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Mikroskopické zbytky spodněpaleozoických obratlovců - metody, systematika, paleogeografie

Microscopic remains of Lower Palaeozoic Vertebrates - methods, systematics and palaeogeography

Bachelor thesis

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I declare that I have prepared this thesis independently and that all information sources and literature used have been duly listed. Neither this thesis nor any substantial part of it has been submitted previously for the award of the same or any other academic degree.

Prague, 30.07.2025 ....

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Abstract

Microscopic vertebrate remains are now commonly used in sedimentological and paleogeographic research of Palaeozoic deposits around the world. Missing data from the Barrandian area, where only occasional finds have been reported, represent a knowledge gap on the palaeomap. However, vertebrate remains often appear in residues collected by micropalaeontologists in Lower Palaeozoic deposits of the Barrandian area. The aim of this bachelor's thesis is to summarize the microvertebrate data from the Silurian and Devonian in terms of their classification, stratigraphic range, geographical distribution and research methods. The focus will be on neighbouring palaeoregions, such as Baltica, where an abundance of comparative material is available. The bachelor's thesis will serve as a prerequisite for a master thesis.

Keywords

Microvertebrates, Microscopic Vertebrate remains, Early Vertebrates, Fish-like Vertebrates, Lower Palaeozoic

Abstrakt

Mikroskopické zbytky obratlovců se dnes běžně používají při sedimentologickém a paleogeografickém výzkumu paleozoických ložisek na celém světě. Z oblasti Barrandienu ovšem máme zprávy pouze o několika náhodných nálezech. Je tudíž nezbytné provést systematickou prospekci, která by doplnila chybějící data na paleomapě. Pozůstatky obratlovců se často objevují ve residuích vybíraných mikropaleontology z rozpuštěných hornin spodního paleozoika Barrandienu. Cílem této bakalářské práce je shrnout publikovaná data o mikrovertebrátech siluru a devonu z hlediska jejich klasifikace, stratigrafického rozsahu, geografického rozšíření a metod výzkumu. Důraz bude kladen na sousední paleoregiony, jako je Baltika, kde je k dispozici dostatek srovnávacího materiálu. Bakalářská práce má sloužit jako teoretický základ diplomové práce.

Klíčová slova

mikrovertebráti, mikroskopické zbytky obratlovců, raní obratlovci, rybovití obratlovci, spodní paleozoikum

Contents

1 Introduction

The aim of this thesis is to summarize microvertebrate data from the Lower Palaeozoic in terms of their classification, stratigraphic range, geographical distribution, and research methods. The thesis is focused on the Silurian and Devonian periods, from which relevant data are available; by contrast, findings from the Cambrian and Ordovician periods are extremely rare. Although microscopic remains occur in many paleontological sites around the world, for the purposes of this work, neighboring areas of the **Barrandian** area—such as **Baltica**—are particularly important for future comparisons with material from the Barrandian itself.

To understand the structure and systematic classification of microscopic remains of the earliest vertebrates, it is essential to provide general information about early vertebrates including research methods, taxonomic groups, and paleogeographic distribution. The processed data should clearly indicate which research methods and taxonomic groups are the most promising for further study and exploration of the **Prague Basin** area.

Microscopic vertebrate remains consist of various body parts, such as teeth, scales, fin spines, tesserae, dermal plate fragments, and bone fragments, which are often called "**ichthyoliths**" or "**exoskeletal remains**" (Janvier 1996; Märss 2006). Exoskeletal microremains of early vertebrates can be classified into taxa based on differences in morphology, sculpture, and microstructure (Märss 2006). Due to the presence of solid inorganic materials, such as **dentin**, **aspidin** and **enamel**, microscopic vertebrate remains were able to fossilize, providing us with important data on the history of vertebrates and their evolutionary development (Lingham-Soliar 2014). Therefore, the study of the earliest vertebrates, including their microscopic remains, holds significant potential for practical applications.

From a paleobiological point of view, the oldest vertebrates represent a phylogenetic line considered to be the stem group of all vertebrates. It has a potential to study evolutionary trends in anatomy, morphology, and ecology in vertebrates. This group can provide important information about the origin of teeth, jaws, and bone tissues (Lingham-Soliar 2014).

From a geological point of view, early vertebrate microremains are used in sedimentological and paleogeographic research of the Lower Palaeozoic, as taxonomically distinct exoskeletal remains are often associated with specific stratigraphic layers (Märss 2006). Therefore, microremains can serve as a valuable tool for subdividing geological sections and for stratigraphic correlation.

The study of ancient vertebrates is possible due to a combination of various laboratory methods, such as acid and non-acid extraction from sediment, along with the use of scanning electron microscopy, and modern imaging techniques like X-ray computed microtomography, synchrotron radiation microtomography, and 3D virtual histology. Up-to-date imaging techniques are so advanced that they allow us to examine fossil material in situ in minute detail non-destructively, enabling it to be preserved and used repeatedly for research.

2 Methods

2.1 Laboratory methods

Small fossilized fish remains are composed of **calcium phosphate**—specifically the mineral **apatite**—like conodonts. Due to their identical composition, similar methods are used for their extraction, such as digestion in diluted weak acids, usually acetic acid (Jeppsson 1974) and formic acid (Jeppsson and Anehus 1995). In addition to weak acids, alternative methods such as digestion in sulfuric acid (Vodrážka 2008) or the use of surfactants (Jarochowska et al. 2013) are also available. However, the approach to extracting fossil remains varies depending on the sediment composition (Table 1) and the type of fossil preservation. Fossils of early vertebrates commonly occur in sedimentary rocks such as limestones, sandstones, shales, dolomites, claystones, and marlstones (Janvier 1996). This thesis, along with future studies, will focus on sediments from the Barrandian area, which consist primarily of limestone (Chlupáč et al. 2011). When dealing with microscopic vertebrate remains, acid digestion is usually required for subsequent analysis using a scanning electron microscope.

Limestones - Fossils preserved in limestones and calcareous matrices can be preparated in diluted acetic and formic acid. Acid preparation should be followed by washing with water, drying and fixing the sample with glue. It is essential to assess the condition of the fossil; otherwise, the disintegration process may cause the formation of endoskeletal microfractures, or the fossil may fall apart (Janvier 1996). Besides weak acids, calcareous fossils may also be extracted using diluted sulfuric acid (Vodrážka 2008).

Sandstones - When preparing fossils from sandstones, delicate remains can be mechanically picked out under a binocular microscope using a needle, but if the rock is too compact and siliceous, the bones can be extracted using hydrochloric acid (Janvier 1996).

Shales - Preservation in shales is often associated with flattening and distortion of the fossilized object. Due to anoxic conditions that prevent a rapid decomposition of non-mineralized structures, some soft tissues can also be preserved as tarry imprints. Since these fossils are preserved as two-dimensional structures, preparation is often unnecessary. However, if the preparation is appropriate, detergents and hydrogen peroxide are used (Janvier 1996).

Dolomites - Fossil extraction from dolomite is particularly challenging due to the inefficiency of weak acids, as dolomite does not dissolve in them (Janvier 1996). Regarding stronger acids, hydrochloric acid cannot be used because it would destroy the fossils (Janvier 1996), although sulfuric acid may be a viable alternative (Vodrážka 2008). As for mechanical preparation, it is also problematic due to the firm attachment of the matrix to the bones. This process can lead to disintegration as a result of extensive recrystallization into fine prisms (Janvier 1996).

The best-preserved Paleozoic fishes are found in **calcareous concretions**. Due to slow decomposition, aided by bacterial metabolic activity, the fish within these concretions are often preserved in their natural position. In **phosphatic concretions**, fossils may also be well-preserved, but they should be prepared mechanically or serially ground and cut (Janvier 1996).

2.1.1 Acid techniques for extraction

Acetic acid - Acetic acid can be used to etch limestone samples, typically at a concentration of approximately 10 percent (Jeppsson 1974; Long 2011). Acid preparation involves placing the rock in a dilute acid bath, followed by rinsing in water. This process is repeated in alternating acid and water baths until the fossil is fully prepared. After digestion, insoluble residues are washed through a series of screens with progressively smaller mesh sizes to separate them into different size fractions. Subsequently, the selected size fractions are processed in bromoform for separation (Jeppsson 1974). The resulting material can then be subjected to further examination and/or processing. Generally, acetic acid is considered safer to use than formic acid; however, the weaker the acid, the more acid bath cycles are required.

Formic acid - Formic acid buffered with calcium carbonate and calcium phosphate (Jeppsson and Anehus 1995) can be used to dissolve dolomite or dolomite grains from residues derived from limestones previously broken down with buffered acetic acid. A 10 percent solution is typically used due to its effectiveness (Jeppsson and Anehus 1995; Long 2011). To prepare the solution, diluted formic acid, calcium carbonate, and tricalcium phosphate are added to the mixture. It is necessary to buffer the solution with both calcium carbonate and tricalcium phosphate; otherwise, if the formic acid is unbuffered or buffered with only one of them, phosphatic fossils may be destroyed. Before preparing the solution, the weight of the dolomite to be dissolved must be estimated. The total amount of solution required is then calculated by using 11 ml of solution per gram of dolomite. During dissolution, the sample must be enclosed in a covered container to prevent evaporation, but gases resulting from the process must be allowed to escape. The liquid inside the container must be kept in constant motion or shaken frequently to prevent density layering (Jeppsson and Anehus 1995).

Sulphuric acid - Sulfuric acid can be used on calcareous rocks such as limestone and dolomite. Before being immersed in acid, samples must be thoroughly dried to prevent changes in acid concentration. The acid bath should be conducted under a fume hood. Samples are then submerged in a container of 38 percent sulfuric acid. The container must be covered to prevent moisture from affecting the acid concentration and to contain any foam produced during the reaction. The duration for which a sample can be submerged in acid depends on the composition of the crust. Generally, samples can be treated for up to two hours before any potential damage occurs to the fossil. After removal from the acid bath, samples must be neutralized—first with continuously flowing tap water, and then with a solution of water and sodium carbonate. Since exposing acid to water can cause unwanted chemical reactions that could damage the fossil, the neutralization process must be completed quickly, within a maximum of five minutes. After neutralization, any remaining residues must be removed using one of the following methods: water blasting, ultrasonic cleaning, or gentle cleaning with a soft paintbrush (Vodrážka 2008).

sediment digestion or preparation	
sediment type	**recommended approach**
limestones	acetic acid/formic acid/sulphuric acid
sandstones	mechanical preparation using a needle
shales	detergents and hydrogen peroxide/none
dolomites	formic acid/sulphuric acid
marls, claystones	surfactant Rewoquat

Table 1: **Recommended chemicals for dissolving sediments, grouped by sediment type.** However, it is necessary to consider the condition of the sediment (as described above) before selecting a treatment.

2.1.2 Acid free technique for extraction

An alternative method for extracting microfossils is the use of the surfactant Rewoquat. It is recommended for microfossil extraction from fine-grained sediments such as marls and claystones. The main advantage of this method is that it dissolves the sediment without the use of acid. Standard acid-based methods are highly inefficient for these sediments due to the tendency of clay components to form aggregates at low pH values. In acid-based applications, these sediments have excessively low porosity, and sample extraction is further complicated by the formation of a clay coating on the sample surface. Moreover, the use of an acid-free method eliminates the risk of damaging the fossils and avoids the time-consuming nature of acid-based sediment dissolution processes (Jarochowska et al. 2013).

2.1.3 Preparation of residues for scanning electron microscope

A scanning electron microscope (SEM) has been proven to be the best-known method for imaging the surface structures of specimens (Table 2); therefore, it is widely used in micropalaeontology. After the initial acid digestion and neutralization treatment, the samples must be prepared for SEM analysis. Unlike biological materials, fossils and other inorganic or dried samples do not require special preparation protocols. Clean samples are placed onto a sample stub using double-sided sticky tape. It is important to ensure that individual samples do not overlap on the sample stub and are firmly adhered to it (Murtey and Ramasamy 2016). Subsequently, the prepared samples must be coated with a gold-palladium alloy for the SEM to function properly (Bremer, Jarochowska, and Märss 2019).

This method is commonly used to study the surfaces of microscopic vertebrate remains, such as scales, spines, teeth, and more. For example, morphology and ultrasculpture of exoskeletal remains of early vertebrates was described and used for taxonomic classification (Märss 2006).

2.2 Non-destructive imaging methods

Non-destructive methods allow us to scan a sample *in situ*, providing a range of data that would not be obtainable through laboratory methods alone, with highly detailed resolution. These methods are often combined to achieve optimal data.

2.2.1 X-ray computed microtomography

Micro CT allows for the study of internal skeletal structures and their organization (Table 2). This method provides high spatial resolution and enables digital acquisition and processing of information without need for dissection or risk of fracturing skeletal elements. It is capable of performing precise morphological measurements and permits digital manipulation of micro CT data for enhanced visualization (Carlson et al. 2003). Entire fossils can be reconstructed by segmenting in transverse, horizontal, and parasagittal planes (Pradel, Denton, and Janvier 2021). However, certain physical obstacles can make this method challenging. Some rock materials, such as heterogeneous matrices or hematite- and pyrite-bearing matrices, prevent X-rays from penetrating. Additionally, bones with very low density or extremely thin bones may not be detected by this method (Janvier 1996).

For example, the neurocranial anatomy and morphology of the placoderm genera *Shearbyaspis* and *Ellopetalichthys*, was described using X-ray computed microtomography (Castiello and Brazeau 2018; Castiello et al. 2020).

2.2.2 Synchrotron radiation microtomography

Synchrotron radiation is a significant approach in modern palaeontology due to its ability to examine samples of various size scales (macro, micro, and nano) and materials of different natures, ranging from synthetic to biological, as well as mixtures of the various types of compounds that fossils often consist of (Prado et al. 2021). Due to its much more intense radiation compared to micro CT, synchrotron imaging can reveal structures in greater detail (Table 2). However, synchrotrons are rare tools; in Europe, there are only a few. The most powerful in the world is the European Synchrotron Radiation Facility (ESRF), located in Grenoble, France (*ESRF The European Synchrotron* 2019).

For example, using synchrotron imaging, the ancestral type of vertebrate dentition has been described in acanthothoracid placoderms, the most basal jawed vertebrates, specifically in the genera *Radotina*, *Kosoraspis*, and *Tlamaspis*, due to the presence of dermal jawbones with tooth rows (Vaškaninová et al. 2020).

2.2.3 3D virtual histology

3D virtual histology is a special application method of micro CT and synchrotron imaging, aiming to visualize histological structures (Table 2). Individual histological layers can be virtually separated into slices using specialized software, distinguished by colour, and examined in fine detail.

For example, the three-dimensional histology of the canal and pore systems in some scales of the osteostracan *Tremataspis* has been visualised (Qu et al. 2015; Bremer et al. 2021; Bremer et al. 2022).

comparison of imaging methods			
imaging method	**scan type**	**requires preprocessing**	**destruction**
SEM	external structures and ultrasculptures	acid or non-acid digestion	gold-palladium layering
X-ray	internal structures (lower resolution)	-	-
synchrotron	internal structures (higher resolution)	-	-
3D virtual histology	internal histological structures	-	-

Table 2: **Comparison of imaging methods, indicating their intended scan types and required preprocessing procedures.**

3 Systematics

Vertebrates divide into two large systematic groups: **Agnatha** (jawless vertebrates) and **Gnathostomata** (jawed vertebrates). Agnathans include Arandaspida, Astraspida, Anaspida, Heterostraci, Osteostraci, Galeaspida, Pituriaspida, and Thelodonti; Gnathostomes include Placodermi, Acanthodii, Chondrichthyes, and Osteichthyes. Most of the vertebrate groups that lived in the Lower Palaeozoic are now extinct (Figure 21). The jawless, fish-like vertebrates living today are lampreys and hagfishes, but both of these groups are likely derived. The jawed, fish-like vertebrates we observe in nature today belong to a successful and highly diversified group of modern bony fishes, and in smaller numbers, cartilaginous fishes such as sharks, skates, rays, and chimaeras. Cartilaginous fishes are a group with many archaic features, making them a valuable source of information. However, in some cases, the study of modern fish can also provide insights into extinct groups, thanks to the application of the theory of actualism.

3.1 Agnatha

Agnathans, comprising all jawless vertebrates, are mostly known from their head shields, isolated scales and bone fragments. In some species, entire body fossils were found, including tails covered with thick bony scales. The bodies of agnathans typically have armour, but the structure of the dermal armour is variable. Ventral and dorsal shields is a typical armour of Arandaspida; a single unit of shield applies to Osteostraci and Galeaspida; armour made of several plates of different sizes is characteristic for Heterostraci. Some agnathan groups, such as Anaspida and Thelodonti, do not have dermal shields, but instead have bony scales covering the entire body, including the mouth, pharynx and gill arches. Agnathans either have only a caudal fin or also possess dorsal and/or anal fins. Only three groups are known to have paired pectoral fins: Osteostraci, Thelodonti, and Pituriaspida (Long 2011).

The shield is formed by the basal bone, the middle vascular layer and the outer ornamental layer; however, the typical structure of the shield also varies in each agnathan group (Long 2011). The base of the bone is composed of laminated **as-**

pidin, an acellular bone tissue. Above the basal layer lies a middle vascular layer containing spaces for collagen fibers and, in rare cases, bone cells (osteocytes)—a feature typical of Osteostraci. An outer ornamental layer is perforated by pores and often covered by a shiny **enameloid** layer over the **dentin** (Roček 2002; Long 2011; Benton 2024).

Bellow, I will briefly outline the main characteristics of jawless vertebrate groups.

3.1.1 Arandaspida

The Arandaspida is an agnathan group from the **Ordovician** of Australia and South America (Janvier 1996).

The arandaspids are characterized by the extremely anterior position of their eyes, located at the tip of the head. A distinctive feature is the T-shaped dermal bone that separates the eyes and nostrils; eyes are positioned on the anterior margin of the dorsal shield. Arandaspids have a head armor consisting of two oval-shaped shields: a slightly flattened dorsal shield and a more convex ventral shield. Both shields have minute and closely set ornamentation with drop-shaped or oak-leaf shaped tubercules. The oral opening is situated ventrally to the dermal bone, and the lower part of the oral opening is covered with rows of scales. Only some body scales and caudal fin scales are known, but there are no ventral or dorsal median ridge scales. Arandaspid body scales are elognated, rod-shaped and arranged in chevrons, similar to those of anaspids; caudal fin scales are minute. Arandaspids have a caudal fin only, other fins are absent (Janvier 1996).

Although the exoskeletal structure is poorly known, some details have been revealed in the genus *Sacabambaspis*. Its exoskeleton consists of three layers: a laminar basal layer, a middle cancellous layer, and a superficial spongy layer that forms the tubercles (Janvier 1996).

3.1.2 Astraspida

The Astraspida is an agnathan group known only from the **Ordovician** of North America and Siberia (Janvier 1996).

The astraspids are characterized by a distinctive thick, glassy enameloid cap on the tubercles of their ornamentation. Other characteristic features include a flat dorsal shield and a convex ventral shield, connected by branchial platelets and eight large, uncovered gill openings (Janvier 1996). The dorsal shield is composed of many polygonal units, while the tail is covered with large, diamond-shaped scales (Long 2011).

Dermal bone consist of four layers: the basal layer of aspidin, a layer of cencellous of spongy bone, a layer of dentin forming the ridges and tubercules and an outer layer with enameloid capping (Long 2011).

3.1.3 Anaspida

The Anaspida (from the Greek *a-* "no" and *aspis* "shield") is an agnathan group that occurred from the **Early Silurian** to the **Late Devonian**, with sites located in northwestern Europe, North America and China (Janvier 1996; Long 2011).

The anaspid body is typically laterally compressed, eel-like shaped, and in some cases, it is covered by elongated, rod-shaped scales arranged in chevrons. Compared to arandaspids, which also exhibit such scale arrangement, anaspids additionally possess a median dorsal series of large ridge scales. The head is usually covered with minute scales or dermal plates, while the mouth is typically round-shaped, with dermal oral plates located on both the upper and lower lips. The eyes are large, laterally placed, and surrounded by structures resembling sclerotic rings, formed by dermal plates. Between the eyes, the pineal foramen and the nasohypopharyngeal foramen are located. Another characteristic feature is the presence of external branchial openings, behind which several triradiate spines (there may be only one spine or multiple) are located. Median dorsal scutes are situated dorsally along the back. The tail is significantly hypocercal, including a dorsally oriented epichordal lobe and a ventrally oriented chordal lobe, where the notochord is situated. Anaspids have paired fins covered with minute scales arranged in thin rows and, in some cases, an anal fin, but no dorsal fin is present (Janvier 1996).

Instead of large continuous dermal shields, they had dermal scutes and scales composed solely of acellular laminar bone tissue (strongly resembling aspidin); the presence of dentin is not observed (Janvier 1996).

Anaspids were probably marine and epipelagic (Janvier 1996). Due to certain morphological similarities, it has been suggested that anaspids are closely related to lampreys (Reeves et al. 2023; Benton 2024).

The phylogenetic relationships among the various forms of anaspids remain unclear; however, some genera—such as *Pharyngolepis*, *Rhyncholepis*, *Pterygolepis*, *Birkenia*, *Lasanius*, *Jamoytius*, *Endeiolepis*, *Euphanerops*, and others-have been well described from Northern Hemisphere (Blom, Märss, and Miller 2002; Sansom et al. 2010; Reeves et al. 2023).

3.1.4 Heterostraci

The Heterostraci (from Greek *hetero-* "different" and *ostracon* "shell") is an agnathan group that includes diverse forms of armoured fishes, which occurred from the **Early Silurian** to the **Late Devonian** (Janvier 1996; Long 2011). Heterostracans are known from North America, northern Europe, Russia, and Ukraine; by contrast, none have been found in the Southern Hemisphere, China, or Indochina (Janvier 1996). The group underwent its greatest radiation during the Silurian and Early Devonian (Long 2011; Benton 2024).

The heterostracans share only one characteristic that distinguishes them from other jawless groups: a single pair of external branchial openings. However, this feature is not entirely unique, as it is also shared by some jawed vertebrates, specifically holocephalans and osteichthyans. The earliest forms of heterostracans share many features with arandaspids and astraspids, including an acellular dermal exoskeleton, an oblong body shape, large dorsal and ventral shields covering the head, oral plates arranged in a fan-shaped pattern, and a dermal ornamentation of oak-leaf-shaped tubercles. Despite these similarities, these features are considered to represent only a generalized morphotype of the earliest vertebrates (Janvier 1996). Other morphotypes typically possess external armor consisting of many distinct plates (Keating 2013). Most heterostracans were small fishes measuring several tens of centimeters, but some forms—such as psammosteids—were large and flattened, reaching lengths of more than a meter (Long 2011). Despite variability of size, proportion, arrangment and number of plates, the head is almost always covered with large median dorsal and ventral shields, along with a pair of elongated lateral branchial plates (Janvier 1996).

Every heterostracan has head armour—dorsal and ventral plates—typically composed of several elements containing canals and the sensory-line system, and a body covered with large scales. The tail is diphycercal or pad-shaped, with small scales (some of which may be larger than others) arranged in radial rows. These rows likely align with the positions of large underlying cartilaginous radials. The body is bordered by a series of dorsal and ventral ridge scales, but median fins (except for the caudal fin) and paired fins are absent. The most distinctive and variable part is the head armour, which can be laterally compressed, fusiform, ventrally bulging, or may have dorsal, rostral, or lateral expansions (Janvier 1996).

The dermal shield consists of three layers: a basal laminal layer, a middle cancellous layer forming honeycomb-shaped cavities—both made of aspidine—and an outer layer of ridges or tubercles made by dentine, capped by enameloid (Janvier 1996; Benton 2024). In only one group, the Psammosteidae, the typical honeycomb-like structure is absent and is instead replaced by a thick spongy layer (Janvier 1996).

The habitat of heterostracans was predominantly shallow marine waters, though in some cases it also included freshwater environments such as rivers and deltas (Janvier 1996).

According to the older phylogeny proposed by Janvier (1996), the diversity is represented by two major, distinct groups: Cyathaspidiformes and Pteraspidiformes. The group **Cyathaspidiformes** is characterized by a single dorsal shield plate formed through the fusion of several smaller dermal plates, featuring longitudinal, more or less parallel dentine ridge ornamentation. The rest of the body is covered with large scales arranged in chevrons or in a vertical orientation. In contrast, the group **Pteraspidiformes** is characterized by a dorsal shield composed of several smaller, independent plates with concentric, laterally serrated dentine ridge ornamentation. The rest of the body is covered with relatively small, diamond-shaped scales (Janvier 1996).

3.1.5 Osteostraci

The Osteostraci (from Greek *osteon* "bone" and *ostracon* "shield") is an agnathan group known from **Early Silurian** to **Late Devonian** (Janvier 1996; Long 2011). Osteostracan finds are known from North America, Europe, Ukraine, Russia, and central Asia. However, the group show signs of endemism, i.e. some subgroups have been found only in certain places of the world (Janvier 1996). The group underwent main radiation in the Early Devonian, while in the Silurian, osteostracans are rare in the fossil record (Janvier 1996; Long 2011).

The osteostracans possess many unique features, such as a head shield with sensory organs referred to as "cephalic fields," which include certain median and lateral shallow depressions on the surface of the dorsal shield (Janvier 1996). The head armor in basal forms exhibits a horseshoe shape, however, the morphology of the head shield is quite diverse, ranging from rectangular or hexagonal forms to those with backward-oriented dorsal spines or rostral spines (Janvier 1996; Benton 2024). The cephalic fields are covered with individual polygonal dermal bone platelets, which are connected to the labyrinth cavity through large, dichotomously branching canals (Janvier 1996). On the head shield there are two close-set round eye holes, and between the eye holes, is situated a smaller, key-shaped, opening for nasal organs and a tiny pineal opening. The underside of the fossilized head shield is mostly open below the mouth and gill cavity, but in life, it was covered by a mosaic of numerous small dermal platelets (Long 2011).

Osteostracans are also notable for having paired pectoral fins attached directly to the head shield, along with a unique horizontal lobe lining the underside of the tail fin, which is sometimes considered a modified anal fin. However, in more derived forms, there is a tendency for reduction of the cephalic shields, paired pectoral fins, dorsal fin, and horizontal lobe; by contrast, the overall body shape remains relatively conservative (Janvier 1996). The pectoral fins are connected to an internally ossified shoulder girdle, which supports a simple paddle-shaped cartilage structure. The tail is covered with thick scales typically organized in vertical rows of rectangular units, topped by smaller ridge scales along the back that connect with a similar series beneath the belly (Long 2011).

Osteostracans differ from other agnathan groups by the diversity, complexity and histological composition of their exoskeleton. The scales and tesserae of the shield are characteristically composed of cellular bone, i.e. osteocytes (Janvier 1996; Long 2011). The only exception is genus *Escuminaspis*, which has acellular bone, covered with a layer of dentinous tissue, i.e. mesodentine. The mesodentine is sometimes also covered by an enameloid layer. The exoskeleton is characterized by a specific system of canals, particularly a horizontal network known as the 'mucous canal' system. This network consists of larger inter-areal canals forming a polygonal pattern along the boundaries of the tesserae, as well as smaller intra-areal canals within the tesserae. In addition, the exoskeleton and endoskeleton are separated by a network of canals with blood vessels supplying the exoskeleton (Janvier 1996).

In addition to the exoskeleton made of cellular bone, the endoskeleton is also ossified, allowing the internal anatomy to be well-documented. This includes the braincase, which encloses the brain and sensory organs, as well as components of the circulatory and digestive systems, and even the canals of the inner ear, which function as organs of balance (Janvier 1996; Benton 2024).

Osteostracans had two types of lifestyles. Less mobile forms with large shields and no pectoral fins lived as bottom-dwellers, while forms with pectoral fins and longer caudal fin were nectonic (Long 2011). They occurred in shallow marine environments, such as lagunas, tidal flats, and deltas, or some could live in rivers (Janvier 1996).

Osteostracans are divided into two distinct groups: cornuate and non-cornuate forms. The group Cornuata is defined by the presence of cornual processes located in front of the paired fins and the posterior closure of the dermal rim of the oro-branchial cavity. It comprises five major subgroups: Cephalaspidida, Zenaspidida, Benneviaspidida, Kiaeraspidida, and Thyestiida (Janvier 1996).

3.1.6 Galeaspida

The Galeaspida (from Latin *galea* "helmet" and Greek *aspis* "shield") is an agnathan group that occured from **Early Silurian** to **Middle Devonian** (except for one species known from the Late Devonian). Their occurrence is associated exclusively to southern China and northern Vietnam (Janvier 1996; Long 2011).

A unique feature of galeaspids is their head armour, consisting of a single bony head shield with a large median opening in the anterior part of the shield (Janvier 1996; Long 2011). This opening may take the form of a longitudinal slit, a transverse slit, a broad oval, or a heart shape (Benton 2024). Additionaly, the openning connects to the ventrally located orobranchial cavity. The dorsal side of the shield has an ornamentally patterned arrangement of the main and infraorbital lateral-line canals. The head shield can be more or less elongated, oval, horseshoe-shaped (similar to that of osteostracans), or feature long rostral processes (Janvier 1996). Galeaspids possessed three dorsal fins, an almost symmetrical hypochordal tail and a pair of ventrolateral fins leading from branchial to caudal part of the body. The ventrolateral fins resemble the paired fin flaps observed in other early jawless jawed-vertebrate relatives—especially the ventrolateral ridges of cephalaspid osteostracans, which also had distinct pectoral fins (Gai et al. 2022). The body was covered with minute, dome-shaped scales featuring a protruding base and a single external tubercle (Janvier 1996).

The dermal bone consists of many minute units that are more or less fused, distinctly different from the larger tesserae of osteostracans. The head shield is composed of many such units, which, through fusion, form a continuous display layer with a laminar structure visible in vertical section. There is no dentine or cellular bone tissue, but some genera possess a transparent, enameloid-like tissue within the external elevations or tubercles—similar to those found in astraspids. The scales share the same structure as the head-shield units, and in some cases, the head shield gradually transitions into a scaly body surface toward the posterior part of the body. Like osteostracans, galeaspids exhibit similar boundary structures between the exoskeleton and endoskeleton, including a subaponeurotic vascular network and large canals of the lateral sensory-line system lined with perichondral bone. Additionally, they share the same endoskeletal structure (Janvier 1996).

Galeaspids were bottom-dwellers, typically found in sandy or muddy areas of coastal marine settings like deltas and lagoons (Janvier 1996).

In systematics, galeaspids are divided into three major subgroups: Eugaleaspidiformes, Huananaspidiformes and Polybranchiaspidiformes (Janvier 1996).

3.1.7 Pituriaspida

The Pituriaspida is an agnathan endemic group known only from the **Lower to Middle Devonian** of Australia (Janvier 1996; Benton 2024).

Pituriaspids are known from only a few specimens. All specimens share the presence of a long rostral process and short cornual process on the head shield. Located on the top of the head shield are the orbits and an adorbital depression, possibly for some sensory organ. The head shield, when viewed ventrally, is quite similar to that of osteostracans; however, dorsally, it appears completely different due to its unique morphology and associated processes. The exoskeleton features minute, rounded tuberculate ornamentation. A distinctive feature of pituriaspids is the area near the cornual processes on the head shield, which appears to be an attachment site for paired fins, suggesting the presence of pectoral fins (Janvier 1996). Pituriaspids are unique due to the absence of a nasohypophyseal opening in the cephalaspid-like shield (Long 2011). Additionally, like some cephalaspids and galeaspids, they possess a perichondrally ossified endoskeleton (Janvier 1996).

The group includes only two, but quite distinct, genera: *Pituriaspis* and *Neeyambaspis*. Both genera of pituriaspids occur in deltaic freshwater deposits, even together with thelodonts and placoderms (Janvier 1996).

3.1.8 Thelodonti

The Thelodonti (from Greek *thele* "nipple" and *odontos* "tooth") is an agnathan group known from **Late Ordovician** to **Late Devonian** (Long 2011). Their distribution was likely worldwide, as suggested by the fossil record (Benton 2024).

Thelodonts lack any bony head shield, yet their entire bodies—and in some cases, even the regions inside the mouth, pharynx, and gill slits—are entirely covered by thousands of small, tooth-like scales (denticles) (Janvier 1996; Long 2011; Benton 2024). They are mostly known from abundant isolated scales, while complete body morphologies are preserved only in a few exceptionally rare specimens (Janvier

1996). Even when whole-body preservation occurs, reconstructing three-dimensional morphology remains challenging due to the lack of an ossified exoskeleton or dermal plates (Janvier 1996). Body length typically does not exceed 15 centimeters, but some larger forms could reach up to 1 meter (Long 2011). Some thelodonts are dorsoventrally flattened, with a broad snout, wide mouth, and eyes positioned on the sides of the head. Their gill openings are located ventrally, while lateral, wing-like pectoral fin folds extend from the sides. They also possess short dorsal and anal fins and a long ventral caudal fin. In contrast, other species are deep-bodied and laterally compressed, with a deep, symmetrical caudal fin that features both an upper and lower fleshy lobe. Furthermore, these forms possess a large stomach—an anatomical feature that once was thought to be absent in agnathans (Long 2011; Benton 2024). Another characteristic feature of some thelodonts is their growing scale base, which develops anchor-like outgrowths or extensions. However, this trait is not universal among all thelodonts, suggesting that the group may not be monophyletic (Janvier 1996). Additionally, thelodont scales vary widely in shape depending on their body location (Long 2011).

There are five major types of thelodont scales, distinguished by differences in their histology: achanolepid, thelodontid, apalolepid, loganiid, and katoporid (Figure 1) (Janvier 1996). A defining characteristic shared across all types of thelodont scales is a non-growing crown composed of dentine, supported by a growing base made of acellular bone (aspidine), and the complete absence of enamel. In addition to these features, thelodonts display a scale and tubercle composition similar to that of many other early vertebrates (Janvier 1996; Benton 2024). **Achanolepid scales** are considered the most primitive scale type among thelodonts, beginning in the Late Ordovician and extending into the Early Silurian. These scales are generally minute, featuring a bulging base without a hollow pulp cavity. Their crowns are composed of a distinctive dentine tissue in which dentine tubules form a network-like pattern, often described as "irregular dentine." This type of scale occurs in genera such as *Kawalepis* and in some specimens attributed to *Loganellia*. **Thelodontid scales** resemble the dermal denticle (placoid) scales of modern sharks, but with key histological differences: thelodontid scales bear a continuously growing base and lack the neck-associated vascular pulp canal typical of shark scales. Their crowns are made

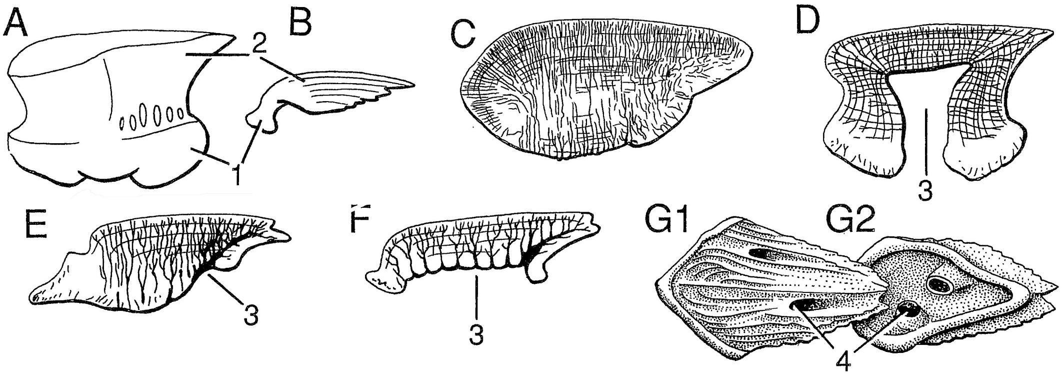

Figure 1: **Thelodonti.** Scales. A *Thelodus*; B *Apalolepis*; C-F vertical section through scales of achanolepid (C), thelodontid (D), loganiid (E), and katoporid (F) types; G *Phlebolepis*, lateral-line scales pierced by sensory-line pores in external (G1) and internal (G2). 1 base, 2 crown, 3 pulp cavity, 4 sensory-line pores. After Janvier 1996 (modified).

of orthodentine and feature ascending dentine tubules. This morphology is found in genera such as *Thelodus*, *Canonia*, and *Amaltheolepis.* **Apalolepid scales** feature a broadly expanded crown composed of orthodentine atop a small, trumpet-shaped base. The pulp cavity is narrow and branching—a distinctive deviation from the typically simple pulp structure seen in other thelodont scales. This scale morphology is characteristic of the genus *Apalolepis* and is generally considered a specialized variant of the thelodontid scale morphology. **Loganiid scales** exhibit a large, swollen base often extending forward as a prong, paired with an extremely narrow pulp cavity limited to the posterior region of the scale. The crown is formed from dentine with densely packed tubule bundles, which originate either from small cavities within the base or directly from the pulp cavity itself. This internal structure closely resembles the mesodentine found in osteostracan scales. This distinctive histology is characteristic of genera such as *Loganellia* and *Helenolepis.* **Katoporid scales** are characterized by a notably large and widely open pulp cavity. From this cavity arise prominent expansions that branch into numerous dentine tubules. The resulting internal structure closely resembles mesodentine seen in osteostracan scales. This particular histological arrangement is characteristic of genera such as *Phlebolepis* and *Katoporodus.* These scale types may represent a continuum between mesodentine and orthodentine, including intermediate, mesodentine-like tissues. However, the polarity of this gradient has not been clearly established (Janvier 1996).

Thelodonts likely exhibited a range of ecological behaviors. According to Turner

(1992), several distinct thelodont lifestyles have been proposed. The larger, flattened species were slow-moving bottom dwellers, similar to modern angel sharks. They may have sifted through sediment for invertebrates or lay in wait to ambush small passing prey. In contrast, the more deep-bodied forms were likely agile swimmers that fed either by filtering suspended particles or by capturing free-swimming organisms. Some other forms, equipped with prominent spines, may have had the ability to raise those spines from a flattened position to an outward-facing defensive posture—resembling the inflation and spine display seen in modern pufferfish (Turner 1992; Long 2011).

Knowledge of the diversity of thelodonts is limited, primarily concerning isolated scale morphology and histology. However, two primary theories have been proposed regarding their relationship to other vertebrate groups. One theory, suggests that thelodonts represent a sister group to gnathostomes, particularly chondrichthyans. This hypothesis suggests that thelodonts are gnathostomes, defined by their scale base, which, in contrast to shark scales, is capable of growth and develops anchorage devices. The alternative theory, argues that thelodonts are generalized stem-group vertebrates from which other groups, such as anaspids, heterostracans, osteostracans, galeaspids, or even gnathostomes, arose. Both theories have their merits and limitations, and neither provides a fully satisfactory explanation. Based on common features in scale morphology and histology, three primary subgroups of thelodonts have been proposed: **Thelodontida**, encompassing taxa with thelodontid and apalolepid scale types; **Loganiida**, including taxa with loganiid and achanolepid scale types; and **Katoporida**, comprising taxa with katoporid scale types (Janvier 1996).

3.2 Gnathostomata

Gnathostomes, jawed vertebrates, include jawed fishes and all tetrapods—that is, all vertebrates except agnathans (Benton 2024). Jawed fish are known from their head and trunk shields, scales, bone fragments, spines, teeth and tooth whorls.

The first evidence of jawed vertebrates was presumed to be in the Late Ordovician in North America in form of isolated scales resembling shark scales (Sansom, Smith, and Smith 1996) and Early Silurian shark teeth from China (Andreev et al. 2022).

There is ongoing debate about the evolutionary development of the jaw and the nature of the structures that preceded it. According to Benton (2024), two main models of jaw origin are currently considered relevant. The first model is the so-called "**gill arch theory**", which proposes that jaws are modified gill arches, while he second model is the so-called "**mandibular confinement hypothesis**," which proposes that jaws are modified lip structures, which were originally not part of the branchial (gill) series but later acquired the developmental pattern of gill arches to become jaws (Benton 2024).

Another ongoing debate is about the origin of teeth. Classic theories propose two contrasting models for the evolutionary origin of vertebrate teeth. One, known as the “**outside-in**” hypothesis, posits that teeth evolved from ectoderm-derived skin denticles which migrated into the oral cavity. The other, the “**inside-out**” hypothesis, argues that patterned odontodes first emerged in the endodermal pharyngeal region and were later co-opted to the jaw margins (Fraser et al. 2010; Lingham-Soliar 2014).

What defines jawed vertebrates, besides the presence of jaws and teeth, is the presence of paired fins and, in some cases, an ossified skeleton or ossified parts of the skeleton (Lingham-Soliar 2014).

The origin and evolution of jaws was one of the greatest events, or revolutions, in the history of vertebrates. Thanks to the emergence of jaws, vertebrates evolved from bottom feeders or parasites to predators. This revolution enabled them to exploit a wide variety of habitats and lifestyles (Lingham-Soliar 2014). Especially in the Devonian, jawed vertebrate groups became significantly dominant, reaching the peak of diversity and suppressing or replacing the jawless groups. Niche replacement is also suggested by the similarity in body shape of some placoderms and jawless vertebrates (Long 2011).

Bellow, I will briefly outline the main characteristics of jawed vertebrate groups.

3.2.1 Placodermi

The Placodermi (from Greek *plax* "plate" and *derma* "skin") is a gnathostome group known from the **Early Silurian** to **Late Devonian** (Long 2011). Based on taxonomic group, environmental context, and geographic region, placoderm diversity varied widely across different parts of the world. While knowledge of their full diversity in the Silurian is limited, they flourished and diversified extensively during the Devonian (Janvier 1996; Long 2011).

A defining trait of placoderms is the presence of a distinct head shield and trunk shield. In rare cases, these shields may fuse into a single composite armour plate (Long 2011). Articulation between the head and trunk shields is not a universal feature among placoderms, but it evolved independently in four subgroups: arthrodires, antiarchs, petalichthyids, and ptyctodontids. Placoderms consistently possess an anterior dorsolateral plate within the thoracic armour and a paranuchal plate atop the skull roof—even in taxa with highly reduced dermal armour, these elements are retained (Janvier 1996). Dermal shields consist of overlapping bony plates arranged in a mosaic pattern, forming their distinctive armored covering. Each armour plate in placoderms is distinguishable by its unique combination of shape, the way it overlaps neighboring plates, the presence or absence of sensory-line canal grooves, and its external (dermal) ornamentation. These features allow individual plates to be identified in the fossil record (Long 2011). The head armour comprises the skull roof along with a variable number of cheek plates—typically up to three—that together form a movable operculum protecting the gill chamber. The skull roof is composed of several plates that are joined by complex sutures or overlap one another, and it is firmly attached to the more or less ossified braincase. When a pineal foramen is present, it pierces a distinct pineal plate (Janvier 1996). In early forms, the braincase is well-ossified, but in later forms, it is composed of cartilage instead (Long 2011). Similarly to the skull roof, the thoracic armour consists of overlapping or sutured plates, typically comprising one or two median dorsal plates and paired anterior dorsolateral, anterolateral, and anterior ventrolateral plates (Janvier 1996). Between the cheek and the thoracic armour on each side lies a single branchial opening. The eyes were large and enclosed in a sclerotic ring composed of four plates. The nostrils

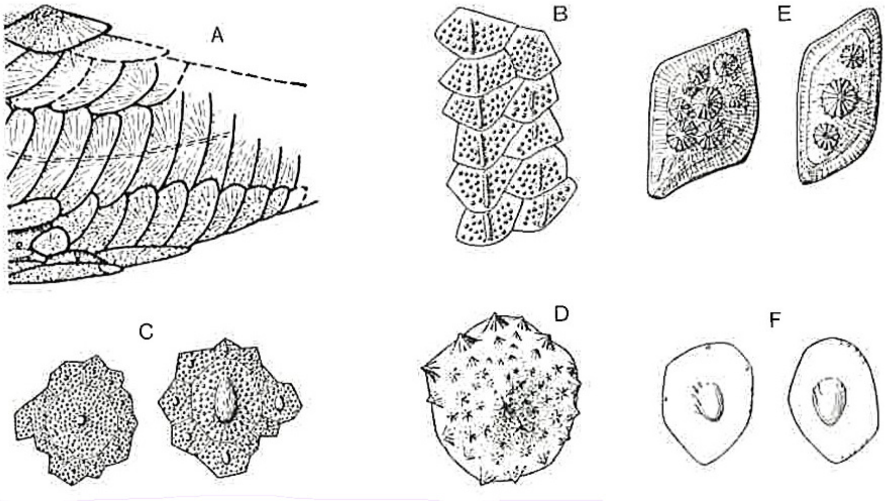

Figure 2: **Placodermi.** Scales and tesserae. A *Sigaspis lepidophora*, flank scales; B *Lunaspis broilii*, flank scales; C *Gemuendina stuertzi*, large scales from pectoral fin; D *Jagorina pandora*, large tesserae; E *Radotina kosorensis*, body scales; F *Stensioella heintzi*, dorsal body scales. After Denison 1978.

were usually positioned ventroanteriorly, though in some taxa they occurred dorsally. Placoderms possess an epicercal caudal fin and a dorsal fin, but the presence of an anal fin is unknown. The pectoral fins are usually well-developed and covered with minute scales; however, in some antiarchs, these fins are encased in dermal plates and modified into distinctive appendages. Pelvic fins are typically small, and only ptyctodontid males bear hook-shaped dermal scutes on the metapterygium, resembling the claspers of chondrichthyans (Janvier 1996). Unarmoured parts of placoderm bodies were usually covered with scales that varied greatly in shape, size, and thickness. Most commonly, these scales were diamond-shaped and tuberculated (Figure 2). Many placoderms, however, lacked scales on the trunk and tail (Janvier 1996).

Most placoderms had a sharply edged lower jaw that opposed a row of approximately eight small bony plates along the upper jaw margin (Benton 2024). For a long time, it was believed that placoderms lacked teeth. However, recent studies shows that certain species of arthrodires, and even the most basal placoderm acanthothoracids, did possess teeth (Vaškaninová et al. 2020; Benton 2024). Arthrodire teeth are located inside the mouth, behind the main shearing bone plates at the edges of the jaws. These teeth most likely evolved independently in placoderms, separate from the origin of teeth in other gnathostomes (Benton 2024). In contrary,

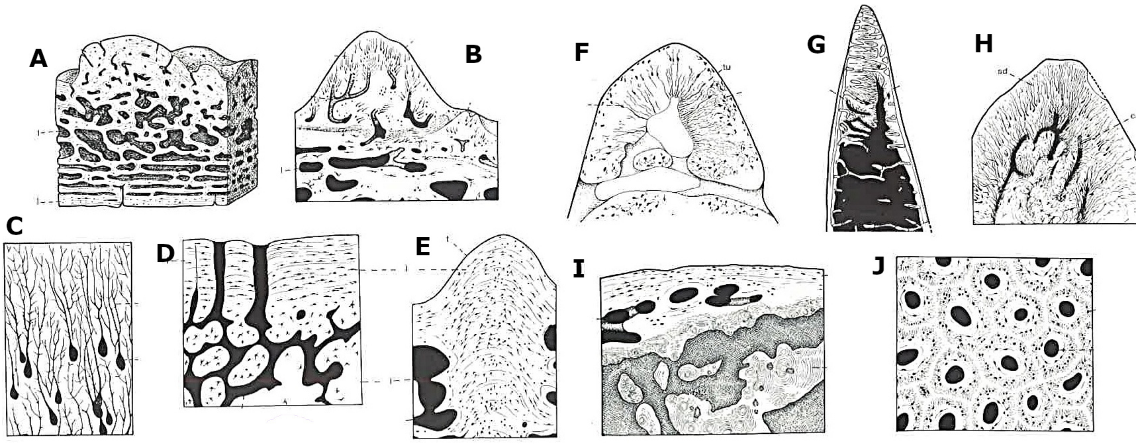

Figure 3: **Placodermi.** Histology. A block diagram of dermal bone of *Arctaspis boeli*; B vertical section through two generations of tubercles on dermal bone of *Phlyctaenius acadicus*; C vertical section through semidentine of *Phlyctaenius acadicus*; D vertical section through superficial layer and part of middle layer of dermal bone of *Phyllolepis* sp.; E vertical section through tubercle of *Asterolepis ornata*; F vertical section through tooth of *Pachyosteus bulla*; G vertical section through biting edge of dental plate of dental plate of *Rhynchodus* sp.; H vertical section through tooth of *Phlyctaenius* sp.; I vertical section through perichondral bone and globular calcified cartilage of mentomandibular of *Plourdosteus canadensis*; J transverse section of cribriform bone of *Asterolepis ornata.* After Denison 1978 (modified).

acanthothoracid dentitions differ fundamentally from those of arthrodires. Their teeth are arranged along the jaw margins, attached to a cheekbone or aligned on a series of small dermal bones. These teeth were added lingually (from the inside edge of the jaw), a pattern mirrored in chondrichthyans and osteichthyans. Some researchers propose that this dental pattern—marginal placement of teeth on dermal jaw bones with lingual addition—represents the ancestral condition for all jawed vertebrates (Vaškaninová et al. 2020).

The characteristic histologic feature of placoderm dermal armor is semidentine, a unique dentine type in which polarized odontocyte cell bodies are embedded within the matrix. The cell spaces in semidentine are drop-shaped, each featuring a single, outwardly directed elongation. This specialized tissue is found in the superficial portion of the tubercles covering the dermal armor bones. Semidentine tissue distinguish placoderms from other early vertebrates (Figure 3) (Janvier 1996).

Placoderms inhabited a wide range of aquatic environments, including marine waters, river deltas, and lagoons. Some species were components of coral reef ecosystems, while others were restricted to sandy shore habitats or bottom substrates.

Among placoderm groups, antiarchs adapted well to both shallow marine and freshwater settings, and arthrodires occupied various zones from benthic to active pelagic zones. Most arthrodire placoderms possessed jaws adapted for crushing and shearing rigid invertebrate exoskeletons—such as crustaceans, brachiopods, and mollusks. In contrast, more advanced arthrodires developed gnathal plates and preyed on other fishes. Ptyctodontids had a markedly different dental arrangement, instead bearing beak-like tooth plates that closely resemble those of modern chimaeras rather than true teeth. Rhenanids—flattened, ray-like placoderms—were almost certainly bottom-dwelling predators, closely resembling modern rays or skates in both body shape and lifestyle (Janvier 1996). Interestingly, placoderms practiced viviparity and internal fertilization—evidence for which comes from fossilized embryos found within the skeleton of the ptyctodontid *Materpiscis* and the arthrodire *Incisoscutum* (Benton 2024).

Placoderms are generally considered a paraphyletic assemblage, meaning some lineages may represent basal jawed vertebrates from which modern gnathostomes (sharks, bony fishes, and tetrapods) emerged, while other placoderm branches, such as arthrodires, likely constitute a separate, monophyletic subgroup (Long 2011). The total diversity of placoderms encompasses approximately 350 genera (Benton 2024). Due to ongoing debate over the polarity and distribution of key anatomical features within the group, it is not possible to construct a universal body plan for a hypothetical generalized placoderm, nor to designate a single taxon as a definitive morphotype (Janvier 1996). However, based on the pattern shape of bony plate, there are major placoderm groups: Arthrodira, Antiarcha, Petalichthyida, Ptyctodontida, Rhenanida, Acanthothoraci, Stensionelida and Pseudopetalichthyida (Long 2011).

The groups **Stensioellida** and **Pseudopetalichthyida** were primitive placoderms with only a few dermal plates developed. They possessed broad, wing-like pectoral fins, and their bodies were covered with ornamented placoid scales. Their phylogenetic relationship to other placoderm groups is considered the most basal, due to the absence of several bones found in more derived groups (Long 2011). Only a few genera have been recognized: *Stensioella*, *Pseudopetalichthys* and *Paraplesiobatis* (Janvier 1996).

The group **Petalichthyida** consists of small placoderms with dorsally positioned orbits (Janvier 1996; Long 2011). They had widely splayed pectoral fins, and their dermal armour was ornamented with characteristic linear rows of small tubercles. Their bones contained sensory-line canals housed within thick tubular channels, which are clearly visible on the internal surface of the skull bones (Long 2011). Like ptyctodontids, petalichthyids also exhibit an X-shaped pattern formed by the intersection of the central supraorbital sensory-line canal and the posterior pit line (Janvier 1996). They were likely bottom-dwellers, although their feeding habits remain uncertain due to the lack of preserved mouthparts (Janvier 1996; Long 2011; Benton 2024). One of the best-known petalichthyids, *Lunaspis*, had the anterior part of its head shield covered with minute scales (Benton 2024). In *Lunaspis*, the body and tail were covered with small diamond-shaped scales and a few very large median dorsal scutes, while the pectoral fins bore relatively large scales (Janvier 1996). Petalichthyids reached their greatest diversity in the Early Devonian and are known from Europe, Asia, Australia, and both South and North America (Long 2011).

The group **Rhenanida** featured a flattened body with reduced thoracic armour and large, wing-like pectoral fins, strongly resembling stensioellid placoderms or chondrichthyan skates and rays (Janvier 1996; Long 2011). Their skulls were variably covered with dermal bone composed mainly of small, polygonal platelets—an identifying feature that sets them apart from other placoderm groups. The trunk shield was notably short, while the tail was adorned with numerous bony platelets of different sizes (Long 2011). Their gnathal plates were flattened and coated with a shagreen of tiny denticles (Janvier 1996). Rhenanids are known exclusively from the Early Devonian of Europe and North America (Long 2011). Although complete rhenanid fossils are rare due to their delicate exoskeletons, their distinctive platelets are frequently found as microscopic ichthyoliths (Janvier 1996).

The group **Acanthothoraci** is distinguished by its heavily ossified armour, which gives the group its name—meaning "spiny trunk shield". This bony armour displays elaborate surface ornamentation (Long 2011). Acanthoracids differ from most other placoderms and jawed vertebrates in the position of the nasal capsule, which is situated between the eyes and lies deep beneath the upper lip; for this reason, these forms are sometimes referred to as “posterior-nosed" (Dupret et al. 2014). They are also characterized by their unique skull bone patterns and relatively short trunk shields (Long 2011). In certain taxa, the skull roof is partially tessellated (Janvier 1996). In juveniles, the plates of the armour were likely separated, appearing fused only in adulthood (Benton 2024). The eyes themselves were heavily ossified by sclerotic capsules and connected to the braincase via a stalk of bone or cartilage known as an eyestalk, a feature shared by both placoderms and modern sharks. The skull of acanthothoracids also contained cavities that housed the brain and cranial nerves, offering valuable insight into the soft-tissue anatomy of early jawed vertebrates (Long 2011). Notably, the structure of the braincase bears a strong resemblance to that of osteostracans and galeaspids (Janvier 1996). Acanthothoracids are primarily known from the Early Devonian and have been discovered in Australia, Europe, Russia, and Arctic Canada (Long 2011). In the Prague Basin, acanthothoracid placoderms constitute a dominant group during the Early Devonian. Representative genera found in this region include *Radotina*, *Kosoraspis*, and *Tlamaspis* (Vaškaninová and Kraft 2014a; Vaškaninová et al. 2020).

The group **Ptyctodontida** is distinguished by robust crushing plates in the jaws, a trait that inspired the group’s name—meaning “beaked tooth”. Their armour is reduced, consisting of a very short trunk shield and a small head shield (Long 2011). They had large heads with prominent eyes. As in petalichthyids, ptyctodontids also display an X-shaped pattern formed by the intersection of the central supraorbital sensory-line canal and the posterior pit line. The trunk shield is very short and forms a mere "ring" of dermal plates. Most ptyctodontids had dermal plates with a spongy surface that were likely covered by skin, although some genera exhibited tuberculate ornamentation (Janvier 1996). Their caudal fin was slender and whip-like, posterior and dorsal fins were long, and anterior dorsal fin was high, supported by a spine on the trunk (Benton 2024). In overall appearance, ptyctodontids resemble modern chimaeras and whipfishes. The group is notable for exhibiting sexual dimorphism, with males possessing dermal clasping organs used for internal fertilization. Fossilized embryos have been found in the genera *Materpiscis* and *Austropyctodus*, providing rare evidence of viviparity. Ptyctodontids are known from the Early, Middle, and Late Devonian, with fossils discovered in Australia, Europe, North America, and Russia (Long 2011).

The group **Antiarcha** comprises small placoderms distinguished by their pectoral fins, which were encased in bony tubes—referred to as pectoral appendages and sometimes informally called "arms." These appendages were usually connected to the trunk shield by joints; only the genus *Remigolepis* lacks them. In more derived forms, these structures were segmented (Long 2011). The head was short, and the eyes, pineal opening, and nostrils were grouped together within an oval-shaped orbitonasal fenestra located at the center of the skull roof. The trunk shield was elongated and typically included two median dorsal plates. In some species, the body and tail were covered with large, prominent scales, while others—such as *Bothriolepis*—lacked this feature. The dermal plates and scales of antiarchs were ornamented with either small tubercles or intricate vermiculate (worm-like) patterns (Janvier 1996). Antiarchs first appeared in the Silurian and Early Devonian of China, later expanding their range and reaching peak diversity in the Middle and especially Late Devonian. This was particularly true for the highly successful bothriolepids and asterolepids (Long 2011).

The group **Arthrodira** is the most diverse and abundant group of placoderms-comprising about 200 genera-with body sizes ranging from just a few centimeters to as much as five or six meters (Janvier 1996; Benton 2024). Arthrodires are characterized by having two pairs of upper jaw plates. Their skulls followed a consistent bony pattern, with the eyes positioned laterally and a distinct cheek unit that was hinged along the side of the skull roof. In more advanced arthrodires, the head and trunk shields were connected by a ball-and-socket joint, whereas more primitive forms retained a sliding neck joint. Arthrodires are generally classified into two major groups: basal forms—such as antarctaspidids, wuttagoonaspidids, actinolepids, and phyllolepids—which possessed long trunk shields with large spinal plates; and more derived forms—such as phlyctaeniids—which had shorter trunk shields, reduced or absent spinal plates, and pectoral fins that were not fully enclosed within the trunk shield (Long 2011). The external skeleton of arthrodires consisted of thick plates made of cellular bone, typically ornamented with costate (ridged) tubercles. Within these tubercles, the outermost layer was composed of pallial semidentine. In brachythoracids, this ornamentation was likely covered by skin (Janvier 1996). Arthrodires are known from Early to Late Devonian deposits and are found in both marine and freshwater environments (Long 2011).

3.2.2 Acanthodii

The Acanthodii (from Greek *akantha* “spine” and -odii, denoting fishes) is a group of gnathostomes known from the **Late Ordovician** to the **Early Permian**, with a peak in diversity during the Devonian (Long 2011; Benton 2024). Most acanthodian taxa had a global distribution, though some lineages were regionally restricted, notably occurring only in Australia and Antarctica (Janvier 1996).

Acanthodians are characterized by the presence of robust, deeply inserted bony spines (Figure 4) located in front of every paired and midline fin, with the notable exception of the caudal fin (Janvier 1996; Long 2011). Sometimes they are referred to as “spiny sharks,” a term inspired by their resemblance to early sharks, to which they are closely related. Knowledge of early acanthodian morphology is based primarily on the shape of the body and fins, as the three-dimensional anatomy of the head remains almost entirely unknown. In contrast, more derived forms possess ossified skull elements and gill-arch structures. Although complete acanthodian fossils are rare, their scales—and occasionally spines—are abundant and widely used for biostratigraphic age determination of Paleozoic sedimentary rocks (Long 2011). Acanthodians had relatively large heads covered with delicate dermal plates or scales, and their prominently positioned eyes were frequently encircled by multiple sclerotic (circumorbital) plates. Some species also possessed a sensory canal system within these dermal plates (Benton 2024). The head of acanthodians was separated from the body by the pectoral (scapulocoracoid) girdle, which in some species was even ossified; however, in general, acanthodians were poorly ossified (Janvier 1996; Benton 2024). The caudal fin was epicercal (Janvier 1996). The entire body was generally small and slender—rarely exceeding 20 centimeters in length—and covered with small, closely fitting scales (Benton 2024).

Acanthodian scales consist of a bone base—typically acellular, though occasionally cellular—supporting a dentine crown, and they commonly display concentric growth layers. These scales frequently exhibit a bulging base and a unique "onion-skin" pattern of growth rings (Janvier 1996; Benton 2024). An exception to this pattern is in the genus *Machaeracanthus*, where successive dentine layers in the scale crown do not fully overlap one another. Instead, they resemble the growth organization found in some Paleozoic chondrichthyans, whose scales exhibit additive growth similar to that observed in *Machaeracanthus.* Some acanthodians possessed scale crowns with a pore-canal system, though markedly different from those found in osteostracans and sarcopterygians, and this network of canals may have been linked to their sensory-line system. Acanthodian fin spines are built from a combination of orthodentine and mesodentine, which form the external ornamentation surrounding a core of trabecular dentine and bone (either cellular or acellular), often encasing a central canal. In climatiids, these spines can superficially resemble the median fin spines of ctenacanthiform sharks. However, ctenacanthid spines differ markedly—they feature a much larger central canal (often widely open at the base), a long basal insertion, a median ridge along the posterior surface, and a thin enameloid layer atop the dentine ornamentation (Janvier 1996). Acanthodians exhibit considerable diversity in dental morphology: some species possess individual teeth or tooth whorls, others display placoderm-like dentition, while several taxa are entirely toothless (Benton 2024).

Although acanthodians were primarily marine, some species occupied freshwater environments (Janvier 1996; Benton 2024). Feeding strategies among acanthodians varied considerably depending on morphology and dentition. Ischnacanthiformes and Climatiiformes were predatory. By contrast, Acanthodiformes lacked teeth and possessed long gill rakers, traits consistent with a microphagous suspension-feeding (Janvier 1996; Long 2011; Benton 2024).

Based on anatomical traits like the presence or absence of pectoral fin–bracing bones, the number of dorsal fins, and the structure of teeth and scales, three primary groups within Acanthodii are commonly recognized: Climatiiformes, Ischnacanthiformes and Acanthodiformes (Janvier 1996; Long 2011).

The group **Climatiiformes** is characterized by robust fin spines with wide bases

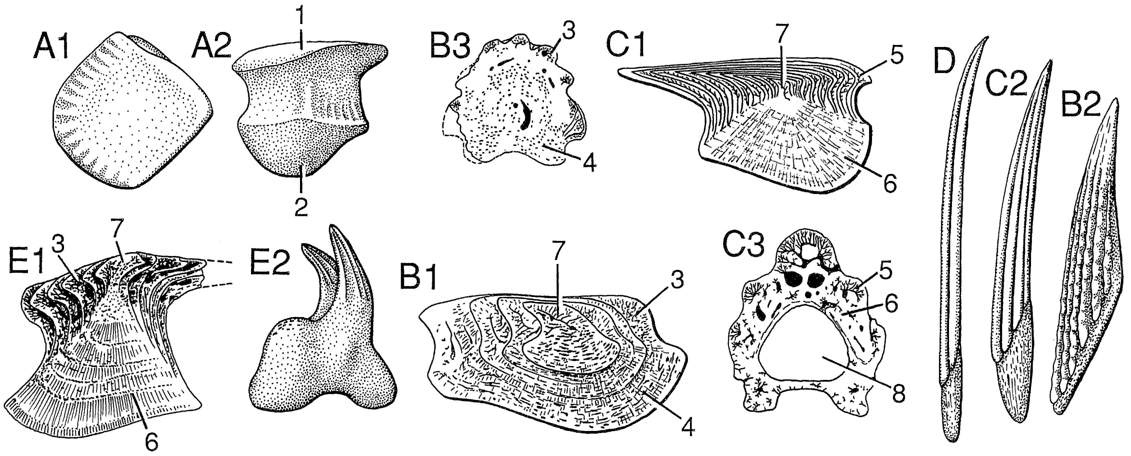

Figure 4: **Acanthodii.** Exoskeleton and histology. A *Gomphognathus*, A1 scale in lateral view, A2 scale in external view; B the Silurian climatiiform *Nostolepis*, B1 vertical section through a scale, B2 fin spine in latelar view, B3 transverse section through a fin spine; C the Silurian ischnacanthiform *Gomphonchus*, C1 vertical section through a scale, C2 fin spine in lateral view, C3 transverse section through a fin spine; D the Carboniferous acanthodiform *Acanthodes*, fin spine in lateral view; E *Machairacanthus*, E1 vertical section through a scale, E2 isolated tooth in lateral view; 1 crown, 2 base, 3 mesodentine, 4 cellular bone, 5 orthodentine, 6 acellular bone, 7 primordial odontode, 8 central canal. After Janvier 1996 (modified).

that are ornamented by prominent, often nodose ridges. They also have numerous intermediate (ventrolateral) spines situated between the pectoral and pelvic fins, and typically possess a well-developed dermal shoulder girdle. The teeth were minute and often petal-shaped, and entire tooth families fused into spiral whorls that likely lacked a mechanism for shedding. They have scales with a cellular bone base and a crown with mesodentine. Climatiiformes include genera *Climatius*, *Euthacanthus*, *Brachyacanthus*, *Ptomacanthus*, *Latviacanthus*, *Culmacanthus*, *Gyracanthus*, *Diplacanthus*, *Nostolepis* (Janvier 1996).

The group **Ishnacanthiformes** typically features robust dentigerous jawbones — bony lower jaws tightly fused with large, triangular teeth. These teeth were added in growing series along the front edges of the jaws, becoming progressively larger toward the symphysis. At the jaw tip, separate toothed spirals (tooth whorls) were present in the symphysial region. The fin spines were generally slender and composed of orthodentine. They have scales with an acellular bone base and a crown with orthodentine. Ischnacanthiformes include genera *Ischnacanthus*, *Uraniacanthus*, *Persacanthus*, *Poracathus*, *Xylacanthus* (Janvier 1996).

The group **Acanthodiformes** lacks intermediate fin spines but possess a single dorsal fin supported by a spine. Most species are toothless—an apparently secondary condition, since other acanthodian taxa bear teeth or tooth whorls and tooth-bearing jaw bones—and their gill arches bear elongated gill rakers. Their scales are minute, featuring an unornamented orthodentine crown atop a base of acellular bone. Three groups are comprised within Acanthodiformes: the Mesacanthidae (genus *Mesacanthus*), Cheiracanthidae (genus *Cheiracanthodus*), and Acanthodidae (genera *Acanthodes*, *Pseudacanthodes*, *Homalacanthus*, *Traquairichthys*) (Janvier 1996).

3.2.3 Chondrichthyes

The Chondrichthyes (from Greek *chondros* “cartilage" and *ichthys* "fishes”) is a gnathostome group that first appeared in the **Late Ordovician** or **Early Silurian** (Long 2011; Benton 2024). The oldest chondrichthyan fossils include isolated microscopic scales and teeth—often assigned to the group Mongolepidida—that date back to the Late Ordovician. These are followed in the Early Silurian by distinct tooth-whorls attributed to *Qianodus* (Benton 2024). The earliest known chondrichthyan articulated body fossils date to the Early Devonian. During the Middle Devonian, chondrichthyans (sharks) rapidly spread across the globe, and by the Late Devonian, they had become truly widespread (Long 2011). The group first experienced significant diversification during the Devonian—when major chondrichthyan lineages emerged—and the Carboniferous—when these lineages underwent extensive evolutionary radiation—followed by a second wave of increased diversity during the Jurassic period (Long 2011; Benton 2024). Some chondrichthyan lineages have persisted to the present day, comprising roughly 970 species of sharks, rays, skates, and chimaeras. Since chondrichthyans are a living group, we have a thorough understanding of their anatomy, physiology, and lifestyle—at least for many extant species (Long 2011).

Chondrichthyans have dominantly cartilaginous skeleton. They have a specialized type of calcified cartilage—known as globular calcified cartilage—that supports their braincase, jaws, gill arches, vertebrae, and fin supporting structures (Long 2011). Calcified cartilage also occurs in placoderms and some jawless fishes. However, chondrichthyans are distinctive in possessing prismatic calcified cartilage, where the surface of their cartilaginous skeleton is arranged as small platelets or prisms (Benton 2024). Since cartilage has a much lower preservation potential than hard tissues, most of what we know about their evolution comes from the most abundant microscopic fossils, teeth, spines, and scales (Janvier 1996; Long 2011). Occasionally, skull fragments or vertebrae are found—but exceptionally complete preservation, where the entire body is fossilized, only occurs under rare, favorable conditions such as those found in Lagerstätten (Long 2011).

Early sharks are known only from their teeth, which exhibit a remarkable variety of forms—underscoring their wide adaptive strategies and diverse ecological roles. Therefore, the identification of chondrichthyans is primarily based on the histology of their teeth and scales (Long 2011). According to Long (2011), chondrichthyan teeth and scales are composed of several tissue types and recognizing these microstructural variations is key to distinguishing different taxa. **Vitreodentin** is the outer enameloid layer of a tooth (absent in some groups such as xenacanthids). Beneath this, the main cusp is formed from a type of dentine surrounding a pulp cavity, with the base composed of spongy trabecular dentine. **Orthodentin** is a type of dentine characterized by distinct growth lines—known as Owen's lines—parallel to the tooth surface. It develops around the pulp cavity and consists of aligned dentinal tubules. **Pallial dentin** forms during the initial phase of dentine development and appears in cross-section as a layer of hypermineralized dentine. **Trabecular dentin** refers to spongy dentine with large cavities (luminae). In cross-section, these cavities may align roughly parallel or semi-parallel to each other. **Pleromin** is a hypermineralized dentine matrix (also called pleromic hard tissue), a term first coined to describe the scales of psammosteid agnathans (Long 2011).

Most shark teeth and scales are built on a base of trabecular dentine—sometimes pierced by fine canals—covered with an orthodentine crown and one or more layers of enameloid. In species adapted for crushing hard prey, teeth may form flattened comb-like structures composed of pleuromic dentine atop a trabecular dentine base, effectively creating a grinding pavement. Shark jaws are formed from two primary cartilages—Meckel's cartilage (lower jaw) and the palatoquadrate (upper jaw)—which support multiple rows of teeth (Long 2011). These teeth grow continuously over the shark's lifetime and are arranged like a conveyor belt: as front teeth are lost or worn out, replacement teeth from behind gradually shift into place (Long 2011; Benton 2024). Sharks and their relatives have placoid scales—also called dermal denticles—that share a very similar tissue structure with teeth. These scales are embedded in the skin but typically do not overlap. Some are simple blade-shaped denticles, while others are more complex—with multiple growth layers on each basal plate—reflecting differences in species and skin region. They possess broad, wing-like pectoral fins and a torpedo-shaped body, which together generate hydrodynamic lift as they swim continuously. Early Devonian fossils of chondrichthyans—such as *Doliodus*—demonstrate that Paleozoic sharks commonly had fin spines positioned in front of one or more of their fins. These well-preserved specimens reveal paired pectoral fin-spines, a feature not seen in most modern cartilaginous fishes (Long 2011).

Chondrichthyans exhibit a range of lifestyles (Long 2011). Early Paleozoic chondrichthyans inhabited only marine environments, similar to most modern taxa (Janvier 1996). They must have been efficient swimmers to avoid being eaten by the giant predators like placoderms that also inhabited the seas (Long 2011).

From their earliest ancestors to modern forms, the fundamental body plan of sharks has remained remarkably enduring. Early jaw and tooth structures are nearly identical to those of living sharks, highlighting their long-term evolutionary stability (Long 2011).

According to Janvier (1996), there are seven groups of chondrichthyans: the Cladoselachidae, Eugenodontida, Petalodontida, Symmoriida, Elasmobranchii, Holocephali, Iniopterygia.

The group **Cladoselachidae** is known exclusively from the Devonian. The full body of genus *Cladoselache* is known from fossil evidence, including rare soft tissue preservation such as kidneys and musculature. *Cladoselache* differs from all modern sharks in one key feature: it lacks pelvic claspers. Its paired fins are supported by unjointed fin radials that articulate either directly with the girdle or along the metapterygial axis, and they include ceratotrichia (fibrous fin rays). Cladoselachids

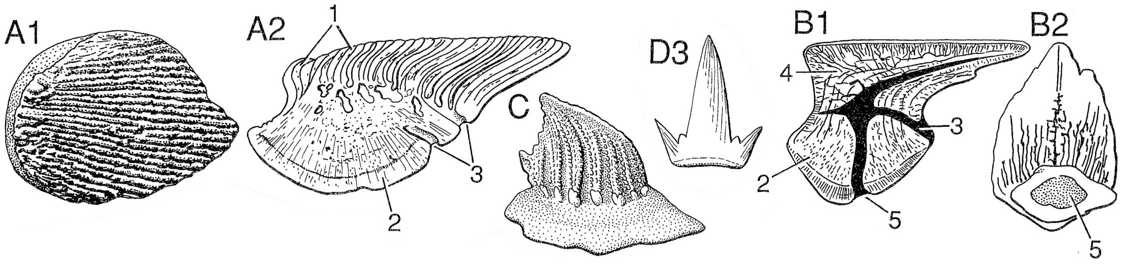

Figure 5: **Chondrichthyes. Cladoselachidae.** A *Mongolepis*, A1 scale in external view, A2 vertical section; B *Elegestolepis*, B1 scale in vertical section; B1 and basal viev B2; C *Pilolepis*, dermal scute in lateral view; D *Cladoselache*, D3 tooth in labial view. 1 odontodes, 2 base, 3 neck canals, 4 microsquamose crown, 5 pulp cavity and basal canal. After Janvier 1996 (modified).

typically had a subterminal mouth and five external gill slits. The teeth were small and tricuspid, commonly referred to as "cladodont" teeth (Figure 5). This tooth type is considered one of the most primitive forms among chondrichthyans. Tooth replacement in *Cladoselache* was likely slow, with multiple rows of functional teeth used simultaneously. The body was nearly scaleless (naked), with only the head and fins covered in compound or mesosquamose scales (Janvier 1996).

The group **Symmoriida** is known from the Late Devonian to Early Cretaceous (Benton 2024). Symoriids are distinguished by an exceptionally elongated metapterygial rod in the pectoral fins, plus a distinctive arrow-shaped skeletal structure just behind the supports of the dorsal fin. In males, the pelvic metapterygium becomes transformed into a clasper—sometimes referred to as a mixipterygium. Their teeth are of the "cladodont" type, featuring a prominent central cusp flanked by smaller ones (Figure 6). They lack typical scales, though there are compound denticles present on the head and fins. Although symoriids first appear in the Late Devonian, their major diversification occurred later in the Upper Palaeozoic (Janvier 1996).

The group **Elasmobranchii** is known from the Lower Devonian through to the present. Elamobranchs are defined by having hypobranchials (gill-supporting elements) that are directed toward the rear, along with a basihyal that is anatomically separate from the basibranchials, and an ectethmoid feature present in the braincase. In the pectoral fins, the radial cartilages articulate with three basal plates—pro-, meso-, and metapterygial plates—which themselves connect to the shoulder girdle

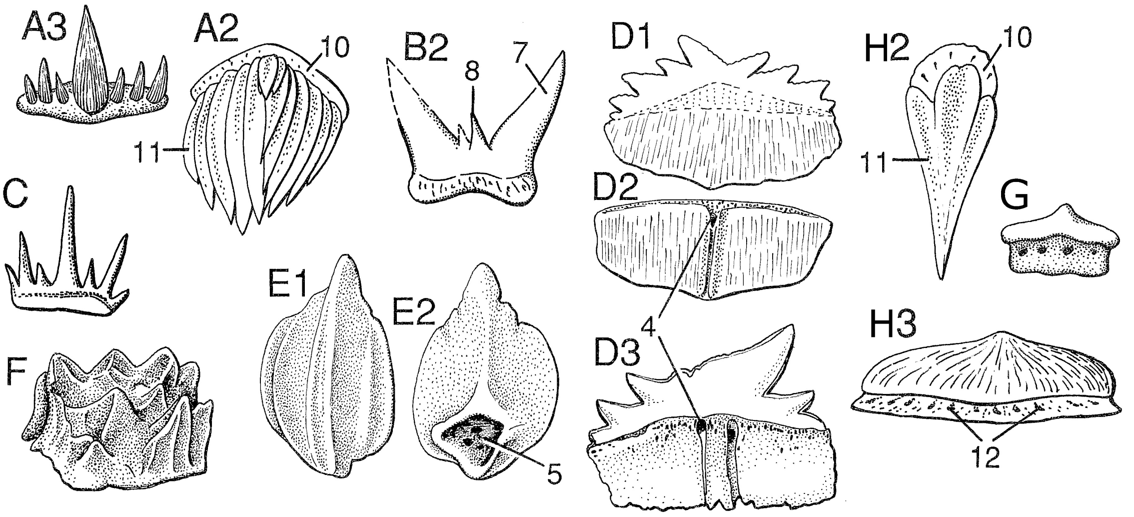

Figure 6: **Chondrichthyes. Symmoriida.** C tooth of a symmoriid. **Elasmobranchii.** A ctenacanthiform *Ctenacanthus*, A2 isolated growing scale, A3 tooth in labial view; B xenacanthiform *Antarctilamna*, B2 isolated tooth; D neoselachian-like *Mcmurdodus*, D1 tooth in anterior view, D2 tooth in basal view, D3 tooth of modern squalomorph *Echinorhinus*; E neoselachian-like *Ellesmereia*, E1 scale in external view, E2 scale in basal view; F *Arauzia*, scale in lateral view; G hybodontiform *Onychoselache*, tooth in labial view; H hybodontiform *Hamiltonichthys*, H2 non-growing scale in external view, H3 tooth in labial view; 4 nutrient canal, 5 pulp cavity, 7 lateral cusps, 8 median cusps, 10 scale base, 11 odontode, 12 nutrient foramina. After Janvier 1996 (modified).

via a narrow joint surface. The group comprises lineages Ctenacanthiformes, Xenacanthiforms, Hybodontiformes, and Neoselachii. Xenacanthiformes first appear in the fossil record from the Early Devonian, persisting through the Triassic. Their teeth are described as “diplodont”—featuring two large lateral cusps that diverge from one another, often accompanied by one or two smaller central cusps (Figure 6). The dorsal fin is typically supported by a long, straight spine devoid of ornamentation, which sits in close proximity to—and is attached to—the braincase. Ctenacanthiformes appeared in the fossil record from the Devonian through the Permian. Their scales are compound structures composed of numerous odontodes anchored to a single base—these posteriorly-oriented odontodes give the scales a resemblance to those found in cladoselachids and eugenodontids. Their dentition is of the "cladodont" type, featuring a large central cusp flanked by smaller lateral cusps (Figure 6). Additionally, the dorsal-fin spines exhibit comb-like (pectinate) ornamentation. Hybodontiformes existed from the Middle Devonian up until the end of the Cretaceous. Their teeth were typically long and low, decorated with winding ridges and perforated by numerous nutrient canals (Figure 6). The fin spines have a rounded cross-section with two longitudinal rows of denticles on the posterior face, and smooth ridges adorn their surface. They also shared placoid scales with neoselachids—non-growing dermal denticles—though some of the earliest hybodontiforms displayed growing scales. Neoselachids are characterized by having at least one layer of haphazardly oriented fibered enameloid present on their teeth and scales. They first appeared during the Mesozoic era (Janvier 1996).

The group **Holocephali** is known from the Late Devonian through to the present. They are distinguished by large, crushing dental plates composed of columnar (or "tubulate") dentine and interstitial pleromin. The earliest representatives, known as "bradyodonts," appeared in the Late Devonian and persisted until the Late Permian. The term "bradyodont" refers to their presumed slow rate of tooth replacement. These forms have been considered closely related to modern chimaeroids based on similarities in tooth microstructure—such as tubulate (orthotrabecular) dentine. Bradyodonts exhibited significant morphological diversity, particularly in the evolution of unusual head appendages. These structures may have functioned similarly to the frontal claspers (tentaculum) of male living chimaeroids. However, in bradyodonts, the frontal appendages—often claw-like, horn-like, spine-like, or whip-like—were generally paired, unlike the single frontal clasper of extant chimaeroids. Both bradyodonts and modern chimaeroids exhibit holostylic jaw suspension, where the palatoquadrate is reduced and fused to the braincase—a trait likely associated with a diet focused on hard prey (durophagy) (Figure 7). Interestingly, certain symoriids share traits with holocephalans as well, such as calcified rings reinforcing the sensory-line canals, large head denticles, and a tentaculum-like reproductive structure (Janvier 1996).

Other chondrichthyan clades appeared in later geological periods. Modern sharks, rays and skates fall within the clade Elasmobranchii, while contemporary chimaeras belong to the sister clade Holocephali (Long 2011; Benton 2024).

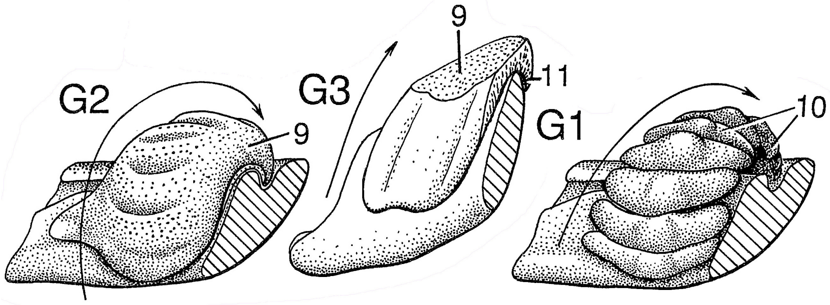

Figure 7: **Chondrichthyes. Holocephali.** G lower jaw and teeth of a generalized holocephalan (G1, based on *Helodus*), a cochliodont (G2, based on *Deltodus*), and a recent chimaeroid (G3, *Callorhinchus*); the arrow indicates the direction of the tooth development or tooth plate growth; 9 tooth plates, 10 tooth family, 11 descending lamina. After Janvier 1996 (modified).

3.2.4 Osteichthyes

The Osteichthyes (from Greek *osteon* "bony" and *ichthys* "fishes") is a gnathostome group divided into two primary lineages based on their fin structure—Actinopterygii ("ray-finned fishes") and Sarcopterygii ("lobe-finned fishes") (Janvier 1996; Benton 2024). However, these distinctions were not clearly defined among the earliest osteichthyans. The oldest osteichthyan fossils—such as the articulated *Guiyu*—date back to the **Late Silurian** and are considered ancestral to both major lineages (Benton 2024). Both the Actinopterygii and Sarcopterygii are regarded to have first appeared in the **Early Devonian** and have persisted to the present day (Janvier 1996; Benton 2024).

Actinopterygii - The name Actinopterygii referrs to fins supported by slender, rod-like structures called lepidotrichia. These fin rays attach directly to jointed skeletal elements known as radials (Benton 2024).

The earliest representatives of this group appear in the Early Devonian, though they remained low in diversity until the Late Devonian (Benton 2024). During the Late Devonian, the first actinopterygian genera began to attain broad geographic distribution (Long 2011). Actinopterygians experienced extensive diversification during the Mesozoic era and ultimately became the most species-rich and widespread group among fishes (Janvier 1996; Benton 2024).

Early actinopterygians typically possessed an elongated body and a single dor-

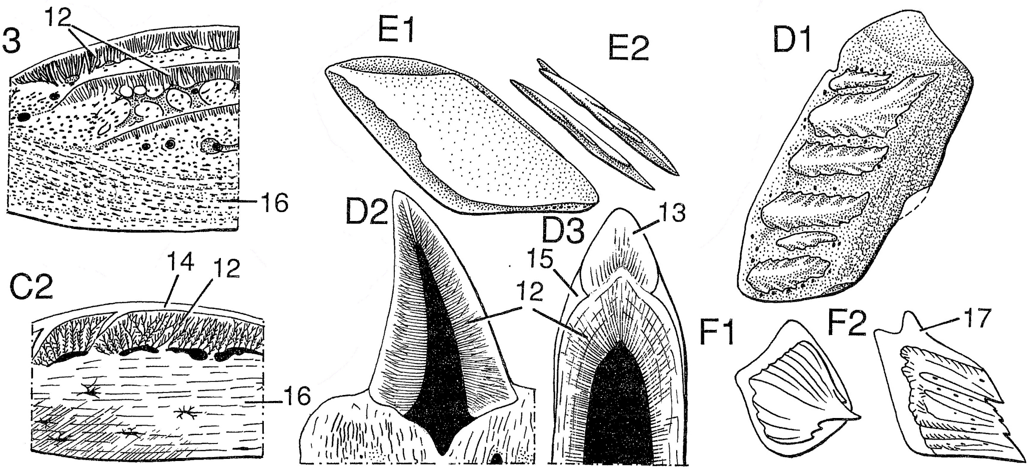

Figure 8: **Actinopterygii.** C *Moythomasia*, C2 vertical section through a scale; D *Lophosteus*, D1 scale in lateral view, D2 vertical section through a tooth, D3 compared to that of a typical actinopterygian tooth (the Mesozoic genus *Semionotus*); E *Andreolepis*, E1 flange scales, E2 possible fulcral scales; F comparative outline of the scales of *Cheirolepis* (F1) and *Moythomasia* (F2); 12 dentine, 13 acrodine, 14 ganoine, 15 collar enamel, 16 bony scale base, 17 dorsal peg of scale. After Janvier 1996 (modified).

sal fin, in contrast to other osteichthyans, which had two dorsal fins. Distinctive traits of actinopterygians include a prominent dentary bone in the lower jaw—the primary tooth-bearing element—which encloses the mandibular sensory-line canal, and a jugal bone in the cheek that contains deep pit-line sensory structures. The heads of early ray-finned fishes were characterized by a wide gape and numerous sharp teeth located on the maxilla and premaxilla of the upper jaw and the dentary of the lower jaw. The braincase was well ossified from multiple centers, remaining separated in adulthood by ventral and occipital fissures. A long parasphenoid bone, bearing teeth, ran along the midline of the palate, while the inner surfaces of both jaws were covered with numerous small toothed bones. In all Devonian and some later species, the spiracular slit remained open. The fins are supported by multiple rows of segmented lepidotrichia and may include specialized leading-edge scales (fringing fulcra). In early actinopterygians, the axial skeleton was only lightly ossified—comprising perichondral bone shells above the notochord. As a result, only the neural and hemal arches are preserved, with no ossified tail skeleton present. Later lineages—such as teleost—evolved fully ossified tail bones (Long 2011).

All early actinopterygians—except the primitive *Cheirolepis*—have teeth capped with a dense tissue called acrodin, consisting of compact dentine. The external ornamentation of actinopterygian bones typically consists of fine, parallel ridges, each topped with glossy ganoine. Teeth were generally sharp and small (Long 2011). Although actinopterygians possess otoliths (ear stones), these structures are extremely rare in Palaeozoic specimens (Janvier 1996). Their body scales featured robust peg-and-socket joints that locked them securely into diagonal rows (Figure 9). Each scale bore a shiny enamel-like layer called ganoine atop dermal bones and the scale itself. This ganoid scale architecture includes a thin ganoine surface layer over a dentine layer with vascular canals, all underlain by a spongy basal bone layer (Figure 8). Later actinopterygians lost ganoine and their scales often become more rounded (Long 2011).

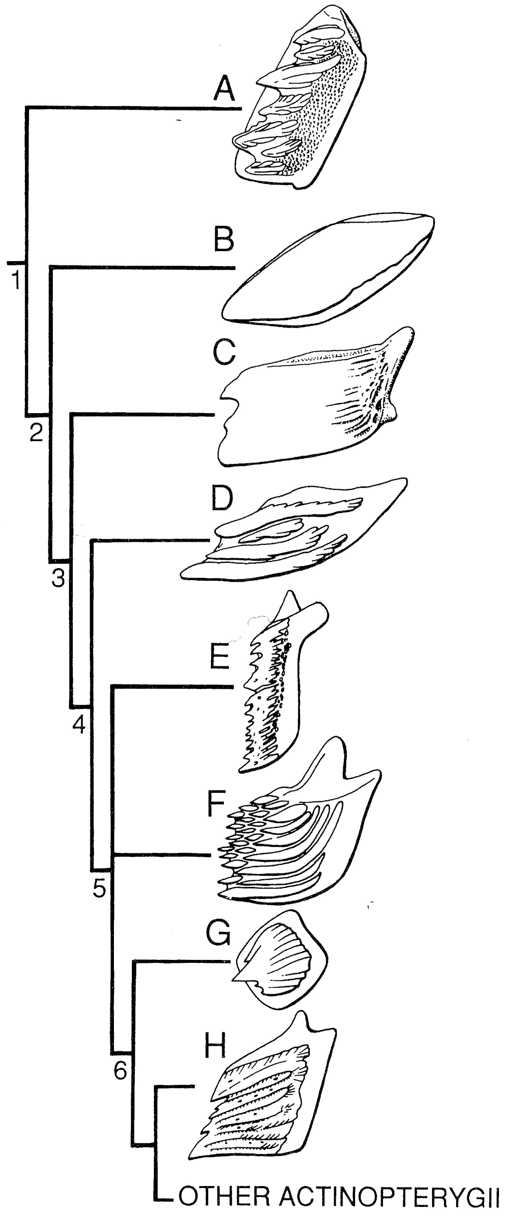

Figure 9: **Actinopterygii.** Interrelationships based on scale structure and morphology. A *Lophosteus*; B *Andreolepis*; C *Naxilepis*; D *Orvikuina*; E *Ligulalepis*; F *Dialipina*; G *Cheirolepis*; H *Moythomasia.* Synapomorphies: 1 rhombic scales with overlaying sequence of dentine denticles and cancellous bone, 2 occasional ganoine layers over dentine and denticles, 3 anterodorsal process, ganoine on dentine denticles, 4 overlaying sequences of dentine denticles without bony base, 5 "peg-and-socket" articulation, peg with narrow base, 6 ganoine layer directly overlying other ganoine layer. After Janvier 1996.

Devonian actinopterygians were generally a fairly uniform group, exhibiting minimal variation — except in cases where they possessed micromeric scale coverings, meaning multiple tiny scale rows per body segment. In Devonian ray-finned fishes, key evolutionary changes included a reduction in gape length and enlargement of the opercular bones, along with a consolidation of the skull roof—where small snout bones were progressively replaced by a consistent pattern of larger elements such as the median rostral and postrostral bones. These fishes also transitioned from a micromeric scale pattern to larger rhombic scales, although the primitive condition remains debated—some early taxa like *Ligulalepis* retained larger rhombic scales. In the most primitive ray-finned fishes, such as *Cheirolepis*, the braincase was sparsely ossified. In contrast, Late Devonian actinopterygians exhibit well-developed ossification in the braincase, displaying both perichondral and endochondral ossification (Long 2011).

All Devonian actinopterygian species are interpreted as marine, likely inhabiting pelagic (open-water) environments (Janvier 1996).

Lower Palaeozoic genera include *Andreolepis*, *Lophosteus*, *Cheirolepis*, *Naxilepis*, *Orvikuina*, *Tegeolepis*, *Ligulalepis*, *Dialipina*, and *Moythomasia* (Janvier 1996).

Sarcopterygii - The name Sarcopterygii denotes paired fins anchored by a single basal bone and include internal musculature that enables adjustment of fin orientations. Sarcopterygii also includes all tetrapods (Benton 2024).

Palaeozoic sarcopterygians exhibited a significantly greater breadth of diversity—especially in their internal anatomical structures—than their contemporaries among the actinopterygians (Janvier 1996; Benton 2024).

Early sarcopterygians are generally elongated in body form, with primitive species possessing a hinged braincase divided into an anterior ethmosphenoid region and a posterior otico-occipital portion. This internal division is mirrored in the skull roof, where the bones form distinct frontal and parietal shields, separated by an intercranial joint. In more derived groups, such as the panderichthyids, this joint becomes immobile due to bone fusion between these shields. Most species have large eyes, and all groups except the osteolepiforms possess paired external nostrils.

Osteolepiforms instead show a single pair of external nostrils and a choana, an internal opening in the palate. The cheek region follows a consistent bone pattern, typically including one or more prominent squamosal bones. The jaws feature robust dentary bones supported by a series of infradentaries. Gill arches are strongly ossified and include large ventral elements (basibranchials), occasionally accompanied by a forward-facing sublingual bone. The shoulder region—including the scapulocoracoid and, in tetrapodomorphs, the limb skeleton—is well ossified. This configuration is most fully developed in groups like the osteolepiforms and rhizodontiforms, which have strong humeri that articulate with radius and ulna bones, resembling the limb structure of higher vertebrates (except limbless ones). Overall, their body shape remains fairly conservative, with no evidence of highly flattened or deep-bodied forms evolving (Long 2011).

Early sarcopterygians possessed prominent fang teeth, in addition to the usual marginal teeth on toothed bones—however, coelacanths are exceptional. In coelacanths, the jaw area dedicated to biting is relatively small, and they feature a unique double-tandem jaw joint—a highly specialized adaptation for feeding. Their teeth were composed of enamel overlaying dentin, and in certain groups—such as osteolepiforms, porolepiforms, and rhizodontiforms—the enamel and dentin exhibit intricate folding. In cross-section, these teeth show exceptional complexity and are known as labyrinthodont teeth. All early sarcopterygians and many primitive members of the group had scales and dermal bones coated with cosmine, though this tissue was frequently lost in later lineages. These scales—typical of most sarcopterygian groups—were thick, rhomboid, and cosmine-covered in initial osteolepiforms and porolepiforms; over time, these forms evolved rounded scales without cosmine. Rhizodontiforms, onychodontiforms, and actinistians retained thinner, more rounded scales. The sensory-line system in crossopterygians was highly developed, visible as arrays of pores and deeply embedded pit-line canals on both their dermal bones and scales (Long 2011).

According to Janvier (2024) seven major subgroups within sarcopterygians were established: Onychodotniformes, Actinistia, Dipnomorpha, Rhizodontiformes, Osteolepiformes, Panderichthyida, Tetrapoda.

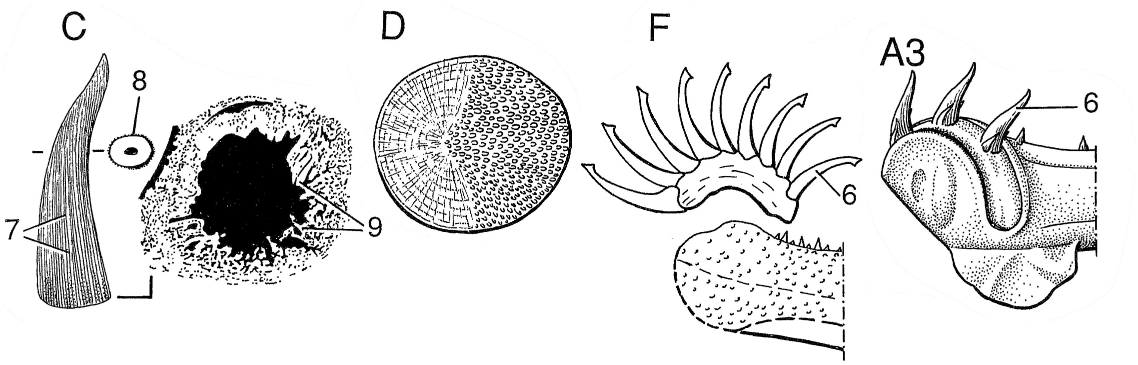

Figure 10: **Sarcopterygii. Onychodontiformes.** External morphology. A *Strunius*, A3 symphysial region of lower jaw in internal view; C-F *Onychodus*, C parasymphysial tooth in lateral view, with apical and basal horizontal sections, D scale in external view, F parasymphysial toothed plate of a form with hamate (hooked) teeth; 6 parasymphysial teeth, 7 striae of enamel, 8 enamel, 9 basal dentine folds. After Janvier 1996 (modified).

The group **Onychodontiformes** is known from the Early to Late Devonian. They possess a single row of large, sigmoid-shaped teeth on the parasymphysial plates located along the lower jaw symphysis (Figure 10). When the mouth is closed, these teeth fit into deep internasal pits in the palate. The teeth themselves are simple in form, with infolded dentine except at the base where minor folds occur, and they are covered by finely striated enamel. In some species of the genus *Onychodus*, the parasymphysial teeth are slightly hook-shaped. The dermal bones of onychodontiform fishes are ornamented with ridges of horseshoe-shaped dentine tubercles. The presence of cosmine in onychodontiforms remains uncertain. Only a few genera are currently recognized within Onychodontiformes, including *Onychodus*, *Grossius*, and *Strunius* (Janvier 1996).

The group **Actinistia**, commonly known as coelacanths, first appeared in the Early Devonian and persist to the present day (Janvier 1996; Benton 2024). Actinistians are distinguished by their anterior dorsal fin, which originates directly from the back without any connection to a basal fin lobe. Their caudal fin is diphycercal (isocercal), meaning the dorsal and ventral lobes are symmetrical. These lobes meet

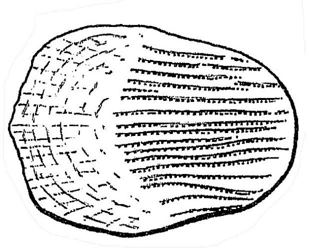

Figure 11: **Sarcopterygii. Actinistia.** *Diplocercides*, scale in externl view. After Janvier 1996.

at the end of the body, which extends horizontally and houses the notochord, culminating in a small rounded tuft. Devonian actinistians were remarkably similar in anatomy to the living coelacanth *Latimeria*, differing primarily in their smaller size. Their scales ranged from ornamentation with horseshoe-shaped tubercles (Figure 11)—comparable to those seen in onychodontiforms—to a thin dentine-based layer. By comparison, the scales of extant *Latimeria* are large, circular, and often decorated with spine-like tubercles. Devonian actinistian genera include *Euporosteus*, *Miguashaia*, and *Diplocercides* (Janvier 1996).

The group **Dipnomorpha** includes two principal groups: Porolepiformes and Dipnoi (lungfish). Porolepiformes are known only from the Devonian. They are defined by their strongly folded teeth encased in attachment bone—the so-called "dendrodont" type. The group includes relatively few genera, such as *Porolepis*, *Glyptolepis*, *Laccognathus*, *Holoptychius*, and *Quebecius.* The most generalized porolepiform morphology is seen in cosmine-covered forms with rhombic scales—like *Porolepis.* In such genera, the pores of the cosmine are bordered anteriorly by a slight crescent-shaped elevation. In later porolepiforms, for example *Heimenia*, the cosmine breaks down into individual tubercles or ridges. In yet other genera, such as *Glyptolepis* and *Holoptychius*, cosmine is completely absent. Their teeth are highly folded—each primary fold contains numerous secondary folds—though the primary-fold axes remain nearly straight, and the attachment bone does not extend between them (the "dendrodont" type). The tooth pulp cavity is small and partially filled with osteodentine. They all inhabited shallow coastal marine environments (Janvier 1996). Dipnoi first appeared in the Early Devonian, and a few genera have survived to the present day. They are typically robust-bodied, with a blunt snout, small eyes, an epicercal tail, and a dorsal fin located far toward the rear. They are distinctive for their large tooth plates, which evolve from modifications of the entopterygoid and prearticular bones, along with a network of tubules within the snout and the symphysial region of the lower jaw. Most Devonian lungfishes had an exoskeleton covered with a cosmine layer similar to that seen in porolepiforms—specifically, enamel typically lined the flask-shaped (bottle-shaped) cavities. Additionally, their cosmine exhibits more or less concentric discontinuity lines known as Westoll lines (Figure 12), which are interpreted as evidence of cyclic resorption

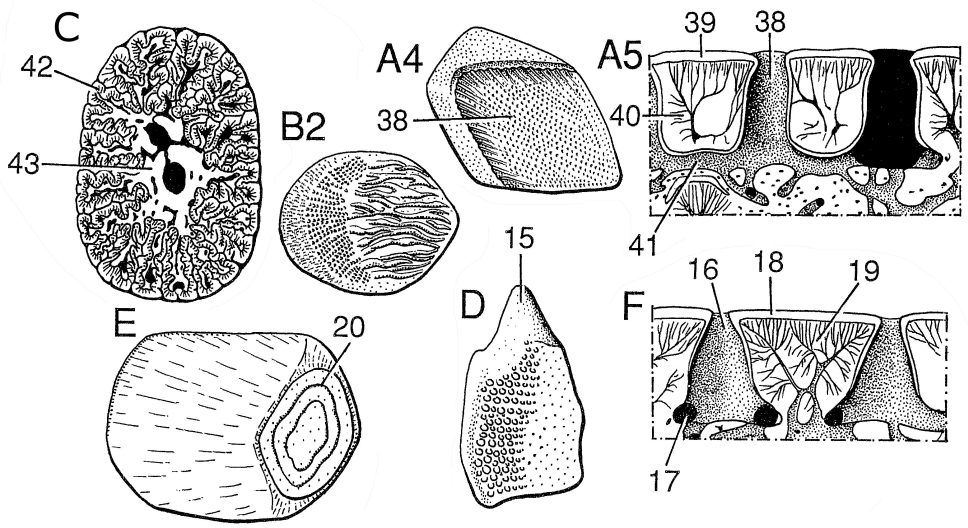

Figure 12: **Sarcopterygii. Dipnomorpha. Porolepiformes.** A *Porolepis*, A4 scale in lateral view, A5 vertical section through the cosmine of exoskeleton; B *Holoptychius*, B2 scale in lateral view; C *Hamodus*, horizontal section through a tooth; 38 pore and flask-shaped cavity of cosmine, 39 enamel, 40 dentine, 41 horizontal canal network of cosmine, 42 dentine (plicidentine), 43 attachment bone or osteodentine filling pulp cavity. **Dipnoi.** D *Dipnorhynchus*, scale in external view (cosmine stippled); E *Rhinodipterus*, scale in external view (cosmine stippled); F *Dipterus*, vertical section through the cosmine of a dermal bone; 15 dorsal peg, 16 flask-shaped cavity, 17 canal of the pore-canal system, 18 enamel, 19 dentine, 20 Westoll lines. After Janvier 1996 (modified).

and redeposition during growth and are unique to this group. Known Devonian dipnoan genera include *Chirodipterus*, *Dipterus*, *Griphognathus*, *Dipnorhynchus*, and *Rhinodipterus*. Devonian lungfishes inhabited near-shore marine environments, often associated with coral reefs, and did not enter fully freshwater ecosystems until the Carboniferous; however, some Devonian specimens have been found in estuarine or fluvial settings (Janvier 1996).

The group **Rhizodontiformes** are known from the Late Devonian to the Carboniferous. Rhizodontiforms are not well known, primarily because their cranial dermal bones were thin, loosely connected, and became scattered after decomposition. A defining feature is that their dermal fin rays (lepidotrichia) have an extended unsegmented portion, covered by a layer of rounded scales similar to those on the lobes. The dermal bones show an ornamentation of bony vermiculations and lack cosmine. Their folded teeth are of the "polyplacodont" type, as in osteolepiforms and tetrapods, although the primary folds are only slightly sigmoid. Their scales are large and rounded, decorated with fine ridges, and have a rounded projection on the inner surface (Figure 13). Devonian rhizodontiforms include the genera *Notorhizodon* and *Sauripterus* (Janvier 1996).

The group **Osteolepiformes** is known from the Early Devonian to the Permian. Osteolepiforms are defined by an enlarged axillary scale or scute located at the rear edge of the basal lobe in both paired and unpaired fins, and by the presence of folded teeth. Similar to porolepiforms, the group includes both cosmine-covered and non-cosmine-covered forms, with the latter considered to be derived from the former. In cosmine-covered osteolepiforms—such as "osteolepids," megalichthyids, and others—the cosmine layer covering the dermal bones and scales appears smoother than in dipnomorphs, as its pores are not bordered by crescent-shaped ridges. The cosmine pores in osteolepiforms are smaller and more widely spaced than those in dipnomorphs, and the flask-shaped cavities are generally not lined internally with enamel. Each cavity is also subdivided by a horizontal septum. In megalichthyids, cosmine resorption can be extensive, leaving only small remnants. In all non-cosmine-covered osteolepiforms, the dermal bones and scales are decorated with bony tubercles, ridges, or vermiculations. The scales of *Osteolepis* are roughly diamond-shaped, while those of *Eusthenopteron* are more rounded (Figure 14). Their folded teeth are classified as either "polyplacodont" or "eusthenodont". In both types, the attachment bone extends between the primary dentine folds, but in the "eusthenodont" type, the pulp cavity is also largely filled with bone and osteodentine. Devonian osteolepiforms include the genera *Osteolepis*, *Gyroptychius*, *Eusthenopteron*, *Megalichthys*, *Koharalepis*, and *Marsdenichthys* (Janvier 1996).

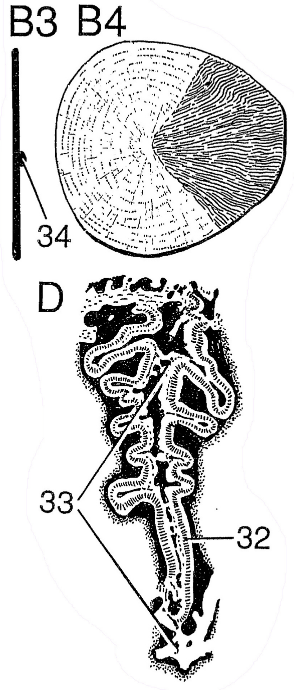

Figure 13: **Sarcopterygii. Rhizodontiformes.** B *Barameda*, B3 scale in transverse section, B4 scale in external view; D *Rhizodus*, horizontal section through a fold of a tooth; 32 dentine (plicidentine), 33 attachment bone, 34 internal boss on scales. After Janvier 1996 (modified).

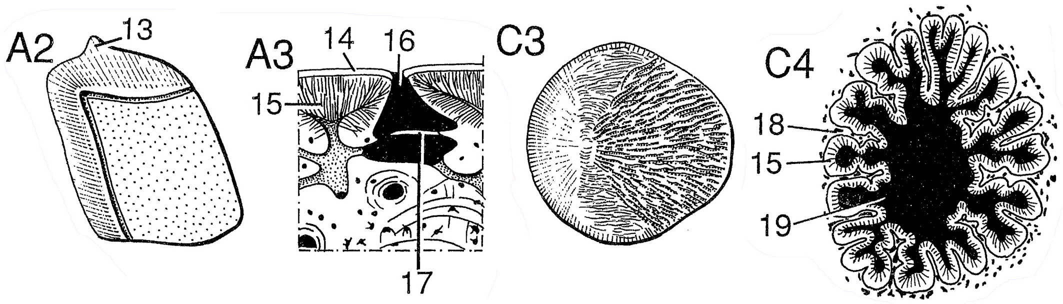

Figure 14: **Sarcopterygii. Osteolepiformes.** A *Osteolepis*, A2 scale in external view, A3 vertical section of the cosmine; C *Eusthenopteron*, C3 scale in external view, C4 horizontal section through a tooth; 13 anterodorsal process of scale, 14 enamel, 15 dentine or plicidentine, 16 flask-shaped cavity, 17 horizontal septum, 18 attachment bone, 19 pulp cavity. After Janvier 1996 (modified).

The group **Panderichthyida** represents a small group from the Late Devonian. Panderichthyid scales are relatively small, diamond-shaped, and show the same vermiculated patterning as seen on the skull (Figure 15). The tooth histology of *Panderichthys* is comparable to that of early tetrapods (especially Ichthyostega), being of the "labyrinthodont" type—characterized by polyplacoid folding and minimal attachment bone between the folds. Panderichthyids are known from only three genera: *Panderichthys*, *Elpistostege*, and *Obruchevichthys* (Janvier 1996).

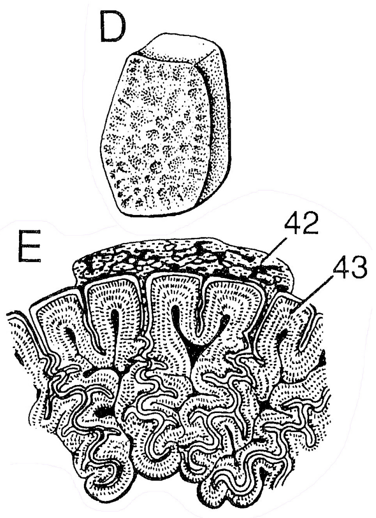

Figure 15: **Sarcopterygii. Panderichthyida.** D,E *Panderichthys*, isolated scale in external view (D), portion of a horizontal section through a main tusk (E); 42 attachment bone, 43 dentine (plicidentine). After Janvier 1996.

The group **Tetrapoda** first appeared in the Late Devonian. Among the most thoroughly documented Devonian tetrapodomorphs are *Tiktaalik*, *Acanthostega*, and *Ichthyostega* (Benton 2024). The teeth of *Ichthyostega* exhibit an advanced polyplacodont (“labyrinthodont”) structure, featuring folded dentine without attachment bone between the folds, and with undulating axes of the primary folds. As in panderichthyids, these dentine folds retain side branches—unlike those in all other tetrapods with advanced labyrinthodont teeth (Janvier 1996). Each of these genera was carnivorous and likely fed on fish. Tetrapods subsequently experienced expansive evolutionary radiation throughout the Upper Paleozoic, Mesozoic, and Cenozoic eras (Benton 2024).

4 Palaeogeography

The Lower Palaeozoic was a key geological period in the evolution of early vertebrates. Understanding continental configurations over geological time is crucial for studying early vertebrates and their paleogeographic distribution, as these factors significantly influenced their evolution and migration (Long 2011). Unfortunately, our knowledge of past continental positions and climate conditions becomes increasingly uncertain the further back we go in geological history. Similarly, the quality and abundance of fossil record tend to diminish towards the geological past.

To understand the distribution of organisms in the past, faunal provinces were reconstructed (Benton 2024). A faunal province is essentially an area on the map where all species share certain characteristics and stand out from other faunal provinces, where different kinds of species dominate. To reconstruct the faunal provinces, it is necessary to identify climatic and landscape factors that determine the distribution of species. Marine faunal provinces in the Early Palaeozoic were reconstructed, based on the distributions of invertebrate fossils. A similar approach was embraced to understand early fish evolution (Benton 2024).

Marine fishes are often considered to have little significance in paleogeography because of their ability to disperse easily through oceans, but are more relevant to ecological biogeography, being bound to climate zones (Janvier 1996). However, if we project the biogeographic patterns of contemporary fish into the geological past, it seems that even early fishes were not as tied to climate zones or ocean currents as they were to geographical regions. Most modern fish live on the continental shelf or around islands and do not usually extend their range throughout the entire ocean; some fish species can even be considered endemic. Apparently, many Paleozoic fish seem to have been tied to nearshore or restricted marine environments—some may have been endemic, while others were likely epipelagic and widespread (Janvier 1996; Long 2011; Žigaitė and Blieck 2013).

In the Ordovician and Silurian, the fish faunas were dominated by agnathans. Additionaly, Silurian fish remains serve as useful biostratigraphical indicators and reliable markers of paleocontinental margins (Žigaitė and Blieck 2013). Although the origin of teeth and jaws is suggested to date back to the Ordovician, the major evolution and diversification of gnathostomes occurred later, in the Devonian (Figure 21) (Žigaitė and Blieck 2013; Brazeau and Friedman 2025). All groups of jawed, fish-like vertebrates underwent the greatest evolution and radiation during the Devonian, ranging from primitive jawed vertebrates, such as Acanthodii, Placodermi, and early Chondrichthyes, to modern Chondrichthyes and Osteichthyes (Brazeau and Friedman 2025).

4.1 Cambrian and Ordovician

Cambrian - In the Cambrian, when the origin of the oldest fish-like vertebrates is estimated, most continents—such as Antarctica, Australia, South America, Africa, and the Indian subcontinent—were located in the Southern Hemisphere, forming the supercontinent Gondwana. Other landmasses lay farther north, though still relatively close to Gondwana, forming major continental blocks such as Laurentia (comprising parts of the regions of Asia and North America), Siberia (Russia), Baltica (northern Europe), or existing as isolated landmasses, including eastern Asia, and North and South China (Figure 16) (Scotese 1998).

The oldest known remains of early vertebrate ancestors are fossil imprints from **Lower and Middle Cambrian Lagerstätten**, such as *Haikouichthys* and *Myllokunmingia* from **Chengjiang** (Shu et al. 2003), and *Metaspriggina* from the **Burgess Shale** (Morris and Caron 2014). The taxa *Haikouichthys*, *Myllokunmingia* and *Metaspriggina* can be considered basal vertebrates that were likely phylogenetically related, sharing common features such as paired eyes, W-shaped myomeres, gill pouches, bipartite branchial bars, and possibly a proto-mandibular bar (Morris and Caron 2014). They may even have had a cosmopolitan distribution during the Lower and Middle Cambrian. However, interpretations of these soft-bodied fossil impressions must be approached with caution due to the fragmentary nature of the material and ongoing debates regarding the identification of key anatomical features. Among these earliest representatives, *Metaspriggina* exhibits the greatest similarity to vertebrates (Morris and Caron 2014).

The oldest known fish remains come from the **Late Cambrian Harding Sand-**

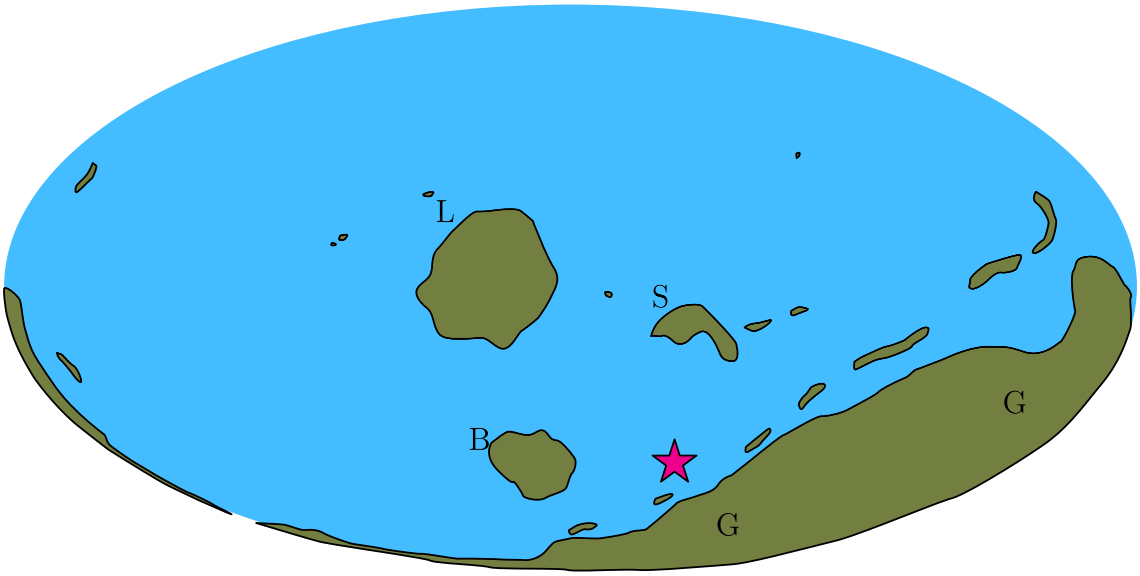

Figure 16: **Palaeogeography of the Late Cambrian**. The asterisk indicates the approximate location of the Barrandian area (within the Bohemian Massif). Abbreviations: L=Laurentia; B=Baltica; S=Siberia; G=Gondwana. After Scotese 1998 and Chlupáč et al. 2011 (modified).

stone Formation in Wyoming, North America. These remains, consisting of dermal fragments, were interpreted as belonging to a heterostracan based on their histological structure and were classified as a new genus, *Anatolepis* (Repetski 1978). However, there are some doubts about this classification due to the limited understanding of scale-like micro-ornamentation in primitive vertebrates, and the histological work conducted so far has been largely inconclusive (Smith and Sansom 1995). Nevertheless, based on *Anatolepis* findings from North America, Greenland, and Spitsbergen, this genus appears to have had a widespread geographic distribution in marine environments during the Late Cambrian and Early Ordovician (Repetski 1978).

Ordovician - In the Ordovician, the supercontinent Gondwana remained in the Southern Hemisphere, but rotated slightly and came to include both North and South China (Figure 17) (Scotese 1998).

Fish remains come from the **Ordovician Harding Sandstone Formation in Colorado**, North America. Some isolated scales were described as the enigmatic species *Skiichthys halsteadi*, though it is not possible to say with certainty whether this species belongs to agnathans or gnathostomes, as it exhibits ambiguous fea-

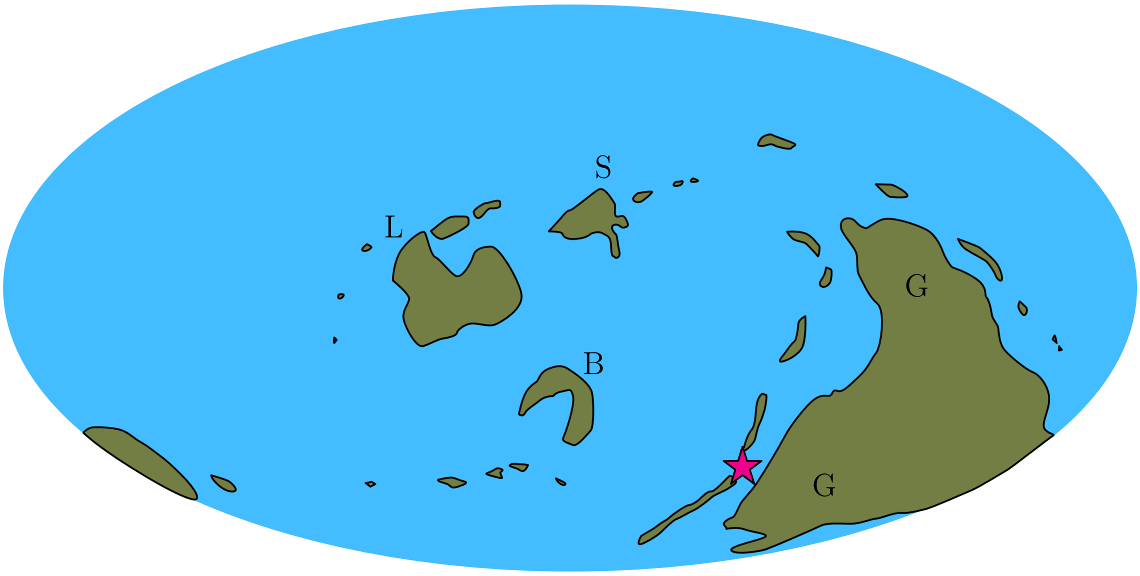

Figure 17: **Palaeogeography of the Middle Ordovician**. The asterisk indicates the approximate location of the Prague Basin (within the Barrandian area of the Bohemian Massif). Abbreviations: L=Laurentia; B=Baltica; S=Siberia; G=Gondwana. After Scotese 1998 and Chlupáč et al. 2011 (modified).

tures. Due to the presence of a variety of histological structures, possible taxonomic relationships have been discussed with groups such as osteostracans, placoderms, acanthodians, and chondrichthyans (Smith and Sansom 1997). Late Ordovician remains consist of scales believed to belong to chondrichthyans (sharks), probably genus *Elegestolepis*, found in association with thelodont scales. Although chondrichthyan scales are present, the remains do not include teeth, so there is no clear evidence for the presence of jaws in the Late Ordovician (Sansom, Smith, and Smith 1996). In addition to the oldest known shark scales from North America, other shark scales were found in the Lower Silurian deposits of Siberia. Furthermore, the oldest remains of thelodonts come from the Late Ordovician of Siberia (Sansom, Smith, and Smith 1996).

The oldest articulated fish are extremely rare. Partially articulated fossils have been found in the **Ordovician Harding Sandstone Formation**, including several specimens of the species *Eriptychius americanus* and *Astraspis desiderata* (Smith and Sansom 1997; Long 2011). Additional articulated and disarticulated fish remains come from the **Ordovician Stairway Sandstone of the Amadeus Basin in Australia** (Kelman and Khider 2018) and **Ordovician Anzaldo Formation of Bolivia** (Davies et al. 2007), where the genera *Arandaspis*, *Porophoraspis* and

Sacabambaspis have been described (Smith and Sansom 1997).

Despite the rare discoveries of early vertebrate fossils from the Cambrian and Ordovician periods, the latest data suggest that the most significant radiation of the earliest vertebrates occurred not in the Silurian, as long assumed, but already in the Ordovician, during the **Great Ordovician Biodiversification Event** (Sansom, Smith, and Smith 1996; Andreev et al. 2022). However, due to the fragmentary and extremely scarce fossil record, defining faunal provinces based on these findings remains problematic.

4.2 Silurian

Silurian - In the Silurian, the supercontinent Gondwana was still located in the Southern Hemisphere, while other landmasses—such as Laurentia, Baltica, Avalonia, and Siberia—began moving closer together, clustering near the equatorial and tropical belt. Shallow seas formed between these landmasses. This configuration influenced the distribution of fish faunas by isolating them through continental barriers (Benton 2024). Eight faunal provinces have been identified (Figure 18): **Tuvan**, **Siberian**, **European**, **Acadian–Anglo-Welsh**, **Central Appalachian**, **Canadian Arctic**, **Canadian Arctic–European Russian** and **South China** (Žigaitė and Blieck 2013; Benton 2024).

One of the most exceptional Silurian vertebrate remains are the tooth whorls belonging to the primitive chondrichthyan species *Qianodus duplicis*, which represent the oldest known gnathostome teeth (Andreev et al. 2022). These isolated tooth whorls, found in the **Early Silurian Guizhou Province**, **China**, provide valuable data on the earliest mandibular dentition of primitive vertebrates (sharks) and even exhibit growth patterns similar to those of modern gnathostome groups (Andreev et al. 2022). This fossil evidence supports the hypothesis that the origin of teeth and jaws is linked to the **Great Ordovician Biodiversification Event** (Andreev et al. 2022).

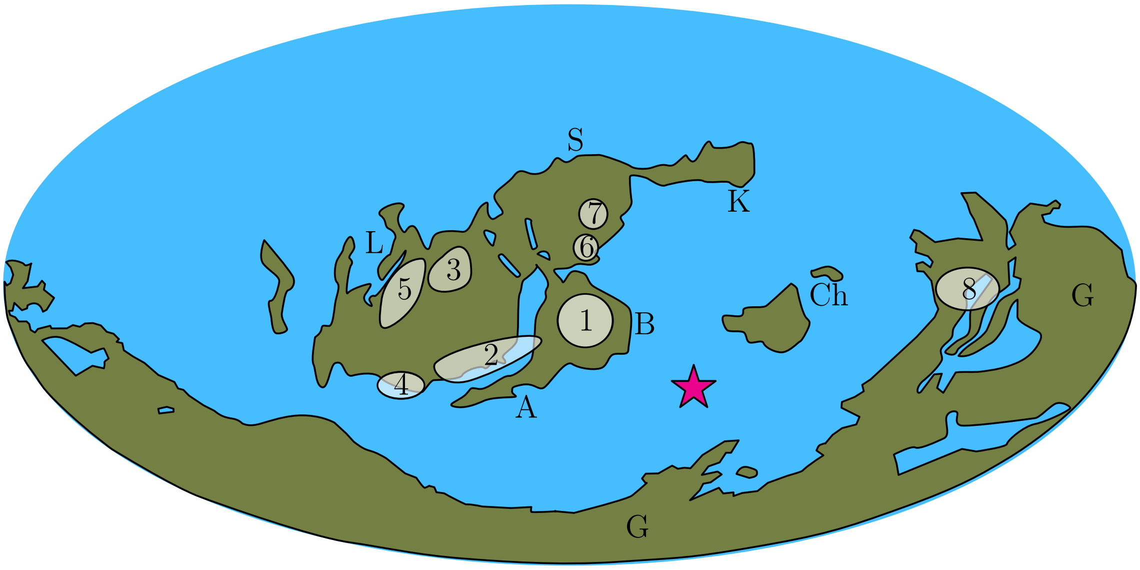

Figure 18: **Paleogeography of the Silurian**. The numbers indicate fish faunal provinces. 1 European; 2 Acadian-Anglo-Welsh; 3 Canadian Arctic-European Russian; 4 Central Appalachian; 5 Canadian Arctic; 6 Siberian; 7 Tuvan; 8 South China. The asterisk indicates the approximate location of the Prague Basin (within the Barrandian area of the Bohemian Massif). Abbreviations: L=Laurentia; B=Baltica; S=Siberia; G=Gondwana, K=Kazachstania, Ch=China. After Chlupáč et al. 2011 and Benton 2024 (modified).

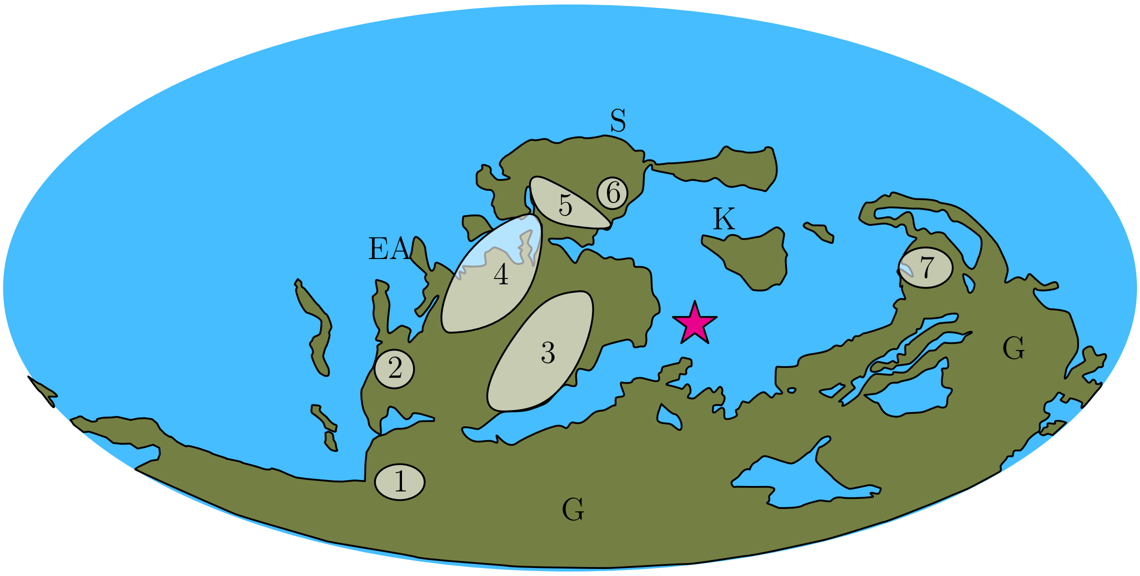

Figure 19: **Palaeogeography of the Early Devonian**. The numbers indicate fish faunal provinces. 1 South American; 2 Rocky Mountain; 3 North Atlantic; 4 Arctic; 5 Angaran; 6 Tuvan; 7 South China. The asterisk indicates the approximate location of the Prague Basin (within the Barrandian area of the Bohemian Massif). Abbreviations: EA=Euamerica; S=Siberia; K=Kazachstania; G=Gondwana. After Chlupáč et al. 2011 and Benton 2024 (modified).

4.3 Devonian

Devonian - In the Devonian, the supercontinent Gondwana, along with other landmasses, shifted significantly northward. Baltica and Avalonia, which were located near the equator, amalgamated and merged with Laurentia, forming a complex landmass. As a result, the shallow seas between these continents disappeared. Due to the disappearance of continental barriers—as previously fragmented continents merged into a more unified landmass—the main trend in Devonian fish faunas was a shift from regional distributions to a more global occurrence (Benton 2024). Seven faunal provinces have been identified (Figure 19): **Tuvan**, **Angaran**, **North Atlantic**, **South American**, **Rocky Mountain**, **Arctic**, and **South China** (Žigaitė and Blieck 2013; Benton 2024)

4.4 Prague Basin (Barrandian area)

The **Barrandian area** represents a fossil-rich region of the **Bohemian Massif**, containing marine sediments from the Lower Palaeozoic—i.e., from the Cambrian, Ordovician, Silurian, and Devonian periods. The central part of the Barrandian area is the **Prague Basin**, which is composed of Ordovician, Silurian, and Devonian sediments (Figure 20). During the Lower Palaeozoic, the Bohemian Massif (including the Prague Basin) was situated on the northwestern margin of the continent Gondwana, in a region referred to as **Peri-Gondwana** (Chlupáč et al. 2011).

Ordovician - The beginning of the Prague Basin sedimentation took place in the relatively cold climatic region of Peri-Gondwana, which at the time was located in the higher latitudes of the Southern Hemisphere (around 60° south latitude) (Figure 17). The development of the Prague Basin began in the earliest part of the Lower Ordovician and continued into the subsequent geological periods (Kraft, Fatka, and Storch 1993; Chlupáč et al. 2011).

The Ordovician forms the largest and outermost part of the Prague Basin, representing marginal marine environments. The sediments are highly diverse, including conglomerates, sandstones, silicites, shales, siltstones, and quartzites (Kraft, Fatka, and Storch 1993; Chlupáč et al. 2011). However, the likelihood of finding any microvertebrate remains in these sediments is minimal. This corresponds to the previously discussed context, which refers to extremely rare findings.

Silurian - In the Silurian, the position of the Peri-Gondwanan Prague Basin shifted toward the lower latitudes of the Southern Hemisphere (around 30° south latitude) (Figure 18). The region was placed within a subtropical climatic zone, and the climate became warmer and more humid. The environment was characterized by shallow warm-water seas. Submarine volcanism was a significant aspect of Silurian geological development of the Prague Basin (Kraft, Fatka, and Storch 1993; Chlupáč et al. 2011). The closest continent to Peri-Gondwana was Baltica, which may provide useful comparative material due to the potential similarity in faunal composition.

Silurian forms the outer part of the central area of the Prague Basin. Typical sediments are black-gray graptolite shales, calcareous shales and bioclastic limestones, whereas towards younger formations, graptolite shales are gradually replaced by limestones (Kraft, Fatka, and Storch 1993; Chlupáč et al. 2011).

Silurian vertebrate finds are quite rare and remain insufficiently explored. However, **thelodont** scales and undetermined vertebrate fragments were found in bioclastic limestone from the Upper Silurian Požáry Formation, Přídolí Stage (Vaškaninová 2014).

Devonian - In the Devonian, the position of the Peri-Gondwanan Prague Basin shifted northwestward, moving closer to the equator (around 10–20° south latitude) (Figure 19). The region was placed within a tropical climate zone, and the climate became even warmer and more humid. Most of the continents were situated near the equator, and the distance between Gondwana and Laurussia was reduced. The marine environment across different continents became increasingly similar, with only local conditions varying. Faunal migration over great distances was possible, and regional differences between faunas gradually disappeared. Due to the similarity of environmental conditions and the closer proximity of landmasses, fossil remains from distant regions can serve as comparative material for those found in the Prague Basin (Chlupáč et al. 2011).

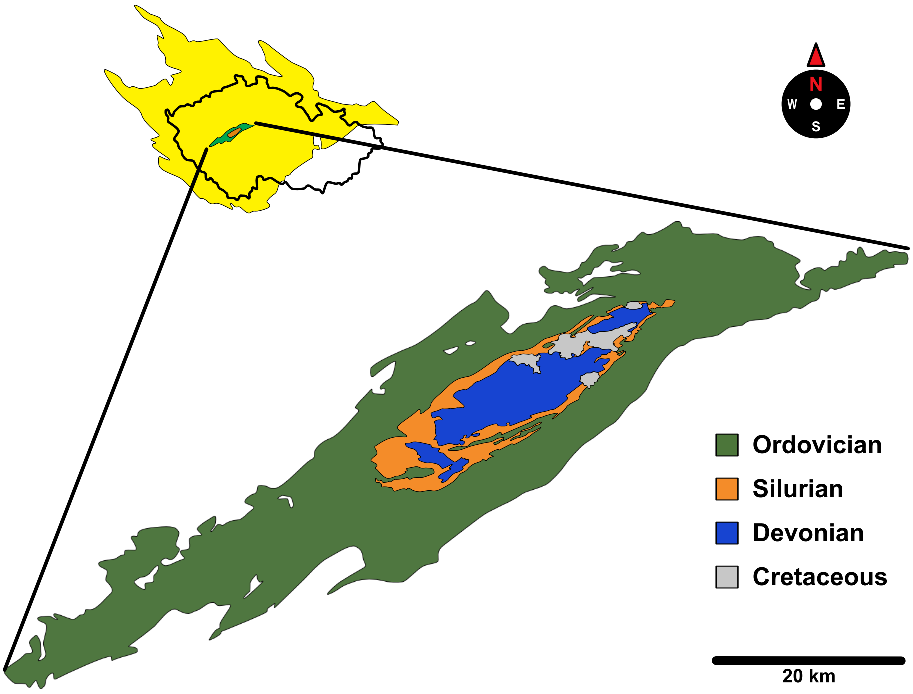

Figure 20: **Map of the Prague Basin.** The yellow colour indicates the Bohemian Massif. After Kraft et al. 2019 and Kraft, Bruthansová, and Mikuláš 2020 (modified).

The Lower and Middle Devonian forms the central area of the Prague Basin, whereas the Upper Devonian stages—the Frasnian and Famennian—are absent from the Prague Basin (Chlupáč et al. 2011). Typical sediments are mostly fine-grained (deepwater) limestones and bioclastic (shelfwater) limestones (Kraft, Fatka, and Storch 1993; Chlupáč et al. 2011).

As mentioned above, the Devonian was a period of significant evolution and extensive diversification of fish, often referred to as the "**nektonic revolution**"—a trend also reflected in the Devonian sediments of the Prague Basin. Several vertebrate fossils—both jawless and especially jawed—have been discovered in these deposits. These include macroscopic fossils, such as dermal shields, particularly from **placoderms** (Vaškaninová and Kraft 2014a; Vaškaninová and Kraft 2014b), spines from large **acanthodians** (Vaškaninová and Kraft 2014a; Vaškaninová and Ahlberg 2017) and, uniquely, dermal shields from **heterostracans** (Table 4) (Vaškaninová and Kraft 2016). Microscopic remains include mostly scales, teeth or tooth whorls, spines and dermal bones of **placoderms**, **acanthodians**, **chondrichthyans**, and **osteichthyans** (Table 3) (Mergl, Vaškaninová, and Žigaitė 2017).

microremains of early vertebrates from the Prague Basin				
systematic group	**classification**	**remain type**	**stage**	**period**
Thelodonti	?	scales	Přídolí	Upper Silurian
Placodermi	acanthothoracid	tesserae	Emsian	Lower Devonian
Acanthodii	*Nostolepis*, *Gomphonchus*, *Laliacanthus*, *Cheiracanthoides*	scales, spines, tooth whorls	Přídolí, Pragian, Emsian	Upper Silurian, Lower and Middle Devonian
Chodrichthyes	*Tassiliodus*	scales, teeth	Pragian, Emsian	Lower and Middle Devonian
Osteichthyes	onychodontid ?, palaeoniscoid ?	scales, teeth, bones	Eifelian-Givetian	Middle Devonian

Table 3: **Summary of microscopic remains of early vertebrates from the Prague Basin.** After Märss 1997, Vaškaninová 2014, and Mergl, Vaškaninová, and Žigaitė 2017.

macroremains of early vertebrates from the Prague Basin				
systematic group	**classification**	**remain type**	**stage**	**period**
Heterostraci	*Schizosteus*, *Drepanaspis*	head shields	Emsian/ Eifelian	Lower/Middle Devonian
Acanthodii	*Machaeacanthus*	spines	Pragian, Emsian	Lower Devonian
Placodermi	*Radotina*, *Kosoraspis*, *Tlamaspis*, *Sudaspis*, *Holopetalichthys*, *Johannaspis*, *Antineosteus*	endo- and exoskeletons	Lochkovian, Emsian,	Lower and Middle Devonian

Table 4: **Summary of macroscopic remains of early vertebrates from the Prague Basin.** After Vaškaninová and Kraft 2014a, Vaškaninová and Kraft 2014b, Vaškaninová and Kraft 2016, Vaškaninová and Ahlberg 2017, Vaškaninová et al. 2020, Vaškaninová 2020.

Despite the rarity of vertebrate remains in the Prague Basin, they represent an important topic for potential research. Although microscopic vertebrate remains of Prague Basin have been little studied so far (with only one article published), it can be assumed that many sediments in the Prague Basin contain such microremains.

5 Conclusion

The thesis is divided into three main chapters—Methods, Systematics, and Paleogeography—which together provide a comprehensive background for the study of early vertebrates.

The methods section offers a general overview of the methods used to study early vertebrates (both macro- and microfossils), including laboratory-based (destructive) and modern imaging (non-destructive) techniques. It also discusses the types of sediments in which early vertebrate fossils are typically found.

The systematics section focuses on the systematic classification of individual groups of early vertebrates, along with their basic characteristics: 1) **Chronostratigraphic and paleogeographic occurrence** – indicating the age and global distribution of the sediments in which these fossils are found, based on previously documented discoveries. 2) **Basic characteristics of body morphology and anatomy**, including a **description of the exoskeleton** (which, along with teeth, is often preserved as microremains). This also covers morphological and micro- and ultrastructural properties of the exoskeleton, including histology, which provides crucial information for determining the systematics of microremains. 3) **Basic paleoecology** (if known), which complements the often ecomorphotypical features of these groups and helps determine the occurrence of certain (sub)groups in specific environments (e.g., freshwater habitats such as rivers). 4) **A simplified systematic division into narrower groups**, along with their phylogenetic relationships. This is particularly helpful for identification, as closely related groups often share similar or identical features.

The palaeogeography section divides the Lower Paleozoic into four consecutive periods. Each period outlines the global configuration of continents and oceans, including marine environments such as shelf and deep-sea areas, along with associated climatic and environmental conditions. Palaeogeography also helps explain the distribution of various early fish-like vertebrate groups across different continents and their present-day localities. It also covers the global position of the Prague Basin during each period, including a description of the sediments—their stratigraphy and lithology—and highlights relevant environmental features. Documented and published remains of early vertebrates from this region are also discussed. Importantly, linking global palaeogeography with the palaeogeography of the Prague Basin provides insight into which regions—based on their paleogeographic rather than modern geographic context—can serve as comparative sources for studying early vertebrate remains. In other words, neighboring paleoregions are likely to contain a similar composition of faunas and and their fossil remains.

The thesis outlines applications for research of microscopic vertebrate remains from the Silurian and Devonian periods in the **Prague Basin**. Given that **limestone** is the most common sediment type, the use of **acetic acid** (and potentially formic acid) is recommended for sediment dissolution and fossil extraction. After extraction, a **scanning electron microscope** will be employed to examine the surfaces of microremains. When necessary, modern imaging techniques—such as X-ray or synchrotron scanning—will be applied to reveal delicate histology.

From a systematic perspective, the follow-up study should focus on the following groups: **Thelodonti**, **Placodermi**, **Acanthodii**, **Chondrichthyes**, and **Osteichthyes**, whose presence in the Prague Basin has already been documented in published studies. However, additional groups such as **Anaspida**, **Heterostraci**, and **Osteostraci** may also be expected, due to their confirmed occurrence in neighboring Barrandian paleoregions—suggesting a reasonable likelihood of encountering these taxa as well.

The Barrandian area (Prague Basin) is relatively poorly explored from the perspective of vertebrates. This is due not only to the relatively rare occurrence of vertebrate finds in the Prague Basin but also to the limited use of research methods for identifying their microscopic remains, which are relatively abundant in sediments containing invertebrate faunas. Therefore, future research on the microscopic remains of early vertebrates in the Prague Basin has great potential to supplement the Barrandian paleomap and to enhance our understanding of Lower Paleozoic Barrandian communities with respect to vertebrate taxa.

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6 Appendix

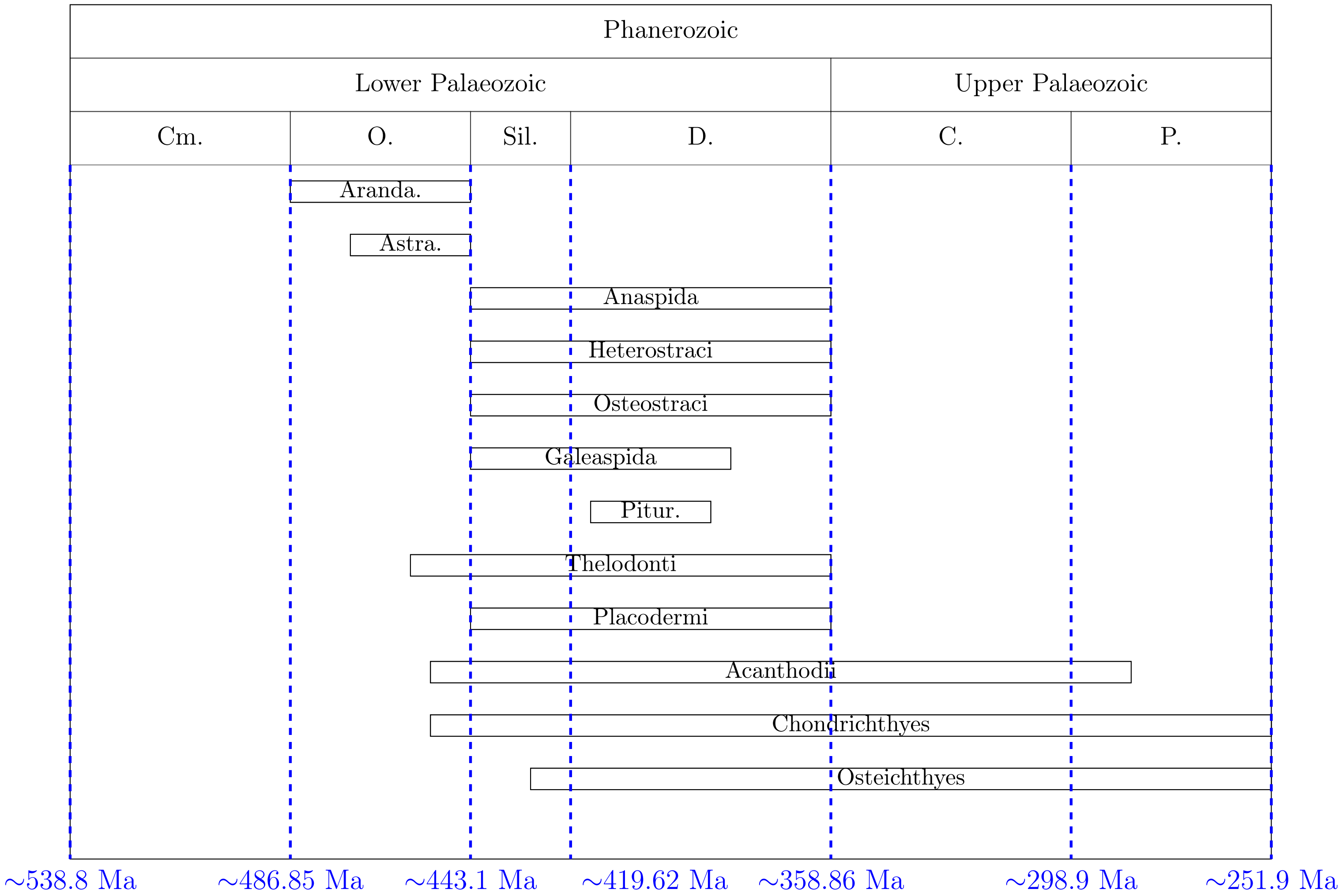

Figure 21: **Approximate occurrences of each systematic group, based on the fossil record.** The groups Chondrichthyes and Osteichthyes have both persisted into modern times. Abbreviations: Cm.=Cambrian; O.=Ordovician; S.=Silurian; D.=Devonian; C.=Carboniferous; P.=Permian; Aranda.=Arandaspida; Astra.=Astraspida; Pitur.=Pituriaspida. After Turner and Miller 2005, and the intervals of geological periods were adopted from *International Commission on Stratigraphy* 2024.