. APW040314.

Hardistiella montanensis Janvier & Lund, 1983

Range: Carboniferous

Phylogeny: Petromyzontiformes **:** * (Paraphyletic Mayomyzoninae) **:::** (Petromyzontidae

Comments: *Hardistiella* is the oldest known lamprey, of uncertain relationships. Lampreys are jawless vertebrates that lack, primitively, any sort of bone tissue or teeth. Modern lampreys have two different life styles. Most are filter feeders, but some have an adult stage in which they predate upon fish by means of sharp cornified rasping projections upon a “tongue”. Hardistiella shows no evidence of rasping structures, but we do not know whether they are mature or not. BILL 061113

Links: Anaspida..

Mayomyzon pieckoensis Bardack & Zangerl, 1962

Range: Carboniferous

Phylogeny: Petromyzontiformes **:::** * (Paraphyletic Mayomyzoninae) **:::** (Petromyzontidae

Characters: Piston cartilage in lingual apparatus (Janvier1997)

Comments: *Mayomyzon* is the best known fossil lamprey and resembles extant lampreys in many respects, except for the somewhat stouter body shape, smaller gill pouches, and coalescent dorsal and caudal fins. Mayomyzon possessed as piston cartilage and, thus, a complex "tongue"-like apparatus. BILL 061113

Links: Hyperoartia - Tree of Life Web.

Pipiscius zangerli Gess, Coates & Rubidge, 2006

Range: Carboniferous

Phylogeny: Petromyzontiformes **:::** * (Paraphyletic Mayomyzoninae) **:::** (Petromyzontidae

Characters: Horny plates or denticles on sucker (Janvier1997)

Comments: A poorly known lamprey that possessed a rouded sucker armed with polygonal horny plates. BILL 061113

Links: Hyperoartia - Tree of Life Web.

Priscomyzon riniensis Bardack & Richardson, 1977

Range: Famennian (Late Devonian) of South Africa

Phylogeny: Petromyzontiformes**:::** (*Mesomyzon* + Petromyzontidae) + *

Characters: large oral disc, the first direct evidence of circumoral teeth and a well preserved branchial basket (Gess et al)

Comments: earliest known lamprey; marine/estuarine form that is more advanced (more conventionally lamprey-like) than the later Carboniferous forms

Links:

Mesomyzon mengae Chang, Zhang & Miao, 2006

Range: Early Cret. EAs

Phylogeny: Petromyzontiformes **:::** *Priscomyzon* + (Petromyzontidae + *).

Links: Hyperoartia - Tree of Life Web.

Petromyzontidae: *Ichthyomyzon, Petromyzon, Caspiomyzon, Geotria, Mordacia, Eudontomyzon, Tetrapleurodon, Entosphenus, Lethenteron*, and *Lampetra*

Range: Recent

Phylogeny: Petromyzontiformes **:::** *Priscomyzon* + (*Mesomyzon* + *).

Characters: Seven gill openings, gill pouches larger and more posteriorly placed, eel-shaped aspect. (Janvier1997)

Comments: Extant lampreys. "The interrelationships of the ten extant genera is still unclear, but it is currently admitted that the organisation of the horny denticles of the sucker in *Ichthyomyzon*, *Petromyzon* and *Caspiomyzon* is primitive for the group. It is also quite similar to that found in one of the fossil lamprey, *Pipiscius*." - Janvier1997

Links: Hyperoartia - Tree of Life Web (same as Janvier 1997 ref); Wikipedia, doubtless more links could be added. See also Hyperoartia links (these haven't been checked in some time though some many may no longer be current). MAK111022

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checked ATW031116, revised MAK111027

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Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Jamoytiiformes

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
     |--Jamoytiiformes
     |  |--Jamoytius
     |  `--Euphanerops
     |--Hyperoartia (= Petromyzontiformes)
     `--+--Conodonta
        `--+--Anaspida
           `--+--Pteraspidomorphi
              `--+==Thelodonti
                 `--+==Cephalaspidomorphi
                    `--Gnathostomata
```

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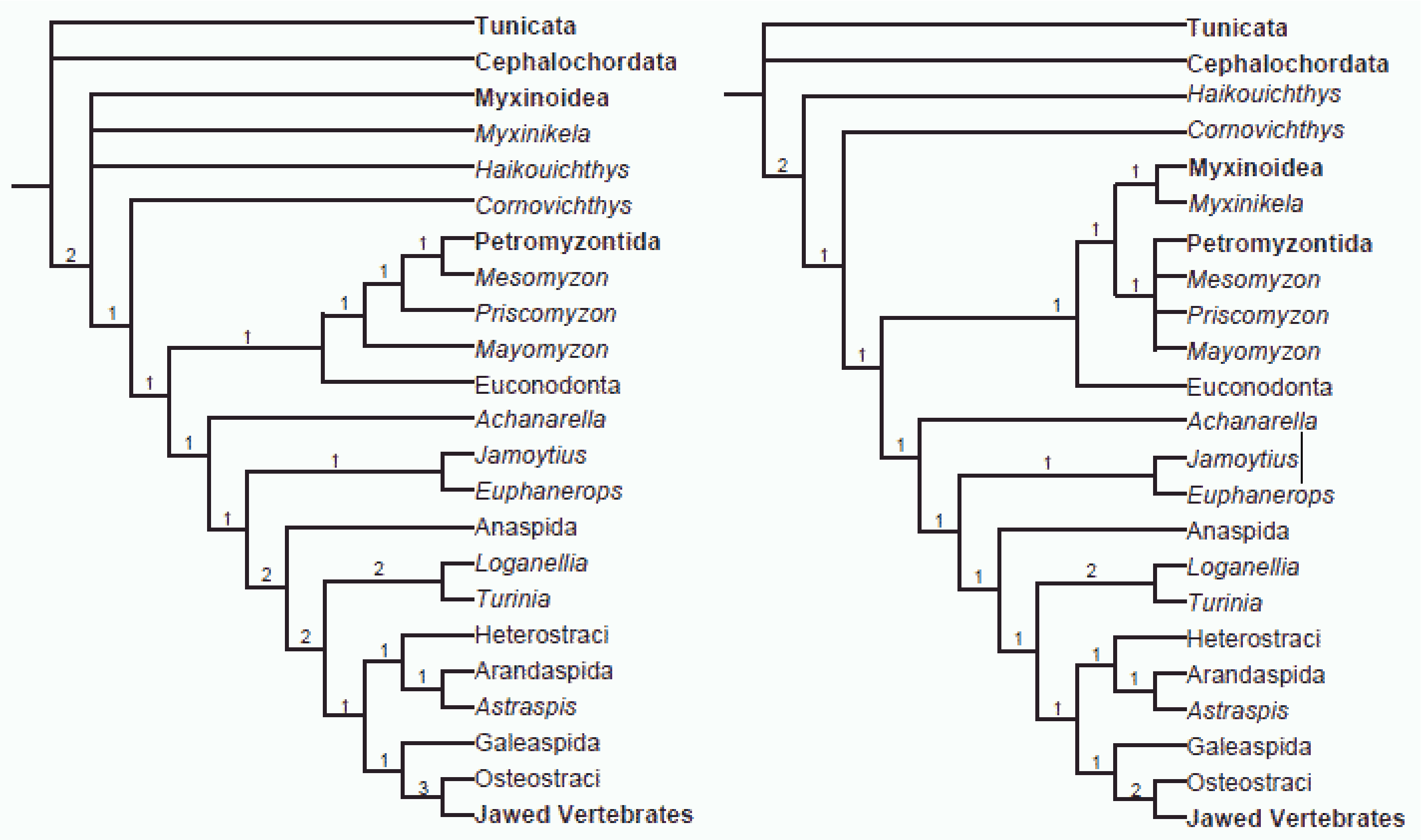
Taxa on This Page

1. *Euphanerops* X
2. *Jamoytiiformes* X
3. *Jamoytius* X

The first fish

Among the ostracoderms, to give the term for a paraphyletic evolutionary grade of jawless fish found in books by Romer, Colbert, etc (Evolutionary Systematics), the Anaspida was an assemblage of unarmoured forms that, like the thelodonts, seem to have become something of a wastebasket taxon for early agnaths that did not belong elsewhere. Leading vertebrate phylogenist Philippe Janvier was the first to make a systematic study of the group on cladistic grounds (Janvier 1996). He argued that the Anaspida are ancestral or basal lampreys, via intermediate forms like *Endeiolepis*. More recently he has modified this original position by distinguishing between more primitive forms like *Euphanerops*, and the Anaspida proper Janvier, 2007b. The former might be on the lamprey stem, whereas the latter are more derived forms. He has also synonymised *Endeiolepis*, *Legendrelepis*, and *Euphanerops* e.g. Janvier 2008, p.1051

An alternative hypothesis is proposed by Sansom and co-workers (Sansom et al 2010) who re-examined the well-known early Silurian anaspid *Jamoytius kerwoodi*, taking into account taphonomic studies, topological analysis, model reconstruction and elemental analysis, to arrive at a more accurate anatomical interpretation, and on this basis provided a new cladistic analysis they discovered that *Jamoytius* and *Euphanerops* (= Endeiolepis) form a clade, which they named Jamoytiiformes, which are stem-gnathostomes rather than proto-lampreys or Anaspida. Their cladogram also revealed the Anaspida to be similarily along the line to gnathostomes, and not related to Petromyzoniformes. So far this agrees with Janvier. Where it differs is that the Jamoytiiformes, including *Euphanerops* are now removed from the Hyperoartia. Apart from leaving the lampreys without obvious ancestors (except possibly conodonts), this means, taxonomically, than the Hyperoartia becomes a synonym of Petromyzoniformes, or vice versa, depending on your choice of terminology. The cladogram is as follows:



Phylogenetic relationships of *Jamoytius* and related taxa, by Sansom et al 2010. *Left*: single most parsimonious tree from the unconstrained phylogenetic analysis with decay support indices. *Right*, Strict consensus of trees resulting from analysis constrained for cyclostome monophyly (according to molecular phylogeny) with decay indices.

Here, the very basal position of the otherwise typically Anaspid- or *Jamoytius*-like form *Cornovichthys* as a stem-vertebrate is supported only by a single equivocal character (anterior otic capsules), and hence may not be reliable. The authors suggets that the stem placements of Cornovichthys and Achanarella are more likely to reflect taphonomic bias resulting from loss of characters through post-mortem decay (Donoghue and Purnell 2009; Sansom et al. 2010). The placement of conodonts as stem-lampreys differs from previous analyses, although it is the most parsimonious on the basis of the morphological data. The addition of other soft-bodied taxa in phylogenetic analaysis will therefore affect hypotheses of euconodont relationships, although trhe premise that euconodonts are vertebrates seems solid (Sansom et al 2010).

All of which pretty much demolishes the Linnaean/Evolutionary Systematic classification of the Anapsida given by Tarlo 1967. This does not mean that any Linnaean style arrangement has to be discarded in every instance, but simply because no one in vertebrate palaeontology is now working in this area, so any coverage is naturally out of data. Elsewhere we will presenting informal Linanean classifications of various taxa, with the proviso that these are not taken too seriously!

Changing the coding strategy for dentine and odontodes results in the thelodonts (represented in the cladograms by *Loganellia* and *Turinia*) being more basal than the pteraspidimorphi. We await further results on this matter before revising all our trees of early vertebrates! MAK111027

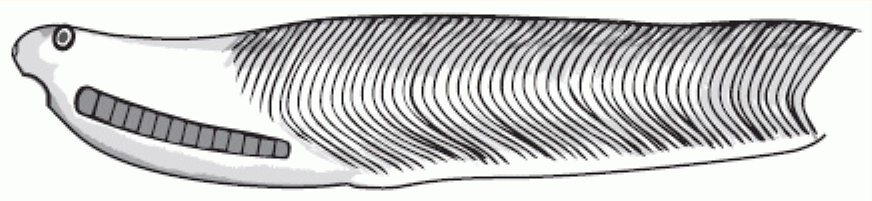
Jamoytiiformes Tarlo, 1967

Range: Early Silurian to Late Devonian.

Phylogeny: two to choose from:
Janvier: Hyperoartia **:** Petromyzontiformes + *Euphanerops* (and by implication Jamoytiiformes) .
or Sansom et al 2010: Vertebrata **:::** (Thelodonti + (Anaspida + (Pteraspidomorphi + + (Cephalaspidomorphi + Gnathostomata))) + * **:** *Jamoytius* + *Euphanerops*.

Characters: ventral mouth and annular cartilage (both homoplastic characters). Sansom et al 2010

Comments: Jamoytiiformes appear cladistically as stem-gnathostomes because of their trunk dermal skeleton, separate anal fin and paired fin folds. They are however are more primitive than Anaspida because of the absence of dermal head skeleton, dentine and lamellar aspidin. Sansom et al 2010 MAK111022



Jamoytius: *J. kerwoodi*

Range: Early Silurian of Scotland.

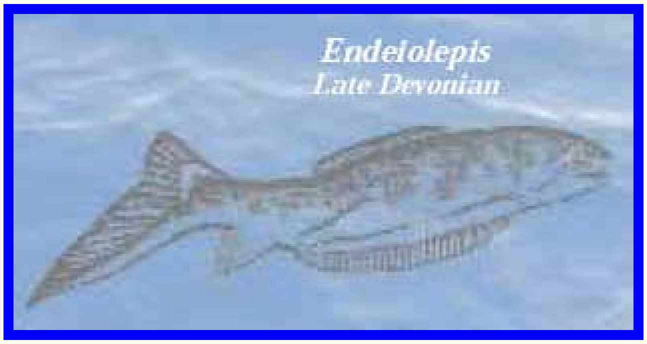
Phylogeny: Jamoytiiformes: *Euphanerops* + *.

Characters: W-shaped phosphatic scales, 10 or more pairs of branchial openings, optic capsules, a circular, subterminal mouth and a single terminal nasal opening. (Sansom et al 2010)

Comments: *Jamoytius* is commonly considered to represent either a primitive anaspid or ancestral lamprey. Analysis by Sansom et al 2010 establishes sister taxon relationship with *Euphanerops*.. Sansom et al 2010. The generic name honours Paleozoic fish specialist J. A. Moy-Thomas (ref Dawkins, *The Ancestor's Tale*, via Wikipedia). MAK111022

Graphic: New reconstruction of *Jamoytius kerwoodi* by Sansom et al 2010

Euphanerops: *E. longaevus*



Synonyms *Endeiolepis aneri*, *Legendrelepis parenti*

Range: Late Devonian.

Phylogeny: two to choose from:
Janvier: Hyperoartia **:** Petromyzontiformes + *.
or Sansom et al 2010: Jamoytiiformes: *Jamoytius* + *.

Characters: tail strongly heterocercal; no mineralized exoskeleton ATW040314

Comment: Probably cogeneric with *Euphanerops* MAK111022

Image: from John Pojeta, Jr.

Links: Vertebrata; Anaspida; DEVONIANO vegetais primitivos (Portuguese); Page 1. ATW040314.

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Vertebrata Dendrogram

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
       |--Jamoytiiformes
       |--Hyperoartia (= Petromyzontiformes)
       `--+--Conodonta
          `--+--Anaspida
             `--+--Pteraspidomorphi
                `--+==Thelodonti
                   `--+==Cephalaspidomorphi
                      `--Gnathostomata
```

Contents

Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
|--Haikouichthys
`--+--Zhongjianichthys
   |--Myxinoidea
   `--Vertebrata
      |--+--Jamoytiiformes
      |  |-- Jamoytius
      |  `-- Euphanerops
      |--+--Hyperoartia (= Petromyzontiformes)
      |  |- Hardistiella montanensis
      |  `--+-- Mayomyzon pieckoensis
      |     `--+- Pipiscius zangerli
      |        `--+-- Priscomyzon riniensis
      |           `--+-- Mesomyzon mengae
      |              `-- Petromyzontidae
      `--+--Conodonta
         `--+--Anaspida
            `--+--Pteraspidomorphi
               `--+==Thelodonti
                  `--+==Cephalaspidomorphi
                     `--Gnathostomata
```

---

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Vertebrata References

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myllokunmingia
`--+--Myxinoidea
   `--Vertebrata
      |--Jamoytiiformes
      |--Hyperoartia (= Petromyzontiformes)
      `--+--Conodonta
         `--+--Anaspida
            `--+--Pteraspidomorphi
               `--+==Thelodonti
                  `--+==Cephalaspidomorphi
                     `--Gnathostomata
```

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- Dendrogram
- References

References

Benton, M. J. 2005. *Vertebrate Paleontology*. Third Edition. Blackwell Publishing
Systematics - Update,

Cameron, CB, JR Garey & BJ Swalla (2000), *Evolution of the chordate body plan: new insights from phylogenetic analyses of deuterostome phyla*. **Proc. Nat'l. Acad. Sci.** 97: 4469-4474.
Craniata., Vertebrata

Chen, J-Y, D-Y Huang & C-W Li (1999), *An early Cambrian craniate-like chordate*, **Nature** 402: 518-522.
Vertebrata.

Delabre, Christiane et al. (2002). "Complete Mitochondrial DNA of the Hagfish, Eptatretus burgeri: The Comparative Analysis of Mitochondrial DNA Sequences Strongly Supports the Cyclostome Monophyly". Molecular Phylogenetics and Evolution 22 (2): 184-192
Systematics - Update,

Donoghue, PCJ, PL Forey & RJ Aldridge (2000), *Conodont affinity and chordate phylogeny*. **Biol. Rev.** 75: 191-251.

Systematics, Vertebrata.

Donoghue, P. C. J. and Purnell, M. A. 2009. Distinguishing heat from light in debate over controversial fossils. *BioEssays*, 31, 178–189.
Jamoytiiformes - Overview.

Robert W. Gess, Michael I. Coates & Bruce S. Rubidge, A lamprey from the Devonian period of South Africa,

Nature 443, 981-984 (26 October 2006), doi:10.1038/nature05150
Priscomyzon

Gürsoy, Halil-Cem; Koper, Dorota, & Benecke, Bernd-Joachim (2000.). "The Vertebrate 7S K RNA Separates Hagfish (Myxine glutinosa) and Lamprey (Lampetra fluviatilis)". *Journal of Molecular Evolution* 50 (5): 456–464. doi:10.1007/s002390010048. PMID 10824089.
Systematics - Update,

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp.
Systematics, Jamoytiiformes - Overview.

Janvier, Philippe. 1997. Hyperoartia. Lampreys. Version 01 January 1997 (under construction). http://tolweb.org/Hyperoartia/14831/1997.01.01 in The Tree of Life Web Project, http://tolweb.org/
Mayomyzon, Pipiscius, Petromyzontidae.

Janvier, P (1999), *Catching the first fish*. **Nature** 402: 21-22.
Craniata, Hyperoartia.

Janvier P (2003) Vertebrate characters and Cambrian vertebrates. *CR Palevol* 2: 523–531
Haikouichthys.

Janvier, P, 2007a , Living Primitive Fishes and Fishes from Deep Time, pp. 1-53, David J. McKenzie, Anthony Peter Farrell, Colin J. Brauner, *Primitive fishes*, Elsevier Academic Press
Systematics - Update,

Janvier P. 2007b Homologies and evolutionary transitions in early vertebrate history. In *Major Transitions in Vertebrate Evolution* Ed by JS Anderson, H-D Sues, Indiana University Press, Bloomington, pp 57-121
Systematics - Update,

Janvier, P. 2008. Early jawless vertebrates and cyclostome origins. *Zoological Science*. 25: 1045-1056.
Systematics - Update,

Janvier, P. 2010, microRNAs revive old views about jawless vertebrate divergence and evolution, Proc Natl Acad Sci USA, November 9, 2010 vol. 107 no. 45 19137-19138 online
Systematics - Update,

Heimberg AM, Cowper-Sal·lari R, Sémon M, Donoghue PCJ, Peterson KJ (2010) microRNAs reveal the interrelationships of hagfish, lampreys, and gnathostomes and the nature of the ancestral vertebrate. Proc Natl Acad Sci USA 107:19379-19383. online
Systematics - Update,

Kuraku, Shigehiro, Meyer, Axel, & Kuratani, Shigeru (2009a). "Timing of Genome Duplications Relative to the Origin of the Vertebrates: Did Cyclostomes Diverge before, or after?". Molecular Biololgy & Evolution 26 (1): 47-59. doi:10.1093/molbev/msn222.
Systematics - Update,

Kuraku, Shigehiro, Ota, Kinya G., & Kuratani, Shigeru, S. Blair (2009b). "Jawless fishes (Cyclostomata)". In S.B. Hedges & S. Kumar. Timetree of Life. oxford University Press. pp. 317-319. ISBN 978-0-19-953503-3.
Systematics - Update,

Sansom, R. S., Freedman, K., Gabbott, S. G., Aldridge, R. A. and Purnell, M. A. 2010a. Taphonomy and affinity of an enigmatic Silurian vertebrate Jamoytius kerwoodi White. *Palaeontology* 53: 1393-1409.
Systematics - Update, *Haikouichthys*, Jamoytiiformes - Overview, Jamoytiiformes, Jamoytius. Hyperoartia.

Sansom, R. S., Gabbott, S. E. and PurnelL, M. A. 2010b. Non-random decay of characters causes bias in fossil interpretation. *Nature*, 463, 797–800.
Jamoytiiformes - Overview.

Shu, DG (2003). "A paleontological perspective of vertebrate origin." *Chinese Science Bulletin* 48 (8), 725-735. p. DOI : 10.1007/BF03187041 . ISSN 1001-6538.
Haikouichthys, Zhongjianichthys

Shu, D-G, H-L Luo, SC Morris, X-L Zhang, S-X Hu, L Chen, J Han, M Zhu, Y Li & L-Z Chen (1999), *Lower Cambrian vertebrates from South China*. **Nature** 402: 42-46.
Craniata, Vertebrata, Hyperoartia.

D.-G. Shu, S. Conway Morris, J. Han, Z.-F. Zhang, K. Yasui, P. Janvier, L. Chen, X.-L. Zhang, J.-N. Liu, Y. Li & H.-Q. Liu, 2003, Head and backbone of the Early Cambrian vertebrate Haikouichthys, Letters to Nature, *Nature* 421, 526-529 (30 January 2003) | doi:10.1038/nature01264;
Haikouichthys.

LBH Tarlo (1967), *Agnatha*, **in** WB Harland *et al.* (eds.), **The Fossil Record**, The Geological Society, pp.629-636.
Jamoytiiformes - Overview.

Wilson, MVH & MW Caldwell (1998), *The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from Northern Canada*. **J. Vert. Paleontol.** 18: 10-29.
Systematics.

Zimmer, C (2000), *In search of vertebrate origins: beyond brain and bone*, **Science** 287: 1576.
Craniata.

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Conodonta: Overview

Abbreviated Dendrogram

```
Vertebrata
|--+--Pteraspidomorphi
|  `--Gnathostomata
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

Contents

"The Jaws That Catch": an Introduction to the Conodonta

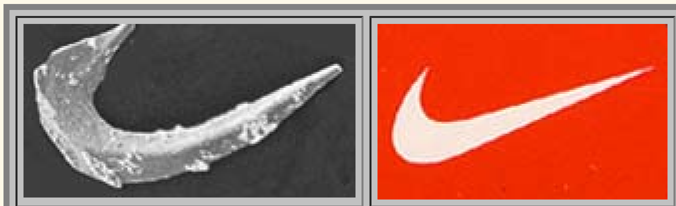
One of the true, great mysteries of vertebrate paleontology concerns the Conodonta, and the relation of the conodont apparatus to vertebrate bones. Indeed, until a decade ago, these matters were sufficiently mysterious that very few suspected a relationship to vertebrate paleontology at all. The very first paper published on conodonts actually had reported them as the remains of some unknown fish. Pander (1856), *vide* Sweet & Donoghue (2001). But this notion was quickly discarded. It is really only since the mid-1990's that Pander's original intuition has been proved correct and these weird Paleozoic worms have been fully initiated into the exclusive sorority of extinct vertebrates. *See, e.g.*, Janvier (1995), Donoghue *et al*. (2000).

> **"We specifically reject terms such as 'conodont- bearing animal' or 'conodont animal' -- at least until our colleagues who study brachiopods or dinosaurs adopt the rubrics of 'brachiopod animal' or 'dinosaur animal' to distinguish between the shells or bones of those creatures and the entire organism." Sweet & Donoghue (2001)**

Conodont Elements & Apparatus

The reason for this long-delayed acceptance into polite society relates -- as it sometimes does -- to the fact that conodonts are entirely too common. Conodont elements, the disarticulated bony remains of the complex conodont oral apparatus, are found as microfossils by the tens of thousands in virtually every Paleozoic marine sediment, everywhere in the world. Further, the various elements occur as isolated pieces, mixed more or less randomly in matrix. With respect to each, as Shelley (1817) noted of another disarticulated relic, "nothing beside remains. Round the decay ... boundless and bare, the lone and level sands stretch far away" It was not until the 1960's that a few, spatially contiguous remains were recognized as "natural assemblages," collections of conodont elements which represented the parts of a complex but unified structure belonging to a single organism which had remained *in situ*, where the conodont had died. With these discoveries came the whole notion of a "conodont apparatus," a unique food-processing machine made up of conodont elements, and the search for the correct three dimensional arrangement and functional biology of the elements was under way.

Although the reconstruction of the apparatus has been a central theme of conodont research in recent years, we will defer any serious discussion of the apparatus until we are positioned to look at the specifics of the Ozarkodinida and the work of Purnell & Donoghue (1997) on this, probably the best-known group of conodonts. Instead, we will take up the very poorly known matter of conodont biology and chordate affinity.

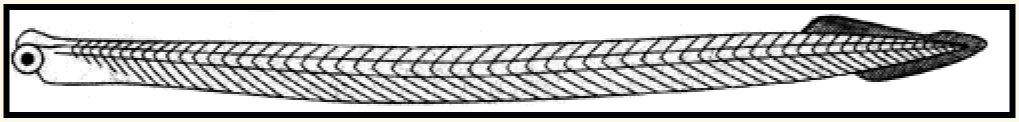


The secret of conodont survival: Evolutionary fitness or corporate sponsorship?
(with apologies to Albanesi & Barnes 2000)

Conodont Biology

As an aside, conodont biology has been the source of one of the strangest social transformations in recent academic history. Consider that, for many years, conodont affinities were unknown, even as to Kingdom, much less phylum. However, conodont elements are very common items and easy to isolate. As a result, conodont elements became key stratigraphic markers. The students of these obscure phosphatic scraps were thus much in demand as petroleum stratigraphers. While stratigraphy is a relatively low academic calling, it pays rather well because of its obvious real-world commercial value. By contrast, vertebrate paleontology has always been a useless, but popular and respected pursuit, although the pay ranges from the execrable to the non-existent. Imagine, then, the dismay of all concerned when conodonts were discovered to be vertebrates. Suddenly, conodont workers were dragged from the oil-stained proletarian legions of Houston and Riyadh petro-imperialism and thrust into the rarified, if ragged, intellectual circles of vertebrate paleontologists.

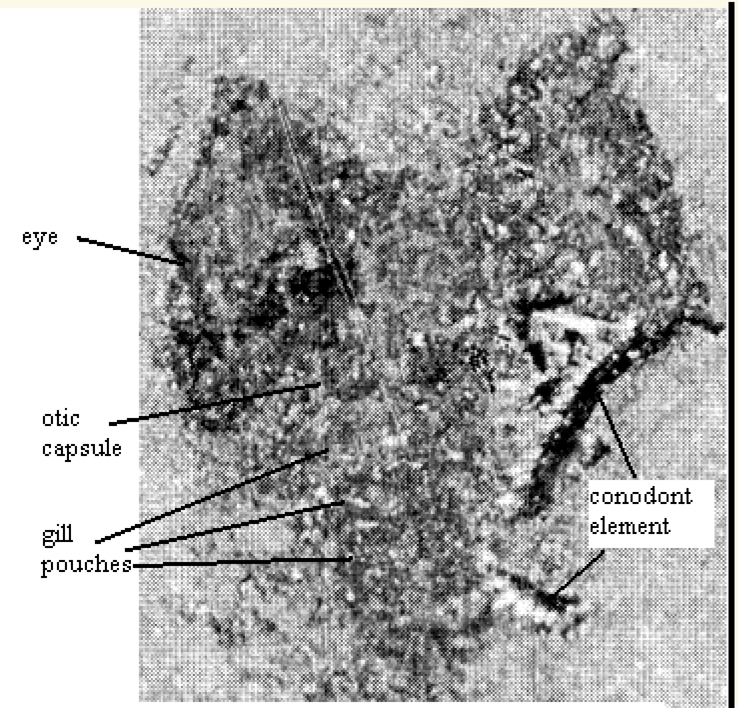
But we must retreat from these sociological speculations to return to the more pertinent, if scarcely less speculative, matter of conodont biology. As noted previously, a very few conodont fossils are preserved as natural assemblages. Of these rare events, a scant handful may also preserve traces of soft tissues on careful, or imaginative, inspection. From these, exceedingly unusual, fossils, conodont workers have recently begun to reconstruct the vertebrate inheritance of these chordate Cinderellas.



A life reconstruction from Sweet & Donoghue (2001) is shown at right. These authors have recently reviewed the evidence for the chordate nature of conodonts. There would be little point in recapitulating this excellent and very readable review. However, we shall do so anyway on the theory that, if the reader had ready access to such materials, he or she would not be spending valuable time on this web site in the first instance. However, unlike Sweet & Donoghue, we will make no effort to strike a linguistically neutral pose, and will use vertebrate anatomical vocabulary without excuse or, perhaps, justification.

Conodonts are elongate worm-like organisms that flourished from the Middle Cambrian through the end-Permian event. After near extinction in that catastrophe, they made a considerable recovery, but dwindled and disappeared by the end of the Triassic or perhaps the earliest Early Jurassic. Their phylogeny is very poorly known . Early Cambrian "protoconodonts" are currently believed to be the unrelated remains of chaetognaths (or "arrow worms"). Sweet's (1988) pre-cladistic taxonomy is still the standard and has been adopted here. As of this writing (020727), a full-scale cladistic study is nearing completion and may see daylight in another two years.

Much of the discussion of other cranial structures is based on a single specimen of *Clydagnathus windsorensis*, which is reproduced at right, with structures identified according to the interpretation of Donoghue *et al*. (2000), Sweet & Donoghue (2001), and concordant sources. Conodonts have a reasonably well-defined head with two large hemispherical or ovoid anterolateral structures which have been interpreted as eyes. For reasons which will be discussed presently, we believe this interpretation is incorrect. Posteromedial to the eyes are a pair of dark, circular structures identified as otic capsules. Posterior and slightly lateral to these are a series of paired vacuities which are interpreted as pharyngeal pouches.



Clydagnathus specimen IGSE 13821 interpreted as in Donoghue et al (2000) and Sweet & Donoghue (2001).

Far less debatably, the long conodont body has obvious V-shaped myomeres throughout its length. A pair of (very probably) dorsal parallel lines also extend the length of the body, and these are believed to represent the outlines of the notochord. Cartilaginous arcualia seem to be associated with the notochord. Last, and most convincingly of all, conodonts bear a distinct tail with a small but clear set of fins supported by very fish-like fin radials.

From this rapid tour of the principle scenic attractions of the taxon, it is reasonably clear that the Conodonta are chordates, and probably vertebrates. The only competing hypothesis -- chaetognath affinity -- provides some alternative interpretations; but the dorsal notochord, tail, and fin radials make this unlikely. For the present, despite many difficulties of detail, we can accept the hypothesis of vertebrate ancestry with a fair degree of confidence. ATW020727.

What Next?

At this point, the reader who has *still* not been induced to depart these precincts in haste, or to resort to some more learnèd and authoritative source, is confronted with a small number of equally repugnant options. They are as follows:

1. Learn why the conodont eye is nothing of the sort. (continues this discussion)

2. Ignore this baseless prattle and **proceed to the phylogenetic summary.**

3. Skip over to the Ozarkodinida for additional rumor and speculation concerning the conodont apparatus.

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Conodonta

Abbreviated Dendrogram

```
Vertebrata
|
|--+--Pteraspidomorphi
|  `--Gnathostomata
|
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

Contents

Taxa on this Page

---

1. Conodonta X
2. Euconodonta X
3. Paraconodontida X
4. Proconodontidae X
5. Protopanderodontida X

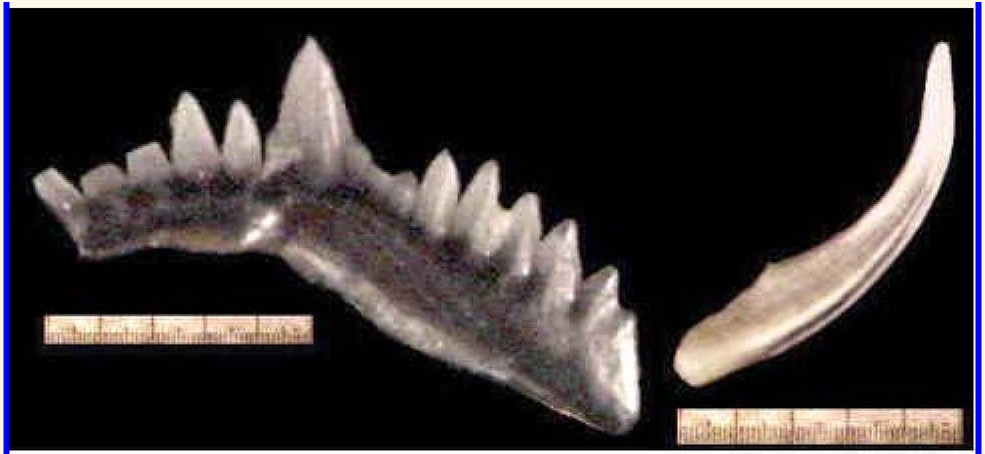
Descriptions

Conodonta:

Range: Middle Cambrian to Late Triassic (near extinction in Early Permian, followed by brief recovery)

Phylogeny: Vertebrata: (Pteraspidomorphi + Thelodonti) + *: Paraconodontida + Euconodonta.

Characters: bilaterally symmetrical



Examples of compound (left) and coniform (right) conodont elements. Scale bar is 0.5 mm

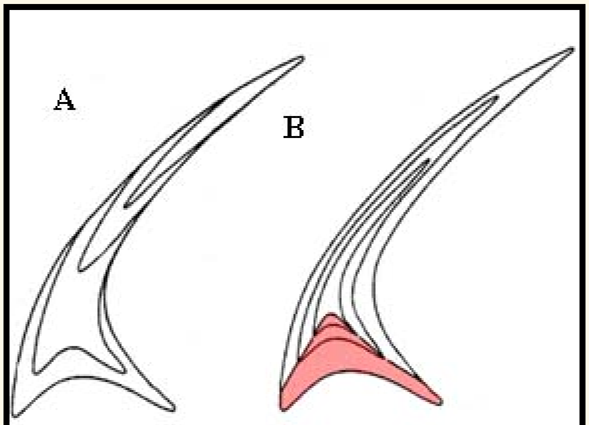
vermiform (worm-like) animals; eyes present; conodont elements appear to be mouth parts; elements grew through successive addition of *apatite* layers around a basal cavity & usually capped by a tooth-like cusp; shapes depend n unequal addition of apatite; processes created by expansions may be capped with denticles, ridges, etc.; V-shaped myomeres; .

Notes: **[1]** the existence of a basal cavity is thought to mean that the elements grew within an epithelial pocket of the animal. **[2]** simple coniform types dominant in Cambrian first half of Ordovician. Compound elements (ramiform, pectiniform, etc.) first occur in Furongian and dominate after the Middle Ordovician. During Early Silurian, coniforms prevalent in off-shore faunas, while compound types were more numerous in nearshore environments. Coniform types disappeared after Early Devonian. **[2]** conodont elements known from ~50My prior to first bony scales from fish (*Sacabambaspis*).

Image: from Conodont Collection, James Davison

Links: Brazilian Conodonts; Euconodonta; Conodont Collection, James Davison; Conodonta; con-nexus; Armed to the teeth; Boggy's links to Conodonts; Conodonta after Sweet & Donoghue, 2001; ICRIODUS; miscinvs.htm; PALAEONTOLOGIA POLONICA, vol. 58; Muzeum Geologiczne - Konodont (Polish); World of Conodonta. APW040316.

Paraconodontida: (= Paraconodonta) *Prooneotodus*



Schematic cross- sections of (A) paraconodont and (B) euconodont elements, showing growth pattern. Red shading indicates portions of euconodont element believed to be homologous to paraconodont element. From Donoghue et al. (2000).

Range: Middle Cambrian to Early Devonian (?)

Phylogeny: Conodonta: Euconodonta + *.

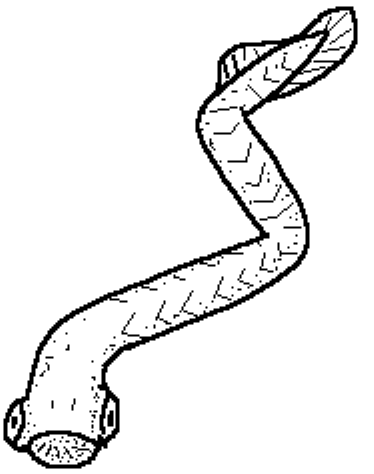
Characters: Relatively simple forms with simple cones [SD01]; single tissue layer probably homologous with basal body of euconodonts [D+00] [SD01]; elements relatively poorly mineralized [D+00]; growth proceeds by adding to margins & base, but not tip [D+00].

Note: no soft tissue remains of paraconodonts are known. However, the group may be paraphyletic and include euconodonts. The material of paraconodont elements, as well as of euconodont basal bodies, is believed to be a dentine homologue.

Links: confabs98.html (Cochrane abstract); Progressive Palaeontology - Titles and Abstracts - PAGE 4 (another Cochrane abstract); Jerzy Dzik's home page; Re: Conodont elements; Re: Conodont elements.

References: Donoghue *et al*. (2000) [D+00]; Sweet & Donoghue (2001) [SD01]. APW040316

Euconodonta:



Rough sketch of a euconodont animal

Range: Middle Cambrian to Late Triassic.

Phylogeny: Conodonta: Paraconodontida + *: Proconodontidae + (Protopanderodontida + Prioniodontida).

Characters: Large, anterior-most cups, believed to be eyes with extrinsic eye muscles; notochord not reaching most anterior portion of cranium; existence of brain inferred from encephalization of sensory structures; complex, poorly-understood tooth-like "conodont elements" formed in calcium phosphate (bone?) in head region; elements include grasping ramiform ('S' and 'M') elements and transverse (biting?) comb-shaped 'P' elements; conodont elements may have rasping function like hagfish and lampreys; 'P' elements may be velum homologue; conodont elements with precise occlusion suggested by microwear; elements formed poorly mineralized, finely crystalline base (probably dentine) and highly mineralized, coarsely crystalline crown (probably "homologous to enamel"); possible gill pouches; long, eel-like body with simple, V-shaped myomeres; fast-twitch fibers may not be present; possible longitudinal septum; 2-lobed (hypocercal?) caudal fin with radials, but no evidence of fin musculature; indeterminate growth

Links: Euconodonta; Conodonts; Hidden World of the Conodonta; Conodont apparatus model; Andrew MacRae - current projects; Conodonts; Scolecodont Definitions; What Are Conodonts?; The Pander Society - International Conodont Research; MsoDockBottom; CMM Research - Dr Anne Kemp; Meeting Reports.

References: Donoghue et al. (2000); Gabbott et al. (1995); Janvier (1995); Purnell (1995); Zimmer (2000).

Note: Estimated 65% of all jawless vertebrate species are conodonts, but the taxon was known only from conodont elements until 1983. A few body fossils are now known primarily from lagerstätten in Scotland and South Africa. The euconodonts are probably descended from the paraphyletic Lower Cambrian Paraconodontida; but this taxon is only known from crownless basal mineralizations and no soft tissue is known. The still more primitive Pre-Cambrian Protoconodonta are believed to be unrelated. APW040316.

Proconodontidae:

Range: Middle Cambrian? to ?

Phylogeny: Euconodonta: (Protopanderodontida + Prioniodontida) + *.

Note: not to be confused with Protoconodontida, which are probably non-chordate (chaetognath) remains. APW040316.

Protopanderodontida:

Range: Early Ordovician to ?

Phylogeny: Euconodonta:: Prioniodontida + *.

Characters: apparatus having a pair of incisor-like (M?) elements in front, a set of four pairs of relatively gracile (S?) elements connected into a single unit by one posteriorly located symmetrical (S_0?) element, and two pairs of robust (P?) elements hidden within the throat.

Links: Protopanderodontida; Jerzy Dzik's home page. APW040316.

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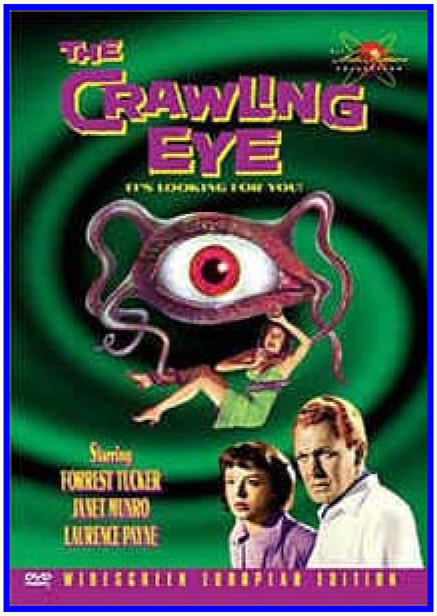
Conodonta: Overview (2)

Abbreviated Dendrogram

```
Vertebrata
|--+--Pteraspidomorphi
|  `--Gnathostomata
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

Contents

"The Crawling Eye": Seeing and Seeming in the Conodonta



On a previous page, we indicated doubt -- in fact outright rejection – of the conodont eye, as interpreted by Aldridge, Donoghue and others. On this page, we present the defense of our position, together with an alternative interpretation of the conodont head based on the same, critical IGSE 13821 specimen.

For reasons much too obvious to discuss, we will refer to the currently floated hypothesis as the "Crawling Eye" theory of conodont structure. In the 1958 movie of this name, a strange radioactive cloud settles on top of a remote mountain. After interminable mood music, and what passes for character development in this genre, an evil alien emerges from the cloud. By some bizarre quirk of interstellar homoplasy, it looks like a giant human eyeball with tentacles. But, supposing this to be true, what are the chances that, over the parsecs and megayears, we can take this similarity at, as it were, face value?

For the same reasons, we must sternly resist the temptation to assume that every large, bilateral, hemispherical structure -- even on an Earthly chordate -- is necessarily an eye. We will discuss a number of factors which make the Crawling Eye interpretation of IGSE 13821 unlikely; following which, we will present an alternative model which seems more consistent with the known information about conodonts.

A Crawling Eye?

Before braving the perils of morphology and differential tissue preservation, let us consider the difficulties of the Crawling Eye model *a priori*. It is a relatively simple matter to make a short list.

1. Not to belabor the obvious, but that's a hell of a big eye for a little beastie like a conodont. What happens to all that visual information? Where is the optic tectum or forebrain necessary to process the images? Heavy reliance on visual information is neurologically expensive and requires a great deal of cerebral overhead -- quite literally – to make proper use of the hypertrophied sensory organ.

2. The orbits bear a close relationship to the adenohypophysis from the point of view of genetic regulation. *See, e.g., The Basisphenoid*. In most basal vertebrates that association is also physical, so that the sella turcica or its predecessor lies in close proximity to the orbits or to an interorbital bar. While this is not always the case, the absence of anything similar here is suspicious.

3. The "accessory lobes," two round, dark patches posteromedial to the "eyes" are supposed to be otic capsules. This should inspire a brief, but urgent, reality check. An otic capsule in an organism without a skull? We need to be looking for the semicircular canals of a labyrinth structure, not the hard tissue of a braincase.

4. The conodont apparatus is taken up in more detail here. According to the careful work of Purnell & Donoghue (1997), the conodont apparatus makes best sense if the affair is largely mounted on bilateral cartilage plates. Given the size of the apparatus and its obvious importance to the organism, these plates should be substantial. Where are they in the Crawling Eye? Similarly, Purnell (2001, 2001a) has shown that the conodont P-elements were capable precise occlusion. Again, this argues for substantial, possibly massive bilateral cartilages associated with the conodont apparatus in the head region. Where are they in the Crawling Eye model? Is it possible that the optic sclera and even the eye itself are partially preserved while these cartilages have completely disappeared?

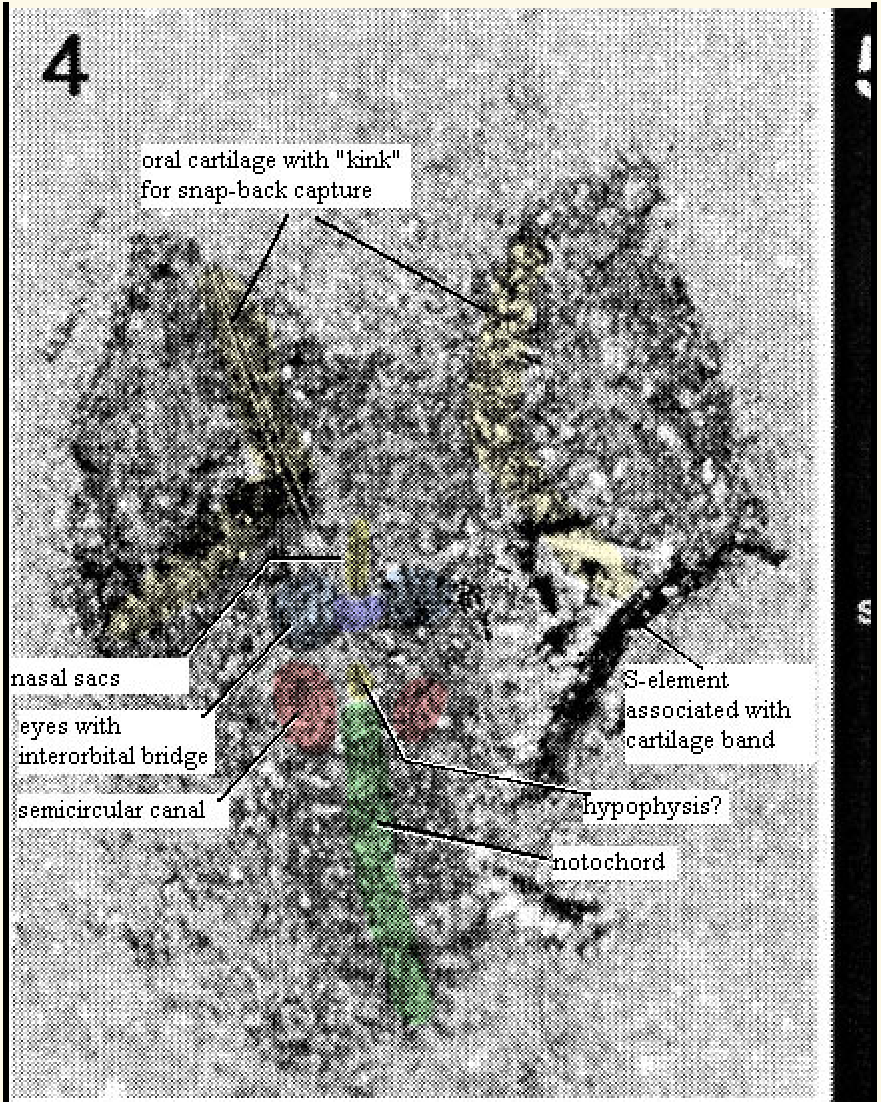
5. What might be the purpose of such large, *laterally placed* eyes in what seems to have been -- by any other design criterion -- a benthic organism? Mud grubbers usually dispense with elaborate eyes relatively quickly.

6. Finally, while not every Paleozoic vertebrate has pineal and/or parapineal foramina, and they would not necessarily be preserved, one typically looks to find such structures in primitive chordates.

The Crawling Mouth

None of the problems above absolutely refute the Crawling Eye model of the conodont head. We probably lack sufficient data to risk any kind of firm conclusions at the present time. However we do assert that it is possible to arrive at a more *likely* explanation for the observed structures -- one that is more consistent with hard information from hard tissues and less reminiscent of B-movies from the 1950's.

Consider, for example, the alternative model to the right. Other than the "eyes" of the Crawling Eye model, the conodont is revealed to be a very ordinary sort of vertebrate. It has two, primitive eyes which are closely paced, dorsal, and joined by an interorbital bridge. The eyes are closely associated with a nasohypophyseal foramen of some kind, just anterior to, and perhaps connected with hypophysis as in many other early craniates,



Clydagnathus alternative interpretation. "Nasal sacs" have been relabelled (051012) light of developments described on the next page.

such as the hagfish.

When suitably magnified, the semi-circular canals on the left side are unmistakable. There are no obvious gill pouches, but there is also no obvious need for them in an organism of this kind. Conodonts cannot have been filter-feeders. Purnell (2001). Thus, a pharyngeal filtering device is unlikely. A very small organism with the extreme elongation of a conodont would not require respiratory gills. Thus the posterior horizontal bands may be the arcualia of a true vertebrate, although they may also be respiratory structures if the organism habitually inhabited an oxygen-poor environment. The point here is that, whichever they are, they are not similar to, or serial homologues of, the semicircular canals.

So what are the "eyes" from the Crawling Eye? It is likely that they are precisely the missing oral cartilages of Purnell & Donoghue (1997). Purnell & Donoghue's structural studies of the ozarkodinid apparatus lead them to suggest that (a) the muscles controlling the apparatus must have operated through tendons running over a pulley - type structure and (b) that the apparatus may have "snapped" back into a retracted position from its everted state. Both of these requirements may be met if we suppose that the rims of the "eyes" are a curved or bent lateral oral cartilages and that the muscles were *lateral* to the cartilages. Thus the "eyeball" is revealed to be a mass of oral musculature and a complex tendon system. When the muscles contracted, tendons running around the lip of the cartilages from the lateral surface would pull the apparatus out and down, or in and up, exactly as envisioned by Purnell & Donoghue. Because the surface is curved, the distal ends of the S-elements would be spread like the ribs of a fan when everted. As the retractor muscles were contracted, these ends would snap inwards (medially) quite rapidly at first, then more slowly as the apparatus was drawn inwards.

ATW020727.

Continued on Next Page

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Conodonta: Overview (3)

Abbreviated Dendrogram

```
Vertebrata
|--+--Pteraspidomorphi
|  `--Gnathostomata
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

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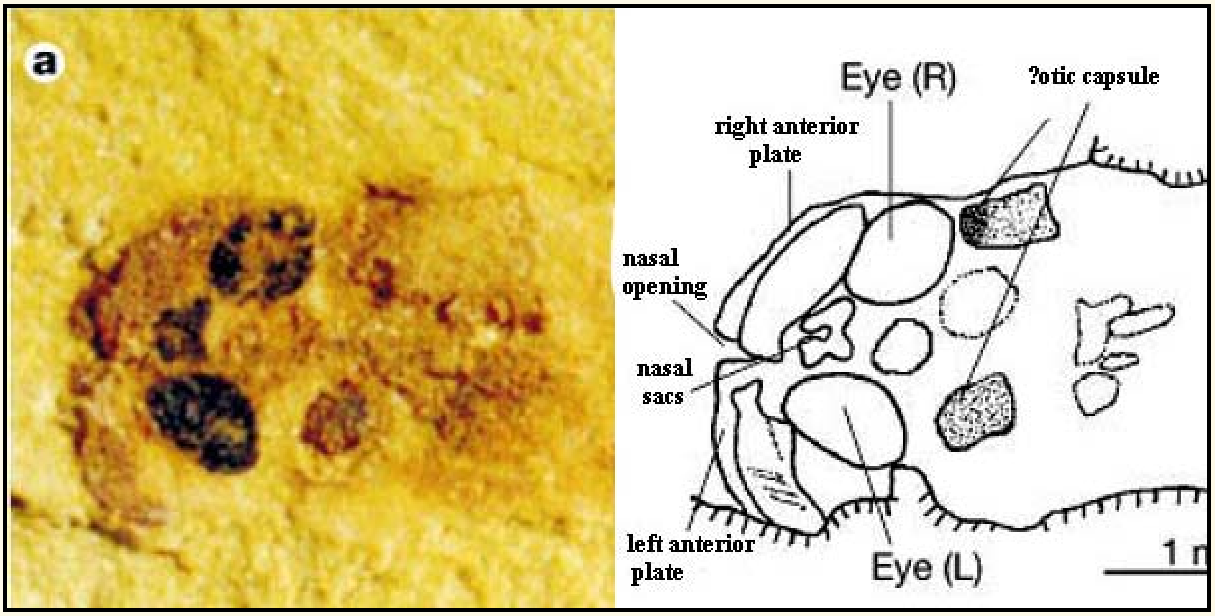
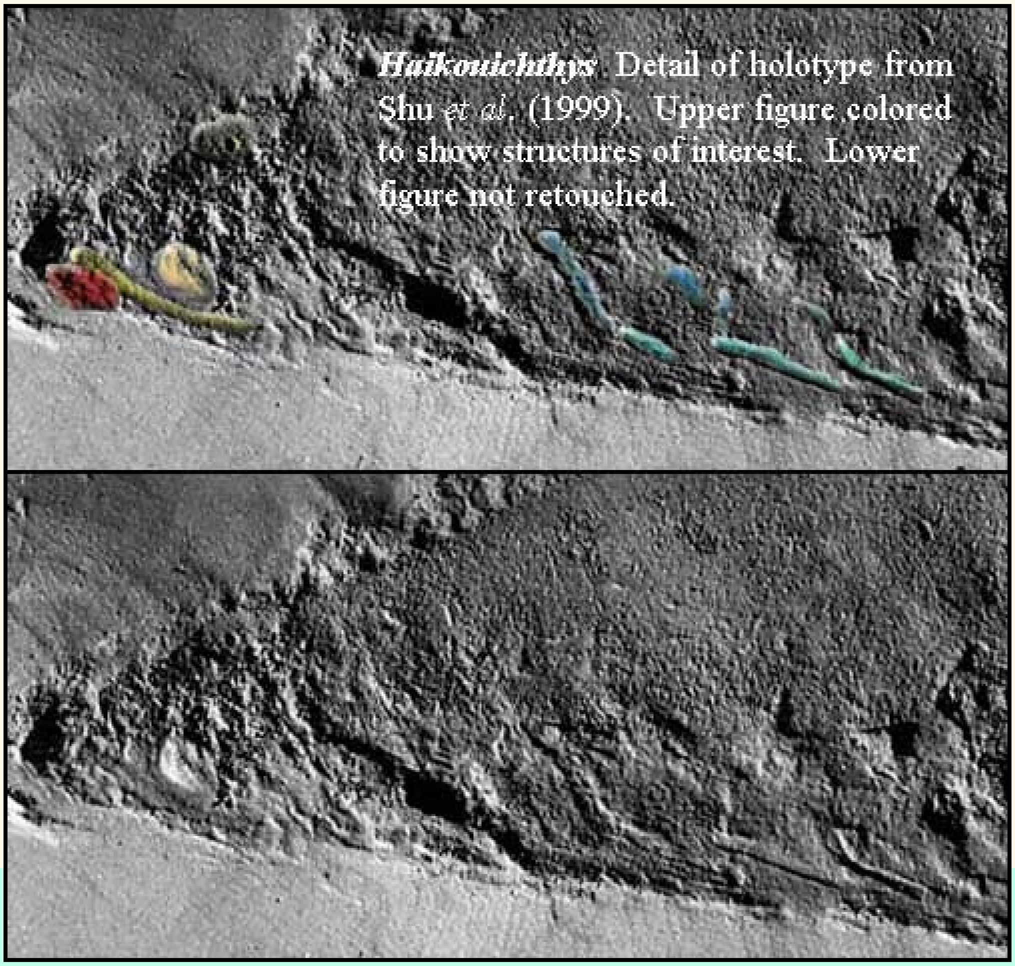
Cambrian Cousins from Kunming



But what's *this*? Could it be some previously unpublished early conodont with extraordinary preservation which we have likewise defaced with our idiosyncratic (or simply idiotic) concept of the conodont cranium? Actually, no. What you behold is the cranium of the Cambrian *Haikouichthys*, as interpreted by an all-star cast, including Degan Shu, Simon Conway Morris, and Phillipe Janvier. Shu *et al*. (2003). To our eyes (which may lack the acuity of a Crawling Eye conodont) it differs only in detail from a conodont. It has only anterior "plates" instead of the hypertrophied pulley system of the later conodonts. The conodont element on the left side is obvious if you are looking for it. It curves around the outside of the "plate," and is present only as a curved section of ?bone with a small, anteromedially directed tooth. The right-hand element is broken, but the curved region and tooth are still evident. The elements may also continue posteriorly, although that may well be an artifact of taphonomy or preparation. The eyes are where they belong, as are the other structures. The otic capsule looks exactly like the same structure in the conodont we labelled on the previous page. The arcualia (better illustrated by other images in the paper) are quite similar. We are forced to concede only the presence of a branchial apparatus. In fact, there is little, and perhaps nothing at all, which distinguishes *Haikouichthys* from a conodont.

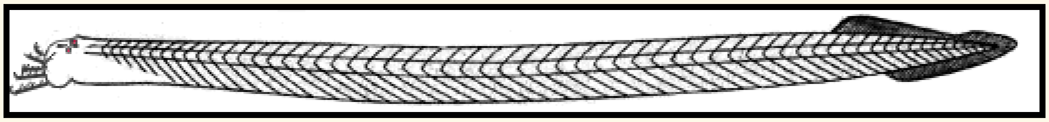

Haikouichthys. Detail of holotype from Shu *et al*. (1999). Upper figure colored to show structures of interest. Lower figure not retouched.

We have now gone so far out on a limb of the tree of life, that our position could scarcely be more insecure. But, at the same time, nothing is likely to make us look any more foolish than we already do. Given these parameters, we unhesitatingly add the obvious from Shu *et al*. (1999): the structure we call a conodont element in *Haikouichthys* also appears to be homologous to the branchial bars, as shown in the image of the holotype of *Haikouichthys*.

If this goes on, we will be forced to take ourselves seriously or abandon the enterprise completely.

ATW051015

Peering or Pouting?



Ultimately, our Paleozoic friend looks a bit more like the figure on the left. Much less cute than the Crawling Eye, but more functional. We have shown the S-elements as if they protruded from the mouth, which is quite unnecessary. The conodont may have, instead, been capable of an enormous pout, with elastic tissue connecting the rami of the S-elements like a gigantic lower lip. This would create a scooping action which might, or might not, have been useful, depending on diet and substrate. However that may be, it clearly makes more sense for the organism to have a big mouth in front, than to peer endlessly off to the side. ATW020727.

In spite of our expectations in 2002, conodont phylogeny remains undeveloped. The most recent tree we know of is reflected in the cladograms at Mikko's Phylogeny **Conodonta**. **Hidden World of the Conodonta** has a good introduction to conodont paleontology -- particularly its practical side.

There are a number of nice on-line collections, including Conodont Collection, James Davison and a small collection of really big images at **Geological collections- IMAGES OF FOSSILS AND ROCKS**.

checked ATW020917

Conodonta: Prioniodontida

Abbreviated Dendrogram

```
Vertebrata
|--+--Pteraspidomorphi
|  `--Gnathostomata
|
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

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1. Balognathidae X
2. Ozarkodinida X
3. Prioniodinida X
4. Prioniodontida X

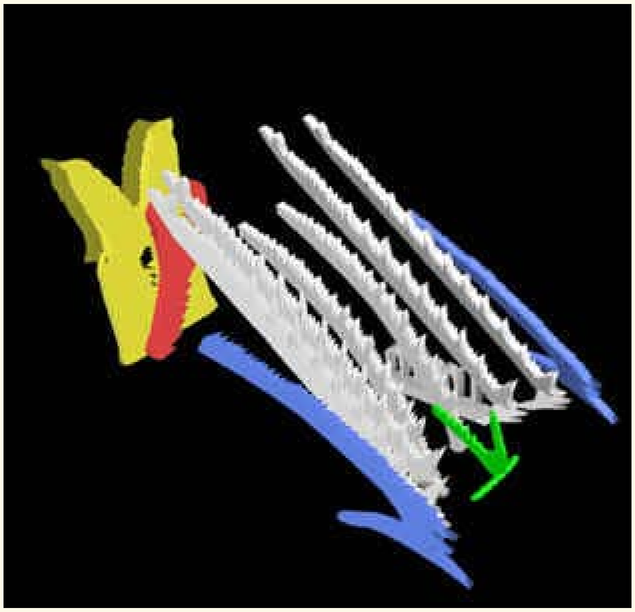
The Ozarkodinid Apparatus

In earlier sections, we have disposed of the contentious and speculative subject of conodont soft-tissue anatomy. We now belatedly turn to the conodont apparatus itself -- hard tissues about which we have hard data. Specifically, we will describe, albeit briefly and without much detail, the apparatus of ozarkodinid *Idiognathodus* which is well known from the work of Purnell & Donoghue (1997) and Purnell (1995, 2001, 2001a).

Ozarkodinids, like most euconodonts, have three basic types of elements. These three basic types are the S, M, and P elements. The precise nomenclature has varied considerably over the years. To the extent it makes a difference, we follow the system described by Purnell *et al*. (2000). The

ozarkodinid elements are better differentiated than the elements of many other groups, which makes them convenient to study.

The reader may note that we have made it a point to use certain terminology which is *de rigueur* in any discussion of conodonts. The point here is not to demonstrate our lamentably poor knowledge of these terms, nor to obscure the facts while purporting to explain them. To the contrary, the objective of our using this "stupid stuff" is, like that of Houseman's Mithradates, to inure the reader to these linguistic poisons by introducing them in small doses and under controlled conditions. **[1]**



S-Elements: In the image of an *Idiognathodus* natural assemblage at right, the S-elements are the long, rod-like bones with straight, transverse *pectinate* teeth and a sort of pick-axe at the anterior or rostral end. More generally, S-elements are frequently curved, as in the *Manticolepis* model below. However, they are all relatively simple in shape, relatively gracile, and with strong longitudinal asymmetry, the base being located much closer to one end than the other. Each conodont has 4 or 5 mirror-image pairs of S-elements, numbered S_1 to S_4 or S_5 In addition, each conodont possesses a symmetrical, unpaired, median S_0 element, shown as green on the figure on the left. The S_0 is an unpaired, bilaterally symmetrical, medial element which is effectively at least *triramous*. Two of its branches create a stout, transverse, *rastrate* bar across the bottom of the mouth, denticles facing upward. The S-element numbering system is symmetrically arranged around this S_0 element, with the first element to the left of the S_0 designated S_1^s, the first to the right S_1^d, and so on (with the superscript designations for *sinister* and *dexter*).

M-Elements: Conodonts have a single pair of M-elements. These are only loosely connected to the S-assemblage and appear to have been attached in the mouth cavity on its dorsal or lateral surface. Their shapes are frequently complex, vaguely reminiscent of anything from a nunchuck to a dart. While the M-elements are structurally obscure, their functional role is clear. They are the fork which held the food item in place as it was sliced or scooped by the S-elements, which acted as a combination knife and spoon.

P-Elements: The P-elements are the stout bones at the right of the right image, the left of the left image, and the bottom of the bottom (*Manticolepis*) image. Contrary to everyone's expectations, they appear to have been oriented vertically, with the two sets of denticles facing and, in fact, interdigitating as shown in the *Idiognathodus* natural assemblage. Purnell has produced convincing SEM images showing regular wear facets. The clear implication is that, at least in *Idiognathodus*, the teeth occluded in a regular and precise way. High resolution images of these facets may be found at Wear on conodont elements.

The Functional Biology of the *Idiognathodus* Apparatus: Purnell & Donoghue reconstruct the functional biology of the *Idiognathodus* along the following lines. The S-elements were attached to the medial surface of (at least) two strong lateral cartilaginous plates, by analogy to the oral apparatus of hagfishes and lampreys. The entire apparatus of S- and M-elements was everted over the anteroventral edge of the mouth. In this position, the distal ends of the S-elements would spread out like the ribs of a fan. The S-element denticles (or *keratinous* "teeth" mounted on them) would grasp and/or slice the food items. The oral plates were then drawn back into the mouth, forcing the S-elements closer together, gripping the food more tightly and forcing it into the oral cavity. The food material was then drawn past the P-elements which crushed, sliced, and sheared it before it was passed to the gut. ATW020728.

Notes: [1] Speaking of stupid stuff, this poem is slightly misquoted at the link, destroying the meter of the critical last two lines. The correct lines are: -- *I tell the tale that I heard told. / Mithradates, he died old.* Furthermore, contrary to various other web sources, the poem *is* by Houseman, not by Auden or Yeats. The concluding lines are an ironic reference to Houseman's own *To an Athlete Dying Young*. The full story behind the poem is interesting, but strains even the elastic notions of relevance which constrain this web site.

Descriptions

Prioniodontida:

Range: Early Ordovician to Middle Triassic (at least)

Phylogeny: Euconodonta:: Protopanderodontida + *: Balognathidae + (Prioniodinida + Ozarkodinida).

Characters: S-elements with hairpin shape; S-elements oriented with cusps rostral and denticles obliquely dorsal [P+00]; P elements less massive & more angular; 3 pairs of P elements; apparatus probably eversible.

Links: confabs98.html; Jerzy Dzik's home page.

References: Purnell *et al*. (2000) [P+00]. APW040316.

Balognathidae: *Distomodus, Icriodella, Icriodus*

Range: from the Middle Ordovician (fl.Llandovery) to Early Devonian

Phylogeny: Prioniodontida: (Prioniodinida + Ozarkodinida) + *.

Note: according to a recent (June, 2003) Pander Society Newsletter, an analysis of the *Distomodus* apparatus is nearing completion.

Image: *Distomodus* Pa element. From **Conodonts** and originally from Leicester University.

Links: Conodonts; PALAEONTOLOGIA POLONICA, vol. 58; APW040316.

Prioniodinida: *Gondolella, Hibbardella, Idioprioniodus, Kladognathus, Neogondolella, Phragmodus, Promissum.*

Range:

Phylogeny: Prioniodontida:: Ozarkodinida + *.

Links: Prioniodinida; PAN 51.(abstracts of Dhanda and Purnell & von Bitter); ALBE R IANA T. APW040316.

Ozarkodinida:

Range:

Phylogeny: Prioniodontida:: Prioniodinida + *.

Links: Ozarkodinida; Muzeum Geologiczne - Konodont; abstract; PandD 97.pdf;. APW040316.

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checked APW040316.

Manticolepis subrecta: model of apparatus after Dzik, labelled according to the scheme of Purnell et al (2000). Model by M. Szubert. Photo by M. Kryzanowski.

Conodonta: References

Abbreviated Dendrogram

```
Vertebrata
|--+--Pteraspidomorphi
|  `--Gnathostomata
|
Conodonta
|--Paraconodontida
`--Euconodonta
   |--Proconodontidae
   `--+--Protopanderodontida
      `--Prioniodontida
         |--Balognathidae
         `--+--Prioniodinida
            `--Ozarkodinida
```

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References

Albanesi, GL & CP Barnes (2000), *Subspeciation within a punctuated equilibrium evolutionary event: phylogenetic history of the Lower-Middle Ordovician **Paroistodus originalis** - **P. horridus** complex (Conodonta)*. **J. Paleontol.** 74: 492-502. Conodonta

Donoghue, PCJ, PL Forey & RJ Aldridge (2000), *Conodont affinity and chordate phylogeny*. **Biol. Rev.** 75: 191-251. Conodonta, Euconodonta, Ozarkodinida, Paraconodontida.

Gabbott, SE, RJ Aldridge & JN Theron (1995), *A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa*. **Nature** 374: 800-803. Euconodonta.

Janvier, P (1995), *Conodonts join the club*. **Nature** 374: 761-762. Euconodonta.

Purnell, MA (1995), *Microwear on conodont elements and macrophagy in the first vertebrates*. **Nature** 374: 798-800. Conodonta, Euconodonta, Ozarkodinida.

Purnell, MA (2001), *Feeding in conodonts and other early vertebrates* **in** DEG Briggs & PR Crowther (eds.), **Paleobiology II**. Blackwell Science: 583 pp. Conodonta, Ozarkodinida

Purnell, MA (2001a), *Scenarios, selection and the ecology of early vertebrates* **in** PE Ahlberg (ed.), **Major Events in Vertebrate Evolution: Palaeontology, Phylogeny, Genetics, and Development**. Systematics Assoc. Spec. Vol. Ser. 61, pp. 187-208. Conodonta, Ozarkodinida

Purnell, MA & PCJ Donoghue (1997), *Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts*. **Phil. Trans. Roy. Soc. Lond. B** 352: 1545-1564. Conodonta, Ozarkodinida.

Purnell, MA, PCJ Donoghue & RJ Aldridge (2000), *Orientation and anatomical notation in conodonts*. **J. Paleontol.** 74: 113-122. Prioniodontida, Ozarkodinida.

Shu, D-G, S Conway Morris, J Han, Z-F Zhang, K Yasui, P Janvier, L Chen, X-L Zhang, J-N Liu, Y Li & H-Q Liu (2002), *Head and backbone of the Early Cambrian vertebrate* ***Haikouichthys***. **Nature** 421: 526-529. Conodonta

Sweet, WC & PCJ Donoghue (2001), *Conodonts: past present, future*. **J. Paleontol.** 75: 1174-1184. Conodonta, Ozarkodinida, Paraconodontida.

Zimmer, C (2000), *In search of vertebrate origins: beyond brain and bone*, **Science** 287: 1576. Euconodonta

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checked ATW031203

Anaspida Overview

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myxinoidea
`--Vertebrata
   |--Jamoytiiformes
   `--+--Hyperoartia (= Petromyzontiformes)
      `--+--Conodonta
         `--+--Anaspida
            |  |--Pharyngolepis
            |  `--+--Pterygolepis
            |     `--Rhyncholepidida
            `--+--Pteraspidomorphi
               |--Thelodonti
               `--+--Cephalaspidomorphi
                  `--Gnathostomata
```

Contents

The Anaspid *Pterygolepis*, a typical representative of the anaspid clade. This little animal was only about 10 or 11 cm in length. Life reconstruction © Mikhail Tikhonov, original url

The Paleozoic (Silurian and Devonian) anaspids (yes, the name is confusing) were a group of early jawless fish that lacked the heavy head shields of the conventional cephalaspidomorphs. Covered in thin scales, their bodies were slender and flexible, with stabililising fins. They are known from the Late Silurian of Europe and North America, but it is almost certain that these active swimmers had a much wider distribution. During the Devonian they gave up a marine existence for life in rivers and lakes. Previously the group was something of a wastebasket taxon for any unarmoured Palaeozoic agnath, but a new study of the early Silurian *Jamoytius* (Sansom et al 2010), shows that it and a related form, *Euphanerops* were actually much more primitive. Given our present synoptic coverage, the remaining anaspids can be reviewed in a single page, although it is hoped in the future that this can be expanded. And while as it stands this is hardly enough material for a Palaeos unit, it is hard to slot these specialised creatures into another category. The anaspida remain for now an intriguing but short-lived experiemnt in the early vertebrate evolutionary tree. MAK111027

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MAK111026

Anaspida

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myxinoidea
`--Vertebrata
   |--Jamoytiiformes
   `--+--Hyperoartia (= Petromyzontiformes)
      `--+--Conodonta
         `--+--Anaspida
            |  |--Pharyngolepis
            |  `--+--Pterygolepis
            |     `--Rhyncholepidida
            `--+--Pteraspidomorphi
               |--Thelodonti
               `--+--Cephalaspidomorphi
                  `--Gnathostomata
```

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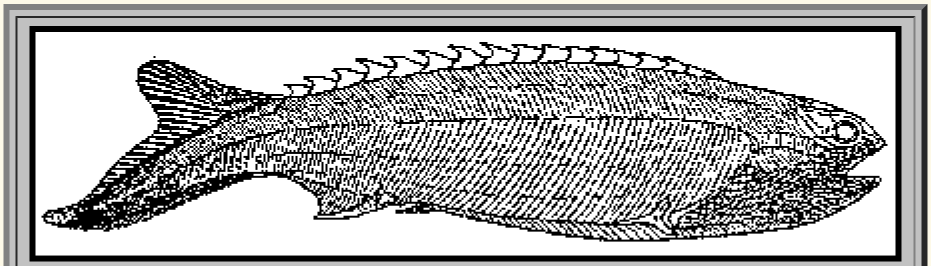
3. *Pharyngolepis* X
4. *Pterygolepis* X
5. Rhyncholepidida X

The Anaspida - unarmoured "ostracoderms"

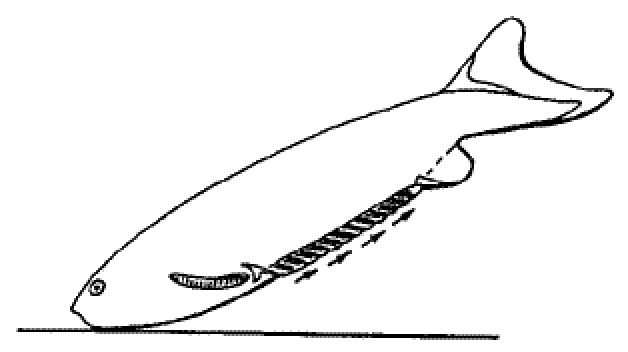


The Anaspida lack the extensive bony plates of their ostracoderm cousins. These jawless fishes had a laterally-compressed scale-covered body. They range from Early Silurian to the Latest Silurian, and are limited to the Euramerica Province. All were quite small, about 10 or 15 cm in length.

***Pterygolepis*. Wenlock (late Silurian) of south-east Euramerica. Length 10 to 15 cm. Graphic from Faktaside om fossile urfisk fra Norge, © 1998 Paleontologisk Museum - University of Olso.**

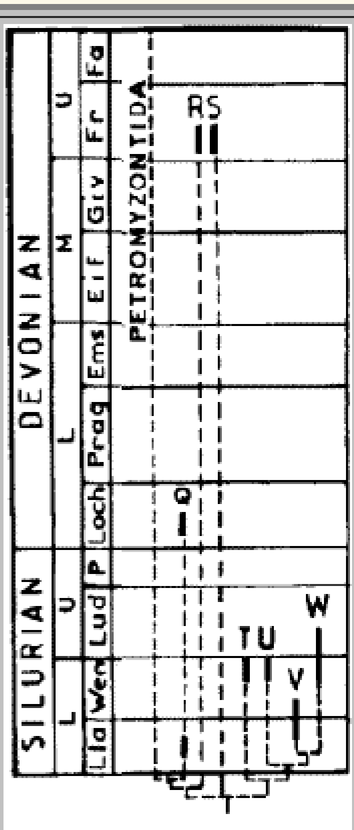
The genera *Jamoytius*, from the Early to Middle Silurian of Scotland, and *Endeiolepis*, *Euphanerops* and *Legendrelepis*, from the Late Devonian of Quebec, are traditionally referred to as anaspids by, among other features, their strongly hypocercal tail, a characteristic which is now known to occur in other vertebrate groups (e.g. thelodonts). Janvier argues that they are apparently more closely related to the lampreys.

The Anaspida are all narrow-bodied jawless vertebrates characterized by triradiate postbranchial spines. They possess rod-like body scales (when not naked), large median dorsal scales or scutes, broad-based paired fins, and a strongly hypocercal (downward- lobed) tail. Their exoskeleton (scales, dermal plates) are made up of acellular bone (aspidin). They may have been awkward, inefficient swimmers, since they lacked the basic stabilizing fins of other fishes -- even many other jawless fishes. A row of crested scales ran along the back, and a pair of bony spines projectedfrom the pectoral area. There was a well-developed anal fin, and the tail was downturned. But none of these features would have stabilized these animals body in the water. It is quite possible however that the small paired fins in forms such as ***Pharyngolepis*** were undulated as a slow displacement device (see diagram below) to provide stabilization.



An interpretation of the paired fins of the anaspid *Pharyngolepis* as a slow displacement device (arrows indicate the direction of the undulation of the fin). Illustration from Janvier (1996).

Their feeding method was probably to plough through the bottom sediment, head-first, scooping up tiny food particles into the small, rounded mouth.



Stratigraphic range and cladistic relationships of the Paleozoic Anaspida and related forms: L = Lower (Early), M = Middle, U = Upper (Late), Q - *Jamaytius*; R - *Legendrelepis*; S - *Endelolepis*; T - *Pharyngolepis*; U - *Pterygolepis*; V - *Birkenia*; W - *Lasanius*; X - *Phlebolepis*; Y - *Loganellia*. Diagram from Janvier & Blieck (1993)

Anaspids are rare as fossils and are apparently restricted to the Silurian. The earliest record consists of isolated scales from the Llandovery of Arctic Canada, and the latest from the Late Silurian of the Baltic area. The Anaspida occur mostly in Norway and Scotland, with some sparse records from eastern Canada, the Baltic area, and a single perhaps dubious record of a "birkeniid" from China.

One of the possible phylogenies of the Anaspida suggests a tendency towards the reduction of the number of gill openings, enlargement of the median dorsal scutes, reduction of anal fin, but is neither corroborated nor refuted by stratigraphy, since most anaspid taxa are of the same age. MAK000113.

Descriptions

Anaspida:

Range: Silurian.

Phylogeny: Vertebrata::: (Pteraspidomorphi + Thelodonti + (Cephalaspidomorphi + Gnathostomata)) + * **:** *Pharyngolepis* + (*Pterygolepis* + Rhyncholepidida).

Characters: 15 cm. Minnow-like, slender with no head shield; some naked; upper & lower margins of round mouth bore dermal bones which may have been used a sort of dentition; orbits large & surrounded by dermal bone, but sclerotic ring absent; single medial pineal and hypophyseal openings; 6-15 gill openings (trend is reduction of #), usually in a slanting line, behind orbits; **$** at least one large, tri-radiate spine behind the series of the gill openings; body covered in elongated scales arranged in chevrons which may reflect underlying myomeres (if so, body musculature extended far ant, perhaps overlapping gills); anal fin usually in far post; primitively, pectorals extended from gills to anal fin; muscles & radials for pectorals inferred from scale structure; no dorsal or separate pelvic fins, but dorsal scutes common & trended to larger, curved or hooked shapes; strongly hypocercal tail, but with large dorsal fin web (possibly this is dorsal fin); acellular, laminar bone similar to aspidine; no dentine & no enameloid caps. Relationship to Petromyzontiformes and to Devonian forms unclear.

Links: Anaspid model ; Anaspid cast; Geol 437 jawless fishes; Anaspida. ATW040314.

Pharyngolepis:

Range: Silurian of Europe

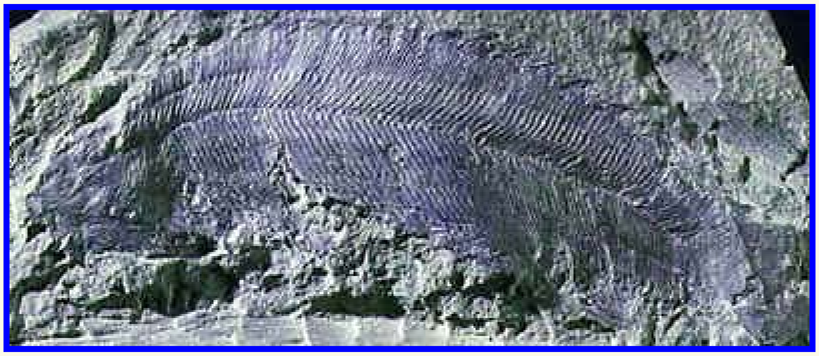
Phylogeny: Anaspida: (*Pterygolepis* + Rhyncholepidida) + *.

Characters: Head covered with relatively large scales compared to other anaspids; distinctive keeled oral plate on ventral surface just under mouth; about 15 branchial openings in postero-ventrally slanting line, terminating in tri-radiate spine diagnostic of anaspids; elongated body; median dorsal ridges small; no dorsal fin (as all anaspids); anal fin present and posteriorly placed; long ventrolateral "fin-fold" from branchial spine to anal fin; "fin-fold" apparently lacks fin rays and perhaps musculature; folds covered with minute scales in thin rows with thicker basal row of scales.

Links: Pharyngolepis oblongus; Annual Conference Abstracts 1999; Anaspida; Volume 16 (V2); Fiskarnas evolution.

Note: believed to be primitive form based on (a) unreduced anal fin (b) relatively large number of branchial openings (c) small dorsal ridge scales. Overall appearance strongly reminiscent of classical thelodonts, but scale histology is supposedly distinct. ATW040314.

Pterygolepis:



Range: Late Silurian (Ludlow).

Phylogeny: Anaspida:: Rhyncholepidida + *.

Characters: "branchial band" of gill openings angled at ~35° from horizontal; <25 dorsal ridge scales.

Links: Pterygolepis nitidus; Anaspida; PPT Slide; Timeline of a Pale Blue Dot; SILURIANO (Spanish). ATW040314.

See also life reconstruction

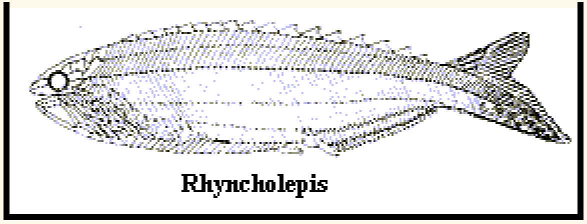
Rhyncholepidida: *Rhyncholepis*.

Range: Silurian

Phylogeny: Anaspida:: *Pterygolepis* + *.

Characters: **$** Reduced anal fin; **$** Shortened paired fins; **$** Large median dorsal scutes.

Links: Anaspida. ATW 040314.



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Anaspida References

Abbreviated Dendrogram

```
Chordata
|
Craniata
|--Myxinoidea
`--Vertebrata
   |--Jamoytiiformes
   `--+--Hyperoartia (= Petromyzontiformes)
      `--+--Conodonta
         `--+--Anaspida
            |  |--Pharyngolepis
            |  `--+--Pterygolepis
            |     `--Rhyncholepidida
            `--+--Pteraspidomorphi
               |--Thelodonti
               `--+--Cephalaspidomorphi
                  `--Gnathostomata
```

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References

Chen, J-Y, D-Y Huang & C-W Li (1999), *An early Cambrian craniate-like chordate,* **Nature** 402: 518-522.
Anaspida

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp.
Overview.

Janvier, P (1999), *Catching the first fish*. **Nature** 402: 21-22.
Anaspida.

Janvier, P & A Blieck (1993), *The Silurian-Devonian Agnathan Biostratigraphy of the Old Red Continent* **in** JA Long (ed.), **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Johns Hopkins Univ. Press, pp.70-73.
Overview.

Long, JA (1993), *Morphological Characteristics of Paleozoic Vertebrates used in biostratigraphy*, **in** JA Long (ed.), **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Johns Hopkins Univ. Press, pp.3-24.

Sansom, R. S., Freedman, K., Gabbott, S. G., Aldridge, R. A. and Purnell, M. A. 2010. Taphonomy and affinity of an enigmatic Silurian vertebrate Jamoytius kerwoodi White. *Palaeontology* 53: 1393-1409.
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Palaeos:

THE VERTEBRATES

PTERASPIDOMORPHI

OVERVIEW

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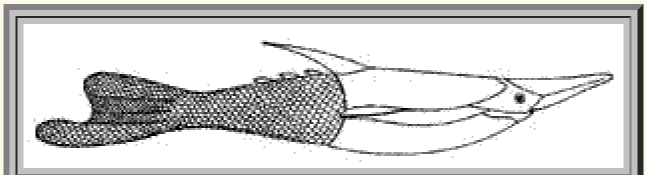
Pteraspidomorphi: Overview

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   `--Pteraspidomorphi
      |--Arandaspida
      `--Heterostracomorphi
         |--Astraspidae
         `--Heterostraci
            |--Cyathaspidiformes
            |  |--Cyathaspidida
            |  `--Amphiaspidida
            `--Pteraspidiformes
               |--Pteraspididae
               `--Psammosteida
                  |--Drepanaspis
                  `--Psammosteidae
```

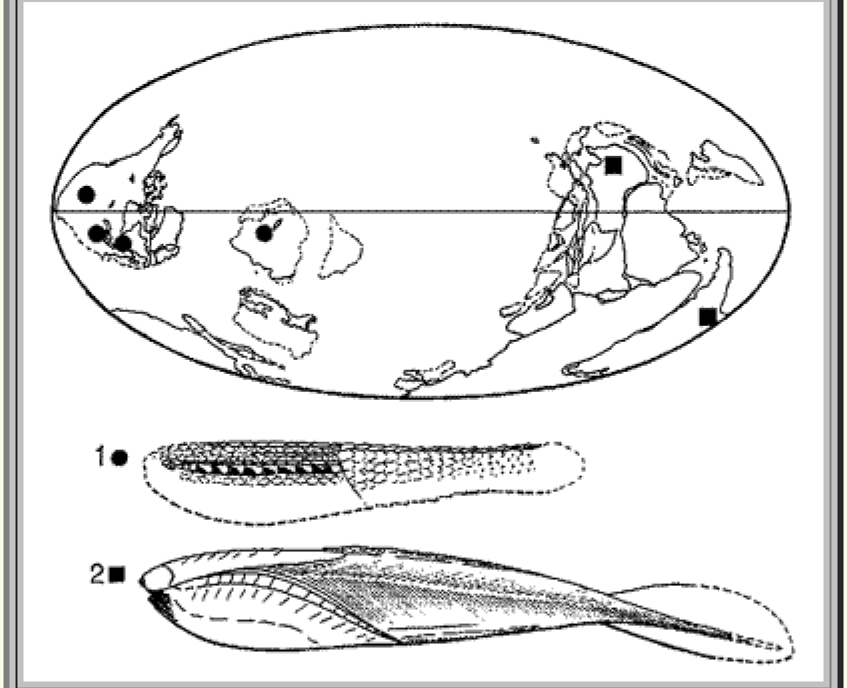
Overview



Pteraspis. **Pragian (Early Devonian) of southeast Euramerica. Length 20 cm. Order Pteraspidiformes**

The Pteraspidomorphi are sometimes referred to as Heterostraci, although that term is more properly applied to the specialised Silurian and Devonian forms. They are an extinct clade of jawless fish, and were the most abundant and diverse vertebrates of the Silurian. They are distinguished by having an exoskeleton or bony shield composed of several plates, usually a dorsal (upper or back) shield, a ventral (lower or belly) shield, branchial (gill) plates, and a number of smaller plates around the areas of the mouth (oral plates) and eyes. These plates consist of a mostly acellular form of bone, called *aspidine*, which is believed to be the ancestral condition for the dermal or skin/exoskeleton bone of all bony vertebrates. The body is covered by many scales, each of which has ornament matching the type seen on the larger dermal bones. In all of the more derived forms, there is only one, common gill opening on each side.

The Pteraspidomorphi include the earliest known vertebrates. The oldest certain remains date to the Early or Middle Ordovician, although the disputed and fragmentary ***Anatolepis*** probably goes back to the Furongian. In any case, by the middle and late Ordovician, there were several different lineages evolving in isolation different parts of the world,



Ordovician Pteraspidomorphs: 1. **Astraspida; 2. Arandaspida**

as this map indicates.

These Ordovician forms, the **Arandaspida**, **Astraspida** and Eriptychiida, were formerly grouped with the Silurio-Devonian **Heterostraci**, but are rather more primitive. These early types share some unique features with heterostracans, such as the presence of large median dorsal and ventral plates, but do not possess common external branchial openings.

By the start of the Silurian period these lineages had died out, possibly as another result of the mass extinction at the end of the Ordovician. They were replaced by the Heterostraci. This latter group underwent an evolutionary radiation, dividing into a number of lineages and reaching their peak during Late Silurian and Early Devonian times, when a variety of different types evolved and flourished, from mud-eating bottom-dwellers to free-swimming filter-feeders. All had the characteristic head shield, which could grow throughout the life of the animal.

By the middle Devonian the Pteraspidomorphi went into decline, with only a single family of giant (by agnath standards) flattened bottom-dwellers, the Psammosteidans, continuing almost until the end of the Devonian, the last and also the largest of the armoured jawless fish. MAK000112.

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Pteraspidomorphi

Anatolepis, Arandaspids & Astraspids

Abbreviated Dendrogram

```
Craniata
|--Conodonta
`--+--Thelodonti
   `--Pteraspidomorphi
      |--Anatolepis
      `--+--Arandaspida
         `--Heterostracomorphi
            |--Astraspidae
            `--Heterostraci
               |--Cyathaspidiformes
               |  |--Cyathaspidida
               |  `--Amphiaspidida
               `--Pteraspidiformes
                  |--Pteraspididae
                  `--Psammosteida
                     |--Drepanaspis
                     `--Psammosteidae
```

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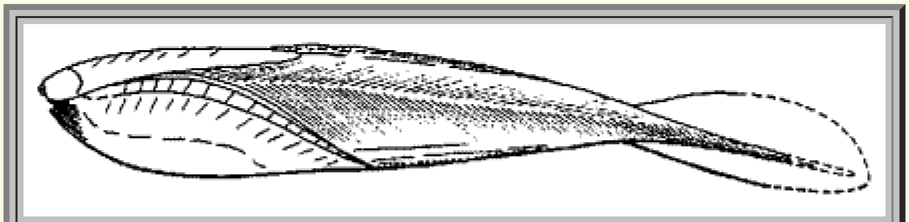
3. Astraspidae X
4. Heterostracomorphi X
5. Pteraspidomorphi X

The Pteraspidomorphi include the earliest vertebrates (other than conodonts) known from reasonably good remains. These Middle or Late Ordovician forms include the arandaspids of the the Gondwanan continents of South America and Australia and the astraspids of North America and the Siberian platform.



***Sacabambaspis*. Sandbian (Late Ordovician) of south east Gondwanaland. Length 25 cm.**

Pteraspidomorphi: Loosely synonymous with "Diplorhina". Probably defined as *Anatolepis* + *Psammolepis*.

Range: Early Ordovician (or Furongian) to Late Devonian.

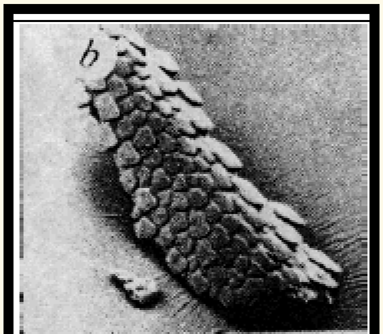
Phylogeny: Vertebrata **:::** "Thelodontia" + * **:** *Anatolepis* + (Arandaspida + Heterostracomorphi).

Characters: 10-200 cm; head very long (40-50% body length); paired nasal capsules, and ? openings; solid anterior plates, with at least a major oblong median dorsal and ventral plates and usually a median rostral plate above mouth; rostra and cornua common; pineal opening (psammosteids?); brain with two semicircular canals; some show internal impressions of arcualia on notochord; body tends to be ventrally flattened (numerous exceptions); mobile tail, generally fan- or pad-like; tail hypocercal; no paired appendages; no unpaired fins except caudal; sensory line system present; no cellular bone (*but see* [H73]); possible traces of calcified cartilage in in some basal lineages; trilaminate aspidine; *grebeshki* ornamentation on dermal plates (lost independently several times); largely marine nearshore.

Links: Pteraspidomorphi; Pteraspidomorphi; Gagnier; Pteraspidomorphi; Faktaside om lungefisk (Norwegian); Class Pterapisdomorphi; Life of the Ordovician; Paleozoic Fossils UK (extraordinary images on this site!).

References: Halstead (1973) [H73]. APW040316.

***Anatolepis*:**



Pantserfragment van *Anatolepis* (Bockelie & Fortey, 1976)

Range: Furongian to Early Ordovician of North America, Greenland & Spitzbergen.

Phylogeny: Pteraspidomorphi **:** (Arandaspida + Heterostracomorphi) + *.

Characters: Known from fragments only. Apatite with scale-like ornamentation; dentine odontodes with pulp cavity; dentine covered by another mineralized tissue of unknown homology; "exclusively tropical, circum-Laurentian, distribution, where it is restricted to outer shelf settings".

Notes: [1] It seems I am not the only one who writes *haiku* about early chordates: see University of Alberta Palaeontological Society Website.

Links: Histology of the first fish (abstract of one of the articles referred to by Gee); A possible Late Cambrian vertebrate from Australia (abstract of the other article referred to by Gee); Molecular Evidence for Precambrian Origin of Amelogenin, the Major ....

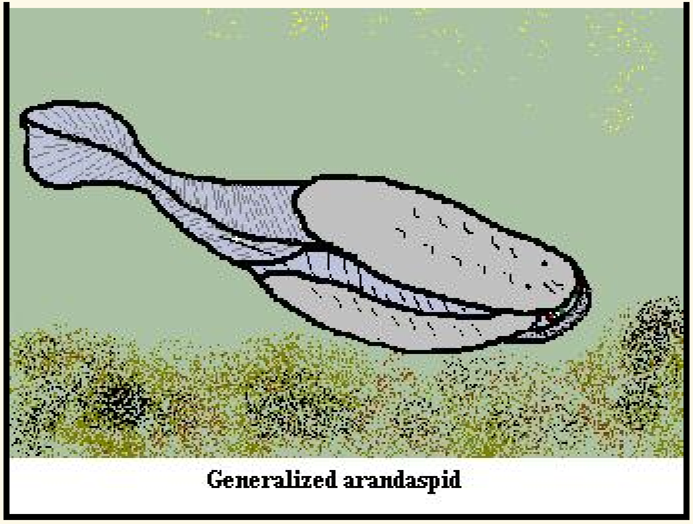
References: Young *et al*. (1996). APW040316.

Arandaspida: *Arandaspis, Sacabambaspis,* possibly *Porophoraspis*. Medium-sized (12-14 cm) very primitive, teardrop-shaped marine fishes.

Range: Early to Late Ordovician of Australia & South America.

Phylogeny: Pteraspidomorphi **::** Heterostracomorphi + *.

Characters: Two large, thin (<1 mm) plates on head (dorsal & ventral); ventral plate convex, dorsal plate flattened; main


Generalized arandaspid

plates ornamented by drop-shaped or lobate tubercles; eyes in extreme anterior; solid sclerotic ring present; nostrils (?) just medial to orbits on embayment in anterior surface just dorsal to mouth; mouth lined ventrally with numerous small scales; possible lingual or velar apparatus; paired pineal (2?) and parapineal (4?) openings on anterior of dorsal plate (which may be endolymphatic ducts instead); probably at least ten gill slits with smaller plates on sides; posterior body & tail may have been laterally compressed; body scales highly elongated and arranged in large chevrons (pointing anteriorly) on each side; no ridge scales; no paired or unpaired fins except caudal (poorly known); caudal fin probably pad-shaped and diphycercal; well-developed small lateral lines on both plates and medioventral surfaces; little or no endoskeleton; scales and plates trilaminar, with basal laminar layer, cancellous central layer (with double walls) and aspidine or cellular bone tubercles. No growth or fusion of scales.

Links: Fischmarkt Bremerhaven (German); Class Pterapisdomorphi; New Page 1 (large image of arandaspid fragment); Boletín de Publicación mensual de (Spanish translation of a National Geographic article on *Sacabambaspis*); life-5-b-Xystridura (exemplary short, encyclopedia-like entry with image of *Sacabambaspis*); Gli Agnati (Italian).

References: Janvier (1996). ATW060209.

Heterostracomorphi: *Eriptychius?*

Range: Late Ordovician to Late Devonian

Phylogeny: Pteraspidomorphi:: Arandaspida + *: Astraspidae + Heterostraci.

Characters: dorsolateral gill openings.

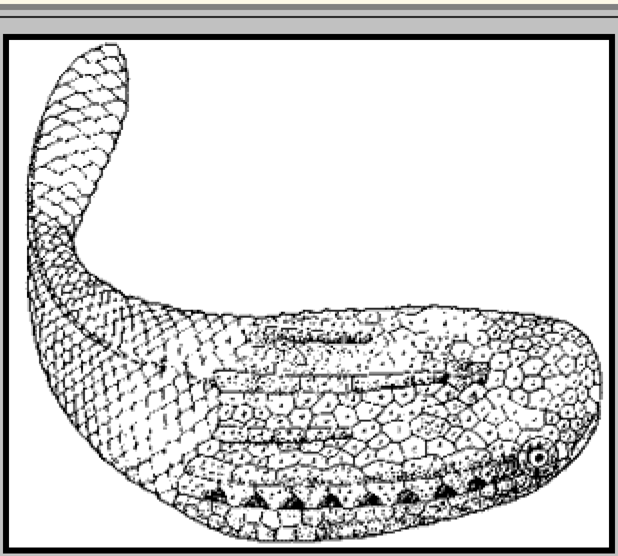
References: Janvier (1996). APW040316

Astraspidae: *Astraspis*.

Range: Middle to Late Ordovician of North America & Siberia.

Phylogeny: Heterostracomorphi **:** Heterostraci + *.

Characters: Head armor massive; plates grew from multiple centers (tesserae) which fused at maximum growth; eyes lateral; multiple (8-10) gill openings; dorsal shield ribbed with strong longitudinal crests; tail covered with large, diamond-shaped scales; sensory-line system with grooves in dermal plates; globular calcified cartilage present, probably(?) forming endoskeleton; tesserae with large mushroom-shaped dentine tubercles with pulp cavity; dentine covered with enameloid cap; trilaminar bone.


***Astraspis.* Sandbian (Late Ordovician) of Laurentia.**

Links: Tree of Life.

References: Janvier (1996). APW040316.

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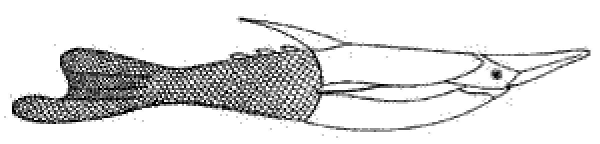
Pteraspidomorphi: Overview

Abbreviated Dendrogram ("Cladogram")

```
CRANIATA
|--CONODONTA
`--+--THELODONTI
   `--Pteraspidomorphi
      |--Arandaspida
      `--Heterostracomorphi
         |--Astraspidae
         `--Heterostraci
            |--Cyathaspidiformes
            |  |--Cyathaspidida
            |  `--Amphiaspidida
            `--Pteraspidiformes
               |--Pteraspididae
               `--Psammosteida
                  |--Drepanaspis
                  `--Psammosteidae
```

? Search

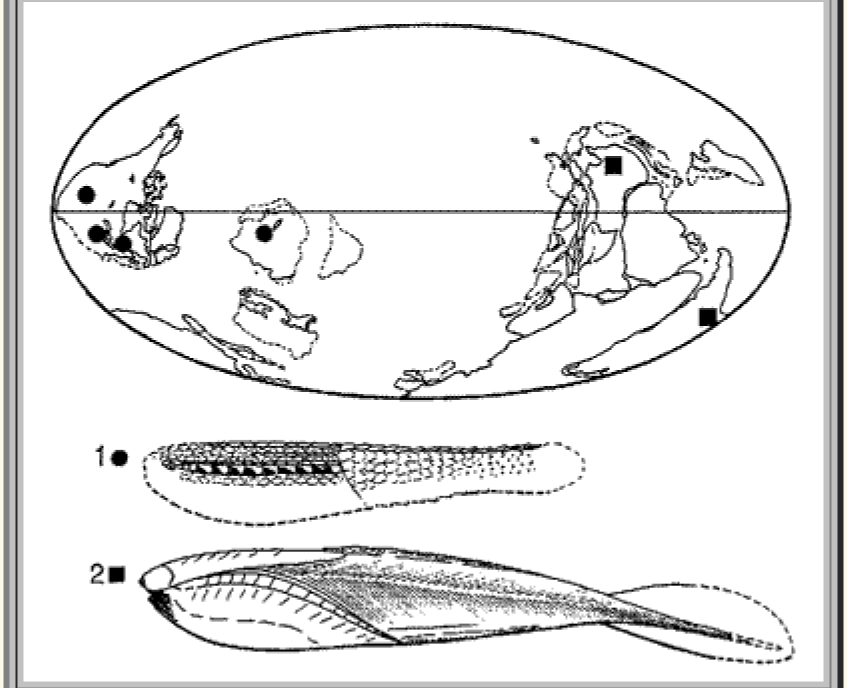
Overview



Pteraspis. **Pragian (Early Devonian) of southeast Euramerica. Length 20 cm. Order Pteraspidiformes**

The Pteraspidomorphi are sometimes referred to as Heterostraci, although that term is more properly applied to the specialised Silurian and Devonian forms. They are an extinct clade of jawless fish, and were the most abundant and diverse vertebrates of the Silurian. They are distinguished by having an exoskeleton or bony shield composed of several plates, usually a dorsal (upper or back) shield, a ventral (lower or belly) shield, branchial (gill) plates, and a number of smaller plates around the areas of the mouth (oral plates) and eyes. These plates consist of a mostly acellular form of bone, called *aspidine*, which is believed to be the ancestral condition for the dermal or skin/exoskeleton bone of all bony vertebrates. The body is covered by many scales, each of which has ornament matching the type seen on the larger dermal bones. In all of the more derived forms, there is only one, common gill opening on each side.

The Pteraspidomorphi include the earliest known vertebrates. The oldest certain remains date to the Early or Middle Ordovician, although the disputed and fragmentary ***Anatolepis*** probably goes back to the Furongian. In any case, by the middle and late Ordovician, there were several different lineages



Ordovician Pteraspidomorphs: 1. **Astraspida; 2. Arandaspida**

evolving in isolation different parts of the world, as this map indicates.

These Ordovician forms, the **Arandaspida**, **Astraspida** and Eriptychiida, were formerly grouped with the Silurio-Devonian **Heterostraci**, but are rather more primitive. These early types share some unique features with heterostracans, such as the presence of large median dorsal and ventral plates, but do not possess common external branchial openings.
By the start of the Silurian period these lineages had died out, possibly as another result of the mass extinction at the end of the Ordovician. They were replaced by the Heterostraci. This latter group underwent an evolutionary radiation, dividing into a number of lineages and reaching their peak during Late Silurian and Early Devonian times, when a variety of different types evolved and flourished, from mud-eating bottom-dwellers to free-swimming filter-feeders. All had the characteristic head shield, which could grow throughout the life of the animal.

By the middle Devonian the Pteraspidomorphi went into decline, with only a single family of giant (by agnath standards) flattened bottom-dwellers, the Psammosteidans, continuing almost until the end of the Devonian, the last and also the largest of the armoured jawless fish. MAK000112.

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Pteraspidomorphi: Heterostraci

Cyathaspidiformes

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

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Poraspis, a representativeCyathaspidiform Heterostracan, life reconstruction © Mikhail Tikhonov, original url

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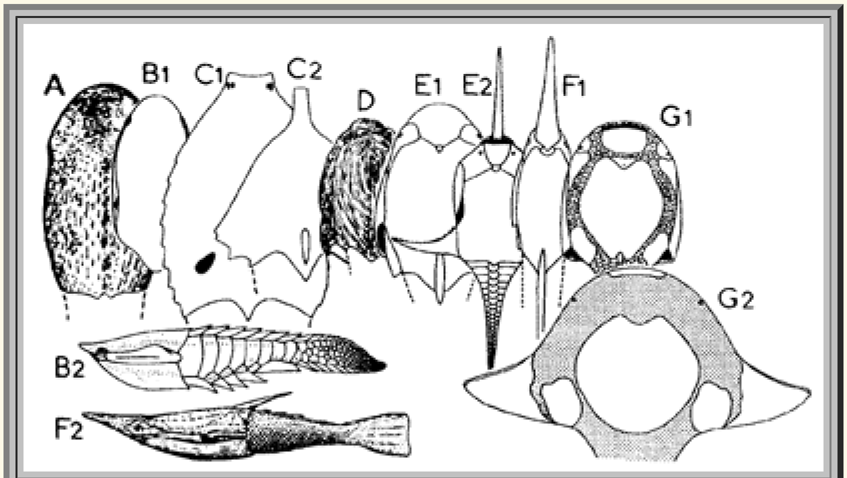
2. Heterostraci X

The Heterostraci



Heterostracan diversity (not to scale). Head shields in dorsal view and reconstructions in lateral view (B2, F2); A - Traquairaspidiformes (*Traquairaspis*); B - Cyathaspidiformes (B1, *Poraspis*; B2, *Anglaspis*); C - Amphiaspidida (C1, *Kureykaspis*; C2, *Eglonaspis*); D - Anchipteraspididae (*Anchipteraspis*); E - Protopteraspididae (El, *Protopteraspis*; E2, *Doryaspis*); F - Pteraspididae (Fl, *Rhinopteraspis*; F2, *Errivaspis*); G - Psammosteida (G1, *Drepanaspis*; G2, *Pycnosteus*). From Janvier & Blieck (1993).

The Heterostracans are an important lineage that includes such ostracoderm types as the pteraspids, cyathaspids, amphiaspids, and many other groups They are restricted to the Silurian and Devonian periods (reaching their height during the Late Silurian and Early Devonian), in the biogeographic provinces of Euramerica, Siberia and Tuva.

The Heterostraci possess a large dermal armor of dentine and acellular bone (*aspidin*), which covers the head region and is pierced laterally by a pair of common external branchial openings. The armor consists of a variable number of plates, which in the amphiaspids of Siberia has fused into a rigid box, while in some other groups it is broken into numerous platelets or tesserae. A number of types developed extraordinary spines and other elaborations

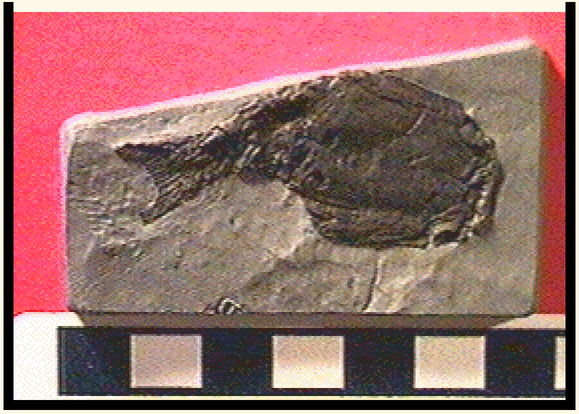
The Heterostracans comprise two major monophyletic groups, the **Pteraspidiformes** and **Cyathaspidiformes** (each of which can be given the Linnaean rank of Order), and a number of minor groups (Traquairaspids, Corvaspids, *Lepidaspis*, and others), some of which may be general primitive forms. MAK000112.

An Early Success

The Heterostraci are arguably the first widely diversified vertebrate clade. But for accidents of history or design (depending on your theoretical and metaphysical preferences), something looking a little like *Athenaegis*, our friend on the left, might now be studying a roughly rectangular slab of rock bearing the bones of our great ancestor: an osteostracan, or some similar form. Instead, we are here and the heterostracan is on the rocks, so to speak. (Images of *Athenaegis chattertoni* courtesy of Dr. Mark Wilson, Univ. of Alberta Laboratory of Vertebrate Paleontology.)

However, in the mid-Silurian, it was the Heterostraci who were lords of the vertebrate domain in what is now the Northern Hemisphere. The Heterostraci are first found in the lower Silurian, about the same time that most of the other major Paleozoic fish groups got their start. They apparently radiated rapidly and evolved a number diverse forms which are now difficult to fit into a cohesive picture, such as *Lepidaspis,* which looks something like a hot dog bun (or, more exactly, a kolache) with the sausage sticking out of one end.

Unlike the ponderous osteostracans or fragile anaspids, the Heterostraci possessed virtually no endoskeleton. Even their dermal



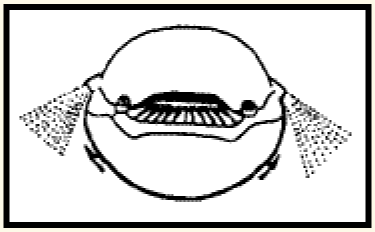
plates were made up of acellular aspidine and dentine, requiring little metabolic investment beyond the initial cost of construction. Only one species (*Torpedaspis*) shows signs of subaponevrotic circulation, the layer of vessels that feeds the cells at the base of living bone. The inner surface of the dermal plates is smooth and shiny, showing no evidence of even cartilaginous attachments. The only evidence of endoskeletal material are the ambiguous indentations radial to the gill lamellae and traces of possible arcualia along the line of the notochord.

The Heterostraci had other advantages, as well. Long before the teleostomes managed the trick, the Heterostraci developed a single common branchial opening, minimizing the surface exposed to parasites and avoiding multiple openings in the body wall. The symmetrical, diphycercal tail, not perfected by gnathostomes until the Cretaceous, was standard equipment on heterostracans in the Silurian.

It is not clear whether heterostracans had precise muscular control of the tail – their only mobile fin – in the same way as fish of the gnathostome lineage. The tail, like the rest of the body, had no internal skeleton and was reinforced only by lines of scales. However, the Heterostraci were not conspicuously flattened fish. They do not seem to have the conventional design of bottom-dwelling fishes, although they are often depicted in that fashion. They may well have been slow and sloppy swimmers compared to later forms. The very fact that they are not found worldwide is a convincing argument that they cannot have been nektonic athletes. Yet it is equally hard to see them as vertebrate barnacles.

Simplicity has its virtues. However, by Mid-Devonian times, the Heterostraci were in relative decline. A few lines, notably the large psammosteids, staged a revival in the Late Devonian, but all were extinct before the Carboniferous. The lesson may be that a simpler body plan gives a clade an evolutionary head start. However, the more complex body plans have a long term advantage because of their ability to adjust to varying conditions. Simplicity of structure necessarily implies simpler responses to the environment. Certainly, any given arrangement of greater complexity is likely to fail, since its needs and requirements are also likely to be complex. However, once conditions permit radiation of the more complex forms to begin, that radiation is likely to be more durable because it inherently contains more diversity. This diversity permits greater success by specialization in good times, and more niche survivors in bad. ATW020510, revised ATW030512.

The Cyathaspidiforms

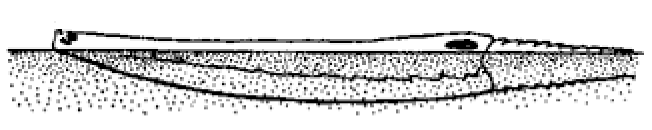


The **Cyathaspidiformes** probably include some fairly active swimmers, although the heavy Armour would presumably slow them down. This clade has both streamlined and flattened forms, distinguished by a head shield ornamented by longitudinal dentine ridges, the dorsal (upper) shield fused into a single plate, and the presence of vertical flange scales on the tail. They appear in the early Silurian with *Athenaegis* (the earliest known Heterostracan), but do not really diversify until the later part of the period (Ludlow epoch). By the end of the Early Devonian they were in decline, and died out at the Emsian/Eifelian (Early/Middle Devonian) boundary.

The Cyathaspidida were quite long-lived types that appeared during the Late Silurian (Ludlovian) and continued to the end of the Early Devonian (Emsian epoch). They are part of the endemic Euramerican fauna. They were generally streamlined forms with fusiform or cigar-shaped head-shields, and deep vertical flange scales arranged along the tail. They were probably fairly active but short distance swimmers.

These jawless fish may have used water jets from their branchial openings as a propulsive or stabilizing device, to compensate for the lack of paired fins. The illustration at the right shows a Cyathaspidiform in anterior (front) view, illustrating this hypothesis of the stabilizing function of the water jet from the common external branchial openings (stipple).

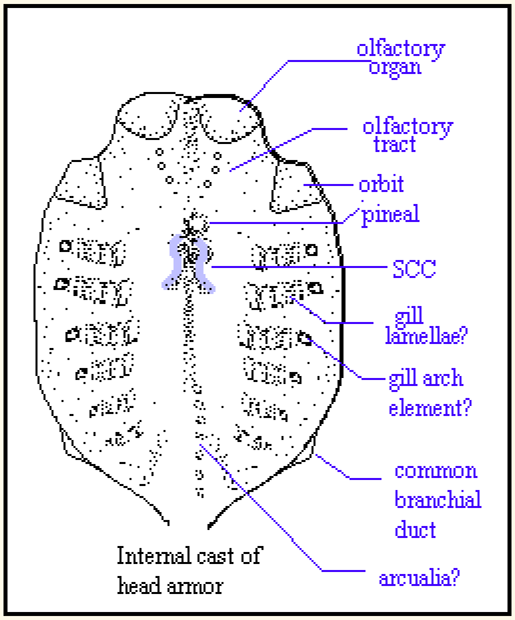
The Amphiaspidida were specialized forms limited to the first half of the Early Devonian (Lochkovian and early to mid Pragian epochs) of the Siberian (Angoran) bio-region. The head-armour is fused into a single unit, and the entire head was flattened, indicating that they were bottom- dwellers, and possibly even burrowers, who would lie mostly submerged in the sand or mud.



Kureykaspis, buried in the sediment, showing the adorbital opening at the very front (far left) of the head
The opening at the right (rear) is the common external branchial opening
illustration from Janvier (1996: 301)

In some forms, the front of the armour is elongated into a tube-shaped structure, and the eyes disappear (*Empedaspis*, *Pelurgaspis*, *Eglonaspis*). In others (*Prosarctaspis*, *Kureykaspis* (illustrated above), *Olbiaspis*, *Gabreynspis*), there is a special opening, the *adorbital opening*, in front of the eyes, which has been variously interpreted as a spiracle, a 'pre-spiracle', or a single nostril. It is probably an inhalant opening that allowed these creatures to live half-buried in the bottom sediments, like modern rays. MAK000112.

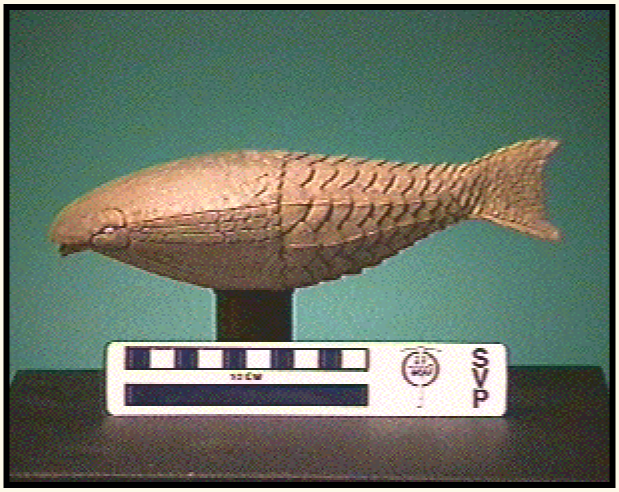
Heterostraci: *Athenaegis*.



Range: Early Silurian to Late Devonian.

Phylogeny: Heterostracomorphi: Astraspidae + *: Cyathaspidiformes + Pteraspidiformes.

Characters: Generally oblong, fusiform shape, with some species dorsoventrally flattened; fan-like lower oral plates; upper oral plate normally rigid; head normally covered with single large dorsal and ventral plates, typically elongated lateral branchial plates; orbits small; **$** single pair of gill openings; possible prenasal sinus or naso pharyngeal tract partially separated from oral cavity; no indication of endoskeleton except head shield impressions of possible arcualia and possible gill arches; head shield has impressions of 2 SCCs, 8-10 transverse gills and possibly gill arch bones radial to gills; ventral plate shows median impression (lingual apparatus?); brain shows 3 segments (pineal, metencephalon or cerebellum, and medula oblongata); where known, posterior covered with large scales; large median dorsal and ventral ridge scales; no fins except caudal; caudal fin primitively di- (poly?-)phycercal with lines of scales rather than fin rays; tail may also be pad-like; no paired appendages; interior of plates smooth & shiny - no evidence of attachment for endoskeleton; subaponevrotic circulation known only in one species (*Torpedaspis*); trilaminar dermal skeleton with basal laminar layer, cancelous aspidine central layer, and tuburculate dentine outer layer showing characteristic *grebeshkis*.



Links: UALVP Fossil Models & Replicas; Class Pterapisdomorphi; Geol 437 jawless fishes (NOT \AGNATHA\), Fall, 1995; Heterostraci; Gagnier; V The four other mass extinctions (French); xrefer - Heterostraci; Lecture Notes, Nat. Hist. Vert., Emporia State Univ.; vista verde news - Frühe Wirbeltiere: Ohne Biss (German); handout9_14; 209 lec s02/20903s02.pdf

Image: (R) after Janvier, P. (1993), *Patterns of diversity in the skull of jawless fishes*, in Hanken, J& BK Hall (eds.), *The Skull*, 2:131-188, U. Chicago Press. Image (L) *Athenaegis chattertoni* model courtesy of Dr. Mark Wilson, Univ. of Alberta. APW040316.

Cyathaspidiformes:

Range: Silurian to Early Devonian of North America and Russia.

Phylogeny: Heterostraci: Pteraspidiformes + *: Corvaspididae + (Cyathaspidida + Amphiaspidida).

Characters: parallel, finely crenulated dentine ridges form ornamentation of dermal plates; flange scales arranged in chevrons.

Links: Tree of Life; Corvaspis; Anglaspis, Cyathaspidiformes. APW040316.

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Pteraspidomorphi: Heterostraci (2)

Corvaspids and Cyathaspids

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Corvaspididae
         |  |  |--Corvaspis
         |  |  `--Corveolepis
         |  `--+--Cyathaspidida
         |     `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

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2. *Corvaspis* X
3. Cyathaspidida X

Corvaspids: Mental Impressions and Ornamental Trees

Between the first Silurian appearance of Heterostraci and the Devonian radiation of definitive Cyathaspidiformes and Pteraspidiformes there is an impressively large group of poorly understood heterostracans: *Athenaegis*, cardipeltids, *Tolypelepis*, Traquairaspidiforms, and the **Corvaspididae**, to name some of the prominent elements of this jawless *lumpenproletariat*. As Janvier (1996: 95, 98) admits, a sensible phylogeny of the Heterostraci can be constructed only by ignoring these groups. This, however, strongly suggests that our current phylogenetic dispositions are perhaps not so sensible. At the moment (030511) we have reviewed only the corvaspids. Thus, we have little basis even for speculation. Nevertheless, the corvaspids do illustrate what some of the problems are.

The Corvaspididae have been around, under one label or another, since the 1930's. Much of the debate on nomenclature is, at bottom, no more than a pointless debate about taxonomic rank. For reasons discussed elsewhere, we decline to get involved in this issue. But, at the same time, it is difficult to arrive at a useful cladistic definition of the relevant group. We have, rather arbitrarily, put the corvaspids in with the Cyathaspidiformes. We have very little confidence in this assignment. The corvaspids might, as easily, be very basal pteraspidiforms or primitive Heterostracomorphi outside the Heterostraci. So, we can't define the corvaspids as a stem group because we don't really know what stem applies. Consequently, we are forced to apply an *ad hoc* crown group definition: "the last common ancestor of ***Corvaspis*** and ***Corveolepis*** and all of its descendants."

What do we know about this tiny group? As it turns out, not very much. The dorsal armor may be a single plate, or may be comprised of as many as nine smaller plates. There may or may not be orbital plates. The ornamentation around the eye includes a unique and distinctive series of concentric rings of dentine, but nothing is known of the mouth or gill openings. The pineal area is located only a little behind the orbits, which is perhaps unusual for the Heterostraci. The main shields are extremely delicate towards their margins and tend to grade into smaller units – particularly on the posterior margin of the dorsal plate. Here, the dorsal shield grades into the body squamation without a definite boundary, at least in some specimens. Since the armor margins are vague, we know little about the overall form of these animals. The armored area is certainly long and, at least by comparison with many other heterostracans, slim. But we cannot guess whether the body was round, deep or flattened. The tail is unknown; and, curiously, no fringing scales have been found. These large, angular scales, normally at the dorsal and ventral midline of the tail, are found in every other heterostracan. Furthermore, since the heterostraci had very little endoskeleton, fringing scales would appear to be necessary to hold the tail rigid enough to swim.

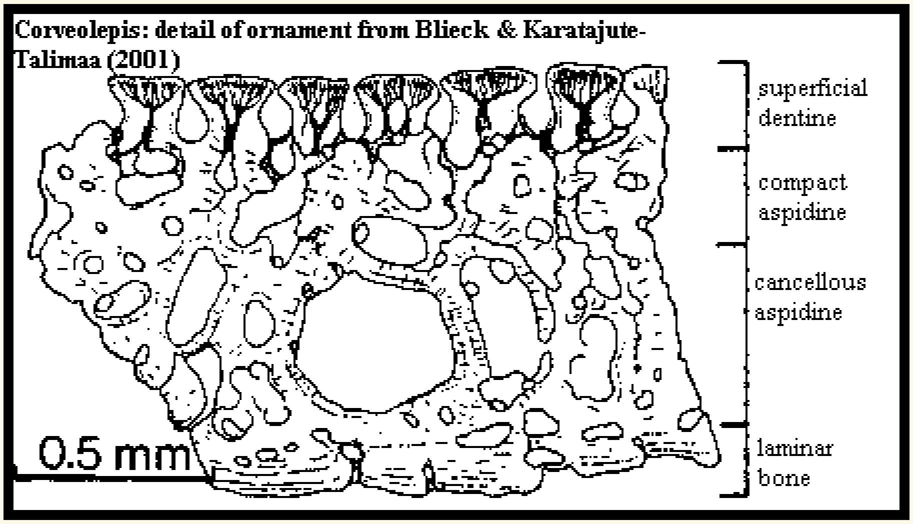
Essentially nothing is known of the internal structure. One photograph of an internal mold of the dorsal shield shows a "faint impression of the brain." Blieck & Karatajute- Talimaa (2001: 644, fig. 4B). This impression (shown at right) gives tantalizing hints of paired structures within and anterior to the medulla oblongata (where there ought not to be any) and a distinct, fan-shaped posterior expansion which is abruptly cut off. There are no impressions suggesting gill arches or lamellae, such as are found in many other heterostracan head molds. However, it is entirely possible that all of these features are artifacts of preservation or transmission, as we are looking at a scan of a photocopy of a photograph of a mold of an impression.

Finally, we arrive -- with much reluctance -- at the part of the journey where most schemes of heterostracan classification have come to grief: the ornamentation of the shield. The good thing about ornamentation is that essentially all early vertebrate fossils have it in abundance. If they did not, we would be unlikely to recognize them as vertebrate fossils. The bad thing is that ornamentation has a long and tortured history of phylogenetic misuse and misleading similarity. To understand how this happened, it is necessary to delve, briefly, into the mindset of science early in the last century. The scientific celebrities of the day, folks like Rutherford, Maxwell, Bohr and Einstein, were theoretical physicists. In practical matters as well, the first generations of adequately trained engineers were applying physical theory to transform the world in very obvious and tangible ways. The paradigm of theoretical development as the key to scientific understanding was transcendent. Zoologists and paleontologists were reluctant to be left off this bandwagon and sought to come up with theoretical approaches of equal breadth and explanatory power. This trend reached its apogee in the works of the Scandinavian school of Stensiö, Jarvik and, most especially, Bjerring (who pushed segmentalist theory almost past the point of absurdity) **[1]**.

Against this background, it was entirely reasonable for Stensiö and others to construct an entire theory of vertebrate evolution based on changes in squamation. Accordingly, the older literature is full of abstruse terms used to describe the supposed development of "agnathan" integument based on equally theoretical long-term trends in the development of scale types. The problem is that squamation can't really tell us much. The basic structure of scales didn't change much during the Paleozoic. Blieck and Karatajute- Talimaa (2001) describe the trunk scales of corvaspids as rhomboidal, bearing parallel ridges of dentine posteriorly and flat-topped tubercles anteriorly (some of which may also bear ridges of dentine), with a small, unornamented anterior margin, and an anteriorly-protruding anchor process on the inner face. As noted below, this description matches scales of unknown Cambrian origin as well as it does the scales of Devonian corvaspids. It is easy to see that these units could be fused in various ways to form the surface ornamentation of various jawless fishes. However, this has relatively little to do with "tesserae," "synchronomorial units" or other, larger-scale organizational features, because the layer below the surface is made of acellular bone (*aspidin*). The aspidin layer may have some contribution from individual scales. Presumably, this is the source of the "compact aspidine" sublayer frequently seen in corvaspids and other Paleozoic fishes. However, the cancellous aspidine layer below is formed by a retreating front of dermal osteocytes, not by superficial cells associated with the squamation. Yet a third layer, the deep layer of laminar bone, is formed by yet a third developmental process, the superficial ossification of the basement membrane.

The point here is *not* that ornament and integument have no phylogenetic value, but that our information on these matters has been so thoroughly warped by scale-oriented theories that it is virtually impossible to sort out fact from theoretical construct. The actual patterns observed are probably rather complex results of the three independent developmental processes noted above, as well as taphonomic factors. A lot can happen to a fish in four hundred million years. Until someone is willing to go through the thankless task of re-analyzing about a century's worth of fish scale observations, we will be left with the decorative, but probably useless, ornamental trees of the Scandinavian school. ATW030511.

[1] Books could be written on the sociology of this movement and the efforts of the post-war generation of European scientists to overcome the dead weight of this paradigm. Phillipe Janvier's **Early Vertebrates** (1996) can, for example, be understood as the logical culmination of the post-war reaction. One of the greatest, but rarely recognized, accomplishments of cladistics has also been its influence in forcing scientists to focus once again on empirical investigation. We have argued elsewhere that empiricism can also be taken too far. The point made there, and here again, is that pragmatism should govern. Both empiricism and theory are only tools. Neither is an end in itself.


Corveolepis: detail of ornament from Blieck & Karatajute-Talimaa (2001)

Corvaspididae: (Corvaspida of [S64]) stem group cyathaspids? [S64] includes the cyathaspid forms *Archegonaspis* & *Poraspis* in a "Corvaspiformes."

Range: Pridoli to Early Devonian (Lochkovian) North America (Arctic Canada), Spitzbergen & Siberia (Severnaya Zemlya) [BJ99]

Phylogeny: Cyathaspidiformes: (Cyathaspidida + Amphiaspidida) + *: *Corvaspis* + *Corveolepis*

Characters: medium-sized [DL76]; dorsal & ventral plates each as single unit [BK01], but appears to be made up of fused scales [J96] (*contra* [S64]: may be two main dorsal plates) (and *questioned* [BK01]: dorsal plate either unitary or assemblage of up to nine plates, including paired orbital plates); orbits round and dorsolateral [BK01]; orbital plate ornamented with concentric ridges near the orbit, grading into short ridges & tubercles arranged in rings; orbital plate containing both supra- and sub-orbital elements (*i.e.*, completely surrounding orbit) [S64] [DL76] (*contra* [BK01]: orbits completely surrounded, but perhaps by dorsal plate); branchial opening unknown [J96]; ventral plate tends to break up into smaller plates anteriorly [BK01]; ornamentation of wide, low, closely-spaced ridges with flattened surfaces and of tubercles with flattened peaks [S64] [DL76]; ridges short, smooth, grouped into units by network of grooves [LD76]; units may be separate or broken off main plates [BK01]; units, and margins of plates may be bounded by small, closely-packed tubercles [BK01]; posterior superficial shield units identical to isolated scales from area posterior to shield [LD76]; shield grades into posterior body squamation [LD76]; posterior body covered with small, rhomboidal scales [DL76] [BK01]; trunk scales with flat-topped crown, wide anterior shelf above thick, anteriorly-protruding anchor process [BK01]**[3]**; trunk scales with crown bearing wide longitudinal ridges with 1+ rows of anterior tubercles [BK01]**[3]**; ridge scales unknown and probably absent (unique among heterostraci) [BK01]; dentine ridges arise in clusters (??), each ridge being associated with 1-2 small pockets communicating with pulp canals [BK01]**[4]**; plate structure as shown in image, but some forms lack distinct compact aspidine layer [BK01] **[4]**; no actual tesserae as all fused together by basal layer of laminar bone [BK01]; sensory line system poorly developed or just poorly known, apparently a simple pit line system [BK01].

Note: **[1]** Stensiö uses the French word "ride" which translates literally as "wrinkle" or "ripple," both of which are more accurate descriptions than the usual English "ridge." On the other hand, who knows what he intended? Stensiö was a Norwegian who wrote in English, but is usually read in French translation. Today, he is best known through the critical work of Janvier, a Frenchman who usually writes in English. **[2]** Whether the orbits are formed by the dorsal plate or by a separate orbital plate, the fact that they are completely surrounded by one plate is considered diagnostic of the family. **[3]** Blieck & Karatajute-Talimaa [BK01] do not figure these scales. However, isolated scales are known which match this description rather closely -- from the Furongian! *See* [S98: 349]. **[4]** Note that the histology of the plates is quite similar to that of psammosteids.

Links: Upper Silurian and Devonian heterostracan pteraspidomorphs (...; 107.htm.

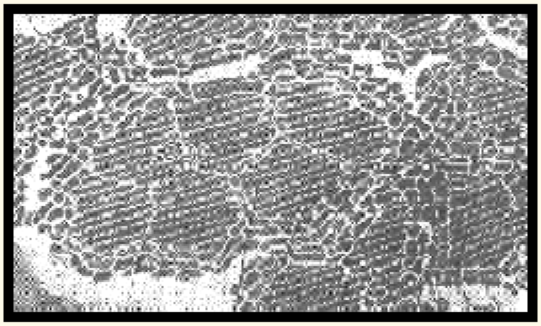
References: Blieck & Janvier (1999) [BJ99]; Blieck & Karatajute-Talimaa (2001) [BK01]; Dineley & Loeffler (1976) [DL76]; Janvier (1996) [J96]; Loeffler & Dineley (1976) [LD76]; Stanley (1998) [S98]; Stensiö (1964) [S64]. APW040316.

Corvaspis: *C. kingi* Woodward, 1934; *C. karatajuteae* Tarlo, 1965.

Range: Early Devonian (Lochkovian) of Europe & North America

Phylogeny: Corvaspididae: *Corveolepis* + *.

Characters: orbits as in *Corveolepis*? [LD76]; flat orbital plates [H73]; may have had separate median, orbital and ridge (or possibly branchial) plates [LD76] (*contra*? [H73]: single median plate with "occasional incorporation of tesserae at the margins"); arched branchial plates [H73]; usually interpreted as being broad and dorsoventrally compressed [LD76]; ornament with polygonal units with sculptured ridges [H73] [L95]; ridges of dentine [H73]; ridges of uniform height & width, with slight crenulation (*i.e.* a tendency to resemble *grebeshkis*) [S64]; tubercles of 2 kinds (a) rather thin & about the same width as the ridges, and (b) and thick, irregular ones located along the margins of the main plates [S64]; anterior portion of dorsal plate divided by grooves into several irregular polygonal fields, which are subdivided by other grooves into 2-5 fairly regular polygons ornamented with anteroposteriorly oriented ridges [S64] **[2]**; anterior and lateral margins with thicker tubercles [S64]; ventral disk also comprised of an epitega with tubercles marginally [S64].

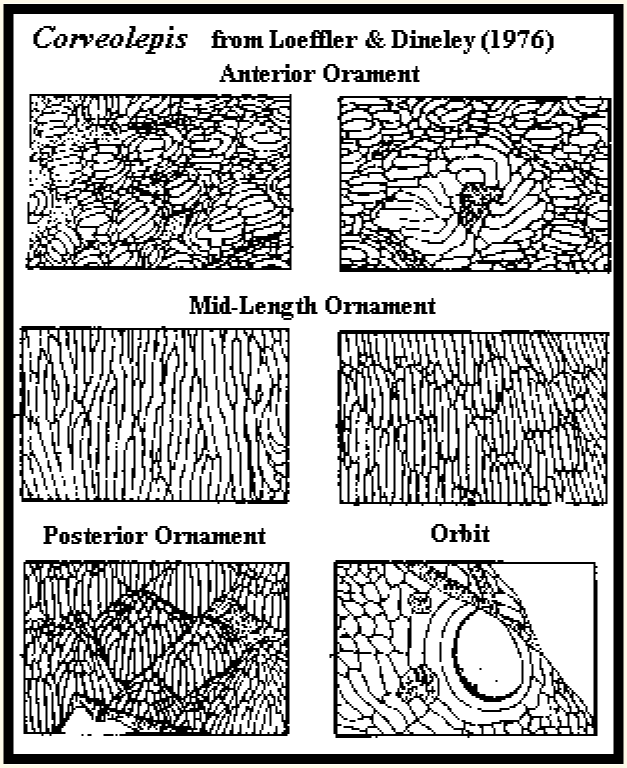


Note: **[1]** From [H73: 293]: The "commonest ornamentation is of synchronomorial tesserae separated from each other by a narrow zone of tubercles. This suggests that the main tesserae were formed before the animal reached its definitive size..." **[2]** See image at right from [S64]. Stensiö argues that these are cyclomorial scale units. The catch, to us, is that the strips of dentine line up *perfectly* from one "field" to the next, so that the same dentine ridge essentially continues from one unit to the next. Thus, it appears that the pattern of dentine ornament was superimposed on a pre-existing polygonal pattern of bone. The ridges could not possibly line up so perfectly if the dentine strips developed independently in separate cyclomorial scale units. In spite of Stensiö's insistence, the fields are *not* "assez régulièrement polygonaux." In fact, they are so irregular and so diverse that the dentine ridges simply could not line up in this manner from field to field if they were independently derived. Note also that the tubercles between fields also tend to form well-aligned strips over moderate distances at a 0-30° to the anteroposterior orientation of the superficial dentine ornament. Unfortunately for our own view, while Stensiö seems plainly wrong about the ornament in *Corvaspis*, his description is an almost completely accurate depiction of the ornament in *Corveolepis*. *See* [LD76] (and image below), [BK01]. This is odd, to say the least, since none of the specimens now known as *Corveolepis* were found (much less described) until at least a year after Stensiö's review was published!

Links: 107.htm; Untitled Document.

References: Halstead (1973) [H73]; Loeffler & Dineley (1976) [LD76]; Long (1995) [L95]; Stensiö (1964) [S64]. APW040316.

Corveolepis: Blieck & Karatajute-Talimaa 2001. *"Corvaspis" arctica* Loeffler & Dineley, 1976; *C. elgae* Blieck & Karatajute-Talimaa 2001. Also includes, *dubitante*, *Corvaspis* cf. *kingi*, *Corvaspis graticulata* Dineley, and unnamed bits & pieces.



Range: Early Devonian (Lochkovian) of Siberia (Severnaya Zemlya) [B+02], Pridoli and/or Early Devonian of North America (Arctic Canada) [LD76], Spitsbergen.

Phylogeny: Corvaspididae: *Corvaspis* + *.

Characters: dorsal shield fused into single plate [BK01]; dorsal shield long, flat, & narrow [LD76]; smoothly rounded rostral margin [LD76]; dorsal shield completely encloses orbits [LD76]; orbits small, circular and anteriorly placed [LD76]; orbits directed dorsally, but located close to margin of dorsal shield [LD76]; orbits surrounded by annular ridges, and annuli by short, peripheral ridges [LD76]; annular orbital ornamentation grades into body ornamentation without sharp boundary [LD76]; pineal macula located slightly posterior to orbits [LD76]; dorsal plate lateral margins downturned to form ventrolateral laminae [LD76]; branchial openings not found or absent [LD76]; ventral shield unknown [LD76]; ornamentation of closely-spaced, smooth-topped dentine ridges [LD76]; ridges of uniform height & typically < 3mm long [LD76] [BK01]; ridge ornaments grouped into small, superficial units separated by grooves or rows of tubercles [LD76] [BK01]; subdivisions not present on rostral and lateral margins [LD76] **[2]**; anteriorly, units of ridges grouped around a single median ridge which is randomly oriented [LD76]; anterior ridges wider than elsewhere [LD76]; at midlength, ridges arranged variably into units, and orientation is uniform [LD76] [BK01]; posterior superficial units scale-like, grading into loosely attached units [LD76] [BK01]; loose rhomboid scales of posterior type associated with body fossils [LD76]; loose scales have unornamented anterior brim of 0.2 mm [LD76].

Note: **[1]** [LD76] described this form as a species of *Corvaspis*. The possibility exists that this may have affected the generality of their diagnosis and description. **[2]** This detail, as well as the superficial nature of the subdivisions, cuts slightly against any conclusion that all of the shield was assembled from true scales, as argued by, *e.g.*, Stensiö [S64]. **[3]** [BK01] note that the actual shape of the body is unknown, as no specimens are free from possibly severe distortion.

Image: from [LD76].

Links: Untitled Document; Upper Silurian and Devonian heterostracan pteraspidomorphs (....

References: Blieck & Karatajute-Talimaa (2001) [BK01]; Blieck *et al*. (2002) [B+02]; Loeffler & Dineley (1976) [LD76]; Stensiö (1964) [S64]. APW040316.

Cyathaspidida: streamlined forms with fusiform or cigar-shaped head-shields.

Range: Pridoli? to Early Devonian of North America and Russia.

Phylogeny: Cyathaspidiformes:: Amphiaspidida + *.

Characters: Entire body covered with plates and large, thick scales; anterior portion with single large dorsal & ventral shields; large plates may be formed from fusion of smaller units, fusing at maximal size; lateral branchial plate; seven pairs of gills; no

known endoskeleton; large deep flange scales; caudal fin nearly symmetrical, but main axis may bend ventrally; no dorsal, anal, or paired fins; marine, later FW.

Image: *Liliaspis* from [L95]. Note the highly-developed sensory line system. Long identifies *Liliaspis* as an amphiaspid. He may be mistaken. The branchial plate seems to be separate, there is no tube-like rostral process as indicated in the figure legend, and the rostrum is broad and suggestive of a primitive pteraspidiform. *Liliaspis* found in the Urals, near the eastern extremity of the Old Red Continent, rather than from Siberia (from whence come all amphiaspids). It is more usually classified as a poraspid cyathaspidiform.

Links: Biology 356; Cyathaspid; Anglaspis; UALVP 17878 Cyathaspididae model; 106.htm; Museum Type Specimen.

References: Long (1995) [L95]. APW040316

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checked APW040316

Pteraspidomorphi: Amphiaspidida

Ctenaspis

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         |     |--Ctenaspis
         |     `--+--Amphiaspidoidei
         |        `--+--Hibernaspidoidei
         |           `--Siberiaspidoidei
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

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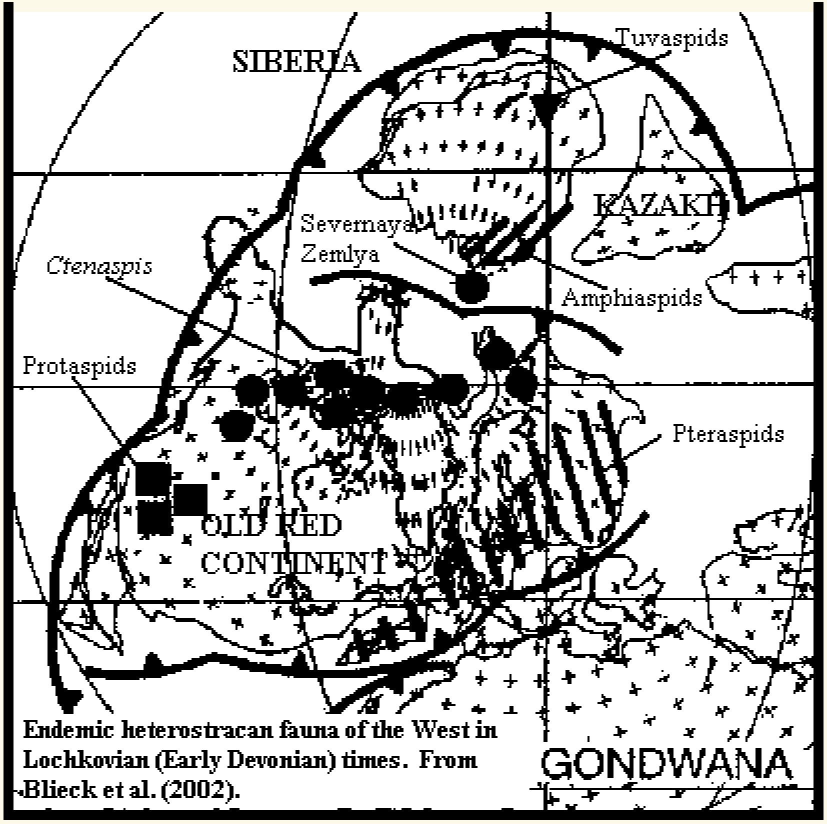
1. Amphiaspidida X
2. *Ctenaspis* X

Amphiaspidida

In the Pridoli and during the Lochkovian Age (the earliest age of the Early Devonian) vertebrates were first becoming major elements of the world fauna. The process was a remarkably slow one. In fact, for perhaps the last time in vertebrate



Endemic heterostracan fauna of the West in Lochkovian (Early Devonian) times. From Blieck et al. (2002).

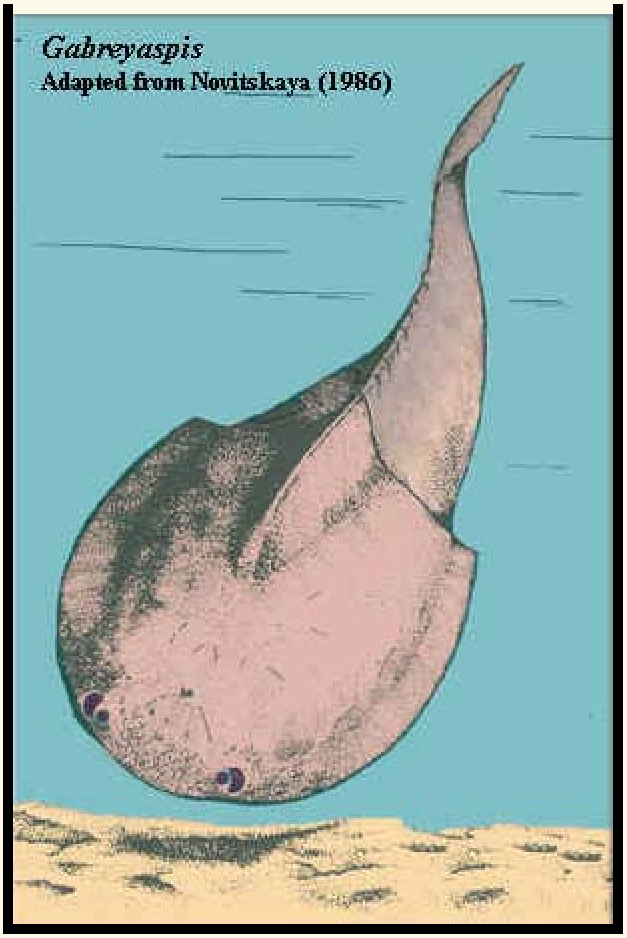
history, the rate limiting factor in global faunal change was dispersal, rather than evolution. By way of contrast, consider the tetrapod radiation which began at the *end* of the Devonian. We really have no idea where our ancestors first walked on land because, as soon as that lineage became successful, its members are found all over the world. Tetrapods radiated in the blink of a geological eye. Undoubtedly, this "blink" took a few hundred thousand years, but, from our standpoint that is virtually instantaneous. Marine vertebrates, in particular, are very mobile. If they are found anywhere, they tend to be found everywhere there is any chance of dispersal.

The case was different at the beginning of the Devonian. Most vertebrate faunas were endemic, that is, local. Protaspidoids dominated in western Laurentia at the western end of the "Old Red Continent" of Laurasia. Pteraspidids inhabited Baltica in the East, and a mixture of ***Ctenaspis***, *Gigantaspis* and various osteostracans held the equatorial zone around what is now arctic Canada. Blieck *et al*. (2002). Each of these lineages radiated separately, with genus succeeding genus for the 10-20 million years of this era. But the process of dispersal was so slow that the rate of faunal replacement between different groups was much slower than the process of evolution within them.

Of all the endemic groups, the **Amphiaspidida** were one of the most stubbornly provincial. They are usually described as inhabiting "Siberia." But that is a gross exaggeration. Amphiaspids are found only in the "Kara-Tajmyr" block, what is now a relatively small strip across the central part of extreme northern Russia. At least one other fauna inhabited the Siberian Platform, the completely unrelated Tuvaspid fauna of Tuva.

The amphiaspids are often described as "bizarre," which is unkind, but accurate. With rare exceptions, the head shield is entirely fused into a seamless coat of bone, typically bearing a sort of brim laterally which was often incised into a series of jagged "teeth." As in all heterostracans, the eyes were small and without sclerotic rings. But some hibernaspidoid forms were completely eyeless and others bore tiny eye spots at the end of a long oral tube, like a built-in straw. In hibernaspidoid and amphiaspidoid species with more or less "normal" eyes, the orbit is partially rimmed by a second, bean-shaped opening of unknown function. It is widely speculated that this opening had an inhalant function. What's particularly odd is that the same sort of structure is found in the *very* primitive, Ordovician fish, *Sacabambaspis*, but is otherwise unknown. There is no real possibility of a direct relationship. Amphiaspids are a late and short-lived breed. Except for the stem-amphiaspid *Ctenaspis*, they appear only in the latter part of the Lochkovian and are gone by the Middle Devonian.

Amphiaspids are typically depicted as bottom-feeding detritivores. Yet, even more than most heterostracans, they tend to be flat on top with convex, even inflated, ventral surfaces. That sort of shape is hard to reconcile with the usual benthic lifestyle. Even if partly buried in sediment, any current would tend to dig these boat-shaped bodies out and lift them off the bottom. Ironically, this is *particularly* true of some of the blind, tube-mouthed Hibernaspidoidei, such as *Eglonaspis*. One amphiaspid, *Siberiaspis*, appears to have had two lateral line systems: a primitive superficial pit line network, and a deeper set of channels. Halstead (1973) (reviewing work of Novitskaya). This tends to reinforce a point made earlier, in connection with the Corvaspididae. The various layers of the heterostracan integument may, to a significant degree, have had independent evolutionary histories consistent with their distinct developmental origins. ATW030513.



Amphiaspidida: (same as Amphiaspida and Amphiaspidae of older sources, more or less the amphiaspidiformes of other sources)

Range: Early Devonian (Lochkovian to Emsian) of Siberia. Survival to Pragian of Middle Devonian per [J96]. Reports of amphiaspids in Arctic Canada and Spitsbergen are based on the occurrence of *Boothiaspis*, which is now believed to be a cyathaspid [B+02]. However, this range is still correct if *Ctenaspis* is an amphiaspid [BJ99]. All occurrences are from warm, marine waters. [BJ99].

Phylogeny: Cyathaspidiformes:: Cyathaspidida + *: *Ctenaspis* + (Amphiaspidoidei + (Hibernaspidoidei + Siberiaspidoidei)).

Characters: up to 40 cm, but typically 10-18 cm [L95]; wide, rounded carapace [N86] [L95] (*contra* [N86]: may be straight anterior border); armor wide & deep [S64]; armor about as wide as long or slightly longer than wide [S64]; some with elongate, tube-like rostrum bearing orbits as well as mouth [N86] [J96] [BJ99]; mouth ventral or terminal, sometimes at the end of an oral tube [S64] [N86]; no supraoral plate [S64]; head is "much flattened" [J96]; loss or reduction of eyes [N86] [L95] [BJ99]; orbits (if not absent or on rostral tube) small, dorsal and usually far anterior [S64]; orbit lined externally with bean-shaped secondary opening which may be functional spiracle [J96]; gill opening usual dorsal or lateral, and rarely on a separate branchial plate (*Putoranaspis*) [H73] [N86]; dorsal surface generally flat [H73]; dorsal surface usually bears a crest or spike [N86]; complete fusion of carapace [N86] [L95] [J96] (*contra* [H73]: some forms have separate dorsal & ventral plates); posterior ventral area sometimes not fused [N86]; in some cases, distinct ornament borders are present between the dorsal, ventral and branchial elements -- and rarely on borders of the suborbital plates (*Aphataspis*, *Gerronaspis*) [N86]; lateral edges of armor are smooth or with jagged "teeth" [N86]; jagged processes may also be present on the posterior margin [S64]; along lateral edges armor forms a flattened rim [N86]; posterior margin, as a rule, has a median ledge [N86]; ventral surface convex [H73]; sensory line is system propagated by furrows and channels, including ‘V’-shaped supraorbital channels, lateral channels, longitudinal lines, and cross commisures [N86]; ventral cross-commisures unique to this taxon [S64]; some forms appear to have had an internal, as well as external sensory line [H73]; ornament of dentine, ridges and mounds with smooth or jagged edges [N86]; ornament of stellate tubercles (= grebeshki?) [S64]; mounds alternate with ridges or entirely cover small areas of the armor [N86]; ridges are generally oriented longitudinally, and sometimes (on the periphery of the armor) – radially [N86]; some forms are tesserated [N86]; in an average part of an armor, there is usually one layer of prominently prismatic chambers [N86].

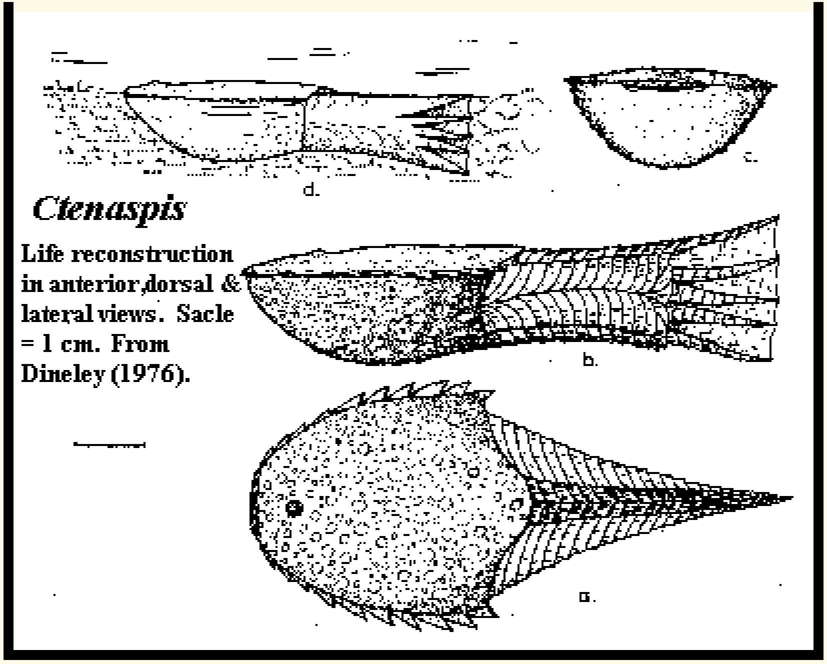
Note: [1] some specimens known with healed bites, presumably from gnathostomes. [L95].

Links: Heterostraci; 420 Text; MsoDockBottom; Biology 356; Upper Silurian and Devonian heterostracan pteraspidomorphs (...;

References: Blieck & Janvier (1999) [BJ99]; Blieck *et al*. (2002) [B+02]; Halstead (1973) [H73]; Janvier (1996) [J96]; Long (1995) [L95]; Novitskaya (1986) [N86]; Stensiö (1964) [S64]. APW040316.

***Ctenaspis*:** *C. dentata* Kiaer 1930; *C. cancellata* Kiaer, 1930; *C. kiaeri* Zych, 1931; *C. obruchevi* Dineley, 1976; *C. ruselli* Dineley, 1976; *C. ornata* Dineley, 1976.

Range: Early Devonian (Lochkovian - Pragian) of North America (Arctic Canada), Lochkovian of Spitzbergen, Siberia (Severnaya Zemlya),



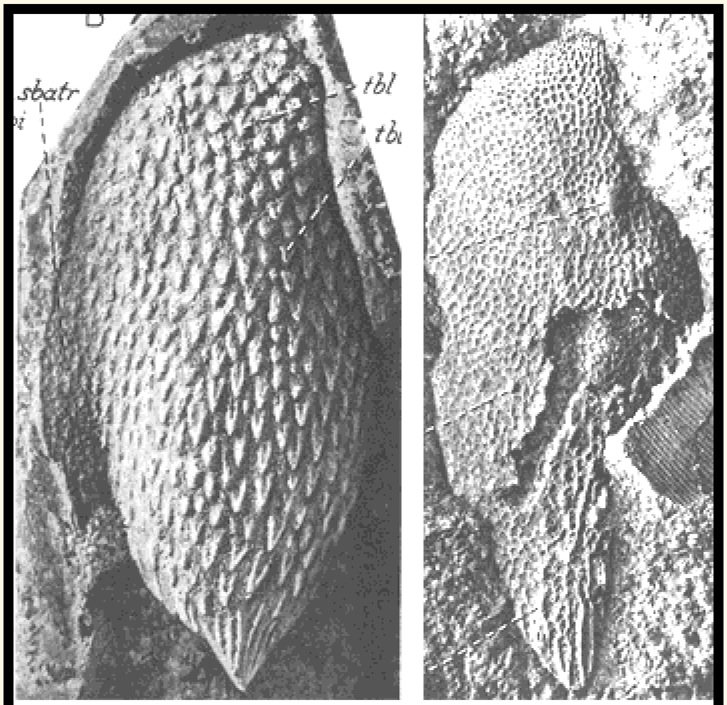
Ctenaspis

Life reconstruction in anterior,dorsal & lateral views. Sacle = 1 cm. From Dineley (1976).

England and Ukraine (Podoli) [D76] [N86] [BJ99]

Phylogeny: Amphiaspidida: (Amphiaspidoidei + (Hibernaspidoidei + Siberiaspidoidei)) + *.

Characters: <10 cm?; adorbital opening (praespiraculum) absent [J96]; only two (dorsal & ventral) plates [D76]; dorsal plates fused with branchials [N86]; plates notably thin [D76]; dorsal plate with jagged lateral margins [N86]; dorsal plate with well-developed lateral brim [D76]; armor rounded and slightly lengthened [N86]; shield short & broad (l/w = 0.7-0.9) [D76]; dorsal shield flat [D76]; short, separate supraoral shelf present with fin anteroposterior striations [D76]; preorbital process well-developed [N86] **[1]**; orbits small and located relatively far anteriorly [D76]; pineal macula well-developed [D76] [N86]; branchial opening located at posterior edge of armor, between dorsal & ventral plates [D76] [N86]; posterior edge of dorsal shield with triangular ledge ornamented with a network of ridges [N86]; ventral shield strongly arched except marginally [D76]; epitega & scale-like units absent [S64] [N86] [SW90]; dentine ridges absent [N86] [SW90]; ornament of stellate tubercles [J96]; ornament of aspidine tubercles (not dentine [D76] **[3]**) and local networks of ridges [N86]; ornament notably coarse [D76]; ornament includes either flat, wide tubercles with a pointed end posteriorly, or a network of delicate ridges [S64]; sensory canals tend to branch [N86]; some elongated scales rows present on body [SW90]; tail *diphycercal* [J96]; tail posterior margin straight or slightly concave [SW90]; dorsal & ventral ridge scales terminating in points [SW90]; up to 6 large "rays" each consisting of a single row of posteriorly tapered scales, supporting fin web [D76] [SW90]; probably no separate muscular control of fin rays [J81]; .



C. dentata (left) and C. kiaeri (right) dorsal shields in dorsal view, illustrating types of ornament. From Stensio (1964).

Note: **[1]** not an elongate rostrum as in most amphiaspids, but a broad, rounded anterior extension of the dorsal plate, more in the manner of pteraspidiforms. **[2]** Dineley [D76] reconstructs *Ctenaspis* as benthic, but a capable swimmer apparently because the tail, being flexible from top to bottom, might have been used for attitude control. **[3]** Stensiö [S64] explains: the dentine layer was reduced in *Ctenaspis* so that the ornament was largely raw bone. Presumably this helps account for the unusually thin plates. Stensiö also analyzes the ornament at great length in terms of primitive cyclomorial units. Following Janvier [J96], I have omitted almost all such discussion as probably pointless.

Links: Upper Silurian and Devonian heterostracan pteraspidomorphs (....

References: Blieck & Janvier (1999) [BJ99]; Dineley (1976) [D76]; Janvier (1981) [J81]; Janvier (1996) [J96]; Novitskaya (1986) [N86]; Soehn & Wilson (1990) [SW90]; Stensiö (1964) [S64]. ATW030509.

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checked ATW031224

Pteraspidomorphi: Amphiaspidida: Amphiaspidida (2)

The three families of amphiaspids

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         |     |--Amphiaspidoidei
         |     `--+--Hibernaspidoidei
         |        `--Siberiaspidoidei
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

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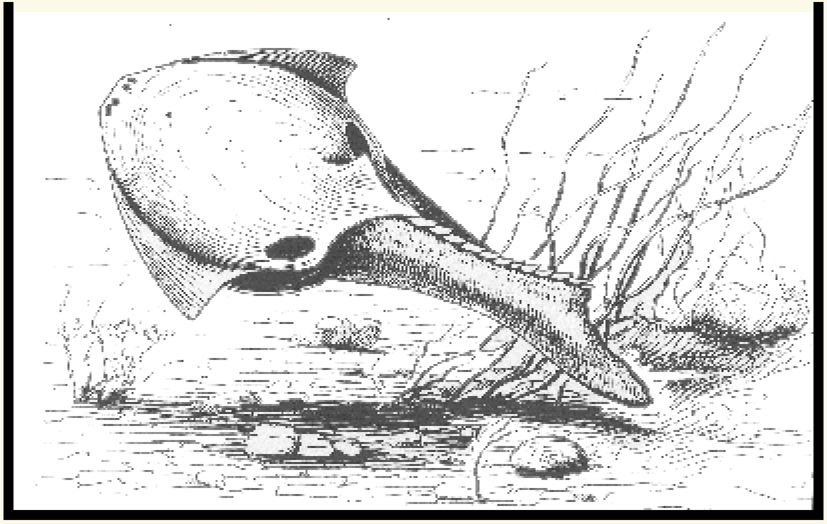
2. Hibernaspidoidei X
3. Siberiaspidoidei X

Amphiaspidoidei: *Amphiaspis, Angraspis, Edaphaspis, Gabreyaspis, Kureykaspis, Olbiaspis, Pelaspis, Prosarctaspis, Tareyaspis*

Range: Early Devonian (Lochkovian to earliest Emsian) of Siberia [N86]



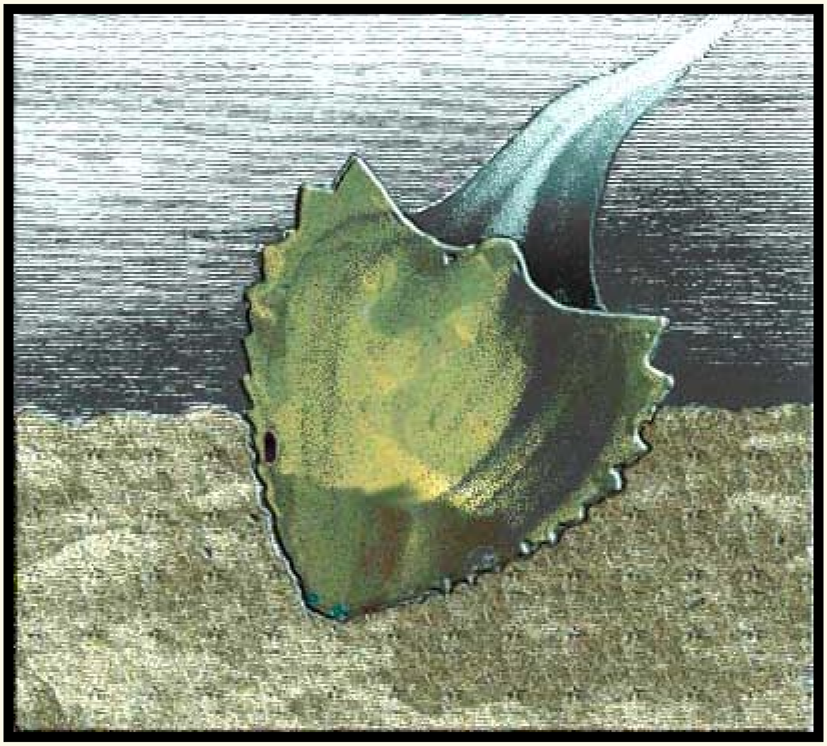
Phylogeny: Amphiaspidida:: (Hibernaspidoidei + Siberiaspidoidei) + *.

Characters: All plates fused, with occasional exception of the posterior ventral area [N86]; anterior margin rounded or straight [N86]; mouth ventral, terminal or subterminal [N86]; oral tubes absent [N86]; orbits at anterodorsal margin of the armor [N86]; praespiracular apertures are present adjacent to orbit [N86]; lateral edges smooth or with "teeth" [N86]; sensory line furrows usually short, slightly curved in the longitudinal lines frequently found? in the alar regions [N86]; sensory line system confined to pit lines, without channels [S64]; ventromedially, sensory lines 'V'-shaped, with anterior commisures forming rectangular figure [N86]; commisures are positioned laterally relative to the longitudinal ventral lines [N86]; pattern of sensory lines unique [S64]; sculpturing present as flattened ridges with smooth edges (in older forms) [N86]; or with tubercles and *grebeshkis* [N86] [S64]; some species have tesserae [N86].

Note: Stensiö wrote when only three amphiaspids were known. His comments refer here only to *Amphiaspis*.

Image: *Angaraspis* from [N86].

References: Novitskaya (1986) [N86]; Stensiö (1964) [S64]. ATW030508.



Hibernaspidoidei: *Aphataspis, Eglonaspis, Empedaspis, Gerronaspis, Hibernaspis, Lecanaspis, Pelurgaspis, Putoranaspis*

Range: Early Devonian (Pragian to Emsian) of Siberia [N86], including Lochkovian of Severnaya Zemlya [B+02].

Phylogeny: Amphiaspidida::: Siberiaspidoidei + *.

Characters: All plates are fused, with the occasional exception of the posterior ventral area [N86]; anterior margin usually extended as an oral tube (absent in primitive forms) [N86]; mouth ventral and subterminal, or terminal in forms having an oral tube [N86]; orbits on lateral margin of armor, or laterally on dorsal surface, or towards the distal end of an oral tube, or absent [N86]; praespiraculum absent [N86]; lateral edges with teeth (except *Putoranaspis*) [N86]; sensory sulci are present and, probably in some species, sensory channels (huh?) [N86]; supraorbital sensory line are not always present [N86]; longitudinal pairs of sulci (medial and lateral) form, with cross-commisures, rectangular figures [N86]; cross commisures usually lateral relative to ventral longitudinal furrows (??) [N86]; sculpturing looks like wide strips with smooth edges [N86]; some species with large, hexagonal tubercles [N86] [S64]; between strips are sometimes interspersed separate rounded tubercles [N86]; tesserae are absent [N86].

Note: Stensiö wrote when only three amphiaspids were known. His comments refer here only to *Eglonaspis* and *Hibernaspis*.

Image: *Hibernaspis* adapted from [N86]. Note that the large oval laterally is not an orbit, but the branchial opening. The orbits are two tiny dots on the dorsal surface of the rostrum.

Links: IX Capitolo - I Primi Pesci.

References: Blieck *et al*. (2002) [B+02]; Novitskaya (1986) [N86]; Stensiö (1964) [S64]. ATW040726.

Siberiaspidoidei: *Argyraspis*, *Dotaspis*, *Litotaspis*, *Siberiaspis*, *Tuxeraspis*.

Range: Early Devonian (Pragian) of Siberia.

Phylogeny: Amphiaspidida::: Hibernaspidoidei + *.

Characters: All plates of the shield are fused [N86]; anterior margin rounded, straight, or superficially excavated [N86]; oral tubes absent [N86]; mouth ventral, terminal or subterminal [N86]; orbits laterodorsal or on lateral edges of armor; [N86]; praespiracula absent [N86]; lateral edges, where known, without jagged projections [N86]; sensory line system present as sulci and channels (the last are definitively known in the Siberiaspididae) [N86]; arrangement of the sensory sulci as in Amphiaspidoidei; sculpturing present as smooth platens or tubercles with smooth or jagged edges (i.*e*. *grebeshkis*) [N86]; tesserae absent [N86].

References: Novitskaya (1986) [N86]. ATW030509.

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Pteraspidomorphi: Pteraspidiformes

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Anchipteraspididae
            `--Pteraspidida
               |--Protopteraspididae
               `--Pteraspidina
                  |--Pteraspididae
                  `--Protaspidoidea
                     |--Protaspididae
                     `--Psammosteida
                        |--Drepanaspis
                        `--Psammosteidae
```

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1. Anchipteraspididae X
2. Protaspididae X
3. Protaspidoidea X
4. Protopteraspididae X
5. Pteraspidida X
6. Pteraspidina X
7. Pteraspidiformes X

The Pteraspidiformes occur first in the Late Silurian but become much more diverse during the Early Devonian. They include streamlined spiny forms like *Pteraspis* and *Doryaspis* , and flattened bottom-dwellers, some of which grew to large size. All pteraspidiforms are characterized, among other features, by a dorsal shield made up of several independent plates. In this they differed from their cousins the Cyathaspidiformes, in which there was the tendency for all the plates to fuse into a single unit.

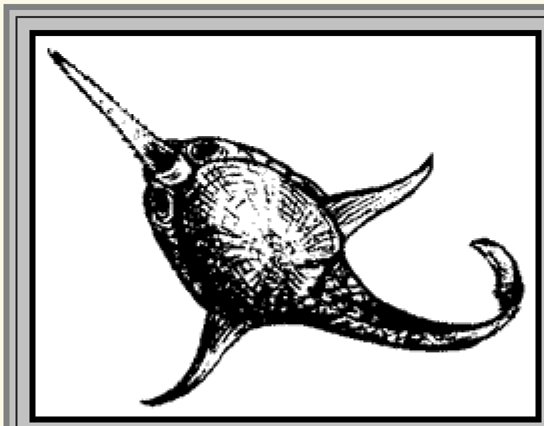
At least five families of pteraspidiforms can be distinguished. The Psammosteida will be covered on the next page. The others are:

The Anchipteraspididae (*Anchipteraspis, Ulutitaspis, Rhachiaspis*) are small primitive forms from the Late Silurian and Early Devonian of the Canadian Arctic (northwest Euramerica), resembling the cyathaspidiforms in possessing only a single fused branchio- cornual plate, and lacking the separate plates that define all other pteraspidiforms. They are close to the ancestral stock from which other pteraspidiforms evolved.

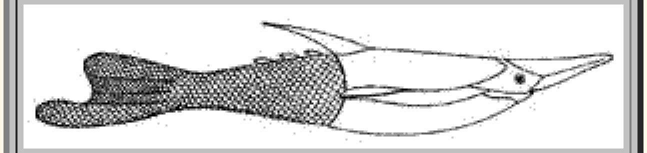
The Protopteraspididae are similar to the Pteraspididae. Some protopteraspidids, such as *Doryaspis* (also called *Lyktaspis*) have a strange snout or rostrum (the elongated median oral plate). There were bony spines set along its length, like the "saw" of a modern sawfish, except that the mouth is located *above*, rather than below, the rostrum. This purpose of this strange appendage is not clear. It may have had a hydrodynamic function, since the shape of *Doryaspis* suggests it was an active swimmer, probably feeding on plankton. Or it may have been used to stir up the bottom mud or sand, to find crustacea or other tiny invertebrates.

Doryaspis also had unusually long, lateral keels growing from the back of the head shield. Their leading edges were also armed with tooth- like spines. It is suggested that these may have acted as hydrofoils, and along with the rostrum and downturned tail, elevated the front of the body during swimming.

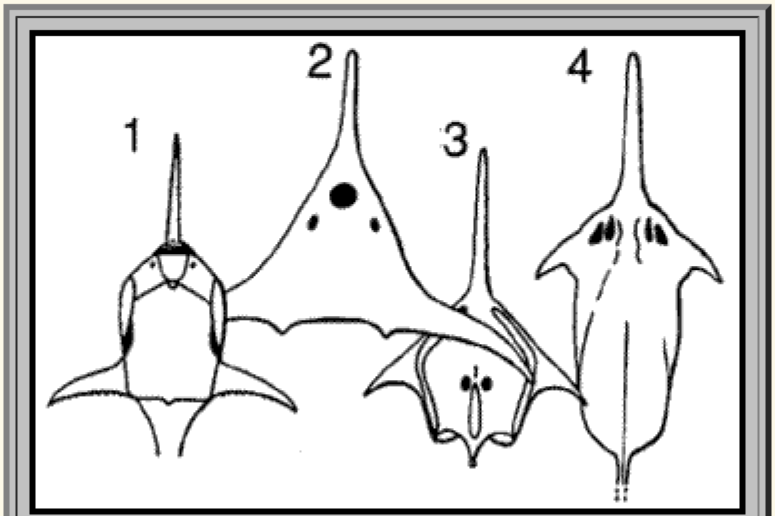
The Pteraspididae are quite similar in overall morphology to the Protopteraspididae, but are distinguished by a supraorbital canal passing through the pineal plate (a feature shared in common with the Protaspididae and Psammosteida). It is likely therefore that the Pteraspididae evolved from the Protopteraspididae, rather than the reverse. Like the Protopteraspididae they were streamlined swimmers, and one genus, *Rhinopteraspis* resembles *Doryaspis* in having a very long rostrum and spinal plate (although in this case located in the normal position, above the mouth).



***Doryaspis*, a protopteraspid from the Lochkovian to Pragian of northern Euromerica. Length 15 cm. Graphic from Faktaside om fossile urfisk fra Norge, © 1998 Paleontologisk Museum,- University of Oslo.**



***Pteraspis*, a pteraspidid from the Pragian of Southeast Euromerica. Length 20 cm.**



Convergent evolution in Early Devonian jawless fishes. The head- shields of (1) *Doryaspis*, a heterostracan; (2) *Asiaspis*, a galeaspid; (3) *Boreaspis*, an osteostracan; and (4) *Pituriaspis*, a pituriaspid.

In *Pteraspis*, the most representative member of the family, the rostrum is of more normal proportions. The Pteraspids became very numerous and diverse during the Late Silurian and Early Devonian. Although lacking paired fins, the pteraspids were probably powerful swimmers. Stability was provided by the wing-like outgrowths from the back of the head shield. A large spine over the back acted as a kind of dorsal fin while 2 rigid 'wings' or keels functioned as pectoral hydrofoils. The long, flexible tail was also hydrodynamic, with the lower lobe elongated to provide lift at the front of the body during swimming. Additional lift was provided by the elongated snout, which was drawn out into a bladelike 'rostrum', below which the mouth opened. It is thought that the pteraspids and protopteraspids fed in mid-water or near the surface of the sea, among the shoals of planktonic, shrimp- like crustaceans.

As with the Protopteraspididae, the rostrum may have served a dual purpose, both hydrodynamic and used to probe the mud and sediment for small organisms. Significantly, the existence of an elongated rostral spine, and sometimes side spines or wings or cornua as well, seems to have been a recurring theme among the early Devonian ostracoderms, as indicated in the following diagram, which shows that some representatives of each of the four major armoured classes developed this feature.

The Protaspididae are early Devonian transitional forms between the Pteraspididae and Psammosteida. The head shield has already become broad and flattened, indicating a shift to a benthic (bottom-living) existence. MAK

Pteraspidiformes:

Range: Late Silurian to Late Devonian.

Phylogeny: Heterostraci: Cyathaspidiformes + *: Anchipteraspididae + Pteraspidida.

Characters: separate orbital, pineal and rostral plates; single median dorsal spinal plate present; separate branchial and cornual plates; dermal ornamentation of concentric, serrated dentine ridges.

Links: Pteraspidiformes, Class Pteraspidomorphi, Heterostraci. ATW020510.

Anchipteraspididae: *Anchipteraspis, Ulutitaspis, Rhachiaspis*

Range: Late Silurian to Early Devonian of North America

Phylogeny: Pteraspidiformes: Pteraspidida + *.

Characters: small; resemble cyathaspidiforms in single, fused branchio- cornual plate. ATW020510.

Pteraspidida:

Range: Early Devonian to Late Devonian.

Phylogeny: Pteraspidiformes: Anchipteraspididae + *: Protopteraspididae + Pteraspidina.

Characters: separate cornual plates, dorsal shield made up of several separate units.

References: Janvier (1996). ATW020510.

Protopteraspididae: *Doryaspis, Protopteraspis*.

Range: Early Devonian to Middle Devonian of North America, Spitzbergen & Russia (Siberia?).

Phylogeny: Pteraspidida: Pteraspidina + *.

Characters:

Links: IGCP, Heterostraci; examples of heterostracans. ATW020510.

Pteraspidina:

Range: Early Devonian to Late Devonian.

Phylogeny: Pteraspidida: Protopteraspididae + *.

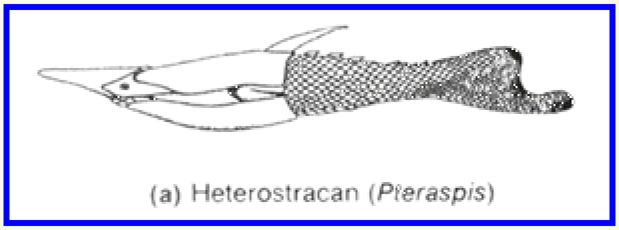
Characters: pineal sensory-line canal passes through pineal plate.

Image: *Pteraspis*: Evol.Page to Print: Clado Pic. Resources. ATW020510.

Pteraspididae: *Errivaspis, Pteraspis, Rhinopteraspis, Unarkaspis*.

Range: Early Devonian

Phylogeny: Pteraspidiformes: Protaspidoidea + *.



(a) Heterostracan (*Pteraspis*)

Characters: supraorbital canal passing through the pineal plate; more separate plates than Cyathaspidida; lateral growth rings; lateral and dorsal spines and keels, smaller body scales, cornua and rostra.

Links: Heterostraci; Pteraspididae; Various Illustrations; Pteraspis rostrata; Siluriano (Italian); ¾î·ù>ÆäÅ×¶ó½ºÇÇ½º (Korean); Fish Replicas - Hanman's Fossils & Minerals; Presse service hos Grafikhuset (Danish -- click on picture for zip file of enormous life image in .tif format).

Image: © 1999 ENSI (Evolution & the Nature of Science Institutes). ATW020510.

Protaspidoidea:

Range: Early Devonian to Late Devonian.

Phylogeny: Pteraspidiformes: Pteraspididae + *: Protaspididae + Psammosteida.

Characters: **$** enlarged, flattened branchial plates; **$** reduced cornual plates. ATW010815.

Protaspididae: *Cyrtaspidichthys* = *Protaspis*.

Range: Early Devonian of North America.

Phylogeny: Protaspidoidea: Psammosteida + *.

Characters: Head shield round and flat; without fragmented dorsal shield areas of psammosteids; concentric growth lines on head shield; cornual plates rudimentary or absent; cornual plate (when present) forms part of median margin of branchial opening [T64]; dorsal surface convex (benthonic?) [H73]; ventral surface broad & flat [H73].

Links: Pteraspidiformes; Heterostraci; Examples of heterostracans; Examples of heterostracans.

References: Halstead (1973) [H73], Tarlo (1964) [T64].

Note: Morphologically intermediate between the classic pteraspids and the psammosteids. ATW030530.

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Pteraspidomorphi: Psammosteida (1)

Drepanaspis

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

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1. *Drepanaspis* X
2. Psammosteida X

On History, Histology and Halstead

"The liveliness of controversies engendered by these animals does not appear to have diminished one iota during the last 150 years. It must be a cause of some surprise that these apparently inoffensive fish should be capable of arousing such passions." Halstead (1973)

1. Histology

In these Notes, we seldom address questions such as "why do we care?" Anyone who reads these words has already manifested a disturbing degree of interest in the arcana of evolutionary biology, as well as a willingness to seek it out in unlikely places. One is not likely, for example, to merely *stumble* on psammosteid histology while searching for celebrity images in varying stages of undress or reproductive receptivity. Second, there are many answers to the question. Some conflict. Some touch on matters which set off crackling visceral reflex arcs, hard-wired deep within the political brainstem of the academic mind. Nevertheless, histology is one of those subjects which, even by the notably lax standards of paleontology, is considered dull, obscure and old fashioned. Thus its presence here requires some sort of justification.

Histology is a word with a phylogeny sometimes more interesting than the science itself. The Greek root seems to be related to *hoist*, with precisely that meaning. The sequence then became: to step (a mast) or raise up > a mast or pole > anything raised up > a (vertical) loom > cloth made on a loom > any web or (living) tissue. With the development of microscopy and artificial dyes, histology became the molecular biology of the Nineteenth and early Twentieth Centuries. There is still a vast arcana of strange, evocative stain terminology: the "Gomori-Takematsu Procedure," "Congo Red," and "Weigert's Iron Haematoxylin." Much of this sounds as if it belonged on an alchemist's parchment or perhaps in some New Age yoga manual. The work itself was highly empirical, "let's add a little of this stuff and see what happens," bench-top chemistry, subject to many artifacts and sometimes requiring an extraordinary amount of individual skill, experience and good luck.

With the advent of more contemporary biochemistry and molecular biology, bizarre acronyms ("cAMP-activated Ca-dependent GTPase") and genetic silliness ("*Sonic Hedgehog*") displaced most of this odd, but dignified, old vocabulary, as well as the odd, but dignified, old professors who had used it. Much was gained by this transition. However, something was lost as well. Few scientists currently work at the tissue level of organization. We have made enormous progress in understanding the molecular basis of life, and are even beginning to assemble this knowledge to attack the cellular level. At the other end of the spectrum, organismal biology and ecology are making a modest comeback. At least by comparison, physiology (organ-level) and histology (tissue-level) studies are presently languishing. Unfortunately, in some cases, tissues are almost all we have. The psammosteids are one of those cases. Most psammosteids consist of pieces of dermal plate, more or less crushed into fragments. Absent some incredible new Devonian lagerstät, that is all we will ever have **[1]**. If we are to understand this group, we must look seriously at their histology.

2. Aspidine (or, sometimes, "aspidin")

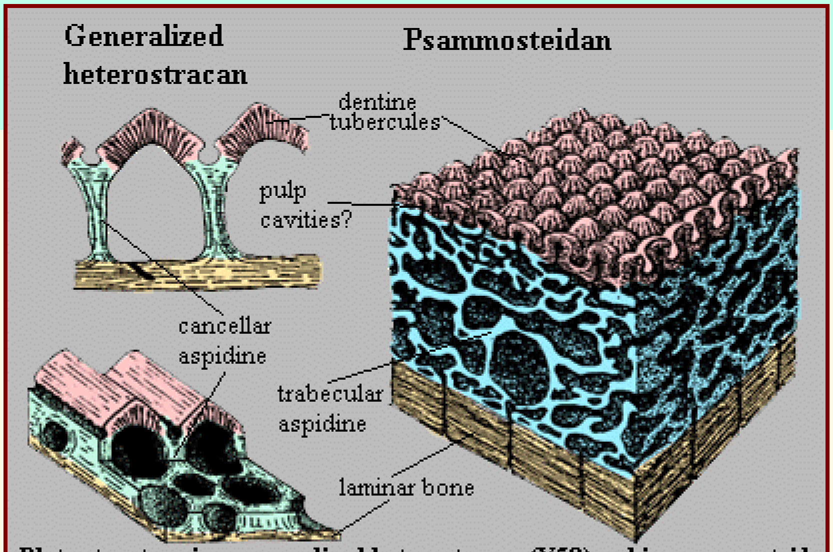


Plate structure in a generalized heterostracan (X50) and in psammosteids (about X30). From Janvier (1996: 89) and Halstead (1973: 306).

The plates of psammosteids, like those of other pteraspidomorphs, are made up of *aspidine*. The difficulty is that no one can define this term. Histology, particularly as applied to fossil material, does not distinguish adequately between bricks and brick walls. That is, the literature does not draw a bright line between the chemical composition of aspidine and its structure. Janvier (1996) suggests that *aspidine* is simply a term for acellular bone. This is useful but, ultimately, only adds a layer of developmental debate to the already existing confusion between structure and composition. Furthermore, Halstead (Tarlo (1964)) argues that psammosteidan plates are not acellular **[2]**.

Since we are dealing with materials from fishes that have been dead, and buried under tons of rock, for some four hundred million years, we cannot assume that their chemistry has been unaffected (even if we knew what it is today). We certainly cannot observe the developmental biology of psammosteidan integument. We can, however, observe that their remains are structurally distinctive, although plainly related to other pteraspidomorph plates. Accordingly, a structural definition seems the most workable.

On a structural level, it is plain that the psammosteidan integument differs from aspidine as it is known from heterostracans (*i.e.* Devonian pteraspidomorphs). As Halstead discusses at great length, in some ways it more closely resembles the exoskeleton of the very earliest pteraspidomorphs, such as *Arandaspis*. To avoid multiplying nomenclature that no one will use anyway, let's refer to the psammosteidan variety as ps/aspidine.

Like "normal" aspidine, ps/aspidine is three-layered. The basement layer is laminar, as in aspidine, and probably consists of dense, cortical bone, like some of the outer layers of endochondral bone. However, the basement layer is (sometimes?) pierced by essentially vertical canals. Unlike aspidine, the middle layer is a thick spongy or*trabecular* space. It lacks the ordered columns of aspidine, although we are dealing with a difference in scale, and there may be less overall difference than meets the eye. A thin layer of cancellous bone left by a line of retreating or dying bone-forming cells is likely to look considerably more like trabecular bone if the layer is thick. In that circumstance, the osteocytes can overlap, slide past one another, and go off at angles. Furthermore, a thick layer is more subject to distortion from shearing and crushing forces, both during development and perhaps even after death. **[3]** Thus the middle layer of ps/aspidine differs from aspidine, but the degree of difference is unclear. Finally, the outer layer of ps/aspidine consists of dentine tubercles. According to Halstead, these dentine caps vary in some particulars from heterostracan dentine, but the differences do not appear to be large. As Halstead notes, the form of the dentine caps changes greatly on a *specific* level within Heterostraci, so one should probably not make too much of divergences between, for example, psammosteidans and pteraspidids.

3. Regeneration?

The interesting bit comes with the irregularities. To make a long story shorter, Halstead's microscopic examination of isolated plates demonstrated that damaged plates show evidence of extensive dentine regeneration. The photographic evidence, at least to the inexpert eye, seems very strong. The regenerated tissue takes the form, not only of new dentine tubercles, but also of *pleromic*, invasive dentine which seems to have filled gaps in the tissue. Halstead's microscopic evidence for regeneration, and thus for living cells, in the bone layers seems less convincing. However, the logic is certainly strong. If the dentine regenerated, it must have contained living cells capable of producing the tissue. These must have been connected to the circulatory system in some way (absent some completely novel symbiotic arrangement). The most straightforward explanation is that, in spite of appearances, the circulatory system pierced the ps/aspidine; and, if so, there is no obvious reason why this peripheral circulation could not have maintained what Halstead calls *aspidinocytes* within the trabecular layer.

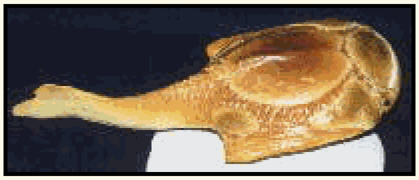
This is a murky area. Only one heterostracan, and *no* psammosteidan, shows evidence of the subaponevrotic vascular network that maintains a living integument in all other vertebrates.**[4]**. As noted, Halstead's own evidence for circulation, and for living cells within the bone framework, seems weak, particularly in comparison to the evidence for dentine regeneration. But, absent something really odd, is some sort of epidermal tissue peripheral to the bone. This seems even less satisfactory. Another odd bit of information noted by Halstead is that the specimens showing regeneration tend to be from specific sites. Conceivably, this geographic bias actually reflects some seasonal or other periodic process allowing a sort of temporary epidermis (with total resorption of the overgrown tissue). Or, we might be seeing a disease process common in some locations. Or, the evidence may reflect proliferation of an internal tissue triggered by traumatic breach of the exoskeleton under locally common conditions. Graduate students take note: these and other possibilities can probably now be examined. In fact, Halstead himself was a pioneer in, for example, the use of electron microscopy. However, the instruments and techniques now available are well beyond the reach of the technology reasonably available to Halstead in the 1960's. Paleohistology deserves a second look in the new millennium. ATW020126

[1] Psammosteids seem to have been restricted to the traditional "Old Red Continent:" the northern parts of Europe and Russia, various Arctic islands, Greenland, and much of North America. Tarlo (1964). Accordingly, there are no psammosteidans in the famous Australian Gogo Formation or the Devonian sites of China and Vietnam.

[2] Then again, a strong case could be made that Halstead's conclusion depends, in turn, on exactly what one means by *acellular*.

[3] As always, please recall that this is personal speculation and not to be taken too seriously.

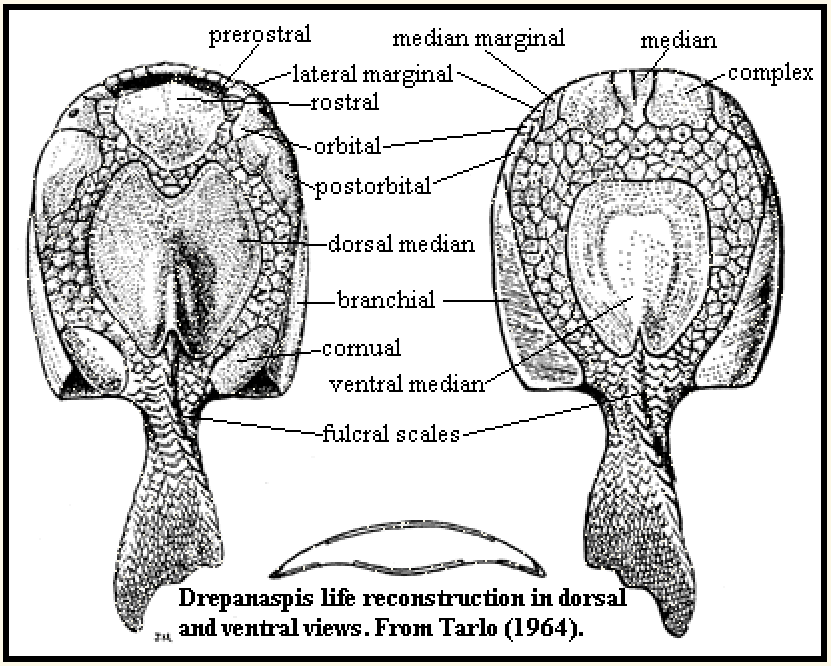
[4] The exception is the cyathaspidiform *Torpedaspis*. Janvier (1986: 92, 94).



Psammosteida: The largest and last of the pteraspidomorphs [JB93].

Range: Early Devonian to Late Devonian of North America, Russia & Europe

Phylogeny: Protaspidoidea: Protaspididae + *. *Drepanaspis* + (Guerichosteidae + ((Pycnosteidae + *Psammolepis*) + Psammosteidae)).



Drepanaspis life reconstruction in dorsal and ventral views. From Tarlo (1964).

Characters: Medium to large (1m) forms [JB93] paddle-shaped [T64] with large, flat, almost round heads; plates similar to Pteraspididae, but with **$** 2 pairs of orbital plates [H73]; orbit pierces anterior orbital plate; individual large plates separated from each other by small, polygonal tessellate platelets during ontogeny (young have no tessellations and large plates are contiguous); platelets capable of growth and have no central tubercle; terminal or subterminal mouth; small paired bone cornual "fins;" cornual plates reduced; branchial plates enlarged, flattened; branchial plates may be downturned in some forms as "outriggers" (?); branchial opening at posterior end of branchial plates [T64]; web-shaped caudal fins; **$** trabecular ("spongy") aspidine (cancellous layer lost -- see figure at *aspidine*); **$** ornamentation of stellate, shiny tubercles; dentine tubercles very diverse in shape, density and size [T64]; dentine tubercles may vary in shape on different parts of same plate [T64]; dentine tubercles showing evidence of resorption & regrowth, thus probably covered with skin [H73]; presence of pleromic (gap-filling) dentine covering or even invading the bone in abraded or injured areas [H73]; sensory line in pore-canal system (?) [T64]; pores usually between tubercles, but may pierce ornament [T64]; sensory line pattern poorly known and may be asymmetrical [T64]; marine, presumably bottom-dwellers; later species restricted to deltas or floodplains.

Links: ??????? (Japanese); Stratený svet c.5/1999 (Czech); Drepanaspis gemuendenensis; Biology 356 (not really certain this is *Drepanaspis*, but its worth a close look).

References: Halstead (1973) [H73], Janvier & Blieck (1993) [JB93], Tarlo (1964) [T64].

Image of *Drepanaspis* model © North Eastern Geologic, courtesy of Gregory S. Gartland.

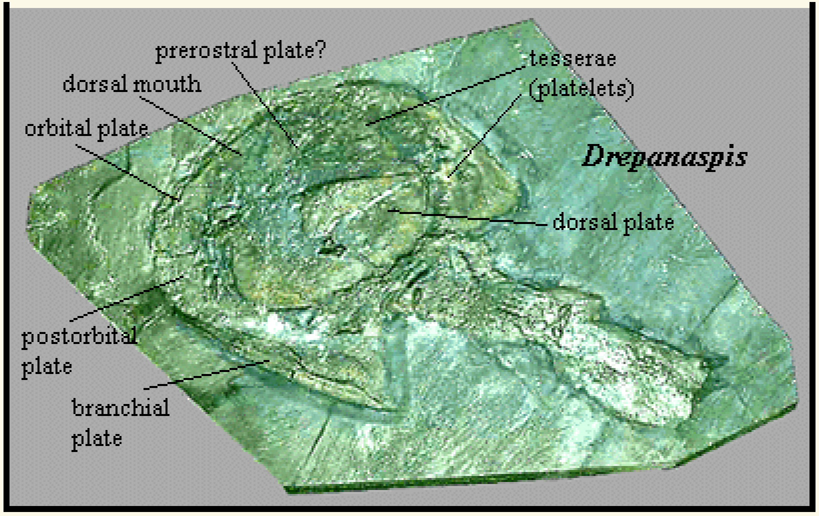
Note: **[1]** The structure and properties of aspidine (also spelled *aspidin*) have been the subject of a great deal of debate. We will tentatively proceed on the assumption that the labels are probably meaningless, although the structural details may be very significant. See *Aspidine*. **[2]** Some very small modifications were made to the figure from [T64] to clarify some of the divisions between plates. **[3]** Halstead and Tarlo are the same person. Tarlo changed his name in 1969 and moved from England (at least for a few years) to the University of Ife in Nigeria. Must be an interesting story there ... . ATW020112.

Drepanaspis**:** (Drepanaspididae) An early, very well known, psammosteidan, "essentially a flattened *Pteraspis*." [H73: 294].

Range: lwD of Eur.

Phylogeny: Psammosteida: (Guerichosteidae + ((Pycnosteidae + *Psammolepis*) + Psammosteidae)) + *.

Characters: **[3]** dorsoventrally compressed and overall slightly convex body form [T64]; mouth



dorsal [H73]; oral plates **[2]** large; 7 oral plates ornamented at terminal margins [H73], [T64]; oral plates fixed to anterior (ventral) margin of mouth [T64]; oral plates held inside mouth in life? [T64]; mouth with median tesserae just below ventral margin [H73] (*contra*, [T64]); thin, transverse prerostral plates across dorsal (= posterior) margin of mouth [H73]; small lateral marginal plate just anterior to orbital [T64]; small (olfactory?) notch between lateral marginal & rostral [T64]; Y-shaped median plate on ventral mouth border, flanked by square complex plates and thin, sigmoidal median marginal plates [T64]; may be small pineal plate between rostral and dorsal median plates [T64]; dorsal median plate with medial indentation anteriorly, matching (but not meeting) posterior extension of rostral plate [T64]; orbital plate triangular [T64]; straight, vertical border between orbital and postorbital [T64]; long postorbital with irregular medial margin [T64]; postorbital articulates posterolaterally with branchial [T64]; ventral margins of lateral marginal, orbital and postorbital visible in ventral view [T64]; branchial plates long and narrow (primitive) [H73]; ventral shield (mainly?) tesserae [H73]; branchial opening dorsal [H73]; in ventral view, posterior end of branchial plate transverse to body axis [T64]; broad tesserated zone between ventral mouth plates and ventral median plate [T64]; ventral median plate oval, but truncated anteriorly & posteriorly [T64]; median ventral with variably deep notch posteriorly [T64]; fulcral scales both dorsal & ventral [T64]; on both surfaces, posterior tesserae grade into caudal scales [T64]; tail almost equilobate [T64]; major plates show continuing concentric growth [H73] [T64]; ornamentation of small, stellate tubercles [T64]; marine [H73].

Links: Drepanaspis gemuendenensis; Biology 356.

References: Halstead (1973) [H73]; Janvier (1996) [J96], Tarlo (1964) [T64].

Note: **[1]** Earliest, but best known, psammosteidan. **[2]** "Oral plates" refers to the numerous, finger-like plates which were attached to the ventral surface of the mouth, either acting to cover it (perhaps as a coarse filter), or projecting anteriorly (perhaps as a scoop), or both. [J96]. As Halstead [H73] comments, the very fact that the oral plates are often found in articulation suggests that they were covered with flesh in life. Halstead [T64] also believes that the plates were held inside the mouth. **[3]** See figure at Psammosteida for plate nomenclature. 020111.

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Pteraspidomorphi: Psammosteida (2)

Guerichosteids, Pycnosteids, Psammosteids & *Psammolepis*

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--+--Guerichosteidae
                  `--+--+--Pycnosteidae
                     |  `--Psammolepis
                     `--Psammosteidae
```

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2. *Psammolepis* X
3. Psammosteidae X
4. Pycnosteidae X

Guerichosteidae: *Guerichosteus, Hariosteus, Schizosteus*

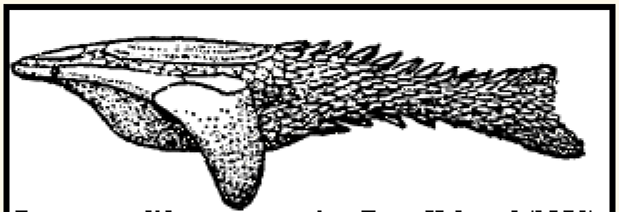
Range: Early Devonian to Middle Devonian (possibly Late Devonian) of Europe

Phylogeny: Psammosteida:: ((Pycnosteidae + *Psammolepis*) + Psammosteidae) + *.

Characters: Oral plates narrow relative to *Drepanaspis* [T64]; postorbital plate tapers gradually posteriorly [T64]; branchial plates wider than *Drepanaspis*, "and their lateral parts are solid and free" [T64]; branchial plates drawn out as sheets laterally and downturned [T64]; cornual plates rectangular [T64]; branchial opening at or medial to posterolateral corner [T64]; ventral median plate convex [T64]; median ventral plate with wide, open posterior notch [T64]; very clear concentric lines of growth in median plates [T64]; development of small, accessory dentine tubercles between main dentine tubercles [T64]; fresh water [H73].

References: Halstead (1973) [H73]; Tarlo (1964) [T64].

Notes: Rather poorly known. ATW020111.


Pycnosteus life reconstruction. From Halstead (1973)

Pycnosteidae: *Ganosteus*, *Pycnolepis*, *Pycnosteus*, *Tartuosteus* (= *Psammolepis*?), *Yoglinia*. Probably the base of the Middle Devonian radiation of psammosteidans.

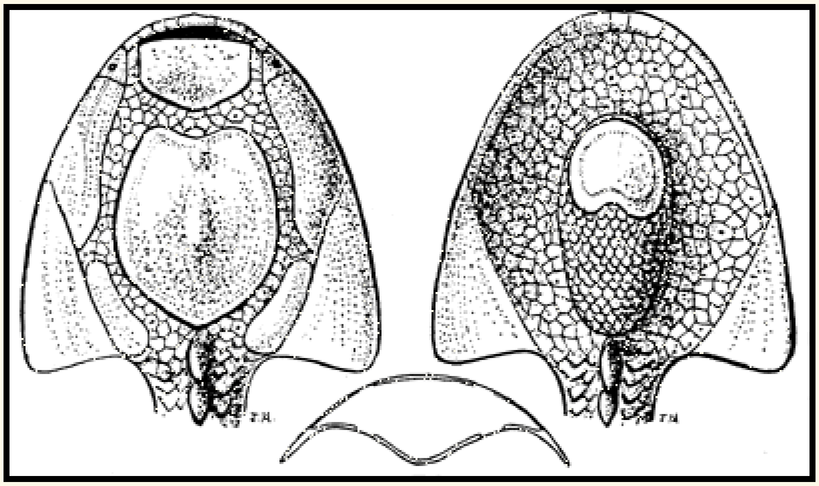
Range: Middle Devonian to Late Devonian of Europe.

Phylogeny: Psammosteida:::: *Psammolepis* + *.

Characters: postorbital elongated [T64]; branchial plates enlarged by successive lines of growth [H73]; branchial plates shortened and extended laterally to form large, thin down-turned "wings" [H73] [T64]; branchial plates show wear on anterior surface, as well as equally on dorsal and ventral surfaces [H73] [T64]; anterior marginal of branchial plate wings anteriorly concave (as in image) in some species [T64]; ventral median plates, long, thin and elaborated ventrally as sled-like runners [H73]; ventral plates show wear in middle region (suggesting horizontal position – mouth well above substrate) [H73]; deep median ventral plate with long shallow groove forming almost flat ventral surface with very steep sides laterally and anteriorly [T64]; notch behind branchial plates filled in, in some forms (*Tartuosteus*) by more tesserae [H73] (? [T64] says groove in median ventral plate is filled in -- which makes more sense); major plates show continuing concentric growth [H73]; major plates also show some growth by accretion of tesserae **[2]** [T64].

References: Halstead (1973) [H73], Tarlo (1964) [T64].

Note: [1] [H73] suggests that *Pycnosteus* cruised through vegetation, knocking small invertebrates loose and filtering them. **[2]** This evidence comes from *Tartuosteus* as stated in [T64]. *Tartuosteus* may actually be a species of *Psammolepis*; but, then again, *Psammolepis* may turn out to be a pycnosteid.... ATW020111.



***Psammolepis*:** (Psammolepididae) Largest (?) of the psammosteidans.

Range: Middle Devonian to Late Devonian of Europe, Russia & North America.

Phylogeny: Psammosteida::: Pycnosteidae + *.

Characters: Growth by addition of tesserae, with growth lines (rings of ornament) on major plates progressively smaller [H73]; subsequent growth by progressive enlargement of component units (tesserae?) of major plates, rather than concentric growth of whole plate (*i.e.*, growth by accretion of tesserae begins to dominate over concentric growth of plates) [H73] [T64]; median plates become covered with tesserae [H73] [T64].

References: Halstead (1973) [H73]; Tarlo (1964) [T64].

Image: *Psammolepis venyukovi* from [T64]. See Psammosteida for plate nomenclature. 020111.

Psammosteidae: *Cranosteus* (*Crenosteus*?), *Karelosteus*, *Psammosteus*, *Rohonosteus*. The last heterostracans, from the uppermost Frasnian.

Range: Late Devonian of Europe, Russia & North America

Phylogeny: Psammosteida::: (Pycnosteidae + *Psammolepis*) + *.

Characters: major median plates covered with superficial tesserae (probably ontogenetic process as in *Psammolepis*) [H73]; dorsal median plate highly variable, *i.e.* flat to concave, but usually with gently curving lateral margin and relatively broad flat keel [T64]; very long postorbitals [T64]; branchial plates extremely short and wide to become "just solid arcuate plates forming the posterolateral corners of the carapace" [T64]; *Psammosteus* may have been sexually dimorphic in width of dorsal median plate [H73]; in *Psammosteus*, branchial plates may have been moveable [H73]; branchial plates with elongated tesserae covering proximoventral surface [T64]; branchial plate distal end with distinct wear facets (suggesting it was moveable) [T64]; growth largely by progressive enlargement of component units (tesserae?) of major plates, rather than concentric growth of whole plate [H73].

Links: Document Gallica (French)

References: Halstead (1973) [H73], Tarlo (1964) [T64].

Note: [1] Document Gallica is a complete, indexed .pdf of Eichwald's (1860) treatise on Russian fossils, with an extraordinary amount of detail on *Psammosteus*. Notwithstanding Halstead's [T64] high opinion of this work, the information is omitted because (a) the author evidently thought *Psammosteus* was a placoderm (b) the genus has been reorganized and redescribed a number of times since, so that the continuing validity of the material referred to *Psammosteus* by Eichwald is unclear; and, mostly, (c) my French is not up to accurate translation of 19th century anatomical or histological terms. 020111.

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Pteraspidomorphi: Cladogram

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

Overview
Pteraspidomorphi
Heterostraci
Heterostraci (2)
Amphiaspidida
Pteraspidiformes
Psammosteida (1)
Psammosteida (2)
Dendrogram
References

Dendrogram

```
Pteraspidomorphi X ToL, MH, Tax
|--Anatolepis •X
`--+--Arandaspida •X Tax
   `--Heterostracomorphi X
      |--Astraspidae •X Tax
      `--Heterostraci X ToL, Tax
         |--Cyathaspidiformes X MH
         |  |--Corvaspididae X
         |  |  |--Corvaspis •X
         |  |  `--Corveolepis •X
         |  `--+--Cyathaspidida •X Tax
         |     `--Amphiaspidida X
         |        |--Ctenaspis •X
         |        `--+--Amphiaspidoidei •X
         |           `--+--Hibernaspidoidei •X
         |              `--Siberiaspidoidei •X
         |
         `--Pteraspidiformes X MH
            |--Anchipteraspididae •X
            `--Pteraspidida X
               |--Protopteraspididae •X
               `--Pteraspidina X
                  |--Pteraspididae •X MH
                  `--Protaspidoidea X
                     |--Protaspididae •X
```

```
`--Psammosteida X
   |--Drepanaspis •X
   `--+--Guerichosteidae •X
      `--+--+--Pycnosteidae •X
         |  `--Psammolepis •X
         `--Psammosteidae •X MH
```

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Pteraspidomorphi: References

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Thelodonti
   |
   Pteraspidomorphi
   |--Arandaspida
   `--Heterostracomorphi
      |--Astraspidae
      `--Heterostraci
         |--Cyathaspidiformes
         |  |--Cyathaspidida
         |  `--Amphiaspidida
         `--Pteraspidiformes
            |--Pteraspididae
            `--Psammosteida
               |--Drepanaspis
               `--Psammosteidae
```

Contents

References

Blieck ARM & P Janvier (1999), *Silurian-Devonian vertebrate-dominated communities, with particular reference to agnathans*, **in** AJ Boucot & J Lawson [eds.], **Paleocommunities: a Case Study from the Silurian and Lower Devonian**. Cambridge Univ. Press, pp. 79-105. Amphiaspidida, Corviaspididae, *Ctenaspis*.

Blieck, A & VN Karatajute-Talimaa (2001) *New corvaspids from the Lochkovian (Lower Devonian) of Severnaya Zemlya, Russia (Vertebrata: Pteraspidomorphi: Heterostraci)*, **in** DK Elliott & MD Gottfried [eds.], 9th International Meeting on Early Vertebrates/Lower Vertebrates. **J. Vert. Paleontol.** 21: 639-650. *Corveolepis*, Corviaspididae.

Blieck, ARM, VN Karatajütë-Talimaa & E Mark-Kurik (2002), *Upper Silurian and Devonian pteraspidomorphs (Vertebrata) from Severnaya Zemlya (Russia): a preliminary report with biogeographical and biostratigraphical implications*. **Geodiversitas** 24: 805-820. WWW Amphiaspidida, Corviaspididae, *Corveolepis*, Hibernaspidoidei.

Dinely (1976), *New species of* ***Ctenaspis*** *(Ostracodermi) from the Devonian of Arctic Canada*, **in** CS Churcher [ed.], **Essays in Palaeontology in Honor of Loris Shano Russell**. Royal Ont. Mus., pp. 73-89. *Ctenaspis*.

Dineley, DL & EJ Loeffler (1976), *Ostracoderm faunas of the Delorme and associated Siluro-Devonian formations, North West Territories, Canada*. **Palaeontol. Spec. Papers**, 18: 214 pp. Corviaspididae.

Halstead, LB (1973), *The heterostracan fishes*. **Biol. Rev.** 48: 279-332. Amphiaspidida, *Corvaspis*, *Drepanaspis*, Guerichosteidae, Protaspididae, *Psammolepis*, Psammosteida, Psammosteidae, Pteraspidomorphi, Pycnosteidae.

Janvier, P (1981), *The phylogeny of the Craniata, with particular reference to the significance of fossil 'agnathans'*. **J. Vert Paleontol.** 1: 121-159. Amphiaspidida, *Ctenaspis*.

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp. Amphiaspidida, Arandaspida, Astraspidae, Corviaspididae, *Ctenaspis*, *Drepanaspis*, Heterostraci, Heterostracomorphi, Psammosteida; Pteraspidida.

Janvier, P & A Blieck (1993), *The Silurian-Devonian Agnathan Biostratigraphy of the Old Red Continent* **in** JA Long (ed.), **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Johns Hopkins Univ. Press, pp.70-73. Heterostraci, Psammosteida.

Loeffler, EJ & DL Dineley (1976), *A new species of* ***Corvaspis*** *(Agnatha, Heterostraci) from the Upper Silurian to Lower or Middle Devonian of the North-West Territories, Canada*. **Palaeontology** 19: 757-766. Corviaspididae, *Corvaspis*, *Corveolepis*.

Long, JA (1995), **The Rise of Fishes: 500 Million Years of Evolution**. Johns Hopkins Univ. Press, 223 pp. Amphiaspidida, *Corvaspis*, Cyathaspidida.

Новицкая ЛИ (1986), "Древнейшие бесчелюстные СССР: Гетеростраки: Циатаспиды, Амфиаспиды, Птераспиды." **Труды ПИН** 219: 159с. [Novitskaya, LI (1986), *The most ancient agnathans of the USSR: Heterostraci: Cyathaspidae, Amphiaspidae, Pteraspidae*. **Trudy Paleontol. Inst. Nauk** 219: 159 pp.] My thanks to Dr. Stella Fitzgibbon for assistance with the translation. Amphiaspidida, Amphiaspidoidei, *Ctenaspis*, Hibernaspidoidei, Siberiaspidoidei.

Purnell, MA (2001b), *Feeding in extinct jawless heterostracan fishes and testing scenarios of early vertebrate evolution*, **Proc. Roy. Soc. Lond. B** 269: 83-88.

Soehn, KL & MVH Wilson (1990), *A complete, articulated heterostracan from Wenlockian (Silurian) beds of the Delorme Group, Mackenzie Mountains, Northwest Territories, Canada*. **J. Vert. Paleontol.** 10: 405-419 *Ctenaspis*.

Stanley, SM (1998), **Earth System History**. WH Freeman & Co., 615 pp. Corviaspididae.

Stensiö, EA (1964), *Les Cyclostomes fossiles ou Ostracodermes* **in** J Piveteau [ed.], **Traité de Paléontologie**. Masson, 4: 96-383. Amphiaspidida, Amphiaspidoidei, Corviaspididae, *Corveolepis*, *Ctenaspis*, Hibernaspidoidei.

Tarlo, LBH (1964), *Psammosteiformes (Agnatha): a review with descriptions of new material from the Lower Devonian of Poland. I. General part* **Paleontol. Pol.** 13: 1-135. *Drepanaspis*, Guerichosteidae, Protaspididae, *Psammolepis*, Psammosteida, Psammosteidae, Pycnosteidae.

Young, GC (1993), *Vertebrate faunal provinces in the Middle Palaeozoic*, **in** JA Long [ed.] **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Belhaven Press: pp. 293-323. Amphiaspidida.

Young, GC, VN Karatajute-Talimaa & MM Smith (1996), *A possible Late Cambrian vertebrate from Australia*. **Nature** 383: 810-812. *Anatolepis*.

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Thelodonti: Overview

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

Contents

Thelodonti: Weighing Scales in the Balance

Among Vertebrata, the Thelodonti are the drifters and vagabonds of Paleozoic phylospace -- a diverse, poorly known group of jawless fish of no fixed address on the phylogenetic tree, without established family or visible means of support. Their only common trait -- one cannot really call it a synapomorphy -- is that they are entirely covered in small (1mm or less in length), thick scales, vaguely similar to the scales of early gnathostomes. In many cases, the scales did not forms lines or patterns as in most other microsquamose (small-scaled) fish, but were arranged randomly, giving them an almost furry appearance in some reconstructions. Their body form is Protean. Take a line drawing of almost any reasonably known Paleozoic fish. Erase the internal lines. Fill in the diagram with tiny half-ellipses representing scales. Chances are that the resulting picture will resemble some known family of thelodonts. Phillipe Janvier's Tree of Life page on the Thelodonti shows some examples. Note that one looks generally like a deep-bodied gnathostome, another like a **galeaspid**, yet another (***Lanarkia***, the one on the left), like nothing in particular.

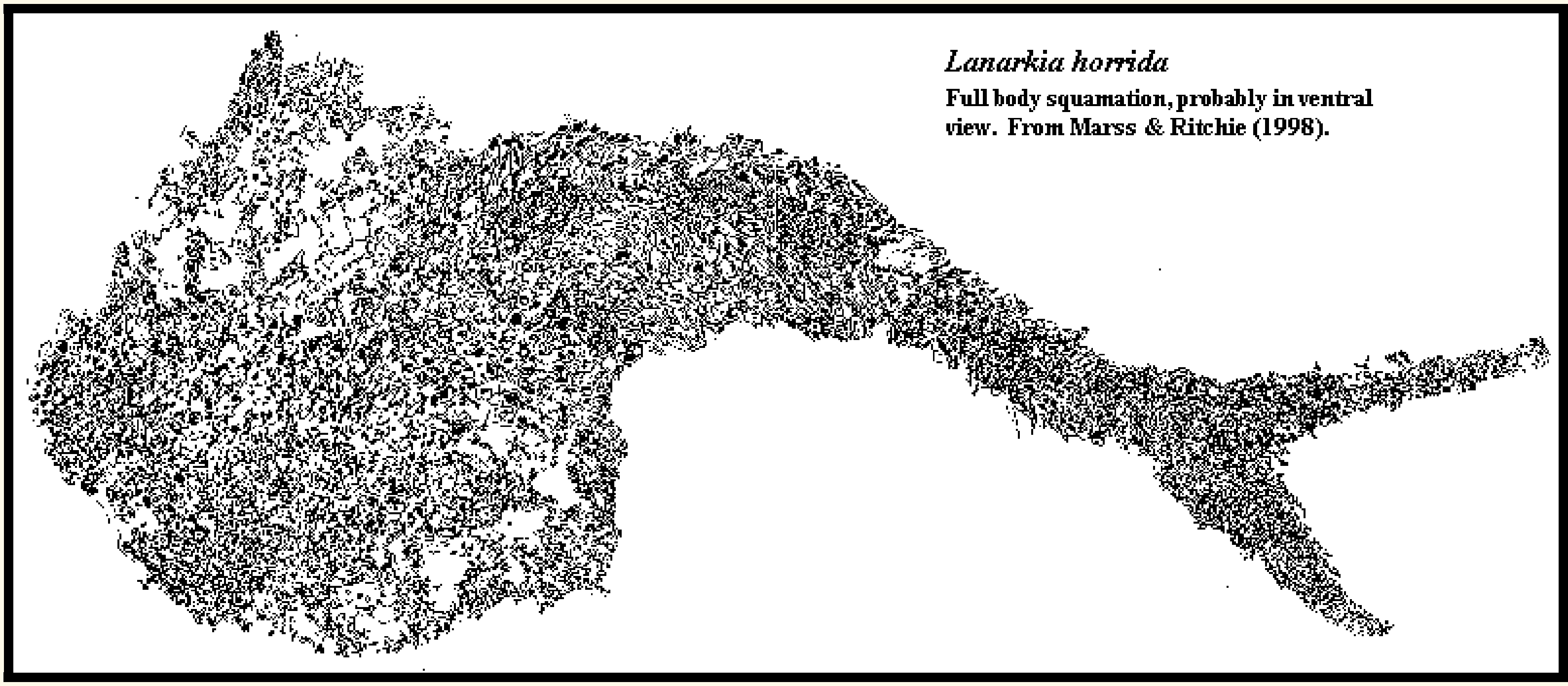
So, why have we chosen this riff-raff as the namesake of a large clade of vertebrates? Like conodonts, the thelodonts were generally ignored in polite society for many years. *Unlike* conodonts, we have not benefited from any sudden enlightenment about their true nature as vertebrates. However, for more than a decade, researchers have suggested that the group may be paraphyletic. This now seems like a sensible working assumption. It is not entirely sensible to assume that their resemblance to all the other jawless fishes is merely coincidental. Based largely on Wilson & Caldwell (1998) and Donoghue et al. (2000), we have taken the plunge here and treated Thelodonti as a huge clade uniting the classical thelodonts with all other recognizably fishy vertebrates other than pteraspidomorphs. For our purposes, we define the Thelodonti, tentatively, as the stem group consisting of all vertebrates having a more recent common ancestor with *Salmo* than with *Psammolepis*.

Previously, "Myopterygia" had an almost equivalent spot on the cladogram. However, Myopterygia was defined by Janvier in terms of physical characters, rather than ancestry, which is risky. In fact, the taxon has more recently been disowned by its creator. We, too, have come to the reluctant conclusion that paired lateral fins, the most obvious synapomorphy of Myopterygia, are not at all unique and have been independently derived in at *least* three taxa, if they are not a plesiomorphic feature of Craniata. Some of the reasons for this conclusion are discussed in connection with ***Ateleaspis*** and in our introduction to the Vertebrates.

As awkward as this arrangement may seem, our arrangement permits the monophyly of the headshield forms, for whom we have recycled the name Cephalaspidomorphi -- galeaspids, **pituriaspids** and **osteostracans**. It also allows ***Loganellia***, a conventional thelodont, to lie closer to the gnathostomes than any of the cephalaspidomorphs. At the same time, other thelodonts resemble heterostracans in, for example, the structure of the tail. It would not be surprising to learn, in another few years, that there are "thelodont" pteraspidomorphs as well, and that what we are calling "Thelodonti" today should be redefined to include all vertebrates other than conodonts, anaspids and hagfishes.

Caveat:

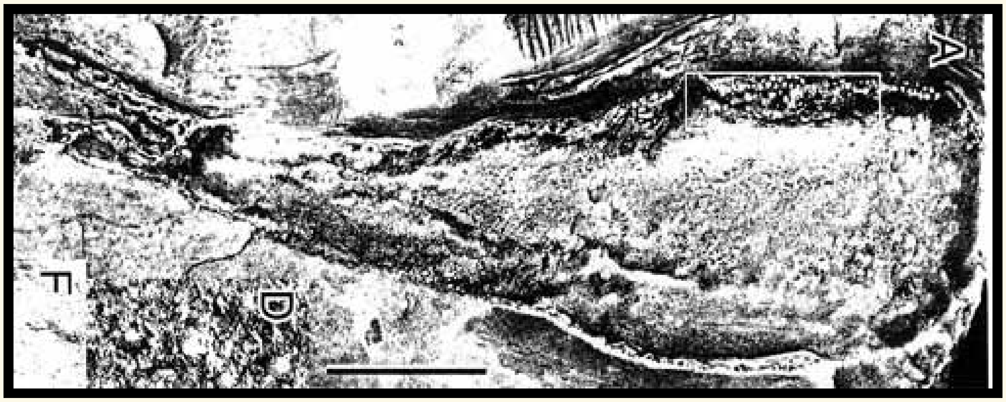
However, we add an important caveat. While it may be didactically useful and instructive to adopt the specific phylogeny described in this section, this phylogeny has no more scientific validity than one of those Victorian portrayals of the *Scala Naturae*: with nasty, brutish labyrinthodonts at the shadowed base, looking up with resentful loathing at the craggy features of some bearded European academician standing in the noble light of Pure Reason at the very apex of Creation. In fact, all "thelodont" groups -- including the one with craggy labyrinthodonts and nasty academicians -- are vertebrates *incertae sedis*. At the present time, there are no reliable phylogenies. The arrangement in this Section is simply one -- not even the most likely one -- of many possible arrangements; and there are no immediate prospects for a closer approach to the True Tree. In fact, one of our secret agents, inserted deep within the thelodont research community, informs us that we are possibly even headed in reverse. That is, the main pillars on which thelodont taxonomy has been constructed (chiefly scale histology) are in the process of being *de*constructed, leading us yet further into squalid ignorance, if that's possible. Some of the first moves in this game are in some of the materials below. ATW030621.


Lanarkia horrida

Full body squamation, probably in ventral view. From Marss & Ritchie (1998).

The Origin of the Thelodonts

Few scientists are courageous enough to speculate in public about the origin of thelodonts. The first undoubted thelodont scales come from early in the Late Ordovician, the Sandbian Age. However, few would be surprised to find an Early Ordovician, or even Furongian, thelodont. These oldest known Ordovician scales are notably simpler in morphology and ornamentation than the scales found in Silurian or Devonian strata [S+96] [S+01]. However, other Ordovician thelodonts, only slightly younger, look much more like "normal" thelodonts, except for an unusually thick base of bone [So+01]. The oldest known scales resembling scales from gnathostomes are essentially contemporaneous with these earliest thelodont remains. So, all things considered, stratigraphy doesn't help much in sorting out thelodont origins and relationships.



One suspects that thelodonts may have been, originally, extremely basic creatures. Take even a simple craniate, on the order of *Pikaia* perhaps, begin adding a few scales, and it begins to look like a basic thelodont. That isn't quite fair, since all known whole-body thelodonts are roughly fish-shaped at least. However, *Archipelepis*, probably the earliest thelodont known from a whole body fossil [S+01], has only eyes, possibly a line of primitive gill orifices, a very simple caudal fin and no other identifiable features.

References: (Sansom *et al* 1996) [S+96], (Sansom *et al* 2001) [S+01], Soehn *et al*. (2001) [So+01].

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Thelodonti

Nikoliviids and Furcacaudiforms

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--+--Nikoliviidae
      |  |  `--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

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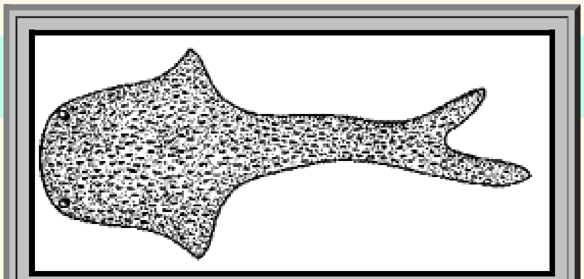
Taxa on This Page

1. Furcacaudiformes X
2. Nikoliviidae X
3. Thelodonti

The Classical Thelodonts



We treat the **Thelodonti** as a very large clade including osteostracans, gealeaspids, gnathostomes, and other forms, as well as the classical thelodonts. We do not mean in the process to forget the traditional thelodonts -- small, jawless fish with thelodont scales.

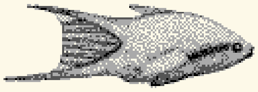
***Lanarkia*: a thelodont, showing the flattened, unarmoured body typical of this group. Graphic from Faktaside om fossile urfisk fra Norge, © 1998 Paleontologisk museum - University of Oslo.**

These "classical" thelodonts differ from the Cephalaspidomorphi (*i.e.* the armored jawless fishes) chiefly in lacking armour plates. Their bodies were covered entirely in tiny placoid-like scales. The scales of thelodonts are small (usually 0.5-1.5 mm) and robust, unlike the large flat scales of anaspids. Thelodont scales are conspicuous in having a dentine-covered crown, sometimes elaborately ornamented, and a bony base with a large central pulp cavity. The base has historically been regarded as "growing," because of the presence of *Sharpey's fibers*. The scales vary in form and size from the orbit, head, gill-covers, fins and trunk areas. Long (1993).

The thelodont fishes range in time from the Middle Ordovician - to the Frasnian Age of the Late Devonian. These scales frequently occur as microfossils and are widespread in the Late Silurian and Early Devonian, known from all the biogeographic provinces, although by the Middle and Late Devonian they appear to have become restricted to Gondwana (Australia, Antarctica, Iran). The only known Late Devonian (Frasnian) thelodonts come from Western Australia They are an important group biostratigraphically, known principally from isolated scales, especially during the Early and Middle Devonian. Thelodont scales have been found in facies from all environments - marine, marginal marine and continental (fresh-water).

It used to be believed that thelodonts were a distinct group or clade of Pteraspidomorphs, related to the Heterostraci but distinguished by their lack of head shields and other features. Many workers now believe that they are an artificial group representing several different lineages that had lost or -- perhaps more likely -- failed to develop, armour. This is still a somewhat controversial point. However, as Janvier & Blieck (1993) note:

> There is no clear evidence of the monophyly of the thelodonts, as such a micromeric exoskeleton is just what can be expected in primitive, generalized vertebrates. Only the peculiar 'handle' which prolongs anteriorly the scale base in most thelodonts may possibly be considered as a synapomorphy (unique feature). Thelodont scales display a wide range of diversity in morphology and histology, and their shapes vary within the individual animal. Their histologic structure varies from orthodentine (*Turinia*, ***Thelodus***) to mesodentine (*Phlebolepis*), but their base is always made up of acellular bone (*aspidin*).



Only a few thelodonts are known from articulated specimens (*Turinia*, *Loganellia*; *Phlebolepis*), some of which allow rough reconstructions. The body shows well-developed paired lateral fins (presumably true pectoral fins), indicating good stability, dorsal and anal fins, and a heterocercal tail (the lower lobe of the tail is elongated). A typical Later Silurian genus like *Lanarkia* had a mouth located slightly ventrally (on the underside) on a flattened head, indicating possible bottom-dwelling habitats and that it fed on the seabed. A few types however, like the furcacaudiform thelodonts from the Early Devonian of Canada shown on the left, had the more typical fish-like body. Whatever their preferred environments, all thelodonts were clearly good swimmers. The cause of their downfall is not clear, but it may be that they were supplanted by the rise of true jawed fishes.

MAK. Revised ATW030621.

Scale Models

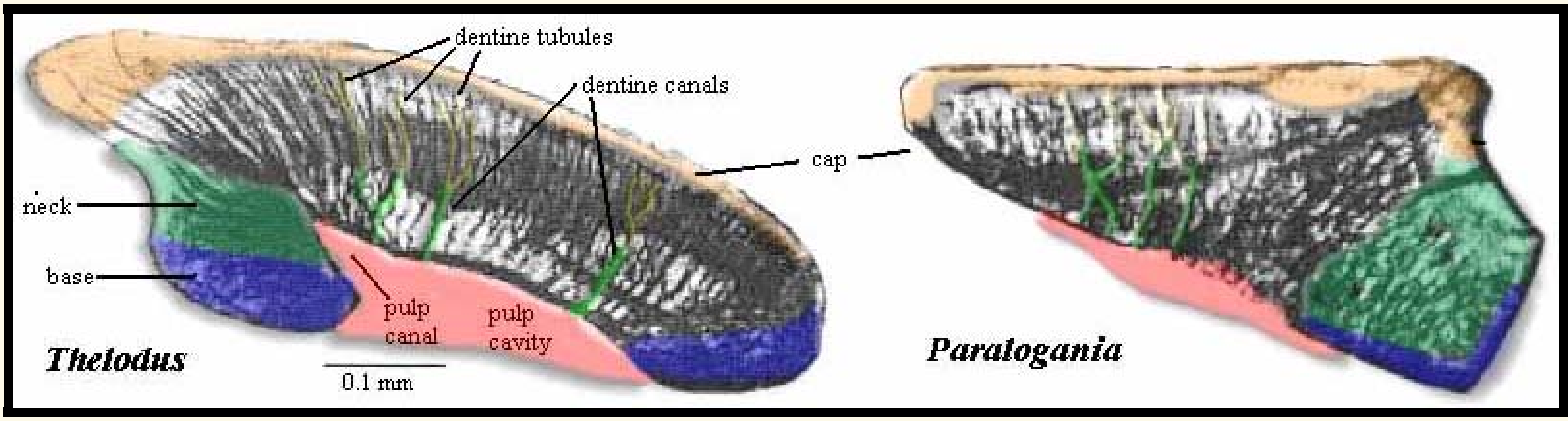
"Thelodonts are the most enigmatic of all Paleozoic jawless vertebrates, because their internal skeleton was not ossified and their exoskeleton was made up of minutes scales which were often dispersed during decay." Van der Brugghen & Janvier (1993).

Most thelodonts are **not** known from articulated specimens. We know them only from scattered scales. These can be found by the thousand in suitable Silurian and Devonian exposures; and they are the most common vertebrate microfossil in most Silurian sediments. Accordingly, thelodont scales, like conodont fossils, have attained a certain currency as stratigraphic markers for the Middle Paleozoic. But this currency is not too widely used. About two thirds of all thelodont papers published in the last decade bear the names of at least one of a tiny group of perhaps half a dozen active thelodont workers.

This combination of stratigraphic interest and a very limited pool of experts is unhealthy for the field. We intend no criticism of the practitioners of the arcane arts of thelodontology. (If nothing else, we would not attempt to pronounce, much less sully, the names of Drs. Tiiu Märss and Valentina Karatajute-Talimaa). The problem is simply one of purpose and numbers. Microfossil stratigraphy is not a phylogenetic or evolutionary study. It is a matter of correlating morphology over disparate samples. The stratigrapher is expected to recognize patterns, similarities and difference between scales from different locations, matrices, portions of the fish's body, and states of preservation. However, morphology is always in the eye of the beholder. When there are only a dozen eyes involved, no matter how experienced and objective those eyes may be, the chance that subjective or idiosyncratic factors have influenced the identification is very high. This is, if you will, an inherent diseconomy of small-scale science.

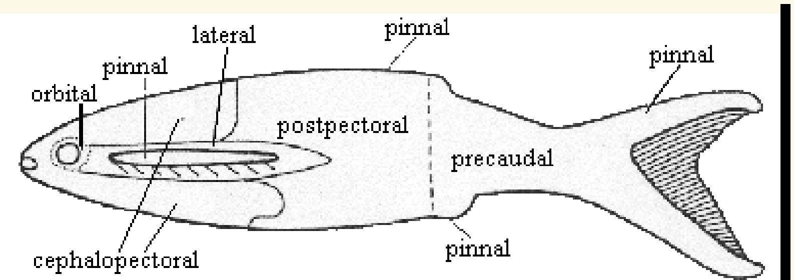
To make matters worse, the field lacks consistent terminology, even for such basic matters as the parts of the animal's body, or reliable definitions even for terms which everyone uses. How, for example does one distinguish between pulp depression, pulp cavity, and pulp canal? Can we be sure that the cap histology is orthodentine or mesodentine? What, exactly, is a "transitional scale"? There are no precise, testable definitions for these terms. Some have wondered, even aloud, whether these terms really have any meaning at all. They may describe vague regions of a continuum, or even completely subjective *gestalt* impressions. The history of vertebrate paleontology is itself littered with the bones of nomenclature which failed for one or both of those reasons.

With all that carping and kvetching said, we still have to deal with thelodont-craft as it actually is today. So we will turn to the scaled-up model of some model scales, below. These are thin sections, cut vertically, through the middle of the scale. We are looking at the scales in lateral view, with anterior to the right.



The first thing to notice is the **base**. The base is conventionally said to be aspidin, acellular bone. Frequently, it is relatively thin; but sometimes it forms a massive structure larger than the rest of the scale. This may be important, since it suggests possible close-packing of the scales in a manner similar to armored fishes. The base is frequently folded back on itself, almost enclosing the pulp cavity, so that only one (or sometimes more than one) pores connect the pulp to the rest of the universe. The *Thelodus* scale has a well-defined **pulp cavity**. This is the home of the living cells that sustained the scale. Part of the base is folded in to create a **pulp canal**. In some scales, both structures are more elaborately developed. There may be several pulp canals. In *Paralogania*, there is only a vague **pulp depression**. Note that the boundary between the pulp depression and the body of the scale is likewise ill-defined in the central region. This is one characteristic of **mesodentine** and of the **katoporid** type of scale. Some workers classify the loganiids within the Katoporida for that (and other) reasons.

Both of these scales have some recognizable **neck** region. This is not always the case. Some scales have no neck, and some have very much better-developed necks between the base and the **cap**. Within the cap, we observe tracks left by the retreating front of *odontoblasts*. The larger tracks are **dentine canals** and the arbitrarily smaller branches are **dentine tubules**. In the orderly **orthodentine** of the *Thelodus* scale, the canals rise almost at 90° to the line of the pulp cavity and branch terminally. In the **mesodentine** of *Paralogania* the odontoblasts are often trapped in spaces within the bone, the canals are wider, and they are not nearly so orderly. Thelodont papers frequently remark on whether or the dentine canals increase in diameter as they approach the pulp cavity. Finally, the cap itself is covered with a layer of dentine or, in some cases, a more hypermineralized tissue referred to as **enameloid**. The surface of the cap may be ornamented in a wide variety of ways, some of which are illustrated below.



Loganellia, with scale regions labelled according to the system of Marss. From Marss & Ritchie (1998).

As we mentioned above, thelodont scales differ significantly depending on the part of the fish from which they are derived. There are two systems in use used to describe this. The traditional system, attributed to Gross, recognizes three rough categories: head ("oral" or "rostral"), "transitional," and trunk. This is generally adequate for most work on isolated scales -- one doesn't have a fish to work with, and it may not be necessary to describe variants in much detail. However, for more exacting work, it is sometimes useful to adopt the system of Marss (1986). This system is rarely used in its full rigor; but, for example, orbital scales are a distinct type in many thelodonts, and there is a rather marked difference between anterior and more posterior scales on the head.

Before developing that point, we should mention that this does not exhaust the catalog of scale types. Others frequently mentioned in the literature include:

1. minute denticles from the *inside* of the oropharyngeal cavity;

2. denticulated plates, apparently formed by the fusion of scale bases, associated with the gill apparatus;

3. scales associated with the sensory pore system, which may contain "holes";

4. dorsal and/or ventral median scales, which are more massive, but lack the degree of specialization found in heterostracan or gnathostome ridge scales;

5. the unusual case of *Lanarkia*, which has two, intermingled populations of scales; and

6. minor dorso-ventral differences.

It may be worth mentioning that the last category is in fact very minor. It is *notoriously* difficult to tell top from bottom in thelodonts. After well over a century, and numerous redescriptions, there is no consensus on whether the famous whole-body fossil of *Turinia pagei* is up or down. *See* review by Donoghue & Smith (2001) (making compelling argument that it is belly-up). Similarly, there are perhaps a dozen good Scottish specimens of *Lanarkia*, but no one is quite sure whether the notochord continued into the lower part of the tail fin, as in most thelodonts, or into the upper lobe. Marss & Ritchie (1998).

During the course of her well-known study on the scales of *Phlebolepis*, Märss (1986) makes some interesting generalizations about scale positions, which go a long way towards imposing order on this mass of details, as well as coming close to reconciling the various systems of terminology in use at that time. The Roman numeral designations in the article have frequently been used by others, and are reproduced below:

I. Head scales, Oral scales, *Kopfschuppen*, or Головные: Usually rhombic; shallow bases bearing vertical projections; round to oval crowns with strong ridges arranged radially about the center. These are often very different from the cephalopectoral scales.

II. Cephalopectoral scales, transitional scales, *Übergangsschuppen Kopf-Rumpf*, or Переходные: larger, oval to rhomboidal scales. The base is shallow and/or protrudes anteriorly beyond crown. The crown is generally notched or ribbed anteriorly and often unornamented centrally.

The next three categories are referred to collectively as **body scales, trunk scales, *Rumpfschuppen*, or Туловищные** (= Туловищые?).

III. Postpectoral scales: often rhomboidal with central longitudinal ridge and several to many lateral ridges. The ornament often includes spines. These scales transition smoothly to precaudal scales.

IV. Precaudal scales: narrower than postpectoral scales an elongate ovoid to cuneiform. The ornament is stronger and often somewhat simplified from the more anterior body scales. There is typically a strong median ridge.

V. Pinnal scales: small, cuneiform scales with a pointed posterior end. The sculpture typically consists of a pattern of ribs and grooves covering the entire crown.

As Märss points out, there are parallels between this pattern and the squamation of living teleost fishes. The implication is interesting. Thelodonts would have had little need for this kind of hydrodynamic refinement unless they swam often enough to benefit from the gain in efficiency, and fast enough to generate the turbulent flows on which the efficiency gain depends. But, unlike modern fishes, most thelodont squamation, especially in the cephalopectoral region, was not *imbricating*. That is, the scales did not overlap so as to create a continuous surface. Thus, if thelodonts were *nektonic*, we might expect to see more dorsoventral asymmetry, since each scale could operate as a tiny hydrofoil, helping to provide lift. ATW030622

Thelodonti: *Salmo* > *Psammolepis*. Obviously, our home-made definition.

Range: From the Late Ordovician.

Phylogeny: Vertebrata:::: Pteraspidomorphi + *: ((Nikoliviidae + Furcacaudiformes) + Thelodontida) + ((Katoporida + Cephalaspidomorphi) + (Loganiidae + Gnathostomata)).

Characters: **[1]** Small (10-20 cm); usually (except furcacaudiforms, probably *Shielia*, and perhaps others) dorsoventrally compressed [DS01] **[4]**; blunt rostrum [DS01]; mouth terminal [DS01]; probably no prenasal sinus distinct from nasopharyngeal cavity (possible **$**) [DS01]; orbits anterolateral [DS01]; orbits small [WC93]; primitively multiple gill openings; homocercal or hypocercal caudal fin [DS01]; many with paired pectoral fins without fin rays (which may or may not be homologous with gnathostome pectoral fins) [DS01**$**]; anal fin may be present [DS01]; *probably* all have lateral line pores enclosed in scales [M86]; small trilaminar scales with pulp cavity; sensory lines in canals, not grooves [DS01**$**]; scale base with *Sharpey's fibers* & assumed capable of growth [T99] **[5]**; head scales usually rhombic, with shallow bases bearing vertical projections, and round to oval crowns with strong ridges arranged radially about the center [M86]; transitional scales oval to rhomboidal, with base shallow and/or protrudes anteriorly beyond crown, and with crown notched or ribbed anteriorly and often unornamented centrally [M86] **[2]**; post-pectoral body scales often rhomboidal with central longitudinal ridge and several to many lateral ridges, the ornament often including spines [M86]; smooth transition between postpectoral & precaudal scales [M86]; precaudal (trunk) scales narrower & elongate oval to wedge-shaped, bearing ornament including sharp median ridge and fewer, but more pronounced, lateral ridges [M86]; caudal & paired fins with small, narrow, *cuneiform* scales with pointed posterior apex, ornamented with high-relief ribs and grooves tending to cover the entire crown [M86]; mostly open shelf and some near-shore environments [T99].

Notes: **[1]** many of the morphological characters do not apply to the possibly unique furcacaudiforms [DS01]. **[2]** Marss [M86] notes that Cenozoic fishes also have *cycloid* scales, without spines, anteriorly, and *ctenoid* scales, with longitudinal patterns, posteriorly. **[3]** Thelodont scales are the most common vertebrate remains in the Early and Middle Silurian [T99]. **[4]** This is inferred from the fact that whole animal fossils are normally found in dorsal or ventral orientation, with the (presumably laterally compressed) tail twisted to one side. [J96]. **[5]** The association of a non-growing crown with non-growing base may be a synapomorphy [J96**$**].

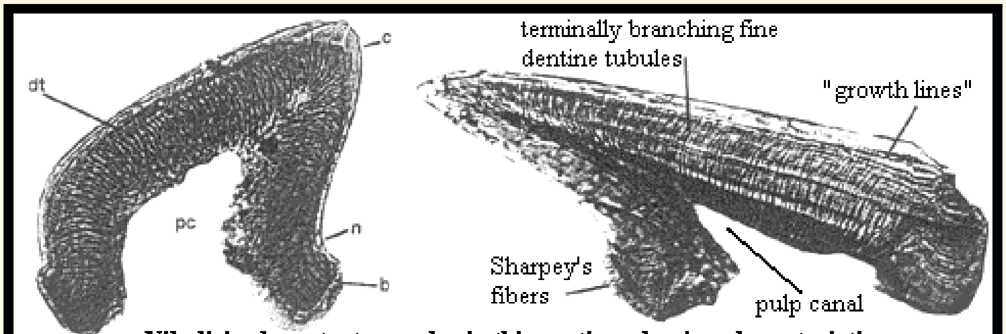
References: Donoghue & Smith (2001) [DS01]; Janvier (1996) [J96]; Marss (1986) [M86]; Turner (1999) [T99]; Wilson & Caldwell (1993) [WC93]. ATW030615.

Nikoliviidae: *Amaltheolepis, Gompsolepis, Nikolivia*

Range: Middle Silurian to Early Devonian (Lochkovian) of Arctic Canada, North America, Spitsbergen, Baltica & Russia

Phylogeny: Thelodonti::: Furcacaudiformes + *.

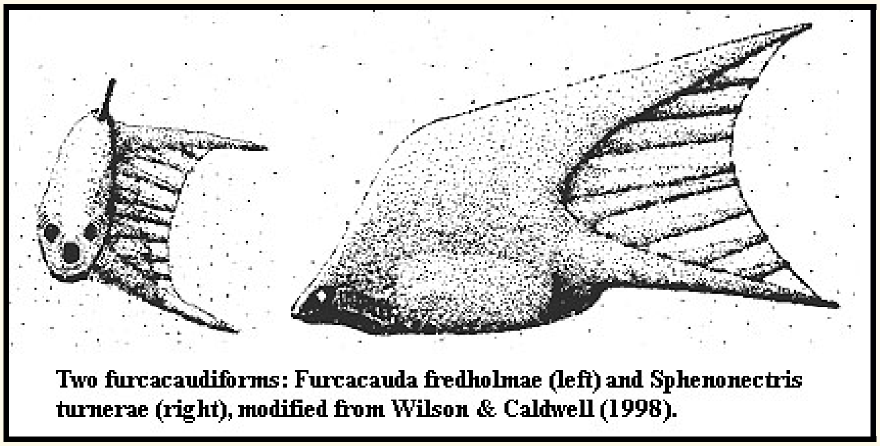
Characters: base small, low & anterior [BG02]; basal layer relatively thin [BG02]; pulp cavity large, with pulp canal [BG02]; dentine canals long & narrow [BG02]; dentine tubules branched [BG02]; crown large [BG02].



Nikolivia elongata: two scales in thin section, showing characteristic nikoliviid scale morphology and histology. From Marss (1999)

Links: Lower Devonian (Lochkovian) thelodonts from October Revolution ...; Untitled Document.

References: Blom & Goujet (2002) [BG02]; Marss (1999) [M99]. ATW060126.



Two furcacaudiforms: Furcacauda fredholmae (left) and Sphenonectris turnerae (right), modified from Wilson & Caldwell (1998).

Furcacaudiformes: *Canonia*, *Cometicercus*, *Drepanolepis*, *Furcacauda*, *Pezopallichthys*, *Sphenonectris*. The goldfish of the Paleozoic.

Range: Middle Silurian to Early Devonian of Arctic Canada [WC98] & Siberia [K02].

Phylogeny: Thelodonti::: Nikoliviidae + *.

Characters: Laterally-compressed, deep-bodied, fork-tailed forms [WC98]; mouth small and terminal [WC98]; eyes lateral and immediately anterior to branchial openings [WC98]; eyes large [WC93]; oralobranchial opening may have expanded ventrally in life [WC98]; branchial openings in a slanted, curved row [WC98]; branchial openings separated by rows of very small, composite scales joined at base, as in *Loganellia* [WC93]; hump-backed appearance [WC98]; large barrel-shaped stomach, tending to sharply rectangular appearance in endocasts [WC98]; short, straight intestine to anal notch [WC98]; caudal peduncle short and dorsoventrally deep [WC98]; caudal fin with long dorsal and ventral lobes and 8-14 intermediate lobes [WC98]; possible scaled connecting web in Devonian forms [WC93]; dorsal fin small or absent [WC98]; prominent paired lateral fins often present extending from base of gill row [WC98]; possible indications of suprabranchial paired fins or flaps in some forms [WC98]; thelodont scales usually < 400µ long, with large central pulp cavity [WC98]; orthodentine? [K02]; scales mostly of nikoliviid or loganiid type [WC93]; distinct base, neck & crown [WC98]; sensory canals probably present [WC98]; probable determinate growth [WC93]; deep water environment [WC98].

Note: [1] Some members of this group were originally described as dorsoventrally flattened forms, perhaps a thelodont version of an Osteostracan. As described and reconstructed by [WC98], the furcacaudiforms are more like thelodont goldfish. This configuration places the rather large orbits in a direct line between the gill slits and the small, terminal mouth. From a functional standpoint, this is downright weird. It also requires the brain to be oriented in a peculiar manner, and leaves no room at all for an olfactory chamber. There is also the matter of the "stomach endocasts" which have a strange, sharply rectangular appearance. However, the laterally flattened interpretation accounts nicely for the structure of the characteristic heterostracan-like tail, which would otherwise be almost impossible to explain.

Links: Untitled Document; Les nouvelles (French); The oldest stomach in the world; Furcacaudiformes; The Journal of Vertebrate Paleontology (abstract of [WC98]); Lower Devonian (Lochkovian) thelodonts from October Revolution ...; EXN.ca | Discovery.

References: Karatajute-Talimaa (2002) [K02]; Wilson & Caldwell (1993) [WC93]; Wilson & Caldwell (1998) [WC98]. ATW030225.

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Thelodonti: Thelodontida

Thelodontids & Archipelepidids

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      |     |--Thelodontidae
      |     `--+--+--Archipelepididae
      |        |  `--Turiniidae
      |        `--+--Apaloepididae
      |           `--Lanarkia
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

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2. Thelodontida X
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Practicing Scales: a Thelodont Key

One of the things we have not done enough of is to provide quick keys to remembering who's who among the vertebrates. Most of us need a few details as reminders to zero in on what we actually know about a taxon. Accordingly we have prepared the following quick reference, keyed to our rather arbitrary cladogram:

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--+--Nikoliviidae: mostly Lochkovian scale taxon; thin bases; very organized orthodentine; crowns with growth lines
      |  |   `--Furcacaudiformes: thelodont goldfish
      |  `--Thelodontida: orthodentine, large pulp cavity, distinct neck
      |     |--Thelodontidae: toroidal scale base; ornament usually simple ridges
      |     `--+--+--Archipelepididae: huge bases, closely packed scales, elaborately branching ornament
      |        |  `--Turiniidae: mostly Devonian, only major Gondwanan group; ornament with strong, converging ridges
      |        `--+--Apalolepididae: Devonian taxon with thin bases and flat, thin crowns
      |           `--Lanarkia: scales dimorphic, heterocercal tail
      `--+--+--Katoporida: mesodentine, often pulp depressions, larger scales
         |  |  |--Katoporidae:
         |  |  `--Phlebolepis: no sharp boundary between head and trunk; elaborate lateral line (pore canal) system
         |  `--Cephalaspidomorphi
         `--+--Loganiidae: flat scales with indistinct neck and pulp depression
            |  |--Loganellia: fusiform, gnathostome-like with fin rays; reversed denticles in oral area?
            |  `--Shielia: paired pelvic fins, even more fusiform, imbricating scales, trunk scales with posterior spines
            `--Gnathostomata
                 |--Placodermi
                 `--o Eugnathostomata
                    |--Chondrichthyes
                    `--Teleostomi
```

ATW030622

Thelodontida: *Boothialepis*.

Range: Middle Ordovician [SE02] to Late Devonian (Frasnian)

Phylogeny: Thelodonti:: (Nikoliviidae + Furcacaudiformes) + *. Thelodontidae + ((Archipelepididae + Turiniidae) + (Apalolepididae + *Lanarkia*)).

Characters: single pulp cavity [K02]; orthodentine [K02]; base narrower than crown [M86]; dentine tubules or canals open directly into large pulp cavity or depression [BG02]; neck usually distinct [BG02]; relatively high, mushroom-shaped, conical or foliate crown [BG02].

Note: "Thelodontida" is sometimes mistakenly used instead of Thelodonti.

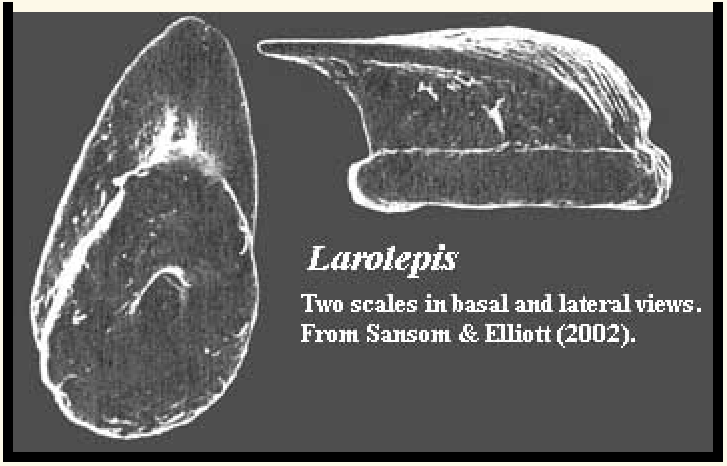
Image: *Lanarkia spinosa* from Museon, het populair-wetenschappelijk museum in Den Haag which also has a few other good images of thelodonts.

Links: Lower Devonian (Lochkovian) thelodonts from October Revolution ....

References: Blom & Goujet (2002) [BG02]; Karatajute-Talimaa (2002) [K02]; Marss (1986) [M86]; Sansom & Elliott (2002) [SE02]. ATW030615.

Thelodontidae: *Larolepis*, *Thelodus*.

Range: Middle Ordovician to Late Silurian (Pridoli) of North America, Greenland, Europe, Baltics, Russia, Siberia.

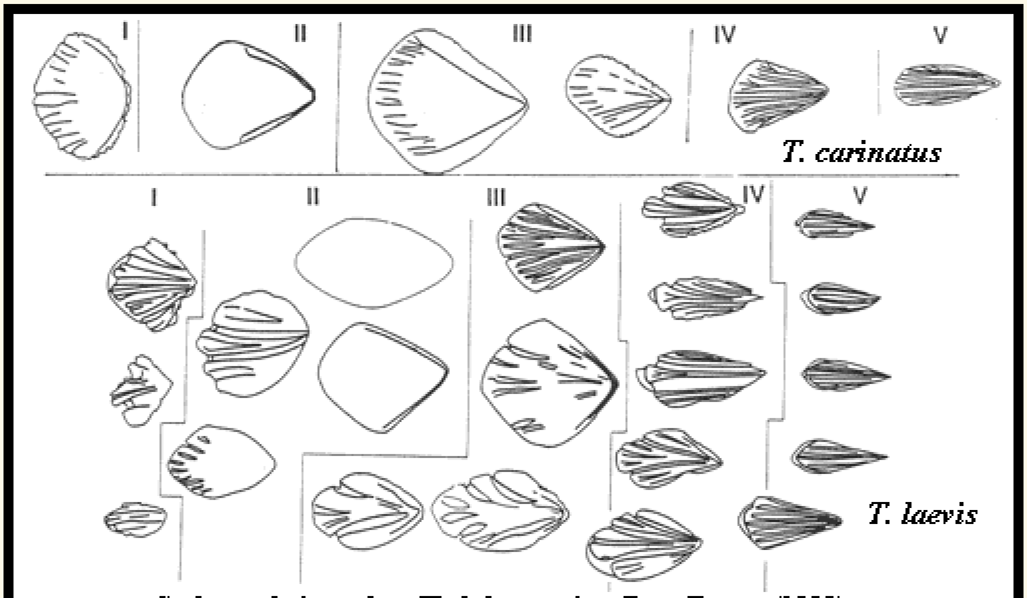

Larolepis

Two scales in basal and lateral views. From Sansom & Elliott (2002).

Phylogeny: Thelodontida: ((Archipelepididae + Turiniidae) + (Apalolepididae + *Lanarkia*)) + *.

Characters: base rounded, smooth, circular or ovate and with a distinct, ring-like (toroidal) rim [SE02]; single, central pulp opening leading to a pulp cavity [SE02]; outline of pulp cavity clear and distinct [K02]; pulp cavity expands in crown? [SE02]; dentine tubules from cavity penetrate base, neck & crown [KM02] **[2]**; dentine tubules dilated near pulp cavity [KM02]; dentine tubules longest & straightest posteriorly [KM02]; crown striated [SE02]; under surface of crown may also be striated [SE02];

Notes: [1] Sansom & Elliott [SE02] place *Larolepis* in the "Coelolepididae," which appears to us to be a garbage taxon. They give no explanation for this placement. Donoghue & Smith [DS01] have proposed to recycle this otherwise useless taxon name to mean a clade of traditional, "flat" Thelodonti (assuming there is such a clade), which seems like a sensible idea. In any case, the very few known scales of *Larolepis* look almost identical to certain scales of *Thelodus matukhini* figured by Karatajute-Talimaa & Marss [KM02: 436, fig. $20P_1$]. Accordingly, we have taken the liberty of placing *Larolepis* in this foster home until more permanent arrangements can be made. **[2]** ***See also*** image at Loganiidae for annotated image of scale histology.



Scale populations of two Thelodus species. From Turner (1999).

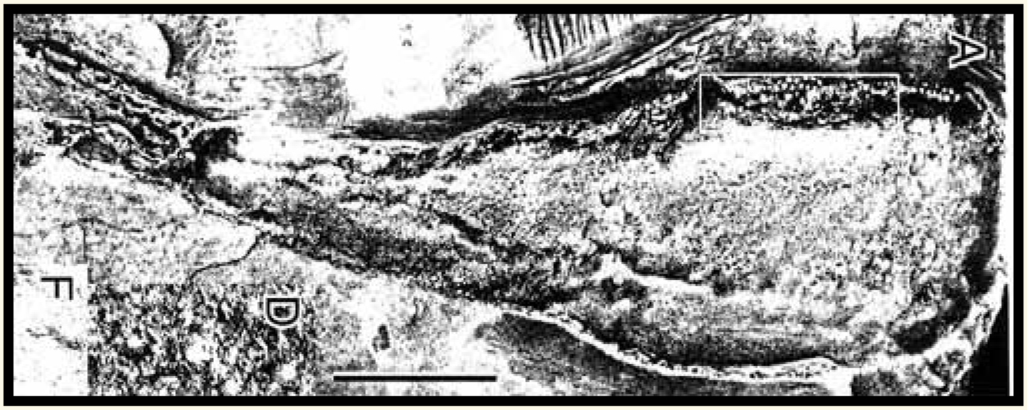
References: Donoghue & Smith (2001) [DS01]; Karatajute-Talimaa (2002) [K02]; Karatajute-Talimaa & Marss (2002) [KM02]; Sansom & Elliott (2002) [SE02]; Turner (1999) [T99]. ATW030606.

Archipelepididae: *Archipelepis*, possibly *Thelodus hoskinsi* and *Boothialepis* **[2]**.

Range: early to middle Silurian of Arctic Canada.

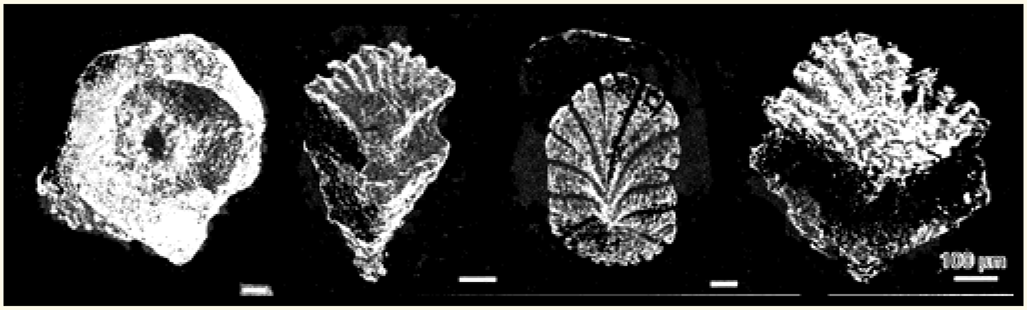
Phylogeny: Thelodontida::: Turiniidae + *.

Characters: ~6cm [S+01]; head broad and blunt [S+01]; body broad [S+01]; no dorsal or anal fins [S+01]; line of robust scales with smooth surfaces down ventral midline which extend into tail [S+01]; dorsal midline and dorsal lobe of tail probably without reinforcing scales [S+01]; tail slender and *hypochordal* [S+01]; no paired fins [S+01]; scale base massive and very (perhaps



uniquely) deep [S+01]; base cuboidal, with sharp edges [S+01]; pulp cavity very large in juvenile scales [S+01]; pulp cavity closure quite variable [S+01]; orthodentine from long, straight, narrow tubules [S+01]; anterior scales often high [S+01]; scale crown 0.15-0.5 mm, much less massive than base [S+01]; scale neck narrow & constricted [S+01]; ornament *turbinate* or stellate, with central apex strongly elevated in anterior scales [S+01]; ornament with complex ridges, bifurcating several times [S+01];

Note: **[1]** as [S+01] note, the very deep (presumably aspidin) base of these scales blurs the line between thelodont scales and heterostracan armor. The bases, being rectangular, are closely packed as in heterostracan armor; and the tubule histology resembles that of some cyathaspids. The style of ornamentation in *Archipelepis* is almost unique, but bears at least a passing resemblance to the *grebeshki* ornamentation which is common in the heterostracan lineage. (Certain Gondwanan turiniids have similar ornament, and others have head scales with ornament much closer to the heterostracan model!) This ornament motif is, however, common to all pteraspidomorphs and may be primitive for the thelodont + pteraspidomorph clade. The structure of the tail is not completely clear, but Soehn believes that it does not resemble the heterostracan model. Finally, note the somewhat corvaspid-style arched scale around the orbit. **[2]** Soehn's [S+01] attempt to distinguish *Boothialepis* Marss [M99] is not completely convincing. The two share a large base, basic style of ornamentation, large pulp cavity, and a few other characters. However, the scale neck in *Bothialepis* is indistinct, *Boothialepis* has prominent posterior protuberances which are missing or very small in *Archipelepis*, and the scale histology may be different. Soehn et al. admit that they have little information on histology, but what they have is different from the bunched tubules which are plainly present in *Boothialepis*. .



Images: *Archipelepis* holotype and detail of scales from [S+01]. Interestingly, there's a *Thelodus* scale species (*T. sculptilis*) with quite similar ornamentation from the Late Silurian of Europe, Russia & Siberia. [T99].

References: Marss (1999) [M99]; Soehn *et al.* (2001) [S+01]; Turner (1999) [T99]. ATW030607.

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checked ATW050524

Thelodonti: Thelodontida: Thelodontida (2)

Turiniids, Apalolepidids & *Lanarkia*

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      |     |--+--Archipelepididae
      |     |  `--Turiniidae
      |     `--+--Apalolepididae
      |        `--Lanarkia
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
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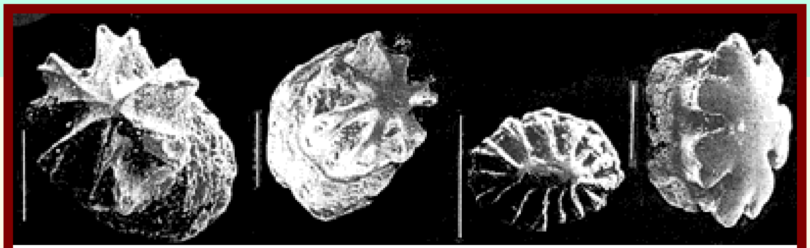
2. *Lanarkia* X
3. Turiniidae X

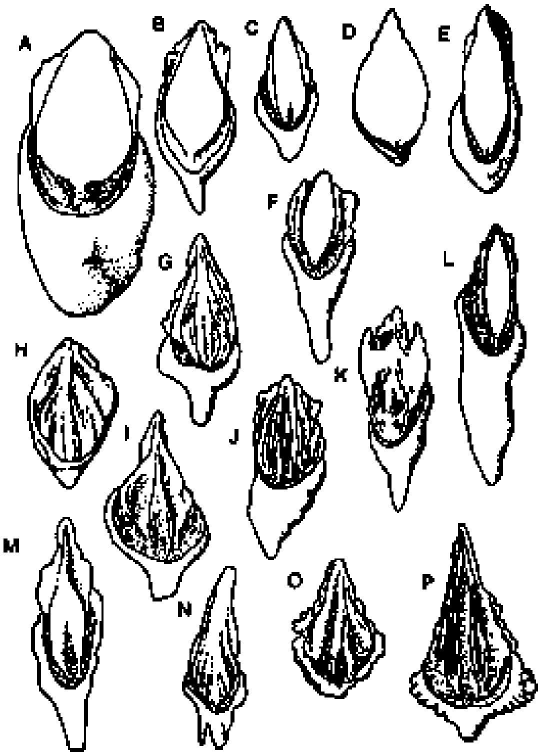


Cephalopectoral scales of Turinia australensis (Early Devonian), showing unusual diversity of form. From Turner (1977).

Turiniidae: *Australolepis*?, *Boreania*, *Turinia*

Range: Late Silurian (Pridoli) to Late Devonian (Frasnian) of Antarctica, Australia, Siberia, South America, Europe, Baltics.

Phylogeny: Thelodontida:::

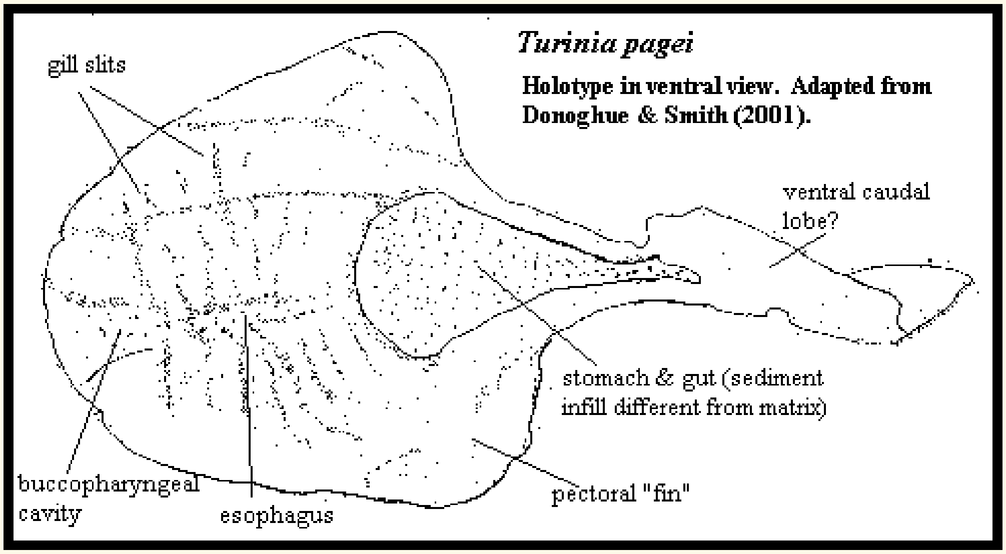


Comparison of a selection of trunk scales from some of the known turiniid populations. A-C, L, type turiniid Turinia pagei, Lochkovian to Pragian, Welsh Borderland; D-E, Turinia polita, Lochkovian, England, France, Podolia; F, Turinia fuscina, Lochkovian?, Victoria; G-H, Turinia australiensis, Emsian-Eifelian?, Western Australia, west Queensland and New South Wales; I, K, M, new turiniid species, Cravens Peak Beds, ? Late Emsian-Eifelian? Queensland; J, Turinia hutkensis, mid-Devonian or Early Frasnian?, Iran; N, Turinia? sp. nov., Late Eifelian - Givenian, Hatchery Creek Conglomerate, NSW and north Queensland; O-P, Australolepis seddoni, Early Frasnian, Western Australia. Not to scale; all turiniid thelodont scales depicted are within length range of 0.5-2.0 mm.

Archipelepididae + *.

Characters: large buccopharyngeal cavity present [DS01]; buccopharyngeal cavity probably lined with very small (~0.5 mm), tear-drop shaped scales tapering anteriorly **[4]** [DS01]; probably 8 ventral gill pairs represented by transverse lines which appear to be divided into medial, lateral and outer segments [DS01]; anteriorly "pointing" minute denticles also associated with lateral regions of lateral ridges [DS01]; cephalothorax ("head" region) terminates rather abruptly, tapering dramatically to trunk region [DS01]; dorsal scale ridge may have been present [DS01]; anal fin ? absent [DS01]; tail hypochordal [DS01]; pectoral fins or equivalent structures without fin rays [DS01]; pectoral fins with dorsal covering of larger, rhombic scales [DS01]; scales 0.2-3.5 mm [BG02]; high scales with large, high, irregular base [BG02]; base more massive than crown [S+01]; 1-2 pulp openings [BG02]; 1-3 pulp canals, often branched [BG02*]; outline of pulp cavity complex and indistinct [K02]; dentine tubules long & often highly dilated towards pulp cavity [BG02] [K02]; crown high [BG02*]; head scales round to oval with crenulated or notched crown margins and vertical lateral ribs [BG02*]; transitional scales elliptical, boat-shaped and often asymmetrical [BG02*]; trunk scales boat-shaped with lateral ridges & their projections on crown [BG02*]; stomach present (sediment infill differs from matrix) and sharply delimited from rest of trunk [DS01]; .

Notes: **[1]** one of the main thelodont families of the Early Devonian of Northern Hemisphere, where *Turinia* is very widely distributed, [BG02] and virtually the *only* Gondwanan thelodont family [T97]. The first appearance of *Turinia pagei* defines the Silurian-Devonian boundary. [BG02]. **[2]** [BG02*] relates to *Turinia*, by far the most common member of the taxon. **[3]** [BG02] note that some turiniid scales resemble nikoliviid scales in crown view, which tends to confirm our suspicion that nikoliviids are closer to thelodontids than to katoporids. **[4]** These scales, if we understand the description correctly, are oriented with the pointed end directed anteriorly for the midline scales, with more lateral scales pointing more anteromedially.



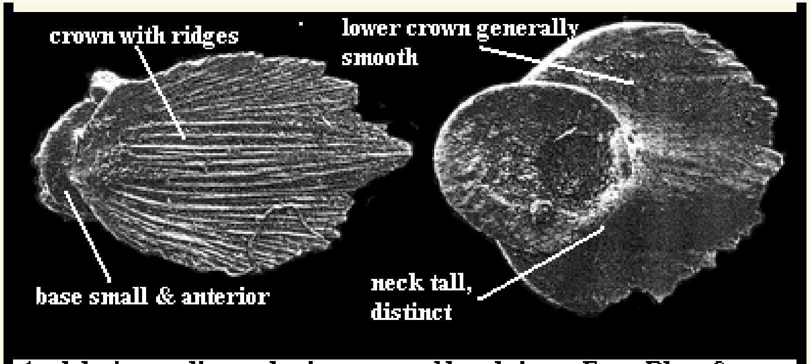
Turinia pagei

Holotype in ventral view. Adapted from Donoghue & Smith (2001).

Links: FISH 00 (**Best on the Web**); MsoDockBottom; MICROVERTEBRATE CORRELATION OF LOWER DEVONIAN STRATA, CENTRAL- ....

References: Blom & Goujet (2002) [BG02]; Soehn *et al.* (2001) [S+01]; Donoghue & Smith (2001) [DS01]; Karatajute-Talimaa (2002) [K02]; Turner (1997) [T97]. ATW030619.

Apalolepididae: *Apalolepis, Skamolepis*



Apalolepis angelica scales in crown and basal views. From Blom & Goujet (2002).

Range: Early Devonian (Lochkovian - Pragian) of Spitsbergen & The Ukraine [BG02].

Phylogeny: Thelodontida::: *Lanarkia* + *.

Characters: scales = 1.25 mm [BG02]; basal layer very thin [BG02]; base very small & anteriorly placed [J96] [BG02]; pulp cavity low & wide, with ? posterior branches [J96] [BG02]; dentine tubules sinuous, slightly irregular & dilated close to pulp cavity [BG02]; neck high & distinct [BG02]; large, usually flat, thin, foliate crown [BG02]; crown broadly expanded, orthodentine [J96]; lower crown smooth & flat or concave [BG02]; crown upper surface with ridges [BG02].

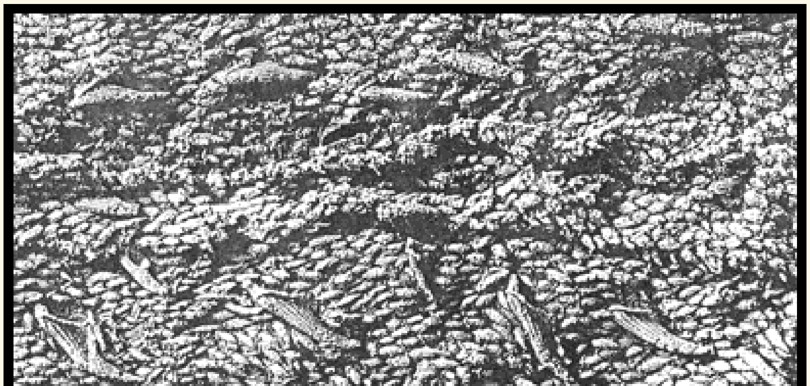
References: Blom & Goujet (2002) [BG02]; Janvier (1996) [J96]. ATW030606.

Lanarkia: Traquair 1898. *L. horrida* Traquair 1898 (= *L. spinosa* Traquair 1898 **[1]**); *L. lanceolata* Marss 1998; *L. spinulosa* Traquair 1898 (fragmentary -- could be *Shielia* per [MR98]).

Range: Early Silurian to Late Silurian (but mostly Wenlock) of Europe (Scotland & Sweden) and North America (Arctic Canada).

Phylogeny: Thelodontida::: Apalolepididae + *.

Characters: small, to 20 cm [MR98]; cephalothorax broad & dorsoventrally compressed (no specimens found in lateral view) [MR98]; mouth nearly terminal [MR98]; rostrum wide & blunt [MR98]; eyes behind anterolateral corners of head [MR98]; pectoral fins reach almost to anterior margin of head [MR98]; broadly separated eyes [J96]; probably 8 gill pairs [MR98]; gills probably ventrally, medial to fins [J96]; crescent-shaped patches of elongated scales just posterior to pectoral fins [MR98]; body narrows rapidly behind pectoral fins [MR98]; forked tail [J96]; dorsal & anal fin weakly developed, with dorsal fin inferred from presence of mid-dorsal ridge of large, conical spines [MR98]; tail slender [MR98]; notochord continues into upper caudal lobe [MR98]; caudal fin *probably heterocercal*, with upper lobe longer & stronger and ventral lobe wider & multilobate [MR98]; small, triangular lateral fins [J96]; dorsal and ventral scale patterns very similar [MR98]**[2]**; pulp cavity wide, narrowing into pulp canal [MR98]; scales spine-shaped, with some very large and aligned in longitudinal rows [J96]; scales conical, lanceolate or trilobate scales alternating with rows of larger (trumpet-shapes) scales [MR98]; most scales with striated or ridged [MR98].



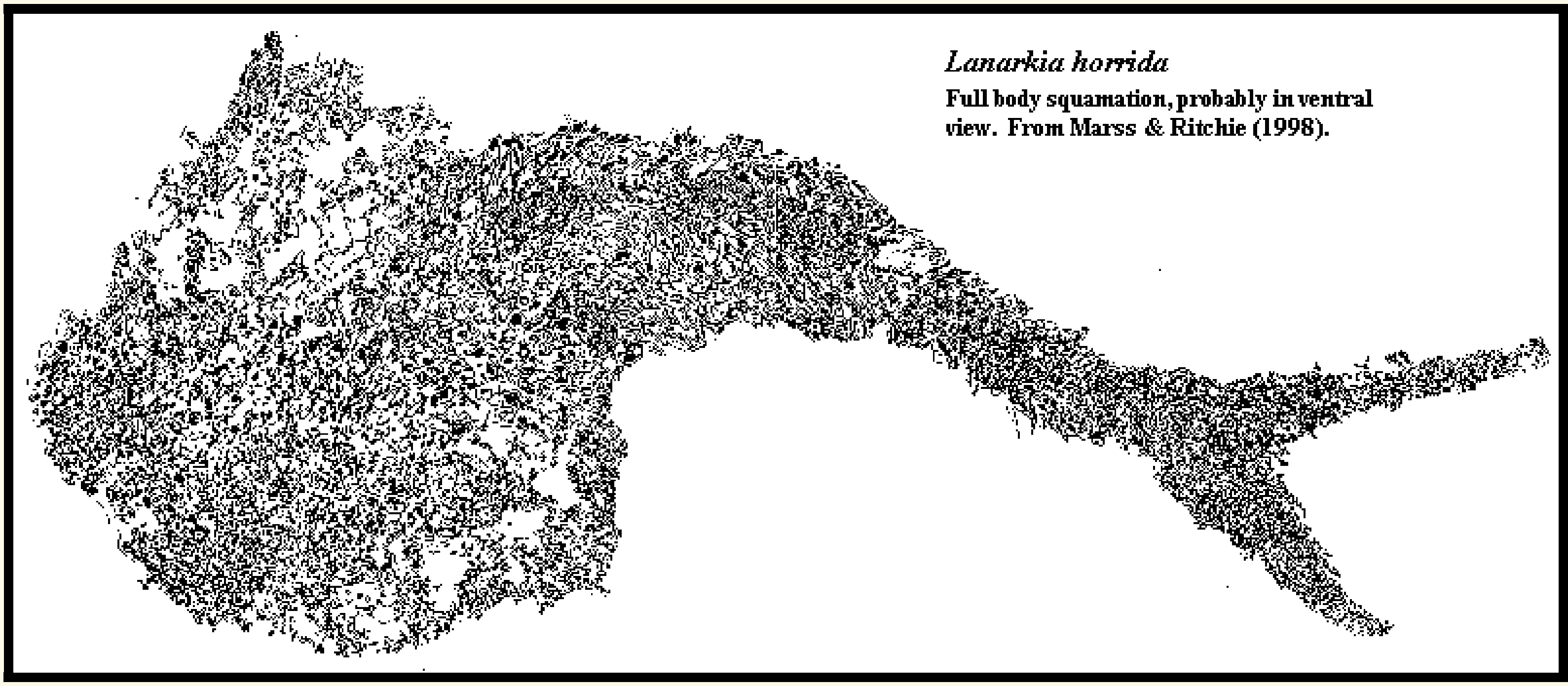
Lanarkia horrida: detail of scales near caudal peduncle, showing rows of large scales and medial scale ridge. From Marss & Ritchie (1998).

Note: **[1]** Marss & Ritchie [MR98] observe that *L. horrida* and *L. spinosa* are two different growth stages of the same species. Other articulated thelodonts sometimes show a mixture of scale sizes. However, those specimens are juvenile, and the squamation becomes more uniform with age. Only in *Lanarkia* does this characteristic routinely persist into adulthood. Interestingly, the juvenile squamation of *Lanarkia* is almost homogenous, consisting of the relatively large, upwardly-directed conical scales with "trumpet-like bases." **[2]** the large scales on the dorsal side are more likely to be nearly vertical and unstriated. The ventral side has fewer large scales with smooth surfaces and may exhibit alternation of denticulated patches with normal scales over the branchial area.

Image: color image of fossil from **PALAEOZOIC FOSSILS UK**.

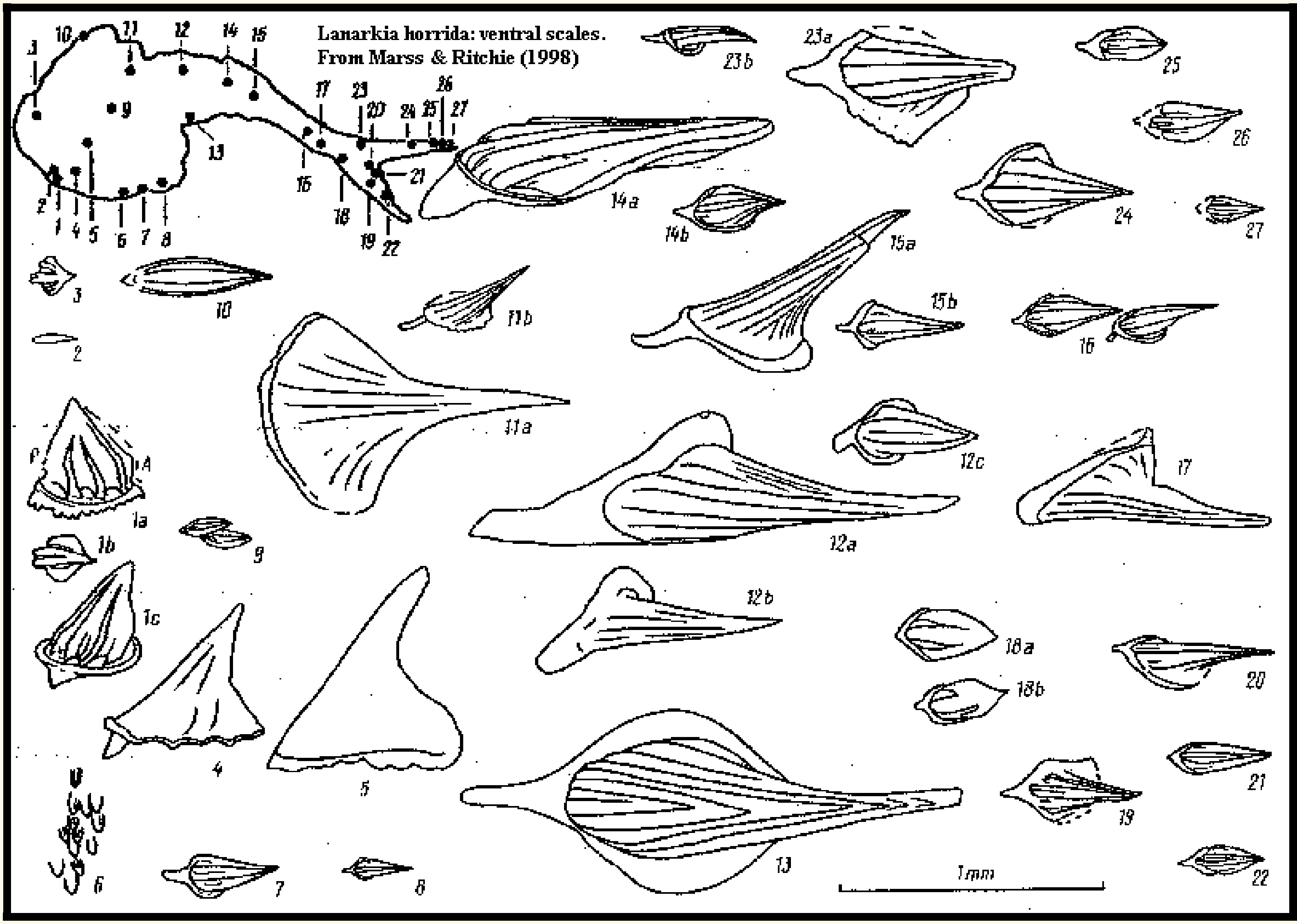
Links: New Page 1.

References: Janvier (1996) [J96]; Marss & Ritchie (1998) [MR98]. ATW030620.



Lanarkia horrida

Full body squamation, probably in ventral view. From Marss & Ritchie (1998).



Lanarkia horrida: ventral scales. From Marss & Ritchie (1998)

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checked ATW050524

Thelodonti: Katoporida

Katoporids & *Phlebolepis*

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  |  |--Phlebolepis
         |  |  `--Katoporidae
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

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1. Katoporida X
2. Katoporidae X
3. *Phlebolepis* X

Katoporida: (= Phlebolepidida = Phlebolepidiformes [S+01]). *Goniporus*, *Sandiva*, *Valyalepis*, *Zuegelepis*.

Range: Late Ordovician to Early Devonian.

Phylogeny: Thelodonti::: Cephalaspidomorphi + *: Katoporidae + *Phlebolepis*.

Characters: anal fin present [DS01]; mesodentine in scales; relatively large scales [S+01]; base wider then crown

[M86]; base with spur-like anterior projection [M86]; single, large, slightly concave pulp cavity and/or 1+ pulp canals present [S+01] [T+99]; dentine canals open into pulp cavity/canal [T+99]; numerous wide, branching dentine canals in crown [S+01]; most with crenulated head scales and grebeshki ornament on transitional scales [S+01]; trunk scales with longitudinal ridges which may be extended as spines [S+01]; lower crown surface ornamented only in *Overia* [S+01];

Links: Thelodonti

References: Blom & Goujet (2002) [BG02]; Donoghue & Smith (2001) [DS01]; Marss (1986) [M86]; Soehn *et al*. (2001) [S+01]; Turner *et al.* (1999) [T+99]. ATW030607.

Katoporidae: *Helenolepis, Katoporodus, Katoporus, Overia*

Range: Late Silurian (Pridoli)of Tuva, North America (Arctic Canada), Europe (incl. Wales), Greenland, Baltics, Russia. Probably extends to earliest Devonian (Lochkovian).

Phylogeny: Katoporida: *Phlebolepis* + *.

Characters:

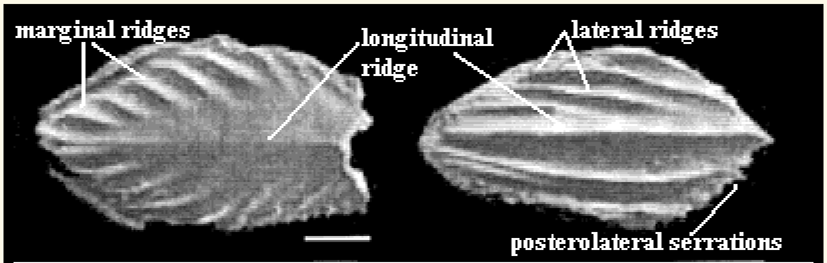
References: ATW051030 (no new information).

Phlebolepis: *P. elegans* Pander, 1856 (= *Coelolepis luhai* Hoppe, 1934); *P. ornata* Marss, 1986.

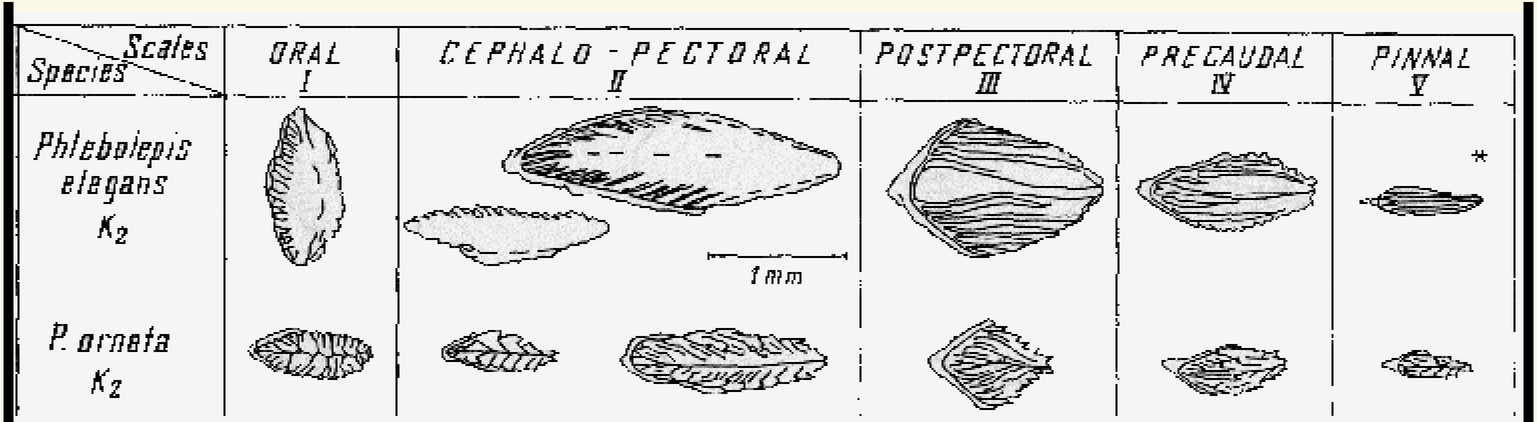
Range: Early Silurian (Llandovery) to Late Silurian (Ludlow?) of North America, Europe, Baltics, Russia & Siberia.

Phylogeny: Katoporida: Katoporidae + *.

Characters: small (<10cm) [T+99]; mouth subterminal and slit-like [M86]; rostrum blunt, with slightly rounded corners [M86]; head region somewhat dorsoventrally compressed [M86]; eyes lateral, immediately rostrum [M86]; two long, curved orbital scales flank eyes [M86] [J96] [T+99]; no visible boundary between head & trunk [M86]; trunk and tail laterally compressed [M86]; small dorsal & anal fins present [M86] [T+99]; caudal fin hypocercal [M86][T+99]; unpaired fins similar to *Loganellia* [J96]; paired pectoral fins present [M86] [T+99]; pore-canal system with various lines & commisures, possibly like cyathaspids [J96] [T+99]; sensory lines present on both dorsal & ventral sides, extending to tail [J96]; scales relatively large (to 2.4 mm) [M86] [T+99]; unusually large number of scale forms on single organism, with transition through intermediate forms [T+99]; scales arranged in longitudinal & diagonal rows [M86]; scales frequently with "extreme thinning" [T+99]; base minimal [T+99] or toroidal, separated from crown by groove [M86] [T+99]; dentine canals/tubules arranged in rows where ornament is ridged [M86] [T+99]; pulp cavity very large [J96], with one pulp canal (except in oral scales) [T+99]; pulp depression widely open [M86] [KM02]; typically, posterior wall of base "closed over to form" pulp canal [T+99]; one (& *only* one) short pulp canal present except in head scales [M86]; dentine canals & tubules penetrate crown [T+99]; crown rhombic or rounded [T+99]; posterior scale edges notched [M86]; head scales rhomboid, oval or rounded with prominent sculpturing [M86] [T+99]; head scales (*P. elegans*) wide & short with transverse angular ridge [M86] [KM02] or (*P. ornata*) long, with zig-zag longitudinal ridge [M86]; head scales with marginal notches [M86]; head scales with short ridges running posteromedially from the margin of the scale [M86]; head & transitional scale bases with small, vertical, bead-like swellings [M86]; head



Phlebolepis transitional scale (left) and trunk scale (right). Scale bar = 0.2 mm. From Karatajute-Talimaa & Marss (2002)



Phlebolepis scale types. From Marss (1986).

with non-*imbricating* scales [T+99]; transitional scales large, elongate, ovoid & flat, with low sculpture of multiple ridges anteriorly [M86] [T+99]; transitional scales large, with crown centrally smooth or single longitudinal ridge, small ridge ornamentation toward edges, small serrations posterolaterally [KM02]; transitional scales with notched crown or short ribs anteriorly [M86]; body scales imbricating [T+99]; posterior scales may show anterior spur from base [T+99]; trunk scales small, wedge-shaped & narrow (not particularly long) with ornament of multiple ("a few" [M86]) ridges [T+99]; trunk scales crown with strong longitudinal central ridge and additional ridges, parallel or fusing with central ridge [M86] [KM02]; trunk scales often with spur-like anterior projection from base [M86]; crown distinctively flat [T+99]; fin scales small, wedge-shaped & narrow, with anterior spur-like projection from base, crown with median ridge and 1+ pairs of additional ridges [M86].

Links: Evol.Page to Print- Clado Pic. Resources (life reconstruction); PPT Slide; Lõuatud (rather unusual life reconstruction).

References: Janvier (1996) [J96]; Karatajute-Talimaa & Marss (2002) [KM02]; Marss (1986) [M86]; Turner *et al.* (1999) [T+99].

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checked ATW050524

Thelodonti: Loganiidae

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            |  |--Loganellia
            |  `--Shielia
            `--Gnathostomata (alternate placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

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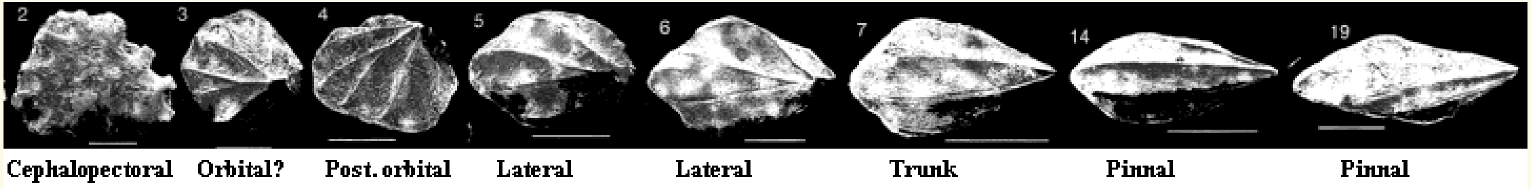
1. *Loganellia* X
2. Loganiidae X
3. *Shielia* X

Loganiids: Derivatives and Development

Despite the rapid progress of molecular biology in recent years, the field is still in its infancy. It may yet be some time before we can say much in detail about animal development on a molecular scale. However, the knowledge that much of development is governed by gradients of signal molecules is at least as old as the classic experiments of Spemann & Mangold. Since then, we have made progress in identifying some of the signals and elucidating the genetic mechanisms which make them work. Against this background, the squamation of*Loganellia* deserves another look. Consider the following series of images, rearranged from the careful work of Henning Blom (1999):



Loganellia scales arranged as an anterior to posterior transformation series. All images from Blom (1999).

This sequence includes essentially all of the scale types found associated with *Loganellia scotica*. Yet, it seems intuitively clear that they can all be explained by invoking a single transformation series or, at most, a very small number of transforming gradients. The crown apex forms, becomes sharp, and moves posteriorly. The marginal crenulation deepens into continuous ridges, meeting at the apex, then flattens out and simplifies as the apex moves progressively to a more posterior position.

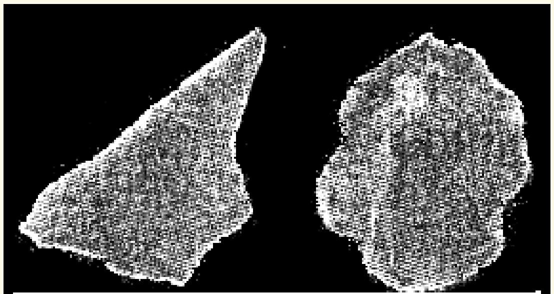
Thelodont scale work has focused on the enumeration of discrete scale types, since the stratigraphic utility of this information depends on the ability of workers to identify isolated scales. However, for, phylogenetic work, we seek to get as close as we can to the genetic processes which determine evolution. Usually, we are required to work with the remains of the morphological results of these processes, *e.g.*, the size, shape, and position of an acromion process, or the presence, articulations and ornamentation of a nasal bone. Thelodonts are poor subjects for such morphological study because they have no bones and are basically amorphous. However, they may have left us something *better*, the actual physical trace of the developmental gradients which created their form, whatever it may have been.

As we are accustomed to morphological thinking, our natural tendency is to be frustrated by the lack of consistent morphology to observe. Recall the quotation from Van der Brugghen & Janvier (1993) near the beginning of our encounter with this taxon. Scales tell us very little about the actual shape and biology of the animal, and scale morphology is notoriously labile and subject to homoplasy. However, this frustration focuses on the end result of the developmental process. The thelodonts exhibit -- not the results of the developmental equation -- but its first derivative. For phylogenetic purposes, this may actually be a better tool, as it is one step closer to actual genetic change.

If this is a workable approach, the key would be to describe thelodont squamation in terms of the developmental gradients the observed patterns presumably reflect. Is the change in scale morphology from rostrum to caudal fin continuous? How many processes is it necessary to invoke to generate the full complement of scale morphologies? Is it necessary to invoke lateral or dorsoventral patterns? Where do these patterning influences begin and end? Do they, merely by way of example, exhibit a *hox*-like influence, beginning abruptly at some anteroposterior position and trailing off posteriorly?

The morphology itself may be uninformative, but the pattern by which it changes is *a priori* likely to reflect significant phylogenetic information. This, ultimately, may be more important to reconstructing thelodont phylogeny. ATW030622.

Descriptions



Possible loganiid trunk (left) and head (right) scales from the Late Ordovician. From Sansom et al. (1996).

Loganiidae: (= Loganelliidae = Loganidae) **[1]**. *Angaralepis*, *Helenolepis* (per [T99], but others place it in Katoporida), *Paralogania*, *Sandivia*, *Stroinolepis*, *Valiukia*, *Valyalepis*.

Range: Late Ordovician (Sandbian) to Late Silurian (Pridoli) of North America, Siberia, Greenland, Europe, Baltics, Russia

Phylogeny: Thelodonti::: Gnathostomata + *: *Loganellia* + *Shielia*.

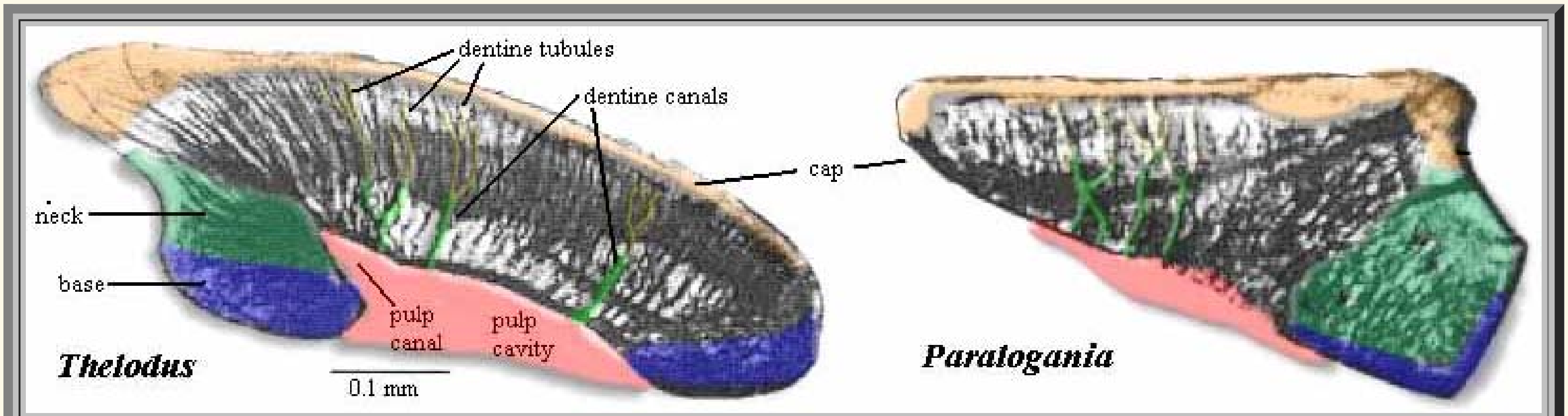
Characters: very small denticulated plates probably derived from pharyngeal cavity [S+96]; scale base large & bulging (???) [J96]; base commonly has anterior prong [J96]; broad, shallow pulp depression with multiple dentine canals emerging from it [SE02]; may lack a pulp cavity, as such, with only a broad pulp depression; wide dentine canals leading to numerous fine dentine tubules [S+96]; pulp cavity thin and may be restricted to posterior part of scale [J96]; no more than one pulp canal present [M86]; bundles of dentine tubules from cavity or cavities in the base, like mesodentine [J96]; neck short & not prominent [SE02]; head scale

Paralogania: head or transitional scale with anterior notches and posterior spine. From Karatajute-Talimaa & Marss (2002).

crown lateral margins usually crenulated and grebeshki-like [SE02]; head scales crowns usually rhomboid or oval, with anterior notches and often 1+ posterior spines [KM02]; plane of crown at a large angle to plane of base in presumed trunk scales [S+96]; trunk scales long [T+99].

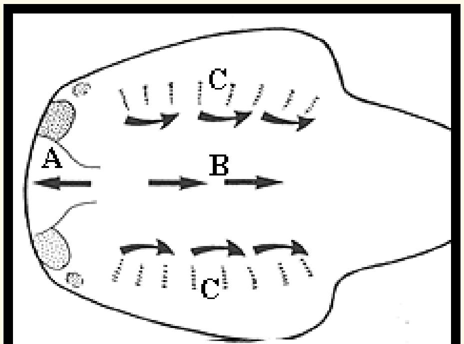
Note: [1] The type genus, *Loganellia* has had its name changed twice, as both previous names were preoccupied [MM99] [T99]. The family name "Loganellidae" is also preoccupied by some obnoxious Cambrian trilobites who refuse to leave. Karatajute Talimaa has consequently attempted to amend the family name to Loganelliidae. *See, e.g.*, [MK02]. That creates an unnecessary junior synonym and invites misspelling. "Loganiidae" is a valid and well-established name. In fact, Karatajute-Talimaa established it herself in 1978. We retain it for the present.

References: Janvier (1996) [J96]; Karatajute-Talimaa & Marss (2002) [KM02]; Marss (1986) [M86]; Marss & Karatajute-Talimaa (2002) [MK02]; Miller & Marss (1999) [MM99]; Sansom & Elliott (2002) [SE02], Sansom *et al*. (1996) [S+96]; Turner (1999) [T99]; Turner *et al.* (1999) [T+99].



Comparison of thelodontid and loganiid scales. The **thelodontid** scale is relatively small and has a rounded crown. It has a more distinct pulp cavity with a uniformly sharp border. The dentine tubules and canals are generally straight and there are relatively few spaces (trapped cell bodies) in the crown. This histology is characteristic of orthodentine. The base is slightly inflated and (although difficult to see in this view) tends to form a toroidal opening to the pulp cavity. The **loganiid** scale is larger and has a rather flat crown. The pulp cavity is barely discernable, and its margin is rough or indistinct in the central region. The dentine tubules form a messy-looking network with numerous spaces. This histology is characteristic of mesodentine. The two examples are both from Karatajute-Talimaa & Marss (2002).

Loganellia: Turner, 1991 (= *Logania* Gross, 1967 = *Loganella* Turner, 1986) *L. ("Thelodus") scotica* Traquair, 1898; *L. asiatica*; *L. cuneata*; *L. grossi* Fredholm, 1990; *L. sibirica*; *L. tuvaensis*. Other species reassigned to *Paralogania* Karatajute-Talimaa.

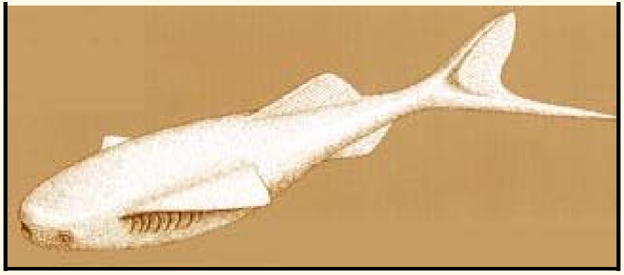


Loganellia: position & orientation of internal denticles. From Van der Bregghen & Janvier (1993)

Range: Late Ordovician to Late Silurian (Pridoli) of North America, Greenland, Europe, & Siberia

Phylogeny: Loganiidae: *Shielia* + *.

Characters: to 28 cm (30-40 cm based on isolated tails [MR98]; cephalothorax dorsoventrally flattened [MR98]; head anteriorly blunt [MR98]; mouth subterminal, appears as horizontal oval slit [MR98]; orbits lateral, just behind anterolateral corners [MR98]; orbits surrounded by 2 large crescentic scales [J96]; 7-8 branchial pouches ventral to lateral fins [J96] [MR98]; "branchial basket" gills similar to *Jamoytius* [J96] [MR98]; trunk narrows continuously behind lateral fin pair to caudal peduncle [MR98]; 1 dorsal & 1 anal fin present, both long [J96] [MR98]; caudal forked, with larger lower lobe [J96]; slightly asymmetrical hypocercal tail [MR98]; caudal fin web with radiating zones of enlarged scales similar to heterostracans [J96]; 22-25 such "fin rays" [MR98]; pectoral fins present [J96]; scales generally small [J96]; scales to 0.6 mm [MR98]; adult scales arranged in longitudinal rows, each scale slightly overlapping scale posterior to it [MR98] **[4]**; base shorter than crown, quadrangular or elongate oval [MR98]; relatively regular dentine tubules arising from weakly developed pulp canal or dentine canals [MR98]; scale neck found as furrows between base & crown [MR98]; cephalopectoral scales rounded, oval, irregular or



rhomboid, with smooth, flat or convex surface [B99]; cephalopectoral scale crowns with strong crenulation & notches arranged radially (anteriorly) or more longitudinally (posteriorly) [B99]; more posterior cephalopectoral scales with swollen (almost toroidal!) bases around central pulp aperture, and crowns with elongated notches and strong posterior spine projecting over base [B99]; orbital & anterior lateral scales round, with moderately, high, ridged conical crown, becoming lower and with crown becoming posterior spine in more posterior scales [B99]; trunk scales with base somewhat anterior (without projecting past crown) and posteriorly placed pulp cavity pore, rhomboidal crown, posterior spine and wide median furrow on a cuneiform central area and usually 2 marginal ridges, converging on the posterior crown apex [B99]; minute internal denticles in snout (A in figure) with pointed ends anterior [VJ93] **[2]**; similar internal denticles in normal orientation ("B") located centrally on head region [VJ93] [MR98]; similar internal denticles, bases fused in linear arrays ("C"), forming denticulated plates near/on gill arches [VJ93] [MR98] **[3]**.

Notes: [1] Marss (1986) notes that the cephalopectoral and postpectoral scales of *Phlebolepis* are dramatically different. Does this merely indicate a more rapid transition, or was there a qualitative difference in the development of scales in *Phlebolepis*? **[2]** Van der Brugghen & Janvier [VJ93] note the similarity with "reversed" denticles in the median dorsal duct of galeaspids. Similar structures have recently been reported by Purnell (2001b) in heterostracans. So much for their phylogenetic significance... but the implication must be that they were physiologically important. Purnell notes that these tiny reversed denticles show no signs of wear in heterostracans. For aught one call tell from the microscopic micrograph in [VJ93], the same may be true in thelodonts. **[3]** I have read over Marss & Ritchie's [MR98] description of the branchial apparatus several times but cannot make out the full sense of it. In this section these authors also state their disagreement with Van der Brugghen & Janvier [VJ93] on the reversed orientation of certain scales. However the reversed scales observed by [VJ93] are not even *in* the branchial area. The problem, at a guess, is linguistic rather than scientific. Scientists are not expected to be masters of clear English exposition; but surely *somebody* should be editing these things. **[4]** based on the difference between large & small specimens, [MR98] speculate that adults were covered with closely-packed rows of scales.

Image: Life reconstruction from **Museon:** het populair-wetenschappelijk museum in Den Haag .

Links: Click on the fossil names above or below to find out more ...; Field Trip to the Lesmahagow Inlier; BGS Education - Fish Page 1.

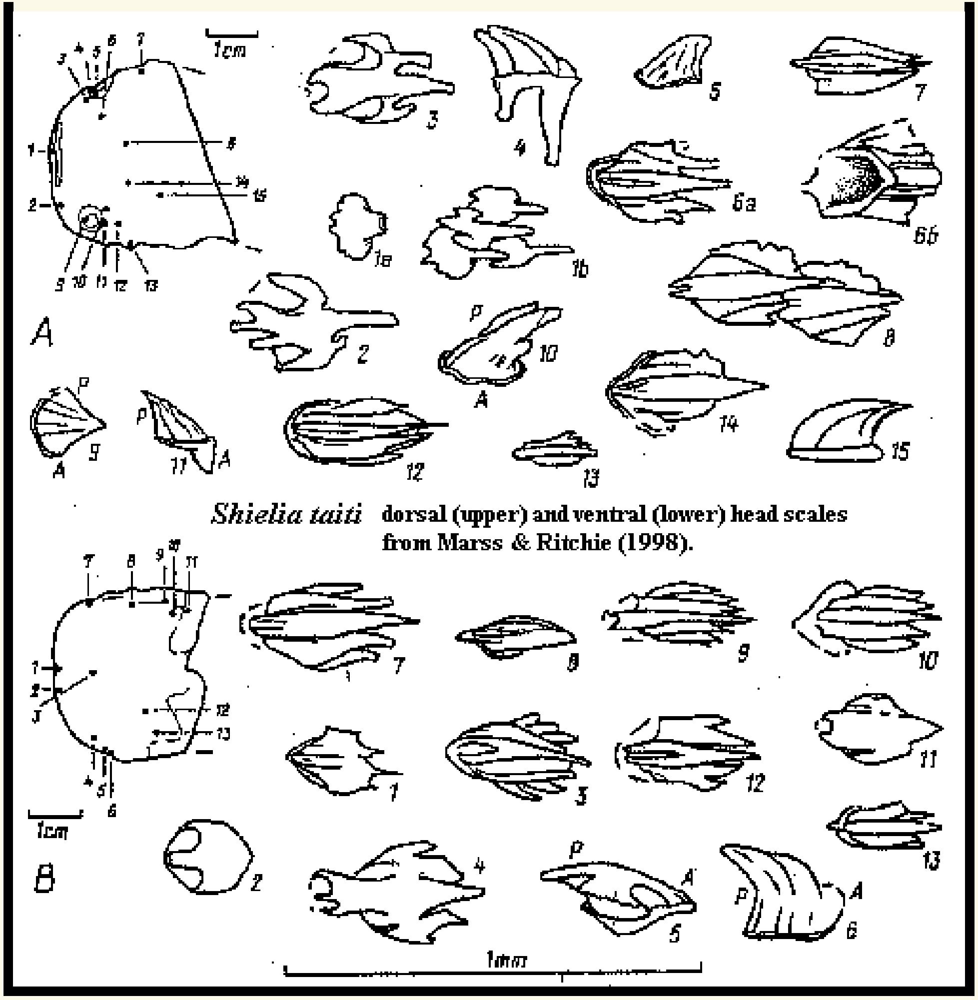
References: Blom (1999) [B99]; Janvier (1996) [J96]; Marss & Ritchie (1998) [MR98]; Turner (1999) [T99]; Van der Brugghen & Janvier (1993) [VJ93]. ATW030620.

Shielia: Marss & Ritchie, 1998; *S. ("Thelodus") taiti* Stetson, 1931 (= *Logania taiti* Gross 1967 = *Loganellia taiti* Turner 1991).

Range: Middle Silurian (Wenlock) of Europe

Phylogeny: Loganiidae: *Loganellia* + *.

Characters: to 13.3 cm [MR98]; entire body fusiform [MR98]; mouth terminal, horizontal slit [MR98]; orbits anterolateral, small, & surrounded by 4-5 rows of distinct tall scales, 3-5 rows of smooth scales with crenulated margins & 1-2 rows of conical scales [MR98]; 8 branchial apertures, located below pectoral fins [MR98]; single dorsal fin [MR98]; caudal fin slightly asymmetrical with longer, stronger ventral lobe &

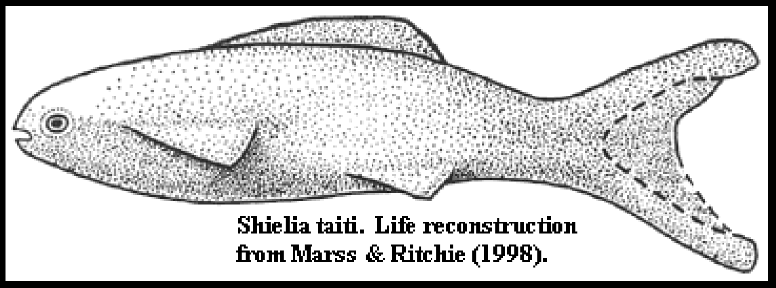


Shielia taiti dorsal (upper) and ventral (lower) head scales from Marss & Ritchie (1998).

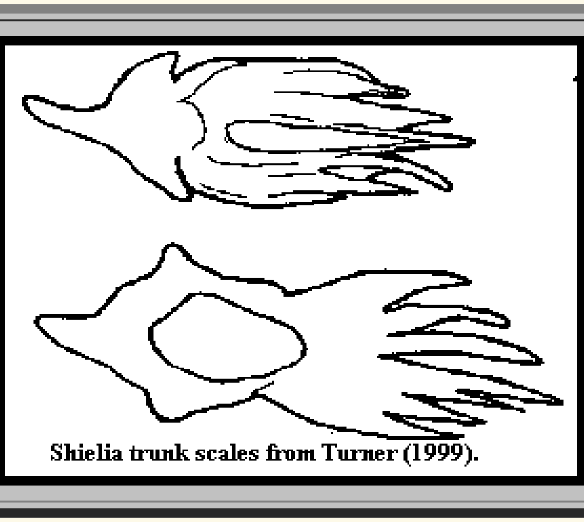
wide flexible web between lobes [MR98]; caudal fin rays absent [MR98]; flexible pectoral fins present [MR98]; paired ventral (?pelvic) fins present [MR98]; scales small (< 0.5 mm) [MR98]; scale base frequently with long anterior spur [MR98]; scale pulp cavity variable in form & size, with up to 3 pulp canals [MR98]; all pulp canals extend well into posterior part of crown [MR98]; dentine canals narrow, from pulp canal or cavity, branching terminally [MR98]; scale neck appears as shallow furrow [MR98]; variable crown forms, but strong tendency towards trilobate organization [MR98]; rostral/oral scales with flat crown projecting anteriorly over base, lateral wings, and posterior margin irregular or with 3 short spines [MR98]; more posterior cephalopectoral scales with 1-2 "wings" separated from central crown by deep furrows, becoming shallower posteriorly & laterally, ornamented by up to 5 ridges projecting over posterior end as short spines [MR98]; orbital scales high, conical & ridged [MR98]; lateral (body?) scales elongate and with fine ridges; all fins with larger & more compact (= closely spaced?) on leading edges; trailing edges of pectoral & caudal fins with very small, tripartite scales [MR98] **[1]**; trunk & pinnal scales imbricating [MR98];

Notes: **[1]** perhaps very much like the unusual tripartite scale shown under Loganiidae, above.

References: Marss & Ritchie (1998) [MR98]; Turner (1999) [T99]. ATW030616.



Shielia taiti. Life reconstruction from Marss & Ritchie (1998).



Shielia trunk scales from Turner (1999).

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checked ATW060126

Thelodonti: Dendrogram

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

Contents

(Note - links to Mikko's Phylogeny (MH) need revising; the pages exist but have been moved to different directories - MAK111024)

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti MH, Tax
      |--+--+--Nikoliviidae •X
      |  |  `--Furcacaudiformes •X MH, Tax
      |  `--Thelodontida X
      |     |--Thelodontidae •X
      |     `--+--+--Archipelepididae •X
      |        |  `--Turiniidae •X
      |        `--+--Apalolepididae •X
      |           `--Lanarkia •X
      `--+--+--Katoporida X
         |  |  |--Katoporidae •X
         |  |  `--Phlebolepis •X
         |  `--Cephalaspidomorphi X
         |     |--Galeaspida X MH
         |     `--+--Pituriaspida •X
         |        |--Osteostraci X ToL, MH
         |        `--Gnathostomata (conventional placement)
         `--+--Loganiidae X
            |  |--Loganellia •X Tax
            |  `--Shielia •X
            `--Gnathostomata (alternate placement) MH, ToL
               |--Placodermi
```

```
          `--+--Chondrichthyes
             `--Teleostomi
```

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checked ATW060126

Thelodonti: References

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     `--+--Pituriaspida
         |        |--Osteostraci
         |        `--Gnathostomata (conventional
placement)
         `--+--Loganiidae
            `--Gnathostomata (alternate
placement)
               |--Placodermi
               `--+--Chondrichthyes
                  `--Teleostomi
```

Contents

Blom, H (1999), ***Loganellia*** *(Thelodonti, Agnatha) from the Lower Silurian of North Greenland*, **Acta Geol. Polonica** 49: 97-104.
Loganellia.

Blom, H & D Goujet (2002), *Thelodont scales from the Lower Devonian Red Bay Group, Spitsbergen*, **Palaeontology** 45: 795-820.
Apalolepididae, Katoporida, Nikoliviidae, Turiniidae, Thelodontida.

*Diekwisch, TGH, BJ Berman, X Anderton, B Gurinsky, AJ Ortega, PG Satchall, M Williams, C Arumugham, X-G Luan, JE McIntosh, A Yamane, DS Carlson, J-Y Sire & CF Shuler (2002), *Membranes, minerals, and proteins of developing vertebrate enamel*. **Microscopy Res. & Tech.** 59: 373-395.
Thelodonti.

Donoghue, PCJ, PL Forey & RJ Aldridge (2000), *Conodont affinity and chordate phylogeny*. **Biol. Rev.** 75: 191-251.

Thelodonti.

Donoghue, PCJ & MP Smith (2001), *The anatomy of* ***Turinia pagei*** *(Powrie), and the phylogenetic status of Thelodonti*, **Trans. Roy. Soc. Edinburgh, Earth Sci.** 92: 15-37.
Katoporida, Thelodonti, Thelodontidae, Turiniidae

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp.
Apalolepididae, *Lanarkia*, *Loganellia*, Loganiidae, *Phlebolepis*, Thelodonti

Janvier, P & A Blieck (1993), *The Silurian-Devonian Agnathan Biostratigraphy of the Old Red Continent* **in** JA Long

(ed.), **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Johns Hopkins Univ. Press, pp.70-73.
Thelodonti.

Karatajute-Talimaa, VN (2002), *Lower Devonian (Lochkovian) Thelodonts from October Revolution Island (Severnaya Zemlya Archipelago, Russia)*, **Geodiversitas** 24: 791-804.
Furcacaudiformes, Thelodontida, Thelodontidae, Turiniidae.

Karatajute-Talimaa, VN & T Marss (2002), *Upper Silurian thelodonts from Severnaya Zemlya Archipelago (Russia)*, **Geodiversitas** 24: 405-443.
Loganiidae, *Phlebolepis*, Thelodontidae.

Long, JA (1993), *Morphological Characteristics of Paleozoic Vertebrates used in biostratigraphy*, **in** JA Long (ed.), **Palaeozoic Vertebrate Biostratigraphy and Biogeography**. Johns Hopkins Univ. Press, pp.3-24.
Thelodonti.

Marss, T (1986), *Squamation of the thelodont agnathan* ***Phlebolepis***. **J. Vert. Paleontol.** 6: 1-11.
Katoporida, Loganiidae, *Phlebolepis*, Thelodonti, Thelodontida.

Marss, T (1999), *A new Late Silurian or Early Devonian thelodont from the Boothia peninsula, Arctic Canada*, **Palaeontology** 42: 1079-1099.
Archipelepididae, Nikoliviidae.

Marss, T & VN Karatajute-Talimaa (2002), *Ordovician and Lower Silurian thelodonts from Severnaya Zemlya Archipelago (Russia)*, **Geodiversitas** 24: 381-404.
Loganiidae

Marss, T & A Ritchie (1998), *Articulated thelodonts (Agnatha) of Scotland*, **Trans. Roy. Soc. Edinburgh, Earth Sci.** 88: 143-195.
Lanarkia, *Loganellia*, *Shielia*.

Mazan, S, D Jaillard, B Baratte & P Janvier (2000), ***Otx1*** *gene-controlled morphogenesis of the horizontal semicircular canal and the origin of the gnathostome characteristics*. **Evol. & Devel.** 2: 186-193.

Miller CG & T Märss (1999), *A conodont, thelodont and acanthodian fauna from the Lower Pridoli (Silurian) of the Much Wenlock area, Shropshire*. **Palaeontology** 42: 691-714.
Loganiidae.

Novitskaya, LI (1998), *The visceral system of Paleozoic agnathans (Heterostraci, Thelodonti) and possible ways of transition to the branchial apparatus of gnathostome verte-brates*. **Paleontol. Zh.** 32: 269-277.

Sansom, IJ & DK Elliott (2002), *A thelodont from the Ordovician of Canada*, **J. Vert. Paleontol.** 22: 867-870.
Loganiidae, Thelodontida, Thelodontidae.

Sansom, IJ, MM Smith, & MP Smith (1996), *Shark and thelodont scales from the Ordovician of Colorado*, **Nature** 379: 628-630.

Sansom, IJ, MM Smith & MP Smith (2001), *The Ordovician radiation of vertebrates* **in** PE Ahlberg [ed.] **Major Events in Early Vertebrate Evolution**, Taylor & Francis, pp. 156-171.
Thelodonti.

Soehn, KL, T Marss, MW Caldwell & MVH Wilson (2001), *New and biostratigraphically useful thelodonts from the Silurian of the Mackenzie Mountains, Northwest Territories, Canada*, **J. Vert. Paleontol.** 21: 651-650.
Archipelepididae, Katoporida, Thelodonti, Turiniidae.

Turner, S (1997), *Sequence of Devonian thelodont scale assemblages in East Gondwana*, **in** G Klapper, MA Murphy & J Talent [eds.], **Paleozoic sequence Stratigraphy, biostratigraphy and biogeography: studies in honor of Dr J. Granville ("Jess") Johnson. Spec. Pap. Geol. Soc. Amer.** 321: 1-45.
Turiniidae.

Turner, S (1999), *Early Silurian to Early Devonian thelodont assemblages and their possible ecological significance*, **in** AJ Boucot & J Lawson [eds.], **Palaeocommunities, International Geological Correlation Programme 53,**

Project Ecostratigraphy, Final Report. Cambridge University Press, pp. 42-78.
Archipelepididae, *Loganellia*, Loganiidae, *Shielia*, Thelodonti, Thelodontidae.

Turner, S, JJ Kuglitsch & DL Clark (1999), *Llandoverian thelodont scales from the Burnt Bluff Group of Wisconsin and Michigan*, **J. Paleontol.** 73: 667-676.
Katoporida, Loganiidae, *Phlebolepis*.

Van der Brugghen, W & P Janvier (1993), *Denticles in thelodonts*. **Nature** 364: 107.
Loganellia.

Wilson, MVH & MW Caldwell (1993), *New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies*, **Nature** 361: 442-444.
Furcacaudiformes, Thelodonti.

Wilson, MVH & MW Caldwell (1998), *The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from Northern Canada*. **J. Vert. Paleontol.** 18: 10-29.
Furcacaudiformes, Thelodonti.

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Checked ATW060126, last modified MAK111024

Cephalaspidomorphi Overview

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           `--Gnathostomata
         |              |--Placodermi
         |              `--Acanthodii
(paraphyletic)
         |                  |--Chondrichthyes
         |                  `--Osteichthyes
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
```

Contents

Hemicyclaspis, a representative Atelaspidiforme Osteostracan, length of original 13 cm; life reconstruction © Mikhail Tikhonov, original url

The name Cephalaspidomorphi was used to include three distinct groups of jawless fish (agnatha), such as osteostracans, anaspids, and lampreys, in the 1920s (by Johan Ki�r and Stensi�) on the basis of a shared single dorsal "nostril", called a nasohypophysial opening. As late as the 1980s, Carroll divided the Class Agnatha into two subclasses, the Pteraspidomorphi or Diplorhina, with two nostrils, and the Cephalaspidomorphi, or Monorhina as they are also called, with a single nostril. Both these groups are now known to be artificial as originally defined. The thelodonts, previously included in the Pteraspidomorphi, are most likely a paraphyletic group, while both the lampreys and anaspids are far more primitive (basal in cladistic jargon) than the osteostraca. Removing those groups from the latter taxon leaves the Cephalaspidomorphi with three groups that are almost certainly closely related: these are the Cephalaspidiforms or Osteostraca proper, a group of bizarre endemic Chinese forms called Galeaspida, and the poorly known and equally bizarre Pituriaspida, from Australia (which during the mid Palaeozoic was still Gondwana). Come to think of it, even the common run of the mill osteostracans were pretty bizarre looking craetures as well, as the above illustration and others show.

The current emerging consensus is that the Cephalaspidomorphi as more recently defined is acttually the parent clade of the jawed vertebrates (gnathostomes) (Janvier2008, Sansom, 2009). At some point these creatures lost their heavy head shield exoskeleton (or not, in the case of the placoderms) and become vaguely ray-like craetures, at first retaining the bottom dwelling habits of their jawless ancestors, but soon radiating out into a diverse range of morphologies, guilds, and ecological niches.

Interestingly, thelodonts, a broad and rather amorphous assemblage that seem to include the ancestors of the cephalaspidomorphs, counted among their number certainly highly specialised forms that were amazingly fish-like in appareance. Weere these the true ancestors of gnathostomes? It wouldn't be hard to make the transition from loganiid thelodont to acanthodian; according to this hypothesis, paired fins and gnathostome-like bone evolved several times, and the placoderms would be a side group who secondarily acquired a heavy armoured bottom-dwelling lifestyle. But if the cephalaspidomorphs are the ancestors of the higher vertebrates, that means that an active, fish-like lifestyle and morphology evolved by convergence at least twice, something that is not at all unlikely, especially considering that Coleoidan cephalopods also converge with fish in many respects, and they belong to a different phylum (Packard 1972 and page)

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Unit Back | Vertebrates Home | Vertebrate Dendrograms | Vertebrate References | Glossary | Unit Next

Cephalaspidomorphi : Galeaspida

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     |     |--Polybranchiaspidiformes
         |     |     `--Huananaspidiformes
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           `--Gnathostomata
         |              |--Placodermi
         |              `--Acanthodii
(paraphyletic)
         |                  |--Chondrichthyes
         |                  `--Osteichthyes
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
```

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1. Cephalaspidomorphi X
2. Eugaleaspidiformes X
3. Galeaspida X
4. Huananaspidiformes X
5. Polybranchiaspidida X
6. Polybranchiaspidiformes X

Cephalaspidomorphi

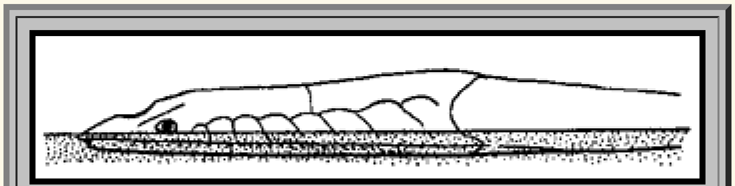
"Cephalaspidomorphi" is an old name of rather uncertain meaning. In some sources, it meant a group consisting – roughly -- of the Heterostraci and Osteostraci, the Galeaspida and Pituriaspida being largely unknown at the time. As the name implies, it included any jawless fish with a head shield. During the last decades of the XXth Century, the term fell out of use because the two groups appeared to be unrelated, and the Osteostraci were suspected to be paraphyletic, or at least the sister group of the Gnathostomata. The way things are presently moving, it seems more likely that the heterostracans will be shown to be paraphyletic. To be specific, we suspect that the Thelodonti are Heterostracomorphi, or perhaps even Heterostraci, and that both the osteostracans and gnathostomes are thelodonts.

However that may be, we now have a perfectly good, and highly descriptive name that isn't being used for anything worthwhile. We have therefore retooled it to refer to osteostracans + galeaspids, a large but otherwise nameless group of jawless fishes with head shields. ATW030604.

Galeaspida

The Galeaspida are a strange group of armored fishes possessing a massive, flattened, one-piece bony shield. The mouth was ventral. The dorsal shield was pierced by a single, large, nostril-like opening situated in the middle of the head in front of the eyes. The head shield was usually an elongate oval or a simple half-moon, but there were also bizarre (possibly nektonic?) forms with long tubular rostra ("nose spikes") and widely flaring cornual processes ("wings"). The body was covered by numerous ornamented scales. The bone structure of galeaspids shows hollow cavities within ornamental tubercles or blisters. These animals may have buried themselves in the sand or mud, with only their "blow hole" showing above the surface.

The Silurian *Hanyangaspis* is perhaps the most generalized galeaspid, having a broad and almost terminal median dorsal opening and forward placed eyes. The more derived galeaspids may be divided into the **Eugaleaspidiformes** and the Polybranchiaspidida. Most of the Polybranchiaspidida (*i.e.*, the Huananaspidiformes) have a long rostral process and slender cornual processes, which parallels the condition in the boreaspid osteostracans.


***Polybranchiaspis*, buried in the sediment, showing the median dorsal inhalant opening at the front (left) of the head, above the eyes. Illustration from Janvier (1996: 301).**

The Galeaspids were geographically limited primarily to the South China terrane (southern China and Vietnam) from the Early Silurian to the Early Devonian. A few are also found in Northern China, and even in Tibet (all of these areas were part of a single geographic region). Thelast known type is from the Late Devonian of Ningxia, northern China.

Descriptions

Cephalaspidomorphi (= Osteostracomorphi)

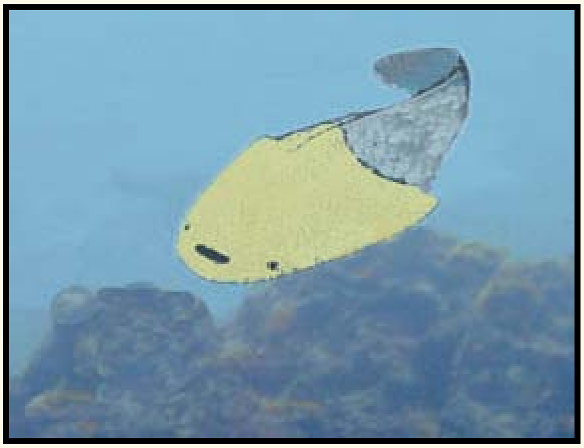
Range: Early Silurian to Late Devonian

Phylogeny: Thelodonti::: Katoporida + *: Galeaspida + (Pituriaspida + (Osteostraci + Gnathostomata))

Characters: massive endo- and exoskeletal head shield. ATW030605. Sclerotic ossicles, paired pectoral fins, a dermal skeleton with three layers (a basal layer of isopedin, a middle layer of spongy bone, and a superficial layer of dentin), and perichondral bone (Sansom, 2009, text via Wikipedia) MAK111026

Comment: Osteostraci, Pituriaspida, and Galeaspida are thought to be either the sister-group of (Benton 2004, Nelson2006), or the larger clade including (Janvier2008), gnathostomes. The term Osteostracomorphi has been suggested, but we have retained the older term Cephalaspidomorphi, albeit in a modified context. Both terms

could be used in either a Linnaean / Evolutionary systematic sense of an ancestral group of armoured jawless fish, or cladistic sense of a larger clade that includes both various armoured forms and the gnathostomes. For an alternative hypothesis of gnathostome origins, see our Thelodont pages.



Galeaspida: *Hanyangaspis*.

Range: Early Silurian to Late Devonian of South China.

Phylogeny: Cephalaspidomorphi: (Pituriaspida + Osteostraci) + *: Polybranchiaspidida + Eugaleaspidiformes.

Characters: Overall morphology similar to Osteostraci. Massive endo- & exoskeletal head shield; endoskeletal shield is solid cartilage lined with perichondral bone and some calcified cartilage; length of shield variable; mouth & gill openings ventral; ventral plates small; orbits usually small & dorsal (anterior in *Hanyangaspis*); $ large anterior median dorsal opening leading to oralobranchial cavity (inhalant duct?); 2 separate nasal olfactory tracts open into this duct; large number of gill openings (up to 45); shield cornua & rostra common (especially in Huananaspidiformes); $ main lateral line has lateral processes on shield, sometimes in scalloped pattern; 2 semicircular canals; body has minute aspidine-like scales with bulging base, usually with enameloid cap; bone acellular with no dentine; boundary between exo- and endoskeleton *is* vascularized (*subaponevrotic* vascularization); shield apparently formed by fusion of scale units & may grade into body squamation. Unlike Osteostraci, no dorsal sensory fields or associated sensory canals, no paired fins; no dorsal or anal fins. Fresh water & marine.

Links: Galeaspida; Class Galeaspida; Geol 437 jawless fishes; Galeaspida.

Image: *Bannhuanaspis* from the Early Devonian Bac Bun Formation of Vietnam, after Janvier (1996). ATW010421.

Eugaleaspidiformes: *Eugaleaspis, Sinogaleaspis, Yunnanogaleaspis*.

Range: Early Silurian to Early Devonian.

Phylogeny: Galeaspida: Polybranchiaspidida + *.

Characters: short, horseshoe-shaped headshield; slit-shaped median dorsal opening; cornual processes short; 6-8 pairs of gill openings with branchial fossae for gills (primitive number).

Links: Galeaspida

References: Janvier (1996). ATW020715.

Polybranchiaspidida:

Range: Early Devonian (to Late Devonian?)

Characters: $ >10 (up to 45) pairs of branchial fossae.

Phylogeny: Galeaspida: Eugaleaspidiformes + *: Polybranchiaspidiformes + Huananaspidiformes.

References: Janvier (1996).

Polybranchiaspidiformes: *Dongfangaspis, Duyunolepis, Polybranchiaspis*

Range: Early Devonian (to Late Devonian?)

Phylogeny: Polybranchiaspidida: Huananaspidiformes + *.

Characters: headshield oval or rounded; median dorsal opening oval or slightly bean-shaped; elaborate rostral and cornual processes absent; most have star-shaped pattern at lateral end of transverse sensory lines on headshield.

Note: [1] Likely paraphyletic stem group of Polybranchiaspidida. [2] includes largest galeaspids (~20 cm).

Links: Galeaspida;

References: Janvier (1996). ATW030404.

Huananaspidiformes: *Asiaspis, Gantarostraspis, Lungmenshanaspis, Sanchaspis, Sanqiaspis*.

Range: Early Devonian of South China.

Phylogeny: Polybranchiaspidida: Polybranchiaspidiformes + *.

Characters: Median dorsal opening may have unusual shapes; $ long, sometimes spatulate, rostra and slender cornua; numerous branchial openings. Janvier suggests some may have been nectonic based on shield shape.

References: Janvier (1996). ATW991113.

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checked ATW050524

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Cephalaspidomorphi: Osteostraci

Pituriaspids plus *Ateleaspis*, *Hirella* and *Hemicyclaspis*

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      |--+--Furcacaudiformes
      |  `--Thelodontida
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--+--Hirella
         |           |     `--+--Hemicyclaspis
         |           |        `--Cornuata
         |           `--Gnathostomata
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
```

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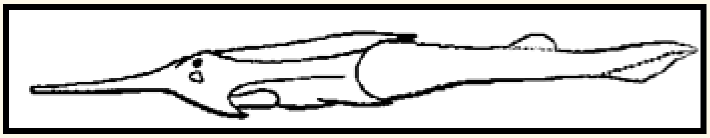
2. *Hemicyclaspis* X
3. *Hirella* X
4. Osteostraci X
5. Pituriaspida X

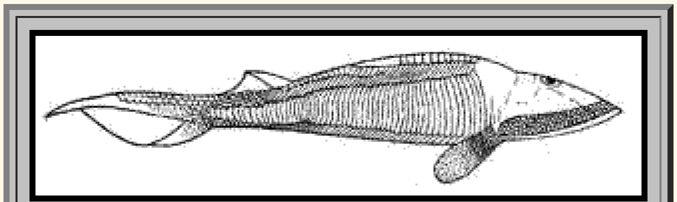
Pituriaspida



Pituriaspida was erected in 1991 based on armours of two genera (*Pituraspis* and *Neeyambaspis*) of rostrate (nose spiked) jawless fishes known as yet from a single locality of sandstones in central Australia (Georgina Basin, Western Queensland). *Pituraspis* (illustrated here) has an elongate headshield (with an area of attachment for paired fins, as in the Osteostraci), *Neeyambaspis* a short triangular one. The exoskeleton is ornamented with tiny rounded tubercles. The outline of the rest of the body shown here is pure fancy. Almost nothing is known of the rest of the body, apart from the headshield, and even that is poorly preserved. These creatures are very tentatively placed close to the Osteostraci on the phylogenetic tree. MAK001204.

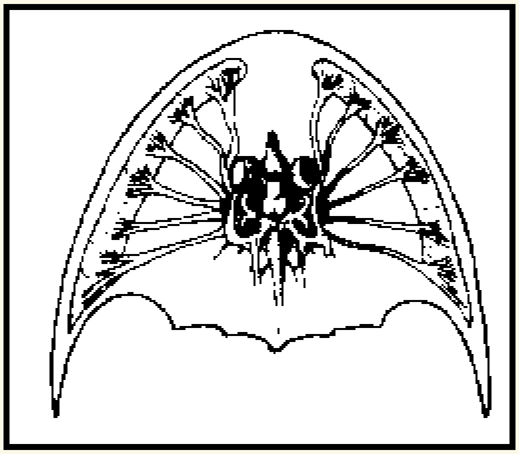
The Osteostraci

The Osteostraci (also called the cephalaspids, meaning 'head shields') are an important group of Silurian and Devonian fishes from the Euramerican province. They were flattened bottom-dwellers (triangular in cross-section) that sucked up food particles from the seabed through a rounded mouth on the underside of the head. Despite their bottom-dwelling habits, they were good swimmers. Unlike many other jawless fishes, some osteostracans possessed paired pectoral (front) fins, a dorsal fin on the back near the tail, and a strong epicercal (upturned) tail. The enlarged upper lobe of the tail produced lift at the rear of the body, keeping the animal's head down while it sucked up food from the seabed. These were possibly active animals and good swimmers, despite their heavy armour.



***Hemicyclaspis*: Pridoli (Latest Silurian), south-east Euramerica (England). Length 13 cm.**

The large and usually horseshoe-shaped head shield (cephalic shield) was made of a single plate of undivided bone. There are many variations in the shape of the cephalic shield, from simple, semi-circular elongate oval shaped forms. In most forms the corners of the head shield were drawn out into keel-like cutwaters, the backwards protruding cornuta or "horns", e.g. *Cephalaspis*, Others forms, like *Boreaspis*, have an anterior rostrum ("nose" spike).



Since the head-shield was made of one piece of bone, it is unlikely that the shield grew during the animal's adult life, unlike the individual bony head plates of the heterostracans. It is thought that osteostracans had an unarmored larva, and that the bony shield developed only when the creature was full-grown.

Another unique characteristic of this group is presence of concentrated patches ("fields") of sensory organs developed on both sides, and on top, of the head shield (referred to as the lateral (front) and median or dorsal (behind the eyes) fields). These are depressions covered with dermal platelets and connected by canals to the otic capsule. These organs were richly supplied with nerves (see left), and must have detected water-borne vibrations. Alternatively, they could have been electric organs. The "fields" have been variously interpreted. They were most certainly of a sensory nature (perhaps generating a mild electric field that allowed the animal to navigate in murky water). The headshield also has two separate eye holes, a pineal opening within a small pineal plate the eyes and a key-hole shaped nasohypophysial opening in front of the eye holes.

The anatomy of osteostracans is well known because of a unique development among these jawless fishes. Bone was laid down inside the body, in a thin layer over the cartilage of the skeleton. From this fossilized bone, the detailed structure of the brain, gills, mouth and even individual nerves and blood vessels can be traced. The brain (above) appears to be similar to that of modern lampreys.

The body is covered with large scales. Both the endo- (internal) and exoskeleton is made up of true bone with cell spaces (the heterostracans have acellular bone). The Osteostraci share a number of unique characteristics - synapomorphies - with the gnathostomes or jawed fish (true bone, epicercal tail, sclerotic ring, endolymphatic openings, dorsal jugular vein, concentrated paired fins) and were clearly closely related.

The Osteostraci are biogeographically limited to the Euramerican Province (Laurentia and Baltica), and are useful biostratigraphic indicators. They are known from the Late Wenlock (Middle Silurian) to the Frasnian (Late Devonian), but were at the height during the period of the Late Silurian and Early Devonian. Strangely, the earliest (Wenlock) occurrences are represented by both very primitive (***Ateleaspis***, *Aceraspis*) and also very advanced (Tremataspididae) members of the group. This indicates either that the diversification of the group took place before the earliest known occurrences, or that the presently accepted phylogeny is completely wrong. Osteostracans are rare in the Devonian of North America (West Euramerica) and practically none of the North American taxa can be assigned with certainty to any of the major European forms.

Most osteostracans belong to a large monophyletic group, the Cornuata, characterized by pointed cornual processes in front of paired fins. The Cornuata comprise five major monophyletic groups, and a few minor groups of uncertain affinities. There are also a few genera of non-cornuate osteostracans which probably represent the primitive osteostracan condition (*Ateleaspis*, *Aceraspis*, ***Hirella***, *Hemicyclaspis*).

Osteostraci: Taking arms against a sea?

The more one studies the Osteostraci, the less one knows with any degree of confidence. The conventional wisdom -- which, right or wrong, is frequently all the wisdom there is -- states that the Osteostraci are the "most advanced agnathans on the evolutionary ladder leading to higher vertebrates." Long (1995). That is, they are jawless fish, but with ossified sclera, paired pectoral appendages (presumably for gripping ladders) and other characters which unite them with gnathostomes. The basic wiring of the brain is fairly well known due to the unique architecture of the skull and Stensiö's destructive thin-sectioning of irreplaceable specimens, an incredible gamble that no one would now be permitted to take, but which paid off remarkably well. The brain turns out to be quite similar to the lamprey brain, which is also taken as a sign that the Osteostraci are but a fruit stand on the broad highway to the gnathostomes.

This general take on the Osteostraci is not disputed, least of all here. The true purpose of this essay, to the extent it has one, is to express frustration with the details of these osteostracan pectoral appendages. They are *probably* homologous with gnathostome pectorals, but there are problems.

The first problem is stratigraphic. Bits and pieces believed to be gnathostome, specifically chondrichthyan, are known as early as the Late Ordovician. Osteostracans are not known before the Early Silurian. Of course paleontology is full of these little stratigraphic anomalies, and they often mean nothing. However, consider that the fossil record of osteostracans is quite good. They have a lot of hard parts, tend to hang around in silty, low-energy marine environments, and have generally shown themselves to be taphonomically friendly to scientists. By contrast, chondrichthyans are an unruly mob with few calcified parts. They often wander about aimlessly in pelagic environments, and have repeatedly demonstrated a willful, even blatant, indifference to the legitimate needs of hominid paleontologists. Under these circumstances, the stratigraphic problem becomes more significant. If the gnathostomes came first, the osteostracan pectoral may be convergent, and not homologous.

The second problem is that the pectoral appendage does not seem to have been a great success among the Osteostraci. In many cases, it not certain that the appendages existed at all. The structure is certainly never elaborated or developed. In osteostracans with elongated shields, the paired limbs could not have existed at all; and no osteostracan shows any sign of paired pelvic fins. To the contrary, the more advanced Osteostraci are cornuates. These osteostracans developed enormously broad head shields, very much like those of a number of galeaspids, with long posteriorly-directed processes at the edges. In these forms, it is difficult to see how the pectoral fin (if it existed) would have been of much use in navigation. Indeed, since the Osteostraci seem to have had only two semi-circular canals, it is difficult to see how *anything* could have been of much help in navigation since the fish evidently lacked the neural wiring to orient themselves well for movement in a three-dimensional medium.

The third problem is structural. The osteostracan pectoral fin is directed antero-posteriorly. That is, it is expressed as a posterior process from the back of the skull, not a lateral process of the trunk. That is not too unexpected, since the pectoral fin girdles are essentially part of the skull even in teleosts. However, the osteostracan paired fin has no well-defined girdle, no fin rays, and no endoskeleton. There are what appear to be attachments for muscles, some scale rows which may have added rigidity, and certainly the fin was integrated with the circulatory system. Still, the appendage is supplied by the branchial artery, not a separate subclavian. The case could perhaps be made that we are looking at the base of a flexible external gill, rather than a limb. The position of the appendage puts it in the hydrodynamic "shadow" of the large head shield. Not a bad place to put fragile external gills, but surely an odd location for control surfaces, and the orientation is entirely different from the pectoral fins of living gnathostomes.

For that matter, the vertebrate pectoral limbs may simply have been external gill supports which were exapted for mobility. One of the leading theories on the subject is not too distant from that view. Still, it seems a long leap from these rather formless flaps of presumably ectodermal tissue to the fins of extant gnathostomes, which seem to be developmentally driven by their mesodermal components. The conventional wisdom is probably quite correct, but there remains room for serious doubt.

Ateleaspis: Fins and Fields

Ateleaspis has one notable distinction for which it deserves more than casual interest. It is the most basal craniate to have unmistakable paired appendages. The *pectoral* fins of this genus are not terribly impressive. They lack any discernible skeletal elements. They may not even be *homologous* (in the phylogenetic sense) with arms. However, there is absolutely no doubt that they exist. The same cannot be said for the often-cited, but rather uninformative, lateral fin folds of anaspids. For more details, see Anaspida.

A second curiosity of *Ateleaspis*, and of most osteostracans, is the presence of sensory fields of unknown function, usually located along the mid-line of the headshield, behind the orbits, and along the lateral margins of the headshield. As mentioned in the main entry. These "fields" are believed to be made up of loose platelets of bone connected to a complex of bifurcating canals, nerve channels, endolymphatic ducts, or whatever. These channels eventually connect with the brain within the *labyrinth*.

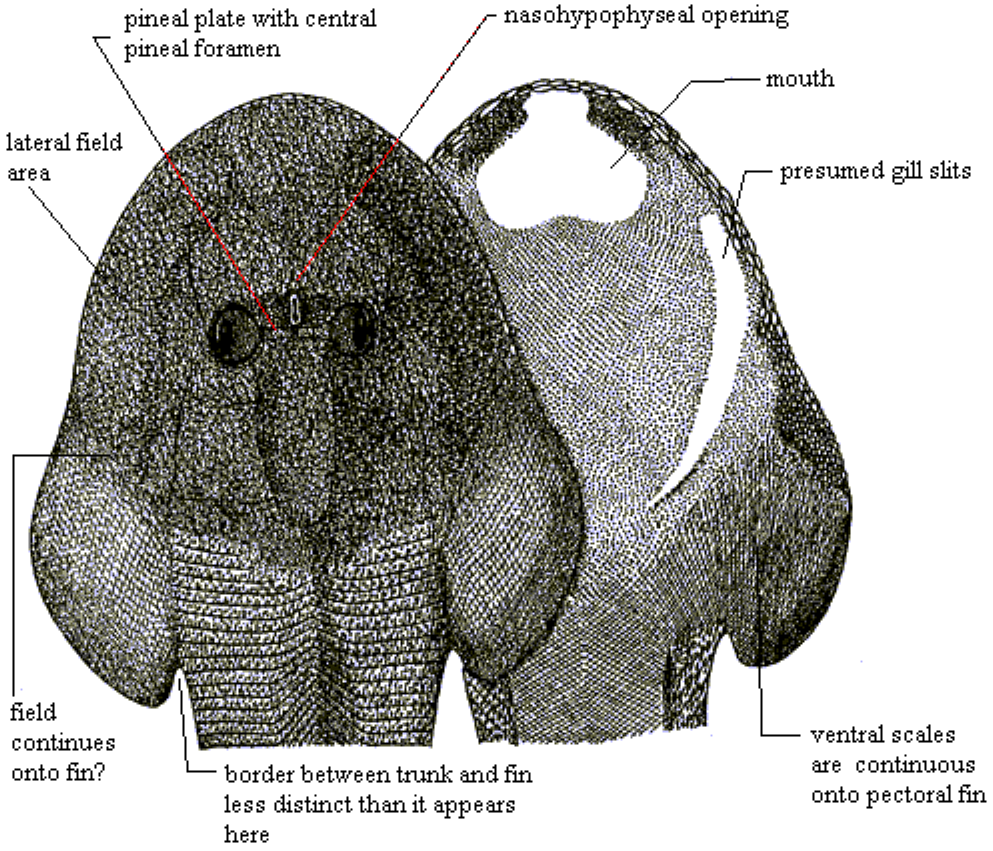


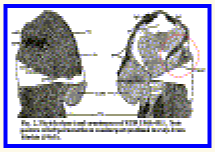
Fig. 1. *Ateleaspis tessellata* headshield and pectoral fins in dorsal and ventral views, modified from Ritchie (1967).

Possibly, these two features are related. Let's review what we know about the fields. They are made up of small platelets which, in the basal *Ateleaspis*, are not at all different from the surrounding *dermal bone* of the headshield. In more derived species, they become more distinct and specialized. However, they seem to have been able to accomplish their essential function as simply generalized bits of dermal bone. These platelets lay over a regular, bifurcating system of channels connected to the labyrinth -- the organs which detect orientation in a gravity field, or acceleration (relativisticly the same things). The Osteostraci, like other pregnathostome craniates, had only two pairs of *semicircular canals* in the labyrinth. That is, their kinesthetic sense was somewhat handicapped in dealing with fully three-dimensional movement. Presumably Osteostraci were able to sense roll and yaw: rotation around an antero-posterior axis and around a dorso-ventral axis, respectively. Since it is impossible to imagine a vertebrate without the ability to detect roll or yaw, it is generally believed that what was missing or deficient was a sense of "pitch," rotation around a horizontal axis, corresponding to motion up or down in the water column.

But, while the Osteostraci lacked a third semicircular canal, they possessed the fields, which were also connected to the labyrinth. The field platelets in *Ateleaspis* look just like the rest of the shield. They aren't specialized sensors. All that happens is that, when the fish moves "uphill," the platelets are pressed down a bit harder on the channels below them. This sends some kind of signal, pressure wave or electrical, directly to the portion of the brain which computes orientation and movement in space. We can be fairly confident in this conclusion because the effect of the mechanical pressure of a small plate on either neural tissue *or* a fluid-filled duct would be to send a signal to the brain -- whether or not this were the "intended" effect. The same, simple system would register a different types and patterns of signal for turbulence caused by currents, waves, or other fish.

This looks well enough, but why bother with this clumsy arrangement when *Ateleaspis* had a perfectly good *lateral line* system, and perhaps even electrical senses? The *neuromast organs* of the lateral line are similar (and closely related to) the receptors in the labyrinth. In modern fish, they are sensitive to very slight water currents. Assuming the osteostracan lateral line is not too different, where is there a need for a gross mechanical receptor of this sort?

There is no simple answer. However, there is also no good evidence that osteostracans actually had lateral line organs except on the head shield. Some, like *Ateleaspis*, had no ventral lateral lines, even on the head. Perhaps their lateral line system was not as effective as in Recent fish. As well, lateral lines are not constructed in a manner which lends itself to detecting flow normal to (towards or away from) the surface -- loosely speaking, movement up and down -- or to making sense of water movements which have both local turbulence and large-scale flow. So, perhaps there was room for a sense which was strong where the lateral line was less dependable.



Whatever the sensory fields do precisely, it may have to do with the pectoral limbs. There is a fairly striking correlation between the extent of the sensory fields and the extent of the pectoral fins. In many cases, the fins are not actually known. However, the extent of the field is fairly closely correlated with the relative size of the fins (where known).

In the primitive *Ateleaspis*, the fields appear to actually extend onto the fins. Although it may be a *taphonomic* artifact, one of the specimens described by Ritchie suggests that the pectoral fin extends well beyond the relatively scaleless dorsal area and is actually limited anteromedially only by the line of the gill arches. The field area of the fin is indicated on the sketch. As Ritchie states, the fin is plainly an extension of the headshield. It is not a lateral breach in, or extension of, the body wall in the manner of modern tetrapods. Thus, the fields and the paired limbs are not only correlated; they are physically associated at least in this basal species.

If the foregoing chain of speculation (one could not call it "reasoning") has any validity, the most probable interpretation is that the fins and fields developed together: a means of stabilizing swimming along with the sense organs to provide feed-back control for it. This reconstruction has the virtue of elegance and economy, but it may suggest that the osteostracan pectoral limb is not strictly homologous with the gnathostome limb. However, this a suggestion built on a speculation -- going a bit too far out on a limb, so to speak. ATW 001016.

Descriptions

Pituriaspida: *Neeyambaspis, Pituriaspis*.

Range: Early Devonian or Middle Devonian of Australia

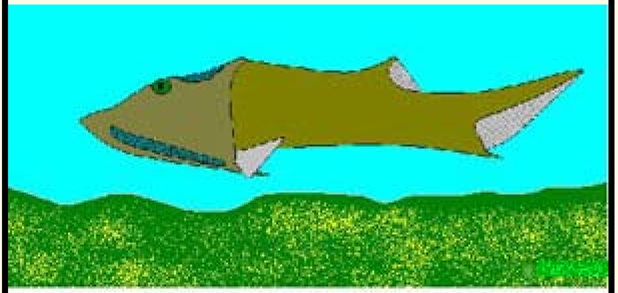
Phylogeny: Cephalaspidomorphi:: Osteostraci + Gnathostomata + *.

Characters: Probable paired pectoral appendages. Similar to Galeaspida. The only unique characteristic of the Pituriaspida is a peculiar pit, of unknown function, ventral to the orbits; marine or deltaic environment.

Links: Pituriaspida; 116.htm; DEVONIANO peixes agnatas. ATW020615.

Osteostraci: (= Cephalaspididae):

Range: Early Silurian to Late Devonian of North America, Europe


Generalized zenaspid, after Janvier (1996)

and Russia.

Phylogeny: Cephalaspidomorphi:: Pituriaspida + Gnathostomata + *. *Ateleaspis* + (*Hirella* + (*Hemicyclaspis* + Cornuata)).

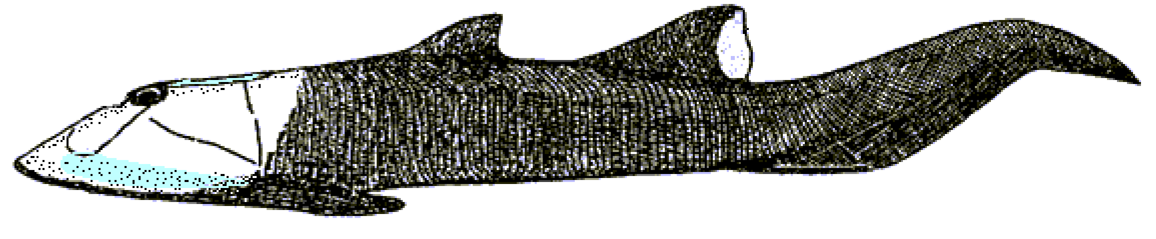
Characters: Armored jawless fish (5-100 cm) with massive cartilaginous skulls and paired pectoral fins. Extensive cephalic endoskeleton of cartilage covered with perichondral bone; large cephalic plates with "cephalic fields" (shallow dorsal depressions covered with small polygonal scales and connected to labyrinth cavity by canals); 2 semi-circular canals; mouth and up to 10 pairs of branchial openings ventral; probably with velum-like pumping organ; orbits close to dorsal midline, with sclerotic ring and commonly ossified sclera; central nasal opening and small pineal opening; cornua common; some with dorsal spines or ridges on head shield or elongated shields; heart in chamber posterior to skull, probably 2-chambered, with ventricle and atrium lying side by side; some details of circulatory system known; ossified dorsal arcualia on notochord; 1-2 dorsal fins or scale ridge; also paired *lateral* scale ridges; heterocercal tail; frequently small horizontal lobe below caudal (modified anal fin?); many have vertical rows of squarish scales on caudal fin; paired fins present as posterior outgrowths from base of broad head shield; pectoral fins with complex musculature but no known fin rays or endoskeleton; pectorals may be stenobasal or eurybasal; from low energy near-shore or estuarine marine sediments; exoskeleton with cellular bone and subaponevrotic circulation; make-up of exoskeleton highly complex and variable, normally with mesodentine outer layer for more detail, see note under Benneviaspidida); lateral line system on trunk; ventral surface of small plates.

Links: Osteostraci; Geol437/ostrac; immune.html; International Meeting on the Evolution of Vertebrates in Lund, Sweden; IGCP406 Publications 1998; UALVP 19145 Cephalaspidid model; Osteostraci; Interactive Fly, Drosophila (fascinating); Origin of Vertebrates; Osteostraci [Cephalaspidiformes]; 120.htm; 122.htm; xrefer - Osteostraci; superEva - guide (Italian); pesciagnati (Italian); Volume 16 (V2). ATW010902.

***Ateleaspis*: (= *Aceraspis*):**

Range: Early Silurian to Early Devonian of northern Europe & Siberia.

Phylogeny: Osteostraci: (*Hirella* + (*Hemicyclaspis* + Cornuata)) + *.


Ateleaspis tessellata, after Ritchie (1967) with minor modifications. "Field" areas (in color) are little differentiated and appear almost identical to the surrounding head shield.

Characters: Primitive, 15-20 cm osteostracan; the most basal known vertebrate with paired fins. Headshield of cellular bone, heavily ornamented with dentine tubercles; tubercle size increases near orbit and headshield margins; headshield flattened, with a broad, flat basal margin containing "fields" (areas made up of loosely attached small plates over poorly understood bifurcating canals connected to the labyrinth area of the brain); endolymphatic duct opens inside a median "field" running along raised peak of posterior headshield; "fields" are larger, but less distinct (less specialized?) than in more derived osteostracans; orbits have ossified sclera as incomplete hollow sphere; orbits closely set and joined by a rod-like pineal plate; pineal foramen runs through center of pineal plate; keyhole shaped nasohypophyseal opening in a "heart-shaped" depression just anterior to pineal plate; poorly-defined ventral mouth; ventral surface of head covered with uniform, minute scales; gill openings along lateral margins of ventral surface; sensory line system present on headshield, perhaps on trunk; cornuate headshield processes absent; cranial endoskeleton poorly developed; two distinct dorsal fins without median dorsal ridge scales; 2nd dorsal and caudal fins have posterior fin membrane; trunk has narrow basal marginal flange; broad-based pectoral fins; gradual transition from both tesserate "field" of headshield margin and brick-like scales of trunk and flange; pectoral girdle and rays (if any) unknown; pectorals appear to be joined to trunk or headshield along most of their length; pectoral appear as extension of lateral headshield. Likely inhabited low-energy marine or perhaps estuarine areas; found as a rare species in association with eurypterids, anaspids & thelodonts.

Links: Osteostraci; Biology 356; Biology 356; The exoskeleton of Ungulaspis and Ateleaspis (abstract, histology).

References: Janvier (1996); Ritchie (1967). ATW031130.

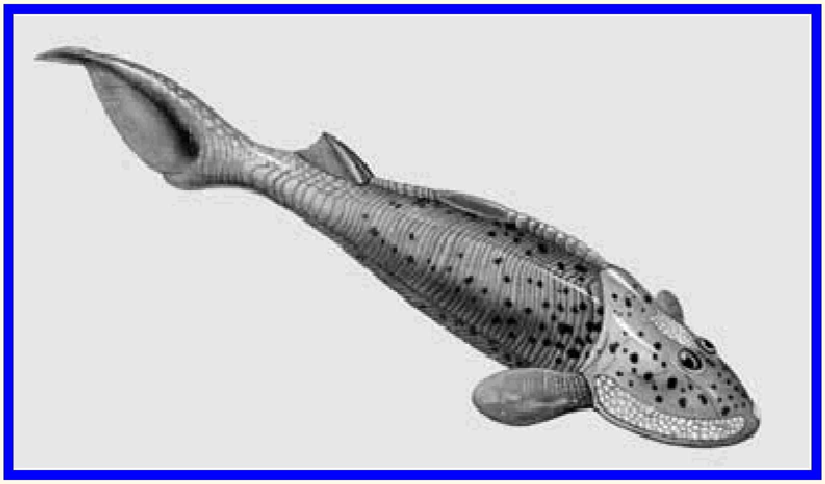
Hirella:

Range: Silurian.

Phylogeny: Osteostraci:: (*Hemicyclaspis* + Cornuata) + *.

Characters: ventral platelets on headshield; pectoral fin base narrow. ATW000624.

Hemicyclaspis: *H. murchisoni*



Range: Late Silurian to Early Devonian of North America & Europe.

Phylogeny: Osteostraci::: Cornuata + *.

Characters: narrowed, more differentiated sensory fields; anterior dorsal fin reduced to large median scute.

Links: Dinosaurs: Model & Collectible Pricelist; Fish Replicas - Hanman's Fossils & Minerals; geologic; Volume 16 (V2) (small, badly drawn, but accurate sketch); 120.htm; museum für naturkunde berlin: glossar geschichte der wirbeltiere (German); view.cgi?page=2&corner=18&file=29 (Japanese); Vertebrate (Korean); Världshaven på Unga Fakta! (Swedish); Genomgång Ostracoderma (Swedish); 古生物学研究的意义 (Japanese); おもちゃのサ·カ·ナ (models); DEVONIANO peixes agnatas; 척추동물아문(Vertebrate, 등뼈를 가진다) (Korean: notes on feeding style?); 展示室にある標本 (Japanese: nice model); The Devonian Period of the Paleozoic Era.

References: Janvier (1996). ATW031022.

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Cephalaspidomorphi: Cornuata

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           |     |--Cephalaspidida
         |           |     `--+--Zenaspidida
         |           |        `--+-
-Benneviaspidida
         |           `--Gnathostomata
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
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3. Cornuata X
4. Zenaspidida X

Cephalaspis as it would have appeared in life. Image from Lucius Fisher's Picasa album, original source unknown

Descriptions

Cornuata:

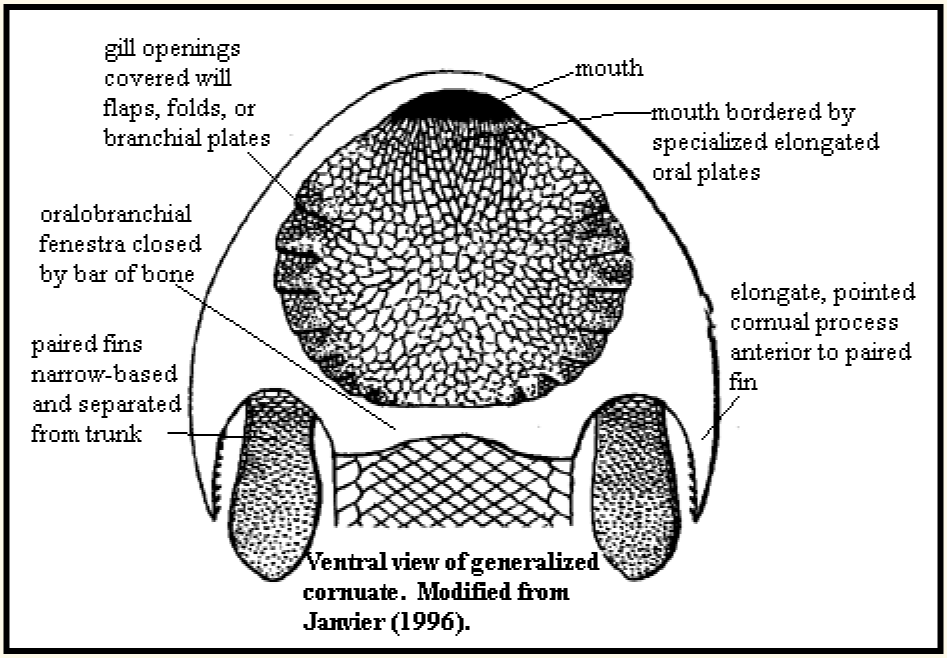
Range: Early Silurian to Late Devonian

Phylogeny: Osteostraci::: *Hemicyclaspis* + *: Cephalaspidida + (Zenaspidida + (Benneviaspidida + (Kiaeraspidida + Thyestiida))).

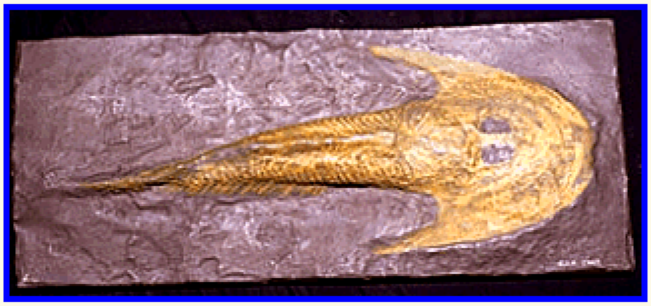
Characters: Mouth lined with elongate oral plates; branchial opening covered by folds or plates; **$** pointed lateral processes (cornua) of the headshield, anterior to paired fins; **$** oralobranchial fenestra posteriorly closed by a bar of dermal bone; paired fins narrow based and separated from trunk musculature.

Links: Untitled Document; Osteostraci.

References: Janvier (1996). ATW020615.



Ventral view of generalized cornuate. Modified from Janvier (1996).



Cephalaspidida: *Cephalaspis*, *Mimetaspis*, *Parameteoraspis*, *Pattenaspis*

Range: Late Silurian(?) to Early Devonian of Europe & Spitsbergen.

Phylogeny: Cornuata: (Zenaspidida + (Benneviaspidida + (Kiaeraspidida + Thyestiida))) + *.

Characters: broad, flattened cornual processes (which may be very broad); lateral sensory fields extend onto cornua; retain some remnant of anterior dorsal fin (primitive); scale microstructure including long ridges and rows of osteocyte lacunae at base [M02].

Image: *Cephalaspis* from Biology 356.

Links: Osteostraci; Cephalaspis tenuicornis; Biology 356; Spittal Quarry; Le Dévonien (10/10); New Page 1 (some of these look almost too good to be true -- but interesting photos nonetheless); fossils.pdf; fish.doc; forelasning4.pdf (Swedish); Ken Mannion Fossil Gallery; Dineley.

References: Janvier (1996); Märss (2002) [M02]. ATW020615

Notes: Ludlovian to Givetian *Cephalaspis* occurs in Britain and Spitsbergen (widespread - northeast to southeast Euramerica). *Parameteoraspis*, is the largest known osteostracan, the crestent-shaped shield reaching 35 to 40 cm in breadth. It is particularly abundant in Spitsbergen (northern Euramerica) but is lacking in Britain and Podolia (eastern Euramerica), and smaller cephalaspidids, such as *Pattenaspis* and *Mimetaspis* occur in Spitsbergen (northern Euramerica), Britain, Podolia, Rhineland (east and southeast Euramerica) and France (adjacent north Gondwana). MAK001023.

Zenaspidida: *Diademaspis, Machairaspis, Scolenaspis, Tegaspis, Zenaspis*

Range: Early Devonian to Late Devonian of Europe and North America

Phylogeny: Cornuata:: (Benneviaspidida + (Kiaeraspidida + Thyestiida)) + *.

Characters: headshield massive; hypophysial part of nasohypophysial opening enlarged; sensory fields posteriorly enlarged; some with tall median dorsal process near posterior of headshield; thick, narrow cornual processes; anterior dorsal scute lost; characteristic ornamentation of large tubercles, surrounded by smaller ones.

Image: *Zenaspis* from BIOLOGY 4402/5402.

Notes: Lochkovian to Frasnian. The Zenaspidida are usually large, massive osteostracans (average length about 25 cm), with a coarsely tuberculated ornamentation and a large hypophyseal foramen. They are abundant in the early Devonian of Britain, Podolia (east and southeast Euramerica) and Spitsbergen (northern Euramerica) MAK001023.

Links: Osteostraci; 309.htm; AGP, Volume 46, Number 3-4, 1996; 118.htm; PPT Slide; Home Page; New Page 1 (two gorgeous pictures of *Zenaspis*).

References: Janvier (1996). ATW021221.

Benneviaspidida: *Belonaspis, Benneviaspis, Boreaspis, Hoelaspis, Tauraspis*.

Range: Early Devonian of Europe (including Spitzbergen) & Russia.

Phylogeny: Cornuata::: (Kiaeraspidida + Thyestiida) + *.

Characters: headshield flat and dorsoventrally depressed; some have *two* rostral processes or the cornual processes are bent anteriorly; first canal to lateral sensory field bifurcates near orbit; short-bodied; anterior dorsal scute absent; no separate tesserae and no radiating canals in the exoskeleton (see **[1]**).

Note: **[1]** osteostracan headshields have a rather complex histology. The outer layer is usually a continuous layer of dentine which may be coated with a thin enameloid. The middle layer is composed of cancellous (spongy) bone and has two divisions. The superficial portion often has a sort of pore-canal system similar to those of many sarcopterygians. The deeper layer is tesselated (tiled) and usually has a pattern of vascular canals radiating from the center of each tile. The inner layer is laminar bone. In Benneviaspidids, the lower part of the middle layer is continuous. There are no visible separate tiles and the radiating vascular canals are absent. **[2]** Lochkovian to Emsian The Benneviaspidida have a very flat head shield and a short abdominal division. They include a group of small forms with long rostral process (Boreaspididae) and other highly derived head-shield morphologies. They are known from Britain, Podolia (east and southeast Euramerica), Spitsbergen and Severnaya Zemlya (northern Euramerica) although the Boreaspididae are restricted to the northern region (hence the name - Boreo- north). At least 14 species of *Boreaspis* are known from fossil deposits of the lagoons of Spitsbergen during the Early Devonian. They differ in the width of their triangular-shaped head shields, and in the length of the bonv spine that grew out from the cheek area on either side. The snout was elongated in all species into a bladelike rostrum. As well as its hydrodynamic function, the rostrum was probably used to probe on the muddy lagoon floor for prey. Another genus in this suborder, *Tauraspis,* is unique in having two forwardly directed horns in place of the usual rostrum. MAK001023

Links: Osteostraci; 309.htm; 118.htm; PPT Slide; Early Devonian osteostracans from Severnaya Zemlya, Russia.

References: Janvier (1996). ATW040717.

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Cephalaspidomorphi: Cornuata (2)

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           |     |--Kiaeraspidida
         |           |     `--Thyestiida
         |           `--Gnathostomata
         `--+--Loganiidae
            `--Gnathostomata (alternative placement)
```

Contents

Taxa on This Page

1. Kiaeraspidida X
2. Thyestiida X

Descriptions

Kiaeraspidida: *Acrotomaspis, Axinaspis, Gustavaspis, Kiaeraspis, Nectaspis, Norselaspis*

Range: Early Devonian of Europe (Spitzbergen).

Phylogeny: Cornuata:::: Thyestiida + *.

Characters: Very small; some with mouths opening anterodorsally; supraoral sensory field present and large; many with lateral sensory fields reduced; cornual processes reduced; headshield extends posteriorly into long abdominal division; anterior dorsal scute absent; first canal to lateral sensory fields bifurcates near orbit; posterior ventral myodome reduced or absent.

Notes: Lochkovian to Emsian. These are tiny forms, barely larger than a fingernail. The cornual "horns" are reduced and there is a tendency also towards reduction or subdivision of the "fields". They are restricted to the early Devonian of Spitsbergen (northern Euramerica). MAK001023.

References: Janvier (1996).

Thyestiida: *Dartmuthia, Procephalaspis, Sclerodus, Thyestes, Tremataspis, Witaaspis*

Trmataspis model

Range: Middle Silurian to Early Devonian of Europe.

Phylogeny: Cornuata:::: Kiaeraspidida + *.

Characters: infraorbital sensory line passes medially to lateral fields; anterior dorsal scute absent; first canal to lateral sensory fields bifurcates near orbit; posterior ventral myodome reduced or absent; loss of. paired fins common; may be burrowers.

Image: from North Eastern Geologic

Notes: Wenlock to Pridoli. These very early osteostracans can variously be considered the ancestral lineage of cornuates (the evolutionary-systematic paradigm) or as the most specialized crown group (the cladistic paradigm). Thyestiida became diversified very early in the Baltic area (central eastern Euramerica) and may have later reached Great Britain, Timan and the Urals but seem to have disappeared by the Early Devonian. Their most primitive members (*Procephalaspis*, *Auchenaspis*) had the typical cornuate shield shape whereas the most advanced or derived (Tremataspididae) had lost paired and unpaired fins, possibly as a consequence of an adaptation to burrowing habits. They were all quite small. *Tremataspis*, an advanced form, was about 8 or 10 cm in length. There is a tendancy in many of these forms towards a reduction of the "fields". MAK001023.

Links: 122.htm; Thyestes verrucosus; 123.htm; geologic; Ovning4.pdf (Swedish).

References: Janvier (1996).

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Cephalaspidomorphi: Dendrogram

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           `--Gnathostomata
         |                |--Placodermi
         |                `--Acanthodii
(paraphyletic)
         |                   |--Chondrichthyes
         |                   `--Osteichthyes
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
```

Contents

(Note - links to Mikko's Phylogeny (MH) need revising; the pages exist but have been moved to different directories - MAK111024)

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida X
         |  `--Cephalaspidomorphi X
         |     |--Galeaspida X MH
         |     |  |--Eugaleaspidiformes •X
         |     |  `--Polybranchiaspidida X
         |     |     |--Polybranchiaspidiformes •X
         |     |     `--Huananaspidiformes •X
         |     `--+--Pituriaspida •X
         |        `--+--Osteostraci X ToL, MH
         |           |  |--Ateleaspis •X
         |           |  `--+--Hirella •X
         |           |     `--+--Hemicyclaspis •X
         |           |        `--Cornuata X
         |           |           |--Cephalaspidida •X
         |           |           `--+--Zenaspidida •X
         |           |              `--+--Benneviaspidida •X
         |           |                 `--+--Kiaeraspidida •X
```

```
         |          |                 `--Thyestiida •X
         |          `--Gnathostomata
         `--+--Loganiidae X
            `--Gnathostomata  (alternative placement)
```

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Cephalaspidomorphi: References

Abbreviated Dendrogram

```
Vertebrata
|--Conodonta
`--+--Pteraspidomorphi
   `--Thelodonti
      `--+--+--Katoporida
         |  `--Cephalaspidomorphi
         |     |--Galeaspida
         |     |  |--Eugaleaspidiformes
         |     |  `--Polybranchiaspidida
         |     `--+--Pituriaspida
         |        `--+--Osteostraci
         |           |  |--Ateleaspis
         |           |  `--Cornuata
         |           `--Gnathostomata
         |                 `--Osteichthyes
         `--+--Loganiidae
            `--Gnathostomata (alternative
placement)
```

Contents

Benton, M. J. 2004. *Vertebrate Paleontology*. Third Edition. Blackwell Publishing
Cephalaspidomorphi

Carroll. R.L. 1988. *Vertebrate Paleontology and Evolution*, Freeman.
Overview

Janvier, P (1996), **Early Vertebrates**, Oxford, 393 pp.
Ateleaspis, Benneviaspidida; Cephalaspidida, Cornuata, Eugaleaspidiformes, Galeaspida, *Hemicyclaspis*, Huananaspidiformes, Kiaeraspidida, Polybranchiaspidida, Polybranchiaspidiformes, Thyestiida, Zenaspidida.

Janvier, P. 2008. Early jawless vertebrates and cyclostome origins. Zoological Science. 25: 1045-1056. **pdf**
Overview, Cephalaspidomorphi

Long, JA (1995), **The Rise of Fishes: 500 Million Years of Evolution**. Johns Hopkins Univ. Press, 223 pp.
Osteostraci.

Marss, T (2002), *Silurian and Lower Devonian anaspids (Agnatha) from Severnaya Zemlya (Russia)*, **Geodiversitas** 24: 123-137.
Cephalaspidida

Nelson, J. S. 2006. *Fishes of the World*. 4th edition. John Wiley and Sons, Inc. New York.
Cephalaspidomorphi

Packard, A. 1972, Cephalopods and Fish: the limits of convergence, *Biological Reviews* 47: 241-307
Overview

Ritchie, A (1967), ***Ateleaspis tessellata*** *Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland*. **Zool. J. Linnean Soc.** 47: 69-81. [This issue, no. 311, was published as a separate *festschrift* volume for Dr. Errol I. White and is sometimes cited -- and filed by librarians -- as "Patterson, C & PH Greenwood (eds.) (1967), **Fossil Vertebrates**. Academic Press"]
Ateleaspis

Sansom, R. S., 2009, Phylogeny, classification and character polarity of the Osteostraci (Vertebrata).*Journal of Systematic Palaeontology* 7(1): 95-115.
Overview, Cephalaspidomorphi

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