

# Teeth of actinopterygians from the Permo–Carboniferous of the Bohemian Massif with special reference to the teeth of Aeduellidae and Amblypteridae

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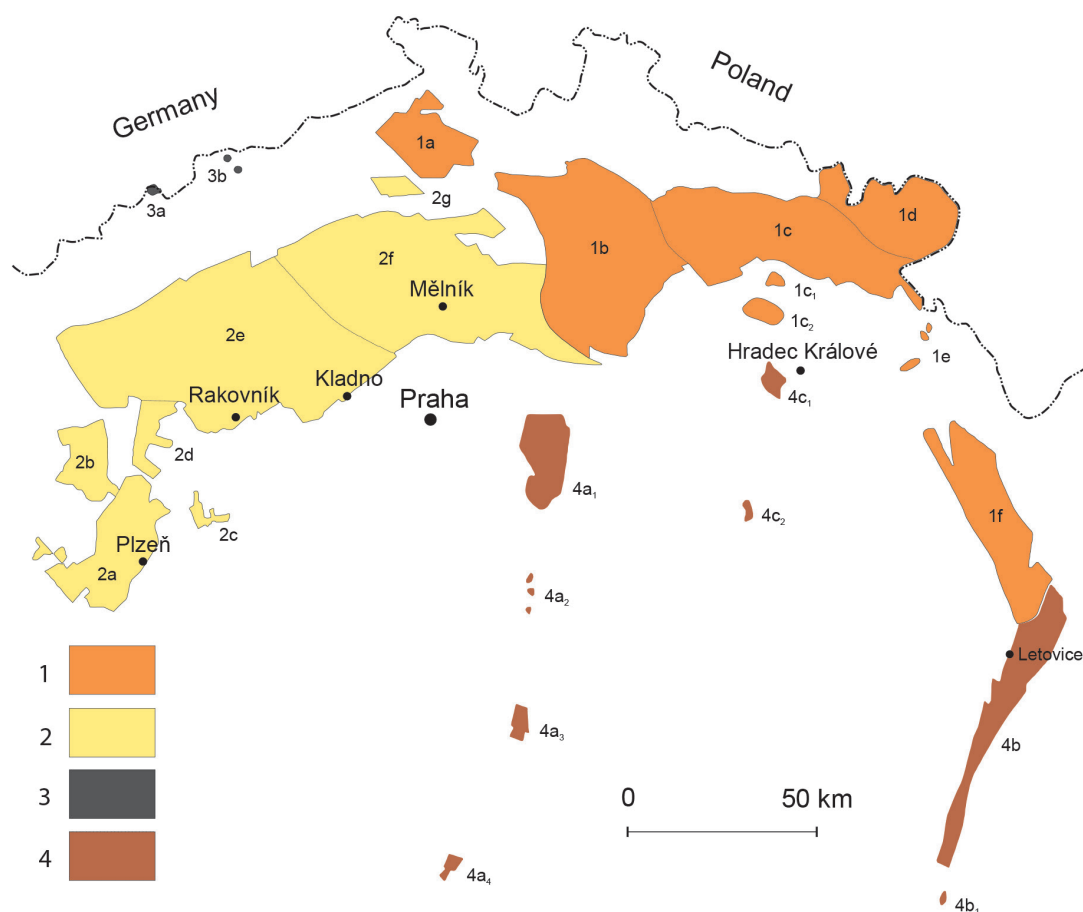
A wide range of different types of dentition is presented in the set of actinopterygians from the Permo–Carboniferous of the Bohemian Massif. They demonstrate variation in the form, size, arrangement, attachment and number of marginal teeth and dentition on the bones of the coronoid series of the lower jaw and the dermal bones of the palate. The wide variety of dentitions suggests their potential utility in taxonomic classification. Three basic types can be distinguished among the described marginal teeth. Special attention is paid to the specialised tubular teeth of Amblypteridae and Aeduellidae. Details of marginal dentition on the lower and upper jaws are described on the basis of *Paramblypterus* sp. from the Boskovice Basin. It appears that the small strong teeth covering the dermal bones of the coronoid series and the dermal bones of the inner side of the upper jaw played an important role in grasping and biting prey. Recently prepared material enables us to recognize tooth morphology, arrangement and changes during ontogenesis of the amblypterid fish *Paramblypterus* cf. *rohani*, *Paramblypterus* sp., aeduellid *Neslovicella elongata* and *Neslovicella rzehaki* from the Krkonoše Piedmont Basin and Boskovice Basin. • Key words: Carboniferous, Permian, Bohemian Massif, Dentition, Actinopterygii.

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The teeth of actinopterygians are one of the important features characterizing species and also fundamentally indicating the individual's way of life and food selection. The dentition varies considerably depending on the food type and foraging mode (Helfman *et al.* 2009). The marginal teeth of the maxilla, premaxilla and dentalosplenial can be distinguished from the teeth in the mouth cavity attached to the prearticular and coronoids of the lower jaw and the dermal bones of the palate of the upper jaw and variably on the ventral surface of the parasphenoid. The main function of marginal teeth is to capture and kill prey, retain prey in the mouth, and aid in swallowing. Marginal teeth show great morphological variation. They differ in their size, shape, number and spacing. It is also important to compare the size of the teeth with the size of the skull. Poplin & Heyler (1993) used as an illustration of this ratio a calculation of the tooth height compared to skull depth in front of the opercular series. The species studied in this contribution belong to the group of “primitive” actinopterygians which are characterized by the maxilla and premaxilla being firmly attached to the surrounding dermal bones.

Together with the neurocranium, they form a firmly connected unit. Indications of a weakening of this firm connection are only visible in Aeduellidae where there is a regression of the posterior maxillary plate, almost vertical suspensorium and mosaic of small bones in the postorbital area. However, the upper jaw is still firmly attached to the surrounding dermal bones. Mouth opening is activated by neurocranial elevation and a special mechanism for mandibular depression in all these “primitive” actinopterygians (Schaeffer & Rosen 1961; Lauder 1980, 1982). Schaeffer & Rosen (1961) assumed a fundamentally predaceous feeding mechanism in the “primitive” actinopterygians. Food items were probably caught by biting and swallowed in one piece with participation of the pharyngeal teeth. However, even in primitive actinopterygians, there is a great diversity among the marginal teeth. This diversity includes the probable original arrangement of teeth in two rows with big teeth in the medial row and more numerous smaller teeth in the lateral row (Poplin & Heyler 1993), teeth that are reduced to one row, or teeth that are specialized. Teeth on the dermal bones of the mouth cavity are also



**Figure 1.** Distribution of the freshwater Carboniferous–Permian basins in the Czech Republic (modified according to Holub & Pešek 1994). Legend: 1 – Sudetic Area: 1a – Česká Kamenice Basin; 1b – Mnichovo Hradiště Basin; 1c – Krkonoše Piedmont Basin (1c<sub>1</sub> – occurrence near Zvičina, 1c<sub>2</sub> – occurrence at the Hořice elevation); 1d – Intra-Sudetic Basin (Czech part); 1e – Permian occurrences in the Orlické hory Mts; 1f – Orlice Basin; 2 – Central and Western Bohemia Area: 2a – Plzeň Basin; 2b – Manětín Basin; 2c – Radnice Basin; 2d – Žihle Basin; 2e – Kladno-Rakovník Basin; 2f – Mšeno-Roudnice Basin; 2g – occurrence near Kravaře; 3 – Krušné hory Mts Area: 3a – occurrence near Brandov; 3b – occurrences between Moldava and Teplice; 4 – Furrows Area: 4a – Blanice Basin (4a<sub>1</sub> – northern part near Český Brod, 4a<sub>2</sub> – central part, the occurrences near Vlašim, 4a<sub>3</sub> – central part, the occurrences near Tábor, 4a<sub>4</sub> – southern part near České Budějovice); 4b – Boskovice Basin (4b<sub>1</sub> – occurrence near Miroslav); 4c – occurrences in the Železná hory Mts and near Hradec Králové (4c<sub>1</sub> – occurrence in the Železná hory Mts; 4c<sub>2</sub> – occurrence near Hradec Králové).

significant. These teeth help to restrain the prey in the mouth and when the prey is bitten repeatedly the teeth perforate the integument. During chewing these teeth lacerate and cause internal damage to the prey (Berkovitz & Schelis 2017).

Actinopterygians form a significant component of the vertebrates in the Permo–Carboniferous basins of the Bohemian Massif. They occur in the limnic basins of the Central and Western Bohemia Area, in the Krkonoše Piedmont Basin, the Intra-Sudetic Basin and the Boskovice Basin (Fig. 1). Twenty-one species of actinopterygians are described from the upper Carboniferous and lower Permian. A wide variation in the size, form, arrangement, attachment and number of marginal teeth and other teeth on the bones of the jaw apparatus and palate can be recognized in this small sample of

species. These range from the tiny fish *Pyritocephalus sculptus* (Frič, 1875) with an absence of teeth, a species for which detritus suction and filtration was probably the main way of obtaining food, to the large carnivorous *Progyrolepis speciosus* (Frič, 1876). The type of dentition in combination with individual size and evaluation of the palaeoecological environment inhabited by the actinopterygians is significant when considering their typical food. The predicted type of food is deduced for each species on the basis of the above mentioned indicators. Data on the teeth of actinopterygians from the Permo–Carboniferous basins of the Bohemian Massif are usually included in the species description. However, teeth preservation is often fragmentary or absent. The finds from recent years complement our knowledge and provide a comprehensive overview of dentition in

the already described taxa from the Carboniferous and Permian of the Bohemian Massif. Further attention is paid to the actinopterygians of the families Aeduellidae and Amblypteridae which constitute the main component of the fauna not only in the Bohemian Massif but also in several other European basins. Their specialised dentition was described in some specimens from Permo–Carboniferous basins of the French Massif Central (Blot & Heyler 1963, Blot 1966, Heyler 1969, Poplin & Heyler 1993, Štamberg 2018), the Saar Basin in Germany (Dietze 2001), and from the Bohemian Massif (Štamberg 2007, 2010). Recently used methods of preparation made it possible to uncover the fine dental structure in the actinopterygians from the Permian of the Boskovice Basin and Krkonoše Piedmont Basin and extend the information gained earlier by Blot & Heyler (1963). The new material enables study of the specialised dentition of Aeduellidae and Amblypteridae species during ontogenesis. The results of this study of actinopterygian dentition from the Czech Republic also allow comparison with those from other European Permo–Carboniferous basins.

## Material and methods

Specimens from the collection of the National Museum in Prague, Czech Geological Survey in Prague, Institute of Geology and Palaeontology of the Charles University in Prague and the Museum of Eastern Bohemia in Hradec Králové were used for this study. The descriptive terminology of the dermal bones of the skull conforms to that adopted by Grande & Bemis (1998). The index of tooth size after Poplin & Heyler (1993) clearly illustrates the ratio of the head depth (dh) to the tooth height (th) in front of the operculum. A number of terms derived from Ørvig (1967, 1978a, b) were used to describe dental structures in *Paramblypterus* sp. The teeth, which were covered with a thin layer of sediment, were cleaned using a Krantz pneumatic needle. Excess rock was removed with a toothbrush and a mixture of abrasive material contained in dishwasher powder and this method was particularly successful in the specimens from the Krkonoše Piedmont Basin. Selected specimens with well-preserved jaws and teeth which had been chosen for grinding were stabilized and cast into two-component resin, Araldit 2020, prior to cutting. Suitable specimens from the Permian of the Boskovice Basin were etched using the acetic acid solution method (Štamberg 2003). Photographs were prepared using a Canon EOS 400D, and most samples were documented using a Hitachi S-3700N SEM.

*Institutional abbreviations.* – DP – Institute of Geology and Palaeontology of the Charles University, Prague; LS – Czech Geological Survey, Prague, Czech Republic;

M – National Museum, Prague, Czech Republic; P, G – Museum of Eastern Bohemia in Hradec Králové, Czech Republic.

## Systematic part

Family Haplolepididae Westoll, 1944

### *Pyritocephalus sculptus* (Frič, 1875)

A minute fish reaching 40 to 60 mm in total length occurring in the cannel coal of the Nýřany Member (middle Pennsylvanian, Moscovian) of the Plzeň Basin. The *Pyritocephalus sculptus* specimens used in this study showed well preserved upper and lower jaws (Štamberg 1978) however teeth were never observed. Westoll (1944) mentioned minute conical teeth on the maxilla of one specimen of *Pyritocephalus sculptus* from Nýřany, but he did not observe teeth on the lower jaw. *Pyritocephalus sculptus* lived in stagnant shallow water with low oxygenation. A large number of invertebrates (Malacostraca, Myriapoda, Arachnida, Insecta, Tentaculitoidea) were described from the same layers of the Nýřany Member. These invertebrates were too big to be preyed by *Pyritocephalus* due to the absence of teeth or possibly in the better scenario, the presence of only very fine teeth. It can be assumed the modification of the fins, a low dorsal fin which could be collapsed, allowed the fish to skim eggs or newly hatched young invertebrates or other planktonic minute fauna under the surface of the water (Westoll 1944). The perforated skull roof suggests movement of the animal just below the water surface. The unusually large paired fenestra, lateral to the frontal and parietal, could have in life contained sensory organs that provided information on the environment, and warned of danger when the animal hunted below the water surface. The genus *Pyritocephalus* is also distributed in several European and North American sites. Westoll (1944) described another species of the genus *Pyritocephalus* from several localities representing a similar environment as the Nýřany Member. Teeth have not been observed in *Pyritocephalus lineatus* (Newberry, 1856) from Linton (Ohio, USA). On the contrary, *Pyritocephalus gracilis* (Newberry & Worthen, 1870) from Mazon Creek (Illinois, USA) demonstrates minute teeth on the lower jaw and maxilla. However, it is not entirely clear whether they are marginal teeth, teeth on coronoids, or teeth from the bones of the palate (Westoll 1944). Elliott (2015) mentioned in *Pyritocephalus youngii* Elliott, 2015 from Westphalian A of Dumgray coal shales (North Lanarkshire, Scotland) the presence of large conical teeth with slightly incurved forwards, with each tooth very close to the next one. These teeth have not been observed in *Pyritocephalus*

*lowneyae* Huber, 1992 from the Pennsylvanian of New Mexico, USA (Huber 1992).

Family Sceletophoridae Štamberg, 2006

***Sceletophorus* Fritsch, 1894**

Figure 2A–C

Family Sceletophoridae is represented in the upper Carboniferous of Central Bohemian basins (middle Pennsylvanian, Moscovian) by *Sceletophorus biserialis* Fritsch, 1894 and *Sceletophorus verrucosus* (Fritsch, 1894). *Sceletophorus biserialis* is a slender fish reaching 10 cm in length. *Sceletophorus verrucosus* reached a length of 14 cm with a dorsally arched trunk. The marginal teeth of both species are of the same type. The following description is focused on the specimens of *S. biserialis* as they provided more information on the dentition. The maxilla is posteriorly extended into an approximately quadrate shape plate that does not protrude in a ventro-posterior direction. The lower jaw is very strong (Štamberg 1983). Although *S. biserialis* are small individuals, the dentition is very robust. The conical teeth are identical in size, sharply pointed (Fig. 2A–C), and arranged close to each other in one row. The teeth on the maxilla spread along the whole ventral margin of the bone, including the ventral margin of the maxillary plate. The lower jaw carries teeth of the same shape and size as the maxilla. Identical teeth are also on the premaxilla. The index of tooth size (dh/th ratio) in *S. biserialis* is 24–27.

Species *Sceletophorus biserialis* and *S. verrucosus* inhabited the same environment as *Pyrtocephalus sculptus*. Both species are known only from the Nýřany Member of the Plzeň Basin. The sediments formed in shallow stagnant water with accumulation of rich organic material. Terrestrial fauna such as Malacostraca, Myriapoda, Arachnida, Insecta are well represented in these sediments. The invertebrate fauna had been flushed, or invaded, from the surrounding vegetation into the aquatic environment, and were very likely to have served as the main source of food for both species of *Sceletophorus*.

Family Trissolepididae Fritsch, 1893

***Sphaerolepis kounoviensis* Frič, 1876**

Figure 2D–F

A small fish reaching 12 to 15 cm. Occurrence of the species is limited to late Pennsylvanian (Kasimovian, Gzhelian) of the Central and Western Bohemia Area and Krkonoše Piedmont Basin. The maxilla and lower jaw are equipped with numerous relatively stout sharp pointed marginal teeth with a length 0.5 mm (Fig. 2D–F).

The teeth of the same size and shape are arranged in one row, with the occurrence of some smaller teeth which probably grew later. The teeth are smooth and terminate with an acrodin apex. Approximately 18 teeth are present on the lower jaw, and the total number does not exceed 20. The upper jaw is equipped with 22 marginal teeth. Sharp pointed teeth cover the whole ventral surface of the vomer except its medial margin which is overlapped by the corpus parasphenoidis. The teeth are similar to the marginal teeth on the jaws. These vomerine teeth are smallest along the lateral margin of the vomer, increasing in size in a medial direction (Štamberg 1991).

*Sphaerolepis kounoviensis* usually occurs in deposits rich in organic matter, in an anoxic environment where organic material decayed. The well-developed caudal fin with a long dorsal lobe allowed the fish to significantly accelerate, suggesting that it was likely to move closer to the water surface and actively capture insects. The most common insects could have been a major component of the fishes' diet. Blattoid insects such as *Neorthroblattina*, *Anthracoblattina*, and *Sysciophlebia* occurred abundantly in some localities of Gzhelian and could have formed the main component of the diet. *Sphaerolepis kounoviensis* probably did not disregard the decaying remains of others actinopterygians or amphibians. It can be assumed that *Sphaerolepis kounoviensis* in Kasimovian and Gzhelian and *Sceletophorus biserialis* together with *Sceletophorus verrucosus* in Moscovian, had the same type of diet judging from the similar type of dentition in these fish. *Sphaerolepis kounoviensis* is the most abundant, in addition to other localities, also in the locality Nedvězí (Krkonoše Piedmont Basin) specifically in the layer with an accumulation of ostracods. They can also be a component of the diet of *Sphaerolepis* (Štamberg 2016). The trunk of *Sphaerolepis kounoviensis* is covered by circular shaped scales. The exposed field of the scales exhibits conspicuous sculptures in the form of sharply pointed posteriorly orientated protuberances which to some extent protected the body from predators. The large carnivorous actinopterygian fish *Progyrolepis speciosus*, selachians *Orthacanthus*, *Sphenacanthus*, *Turnovichtys*, and *Lissodus*, or even some amphibians were potentially predators of *Sphaerolepis kounoviensis*.

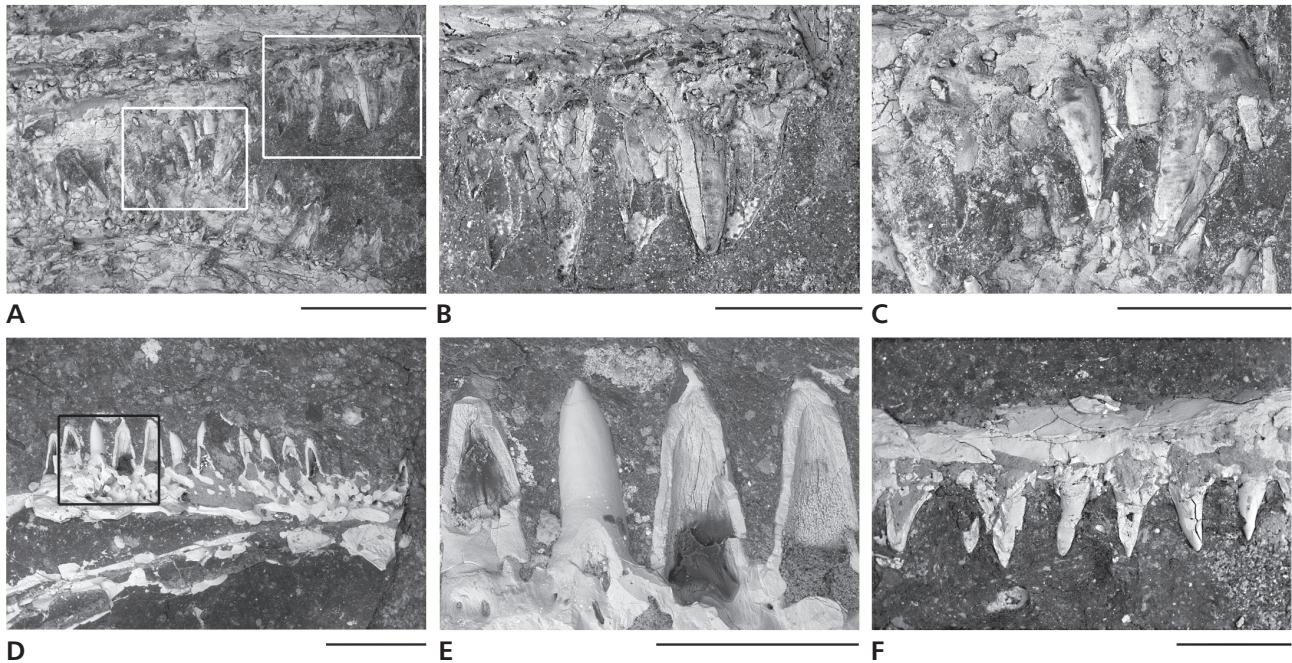
Family Acrolepidae Aldinger, 1937

***Progyrolepis speciosus* (Frič, 1875)**

Figure 3A–D

A large carnivorous fish reaching 60 cm in total length. It occurs in sediments of the late Pennsylvanian (Kasimovian, Gzhelian) in the Central and Western Bohemia Area and Krkonoše Piedmont Basin. The fish has typical predatory dentition where the teeth on the





**Figure 2.** A–C – *Sceltophorus biserialis* Fritsch, 1894. Moscovian, Plzeň Basin. M 1422; A – upper and lower jaws with teeth. The white frames mark the views at B and C of this figure, scale bar = 1 mm; B – detail of teeth on the maxilla, scale bar = 500 µm; C – detail of teeth on the maxilla, scale bar = 500 µm. • D–F – *Sphaerolepis kounoviensis* Frič, 1876. Kasimovian, Kladno-Rakovník Basin; D – lower jaw. The black frame marks the view at E of this figure. P 81329, scale bar = 1 mm; E – detail of teeth of the lower jaw. P 81329, scale bar = 500 µm; F – fragment of the maxilla with teeth. P 81367, scale bar = 1 mm.

lower and upper jaws are arranged in two rows. These teeth are well preserved on the lectotype M 1217 (Fig. 3A). The medial row contains large conical teeth that are 3–5 mm long with a 2 mm wide base. The anteriorly placed teeth are a little shorter than the posteriorly placed teeth. The lower jaw bears 11–12 large conical teeth. Much smaller and more numerous sharp pointed teeth form the lateral row (Fig. 3B). On an individual specimen they are maximally 1.2 mm long but there are also some which are only 0.5 mm long. The teeth in the lateral row are 4–5 times shorter and more numerous than the large teeth on the medial row. In the gap between two large conical teeth on the medial row, there are 4–5 small teeth on the lateral row. The teeth of the lateral and medial rows terminate with an acrodin apex, which in the large conical teeth is 0.5 mm long. The index of the tooth size (dh/th ratio) in the sense of Poplin & Heyler (1993) is about 26.

Dental morphology of *Progyrolepis speciosus* is traceable, beside the lectotype M 1217 and lower jaw M 884, also on other isolated teeth (Fig. 3C, D). With the exception of the acrodin tip, the corpus of the tooth is sculptured with shallow ridges uniformly directed from the acrodin apex to the base of the tooth. Because there are 11 or 12 of these longitudinal ridges on the visible half of the tooth; it can be supposed there are 22 to 24 longitudinal ridges around the whole periphery of the

tooth. A different fine microsculpture is observable on the whole surface of the tooth, with the exception of the acrodin apex. This fine microsculpture is formed by fine protuberances convolutedly distributed over the surface of the tooth. The elliptical protuberances are proximo-distally elongated and confluent in several places (Štamberg 2016). The distribution of the protuberances corresponds to the description of the tooth ornamentation in *Progyrolepis speciosus* type material by Fritsch (1895, pl. 32, figs 4–6).

The teeth of *Progyrolepis speciosus* are similar to the teeth of *Progyrolepis heyleri* Poplin, 1999 from the Permian locality Buxières-les-Mines in Bourbon l'Archambault Basin in France. There is strong correspondence between these two species in the arrangement of the teeth and also their morphology. Microsculpture on the large laniaries teeth and smaller teeth on the lateral row also match with the microsculpture of *P. speciosus*. Differences can be found in the number of large conical teeth in the medial row, the medial row of *Progyrolepis heyleri* contains 12–14 conical teeth and the index of the tooth size (dh/th ratio) is 22 (Štamberg 2018). The study of *Progyrolepis heyleri* was based on a greater number of individuals (Štamberg 2018) than the study of *Progyrolepis speciosus*. It was possible to demonstrate changes during the ontogenetic development of the specimens such as how the number of conical teeth in the medial row fluctuates, changes in their

arrangement and in their shape. Well-preserved material of *P. heyleri* made it possible to identify small short sharply pointed teeth covering the dorsal surface of the coronoids on the lower jaw, also on the medioventral surface of the ectopterygoid and dermometapterygoid and on the ventral surface of the parasphenoid (Štamberg 2018). It is very likely that the palate bones and coronoids of *Progyrolepis heyleri* also exhibit similar small teeth.

*Progyrolepis speciosus* was powerful swimmer which actively hunted other fishes or amphibians. Diagonally arranged ridges on the outer surface of the scales, which were oriented antero-posteriorly to the animal's body, directed the flow of water around animal's body and they thus contributed to its stability during rapid attacks. The same type of scale sculpture occurs also in other Permo–Carboniferous actinopterygians (*Rhabdolepis*, *Elonichthys*) with the same method of hunting.

Family Elonichthyidae Aldinger, 1937

### *Elonichthys krejci* (Fritsch, 1895)

Figure 3E, F

Fishes of the genus *Elonichthys* have been discussed previously. Their revision in the recent past (Štamberg 1991, 2010), and a new revision of the type species *Elonichthys germari* Giebel, 1848 from the Saal Basin in Germany by Schindler (2018) confirm the presence of *Elonichthys krejci* (Fritsch, 1895) in the Bohemian Massif. *Elonichthys krejci* is a small predatory fish not exceeding 15 cm in length. It lived in the limnic basin of the Central and Western Bohemia Area and Krkonoše Piedmont Basin during late Pennsylvanian (Kasimovian, Gzhelian).

The dentition is recognisable on the type specimen M 1208 from Plzeň Basin (Štamberg 1991). It is formed of two distinct rows of teeth. The outer row consists of numerous 1 mm long minute teeth while the teeth on the inner row are three times longer, conical, sharply pointed but less numerous. The teeth on the outer and inner rows have a distinct acrodin apex.

Numerous finds of isolated teeth from the Stephanian C of the Krkonoše Piedmont Basin can be assigned to *Elonichthys* (Štamberg 2016) on the basis of comparison with the type material of *Elonichthys krejci*. The slender, sharp pointed teeth are 1.5–1.7 mm in length (Fig. 3E, F).

The width at the base is 0.6 mm. The distinct acrodin apex has a length of 0.3 mm. The entire outer surface of the teeth, with the exception of the acrodin apex, is covered by microtubercles shaped like short proximodistally elongated ribs arranged close to each other.

The basic arrangement of teeth of *Elonichthys krejci* from Plzeň Basin and isolated teeth of *Elonichthys* from the Krkonoše Piedmont Basin are similar to the dentition in *Progyrolepis speciosus*. However, they differ in the more slender teeth of *Elonichthys krejci* and absence of longitudinal ridges on the periphery of the large conical teeth which are recorded in *Progyrolepis speciosus*.

It can be assumed that the small predatory fish *Elonichthys krejci* fed on insects or juvenile actinopterygians such as *Spinarachthys dispersus* or *Sphaerolepis biserialis* or larvae of amphibians.

Family Igornichthyidae Heyler, 1977

### *Igornichthys bohemicus* Štamberg, 2016

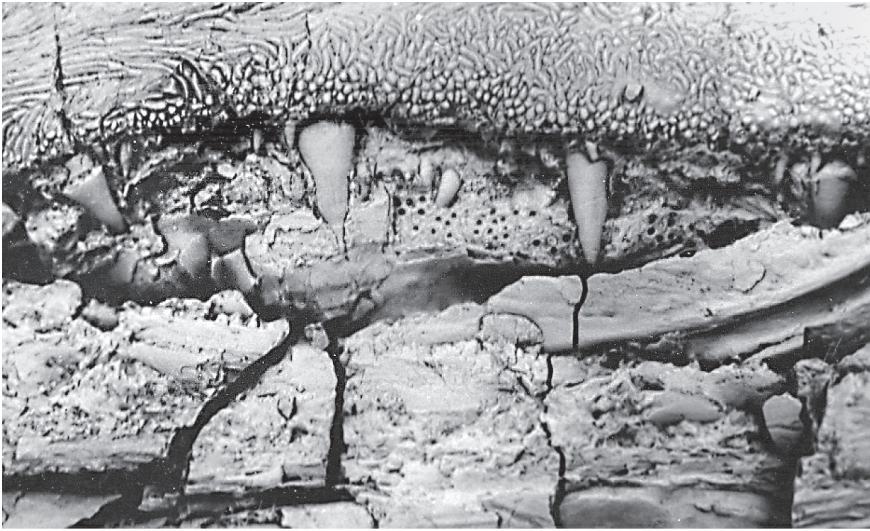
Figure 4A–C

A very small fish; which as an adult probably did not exceed 8 cm in total length. It occurs in the lower Permian (Vrchlabí Formation, Asselian) of the Krkonoše Piedmont Basin. The dentition is well developed on the upper and lower jaws, and it consists of a single row of straight, conical teeth of equal size and shape (Fig. 4A–C). The teeth have a wide base, and the height is twice that of the base width. The tooth surface is smooth. A small acrodin apex, which sometimes narrowing, is present. The teeth are arranged in a single row, and they interlock when the jaws are closed (Fig. 4B). There are 24–27 marginal teeth along each of the upper and lower jaws. The index of tooth height compared to the depth of the skull in front of the opercular series (dh/th ratio) results in a ratio of 40. The dermal bones on the inner side of the palatoquadratum exhibit small sharply pointed teeth. Minute teeth also cover the ventral surface of the parasphenoid processus cultriformis (Štamberg 2016).

*Igornichthys bohemicus* has been only rarely found in the site Rybnice “Hoňkuv potok” (Vrchlabí Formation, Asselian) in the Krkonoše Piedmont Basin. It is known only from two specimens. Conchostracans and syncarid

**Figure 3.** A–D – *Progyrolepis speciosus* (Frič, 1875); A – part of the maxilla in lateral view with conical teeth of the inner row and several small teeth of the outer row. Kasimovian, Kladno-Rakovník Basin. M 1217, scale bar = 5 mm; B – lower jaw with large conical teeth of the inner row and small teeth of outer row. Kasimovian, Kladno-Rakovník Basin. M884, scale bar = 5 mm; C – distal part of isolated tooth with smooth acrodin apex and shallow ridges uniformly directed from acrodin apex to the base of the tooth. Kasimovian, Krkonoše Piedmont Basin. LS84 – Št5, scale bar = 300 µm; D – fine elliptical protuberances on the periphery of the tooth are proximo-distally elongated. LS84 – Št5, scale bar = 100 µm. • E–G – *Elonichthys krejci* (Fritsch, 1895). Gzhelian, Krkonoše Piedmont Basin. M 4900; E – isolated whole tooth from locality Ploužnice, scale bar = 1 mm; F, G – microtubercles on the periphery of the tooth, scale bars = 100 µm.

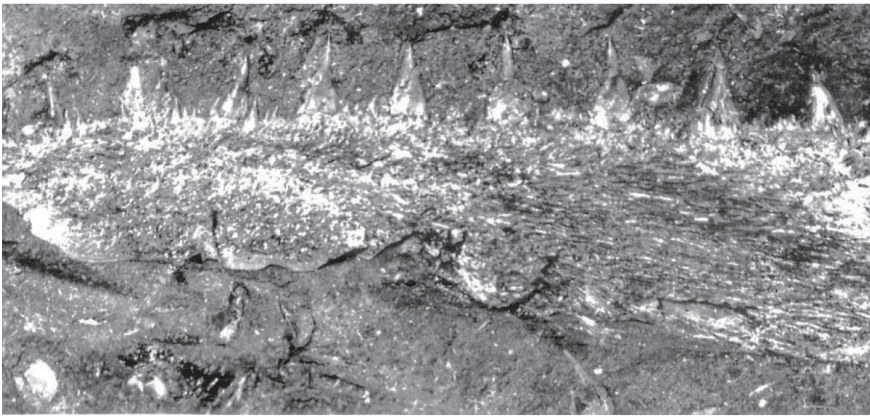




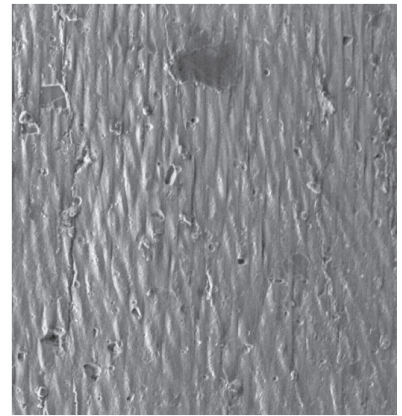
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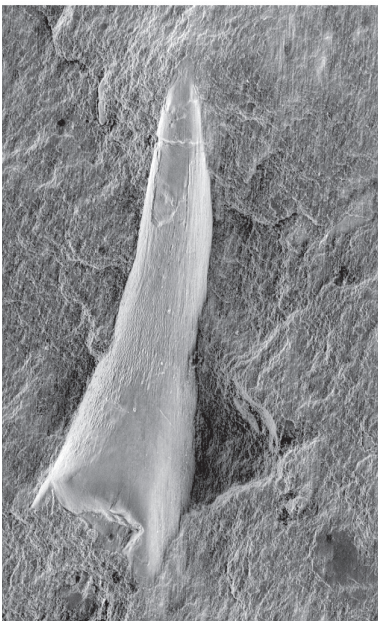
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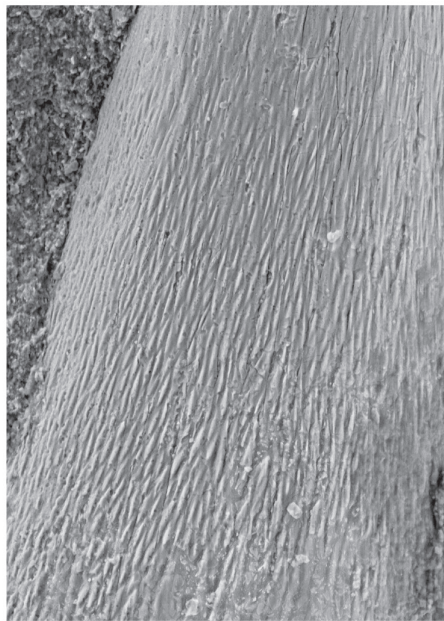
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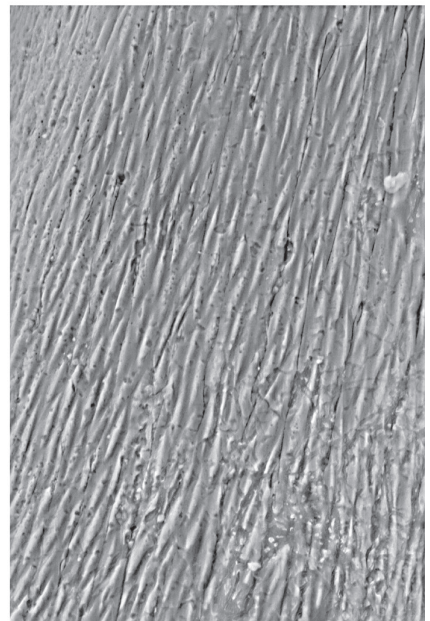
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G



malacostracans *Monicaris rudnicensis* Štamberg, 2000 occur abundantly in the same locality. Based on the dentition, the probable main food source of *Ignornichthys bohemicus* are syncarid malacostracans which are only known from this locality. The scales covering the body of *Ignornichthys bohemicus* have one or two sharp pointed spines directed posteriorly on their surface. These could form some protection for the animal against predators such as xenacanthid sharks *Bohemiacanthus* which occur in the same locality.

*Ignornichthys doubingeri* Heyler, 1972 described from the Igornay Formation of Autun Basin (France) show an alternation of large and smaller teeth on the jaws (Heyler 1969) whereas the larger teeth have the same size and shape as the teeth of *Ignornichthys bohemicus*, the smaller ones are only marginally smaller than the large teeth.

Family Palaeonisciformes Hay, 1929

### ***Letovichthys* Štamberg, 2007**

Figure 4D–J

Genus *Letovichthys* is represented in the lower Permian (Asselian) of Boskovice Basin by *Letovichthys tuberculatus* Štamberg, 2007 and *Letovichthys multidentatus* Štamberg, 2007. The total body length of both species is estimated to range from 15 to 20 cm. They have strong lower jaw and maxilla with a large posterior maxillary plate which extends ventroposteriorly into a large projection. The maxilla and lower jaw carry two types of teeth in two rows.

*Letovichthys tuberculatus* has outer row with numerous sharp pointed teeth, while the inner row carries large conical teeth that are three times higher than those of the outer row (Fig. 4D, E). The large conical teeth in inner row are less numerous with large gaps between neighbouring teeth. There are about 16 large conical teeth per jaw. The teeth have apical acrodin caps. The lower jaw dentition is similar to that on the maxilla.

Marginal teeth of *Letovichthys multidentatus* are also arranged in two rows. The outer row contains numerous small, sharply pointed teeth; similar to the condition of *L. tuberculatus*. The inner row contains large conical teeth which are lined up close together without gaps (Fig.

4F–J). The teeth are bluntly pointed and the acrodin cap is observable on the apex of some teeth. It is estimated that *L. multidentatus* had at least 40 large teeth in each jaw. This considerably different marginal dentition of *L. multidentatus* could perhaps be caused by a replacement process involving some of teeth of outer row.

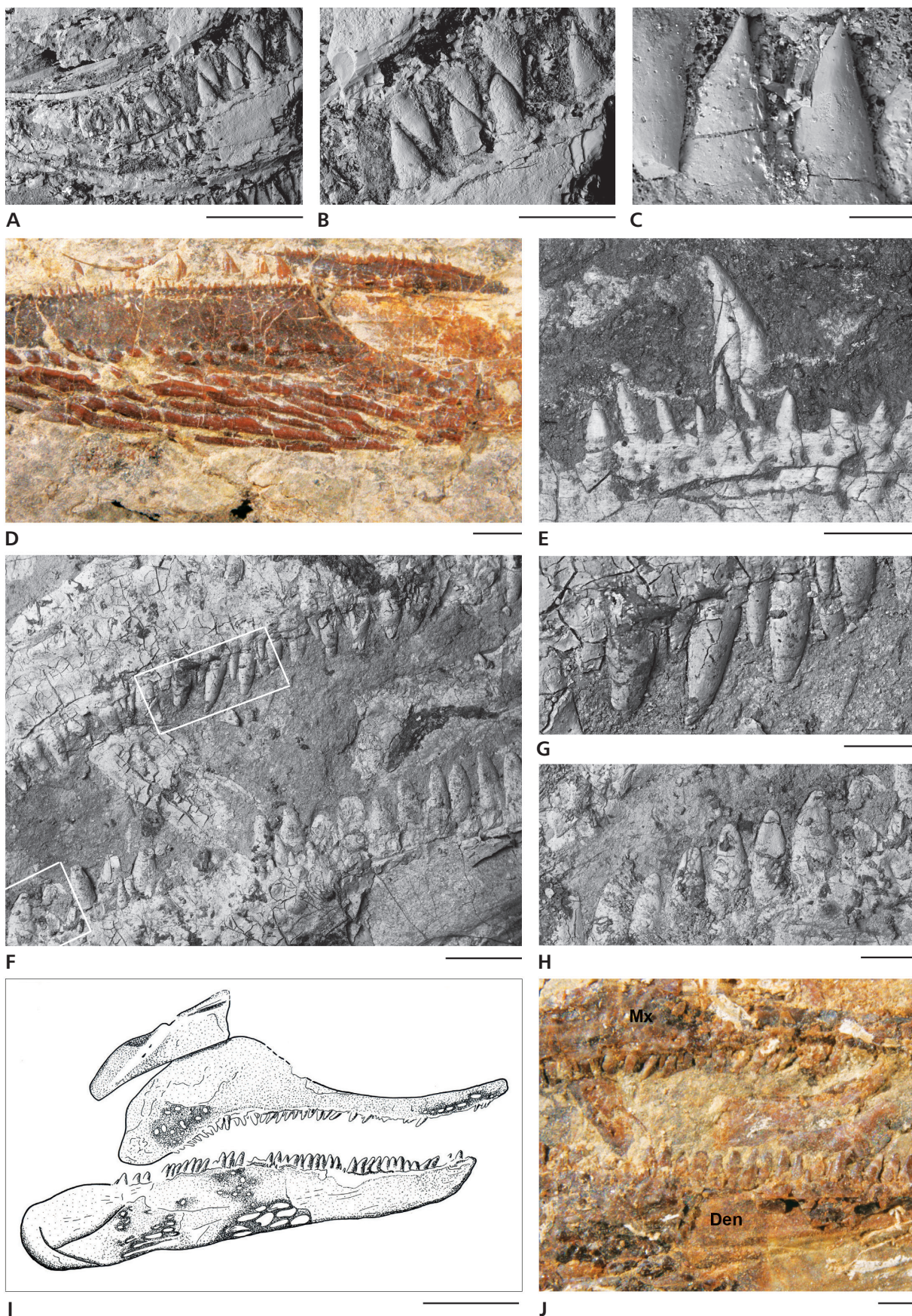
Both species of the genus *Letovichthys* have a slender body shape, strong caudal fin, and robust jaws equipped with two rows of teeth. Accordingly, *Letovichthys* is reconstructed as a carnivorous fish that actively preyed upon other swimming animals. Body fragments and pieces of skin of acanthodians lying close to specimens of *Letovichthys* within the sediment suggest that small acanthodians formed its main diet (Štamberg 2007).

Family Amblypteridae Romer, 1945

Amblypteridae is represented in the Bohemian Massif by the genus *Paramblypterus* and together with the species of genera *Bourbonnella* and *Neslovicella* of the family Aeduellidae are the largest groups of actinopterygians occurring in the Permian of the Bohemian Massif. Both families are characterized by a brush arrangement of tubular teeth. These teeth consist of a long tubule with a small acrodin cusp distally. This specialised dentition was first described in *Paramblypterus* and *Aeduell* from the Stephanian and lower Permian of the French Massif Central by Blot & Heyler (1963), Blot (1966) and Heyler (1969). Preservation of the tubular teeth and jaw apparatus of amblypterids from the Krkonoše Piedmont Basin and Boskovice Basin enable us to recognize tooth morphology, arrangement and changes during ontogeny. Amblypterids belong among the most numerous vertebrates in the sediments of the lower Permian of the Bohemian Massif. They are represented currently by *Paramblypterus rohani* (Heckel & Kner, 1861), *Paramblypterus zeidleri* (Fritsch, 1895), *Paramblypterus kablikae* (Geinitz, 1860), *Paramblypterus vratislaviensis* (Agassiz, 1833), *Paramblypterus feistmanteli* (Fritsch, 1895) and other unidentified species of the genus *Paramblypterus*. Dentition consisting of tubular teeth is a common feature for all species of this genus. Dentition of two groups of amblypterids will be discussed in the following text, namely *Paramblypterus* sp. from the Boskovice Basin

**Figure 4.** A–C – *Ignornichthys bohemicus* Štamberg, 2016. Lower Permian (Asselian), Krkonoše Piedmont Basin, P 30866; A – general view of the teeth of upper and lower jaws, scale bar = 1 mm; B – detail of the teeth of the upper and lower jaws, which interlock, when the jaws are closed, scale bar = 500 µm; C – teeth of the lower jaw, scale bar = 100 µm. • D, E – *Letovichthys tuberculatus* Štamberg, 2007. Lower Permian (Asselian), Boskovice Basin. Posterior region of the lower jaw with the prearticular on the right side above. P 72419, scale bar = 1 mm; E – outer row of small teeth and large conical tooth in inner row of the lower jaw, scale bar = 500 µm. • F–J – *Letovichthys multidentatus* Štamberg, 2007. Lower Permian (Asselian), Boskovice Basin; F – lower and upper jaws with marginal teeth. Small white frames indicate the portions of the dentition magnified in G and H of this figure. P 72436, scale bar = 1 mm; G – the teeth of outer and inner rows on the upper jaw, scale bar = 500 µm; H – the teeth of inner row on the lower jaw, scale bar = 500 µm; I – lower and upper jaws and fragment of the preoperculum in lateral view, P 72436, scale bar = 5 mm; J – maxilla and dentalosplenial with the dentition. P 72436, scale bar = 1 mm. Abbreviations: Den – dentalosplenial; Mx – maxilla.







and *Paramblypterus* cf. *rohani* and *Paramblypterus* sp. from the Krkonoše Piedmont Basin.

***Paramblypterus* sp. from the Boskovice Basin**  
Figures 5–7

Unidentified species of the genus *Paramblypterus* are abundant in the lower Permian (Asselian) of the northern region of the Boskovice Basin. They occur together with abundant discosauriscid amphibians. The mass death of vertebrates bound to aquatic environment is probably due to the loss of oxygen during water level fluctuations or overheating of the water in lake. Skeletal remains of animals are deposited in the limestone or calcareous claystone. Cadavers of these animals were covered with fine sediment shortly after the animal died, and thus the bones were not washed away after decomposition of the animal. Another advantage of this type of fossilisation is the possibility to use chemical preparation (acetic acid) of the fossils (Štamberg 2003). A number of important skeletal details, and hence fine dentition, can be preserved (Figs 5, 6, 7A).

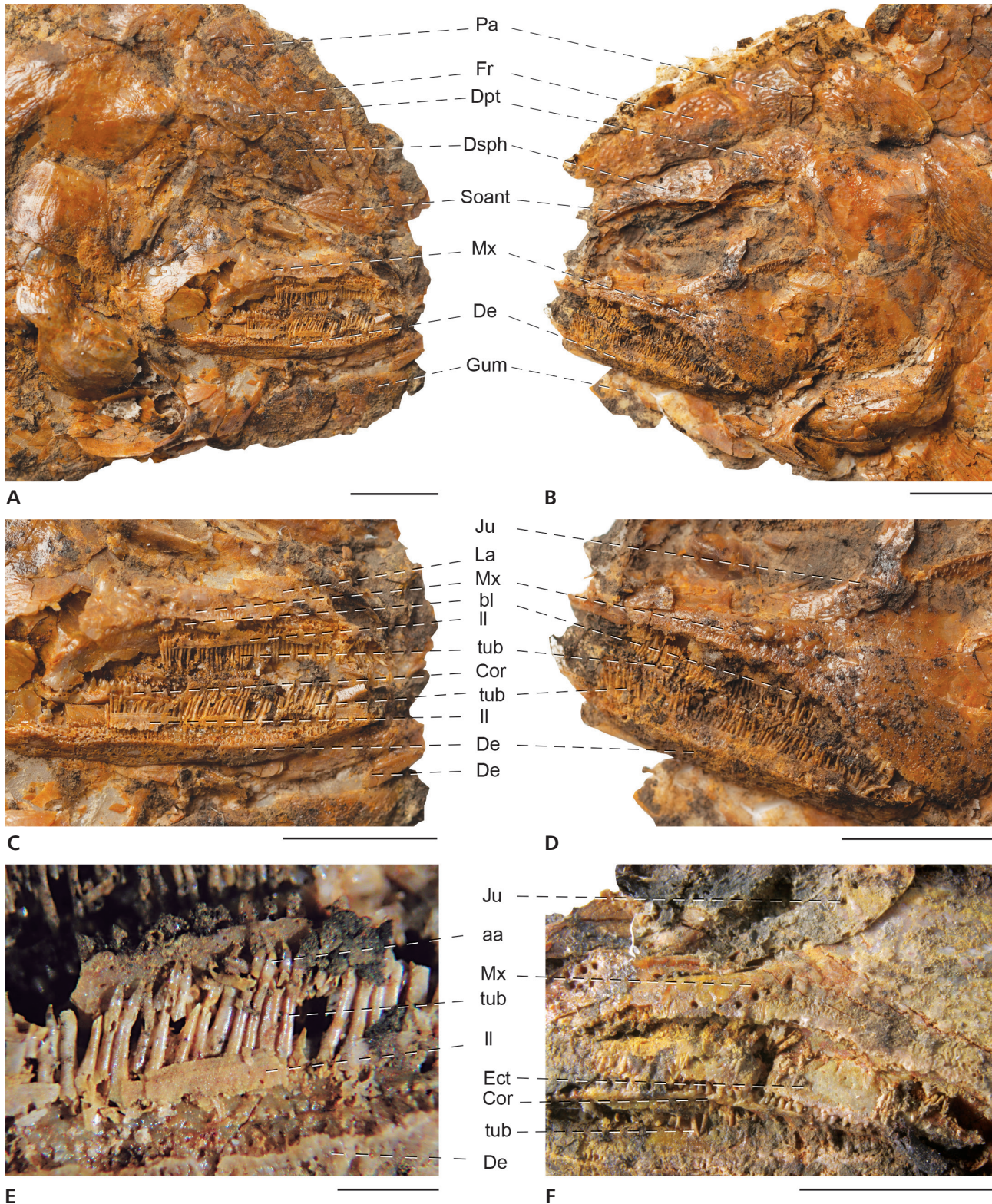
*Paramblypterus* sp. from the Boskovice Basin reach 10–20 cm in length. Marginal teeth on the upper and lower jaws are formed of long tubules terminated with a sharp pointed acrodin apex. Marginal tubular teeth were also well developed in juvenile specimens. Long tubules terminated with a sharp pointed acrodin apex were observed in a 5 cm long juvenile specimen of *Paramblypterus* sp. The acrodin apex joins smoothly with the tubule as figured by Heyler (Blot & Heyler 1963, fig. 2a), and not as figured by Blot (Blot & Heyler 1963, fig. 3). The tubules are hollow and the cavity also passes into the inner part of the acrodin apex. The hollow part of the tooth served as pulp cavity, and so, it can be assumed it was filled with soft tissues such as blood tissues and nerve fibres during the life of the animal. The tubules on the fossil material show longitudinal grooves on their outer surface which were created by a partial warping of the tubules after the internal material of the tube disappeared after the animal died. The circular wall of the tubules is made of dentin (Fig. 6E), and the thin outer layer is of enamel which is visible when crossed nicols. The acrodin apex has the shape of a straight cone or is slightly curved posteriorly (Figs 5E; 6A, B). Posteriorly bent tooth tips are mainly seen in teeth in the anterior part of the jaws. The acrodin apex constitutes about  $\frac{1}{6}$ – $\frac{1}{8}$  of the total tooth length in adult specimens. For example in adult specimens G 201, P 80385, P 80377

(Fig. 5A–D) with length of maxilla 16 mm, the length of whole tubular teeth is 1.3 mm, and the length of the acrodin apex is 0.2 mm. Tubular teeth are placed close together and have a brush-like type of arrangement. The bases of the teeth coalesce to form a thin basal lamella which adheres to the dentalosplenic (Figs 5A, D; 7B). If the teeth are separated from the lower or upper jaw during the initial stage of skull decomposition, the entire set of tubular teeth, including this basal lamella, is usually separated. It can be assumed that this basal lamella did not form a firmly connected unit with the lower or upper jaws. During the death of the animal and subsequent processes of decomposition, it was relatively easy for this basal lamella to become separated and with it the entire set of teeth. It is also the reason why this type of dentition is rarely preserved. The series of tubular teeth are laterally covered by a very thin lateral bone lamella (Figs 5A–D; 7B). This lamella laterally covers the tubular part of the teeth along the dorsal rim of the dentalosplenic and ventral rim of the maxilla. Only short distal parts of the tubules and sharp pointed apical acrodin cusps overlie this lamella. This lateral lamella adheres to the tubular part of teeth, and usually the tubules can be seen outlined under this lamella in lateral view. The lateral lamella together with the tubules were called by Blot & Heyler (1963, fig. 1) “os tubulifère”. No suture is present between the lateral lamella and the dentalosplenic or maxilla. The lateral lamella probably expanded in a vertical direction along the dorsal border of the dentalosplenic or ventral border of the maxilla with the growth of the tubules during the individual’s development.

The teeth on the coronoids and dermal bones of the palate also play an important role, and are well preserved in *Paramblypterus* sp. from the Boskovice Basin. These teeth are strong and short (Figs 5C, D, F; 6; 7). Outer surface of these teeth is smooth, and acrodin apex is missing. Their development begins as bulges on the dermal bone and are therefore firmly attached to it. The teeth on coronoids and dermal bones of the palate are much stronger compared to the distal parts of the marginal tubular teeth. Cutting and grinding of the jaws with teeth showed partial construction of the teeth on the coronoids and dermal bones of the palate (Fig. 6C, D, F). The pulp cavity, surrounded by a thick layer of dentin with dentinal tubules diverging radially, is easily observed. Enamel, visible when crossed nicols, forms a very thin surface layer on the tooth but is absent on the basal  $\frac{1}{4}$  of the tooth height. There are teeth on the dermal bones on the inner side of the mouth in which the pulp cavity is absent.

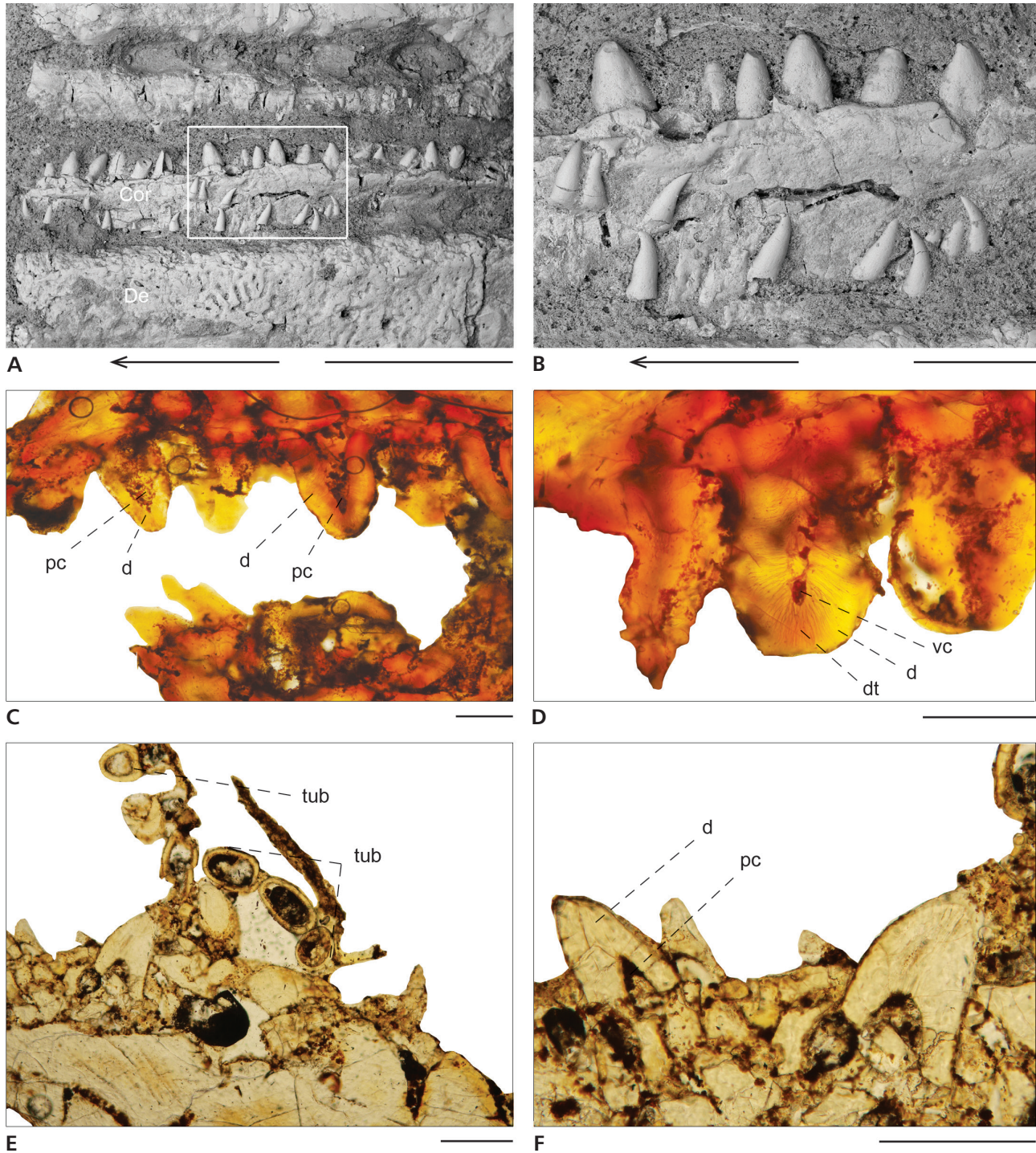
**Figure 5.** Representatives of *Paramblypterus* sp. From the lower Permian (Asselian) of the Boskovice Basin; A – the skull in lateral view with well-preserved dentition. P 80377, scale bar = 5 mm; B – the skull in lateral view. P80385, scale bar = 5 mm; C – upper and lower jaws with the series of tubular teeth covered by a very thin lateral lamella. The coronoids with short and strong teeth firmly fixed to the bone. Lateral view. P 80377, scale





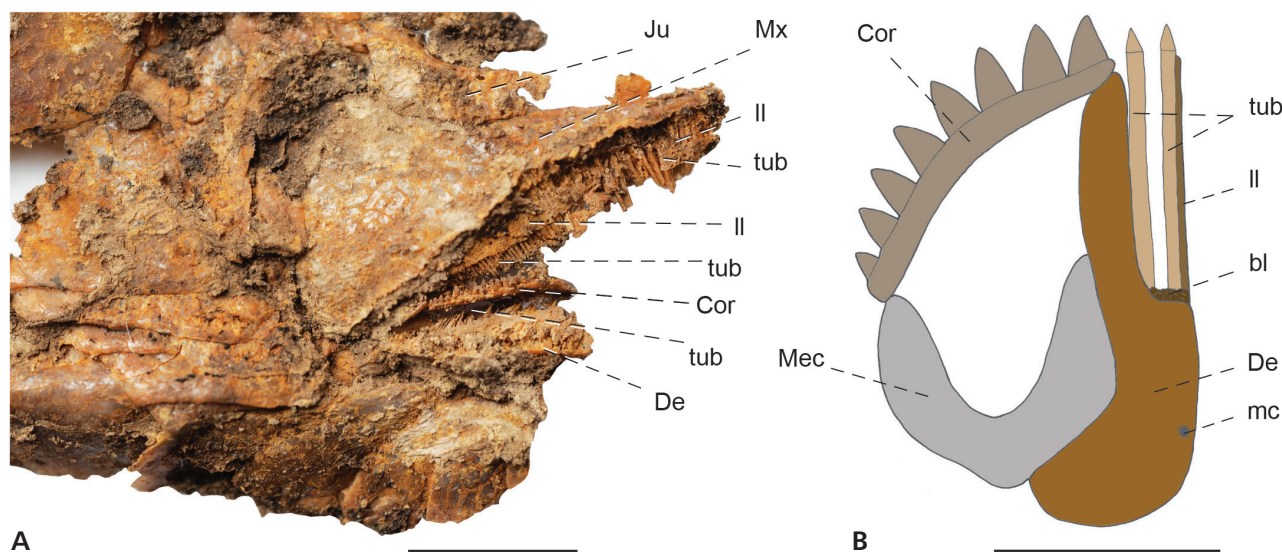
bar = 5 mm; D – series of tubular teeth on the maxilla and lower jaw in lateral view and rests of thin basal lamella. P 80385, scale bar = 5 mm; E – lower jaw with long tubules terminated with a sharp pointed acrodin apex. P 80377, scale bar = 1 mm; F – the coronoids of the lower jaw and ectopterygoid of the upper jaw with strong teeth. Lateral view. G 204, scale bar = 5 mm. Abbreviations: aa – acrodin apex; bl – basal lamella; Cor – coronoid; De – dentalosphenial, Dpt – dermopterotic; Dsph – dermosphenotic; Ect – ectopterygoid; Fr – frontal (parietal); Gum – gular medial; Ju – jugal; La – lachrymal; Il – lateral lamella; Mx – maxilla; Pa – parietal (postparietal); Soant – supraorbital anterior; tub – tubular teeth.





**Figure 6.** Representatives of *Paramblypterus* sp. from the lower Permian (Asselian) of the Boskovice Basin; A, B – anterior part of lower jaw with acrodin apexes of marginal tubular teeth and the teeth on coronoids. A row of acrodin apexes without the tubules appears above the dentalosplenial. The coronoids bear short and strong teeth firmly attached to the bones. The teeth on the coronoids are significantly stronger compared to the acrodin apexes of marginal tubular teeth. Small white frame indicates the portions of the dentition magnified in B of this figure. Arrows indicate *directio cranialis*. G 122, scale bar of A is 2 mm, scale bar of B is 500  $\mu$ m; C – cross section of palatal bone showing the teeth firmly fixed to the bone. The teeth contain pulp cavity surrounded by thick layer of dentine with dentinal tubules. G 263, scale bar = 200  $\mu$ m; D – palatal bone showing cross section of the tooth in stadium of odontode with the vascular canal and dentinal tubules fan-shaped away from the vascular canal. G 263, scale bar = 200  $\mu$ m; E – cross section of tubules of the tubular teeth on the lower jaw. G 264, scale bar = 200  $\mu$ m; F – coronoid showing the section of two teeth with the pulp cavity surrounded by thick layer of dentine. G 264, scale bar = 200  $\mu$ m. Abbreviations: d – dentine; dt – dentinal tubules; pc – pulp cavity; tub – tubular teeth; vc – vascular canal.





**Figure 7.** *Paramblypterus* sp. from the lower Permian (Asselian) of the Boskovice Basin; A – the skull in lateral view with well-preserved dentition. G 214, scale bar = 5 mm; B – schematic cross section of the lower jaw. The ratio of the size of the marginal teeth and the coronoid teeth is maintained, scale bar = 1 mm. Abbreviations: bl – basal lamella; Cor – coronoid; De – dentalosplenial; Ju – jugal; II – lateral lamella; mc – mandibular canal; Mec – meckel cartilage; Mx – maxilla; tub – tubular teeth.

The tooth with a wide base has central vascular canal surroundings with the dentine. The dentinal tubules extend in a fan-like manner from the vascular canal (Fig. 6D). Another tooth exhibits a short vertical vascular canal from which the dentinal tubules extend laterally, and diverge from the distal end of the canal in a fan-like manner. The last two teeth described are in the stadium of odontodes in the sense of Ørvig (1978a, b), and teeth with typical pulp cavity were still developing.

#### *Paramblypterus* cf. *rohani* (Heckel & Kner, 1861)

from the Krkonoše Piedmont Basin

Figures 8, 9

Somewhat different conditions for fossilization occurred in the Krkonoše Piedmont Basin during deposition of the lower Permian sediments. Digestive processes took place in most cases, the cadavers decomposed, the skull bones were often scattered, and jaws with teeth are very rare. Partly preserved tubular teeth were found in *Paramblypterus kablikae*, *Paramblypterus zeidlereri* from the Krkonoše Piedmont Basin as well as in *Paramblypterus vratislaviensis* from the Intra-Sudetic Basin.

Specimens of *Paramblypterus* cf. *rohani* from the Rudník Horizon (Vrchlabí Formation, Asselian) of the Krkonoše Piedmont Basin provide significant knowledge about dentition during their ontogenesis.

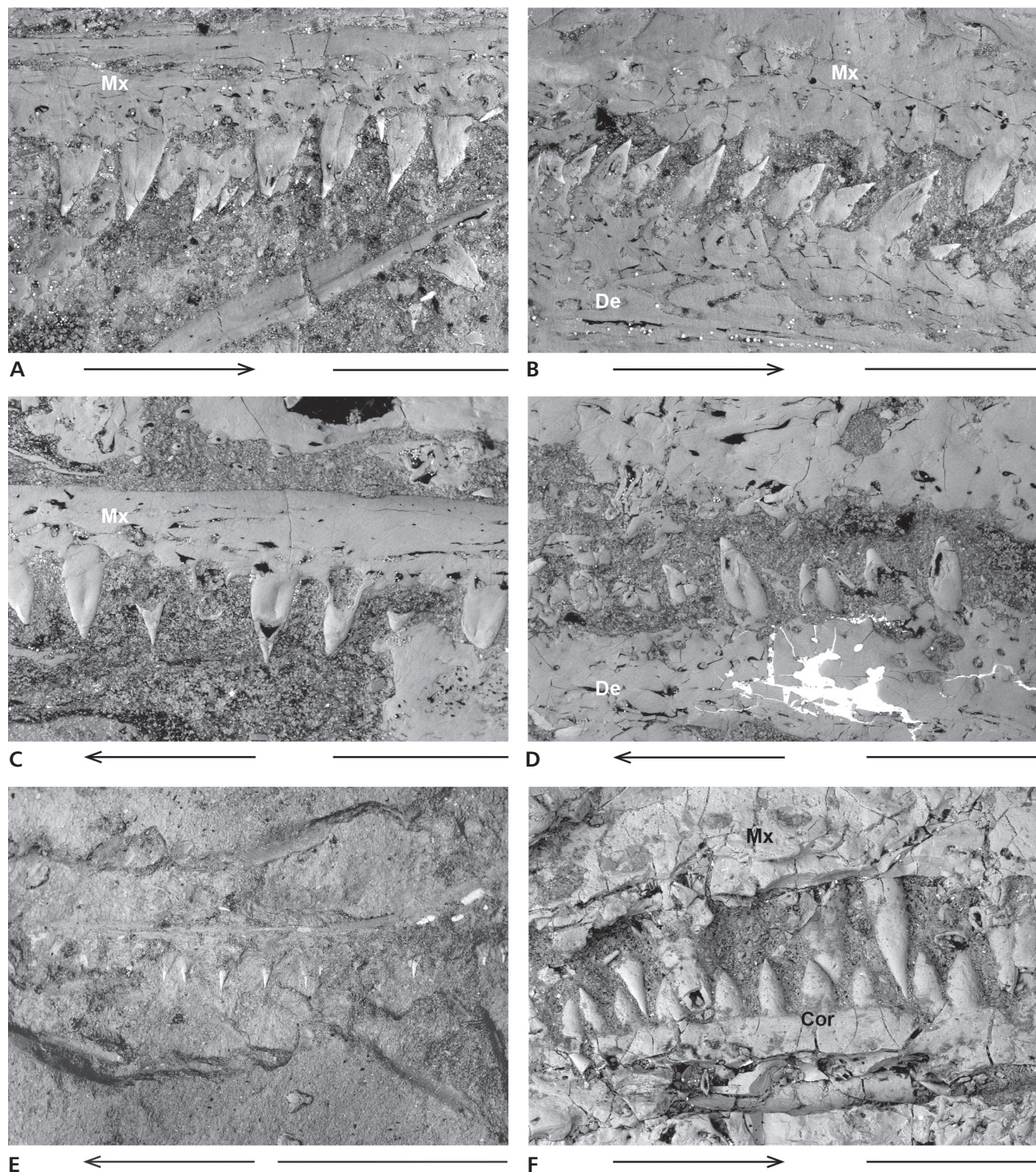
Typical tubular teeth are documented in adult specimen P 70046 of length 190 mm and maxilla length 23 mm (Fig. 9F). The tooth consists of a long tubule which is terminated by a sharply pointed acrodin apex. The acrodin apex has a conical shape but on the teeth in the anterior

part of the jaws it is more slender and curved posteriorly. Whole tooth is 1.2 mm long.

Numerous *Paramblypterus* cf. *rohani* findings from the Rudník Horizon (Vrchlabí Formation, Asselian) of the Krkonoše Piedmont Basin make it possible to identify the dentition in adult and juvenile individuals at various stages of ontogenesis. Dentition can be assessed on number specimens of different ages. The youngest specimens (DP 2620, P 64830) with dentition are 50 mm long. Marginal teeth on the upper and lower jaws have a conical shape with small acrodin apex (Fig. 8A, B). The base of the teeth is relatively wide (Fig. 8A, B, E) and teeth are separated from each other by gaps (Fig. 8E). The length of the teeth increases during the gradual growth of the individual. Specimen P 30738 represents a juvenile fish of 67 mm in length with an 11.5 mm long maxilla. The maxilla carries slightly elongated tubular teeth, and the coronoids of the lower jaws have short robust conical teeth (Fig. 8F). Individuals with the maxilla of length 13–17 mm (P 81434, P 86523, P 80154, P 64823) have the teeth of an elongated conical shape with a narrow base compared to the tooth length (Fig. 9A–E). The teeth on the coronoids are also well developed in young individuals beside the marginal teeth. They are very strong and firmly attached to the bone (Fig. 8F). Adult specimens with the length of the maxilla over 20 mm have tubular teeth with long tubule as was described on P 70046 (Fig. 9F).

The significantly different structure of the dentition shows the specimen P 27571 from the lower Permian of Prosečné Formation (Asselian) of the Krkonoše Piedmont Basin. Disarticulated bones of the skull including lower



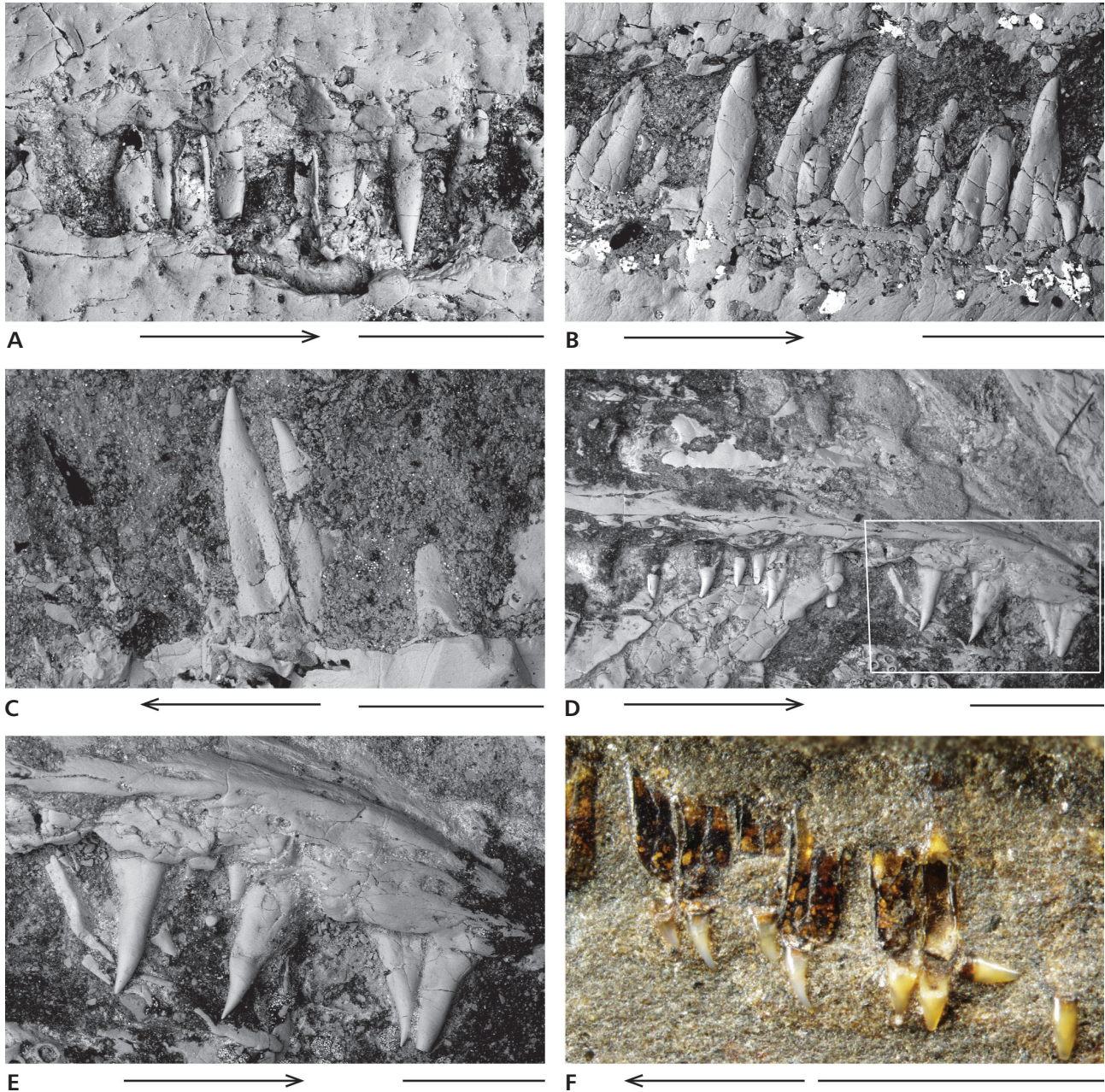


**Figure 8.** *Paramblypterus* cf. *rohani* (Heckel & Kner, 1861). Lower Permian (Asselian), Vrchlabí Formation, Rudník Horizon, Krkonoše Piedmont Basin. Arrows indicate *directio cranialis*; A, B – a juvenile specimen of the total body length 50 mm with dentition. Marginal teeth have conical shape with wide base and small acrodin apex. DP 2620, scale bars = 500 µm; A – dentition on the anterior part of right maxilla; B – dentition on the posterior part of right dentalosplenial; C, D – a juvenile specimen of the total body length 75 mm (length of the maxilla is 10.5 mm). Conical teeth are slightly elongated. P 64828, scale bars = 500 µm; C – dentition on the anterior part of left maxilla; D – dentition on the middle part of left dentalosplenial; E – dentition on the left maxilla of juvenile specimen of the total body length 50 mm (the length of the maxilla is 8.5 mm). P 64830, scale bar = 2 mm; F – a juvenile specimen of the total body length 67 mm (the length of the maxilla is 11.5 mm). Set of the teeth on coronoids and elongated marginal teeth on the right maxilla. P 30738, scale bar = 500 µm. Abbreviations: Cor – coronoid; De – dentalosplenial; Mx – maxilla.



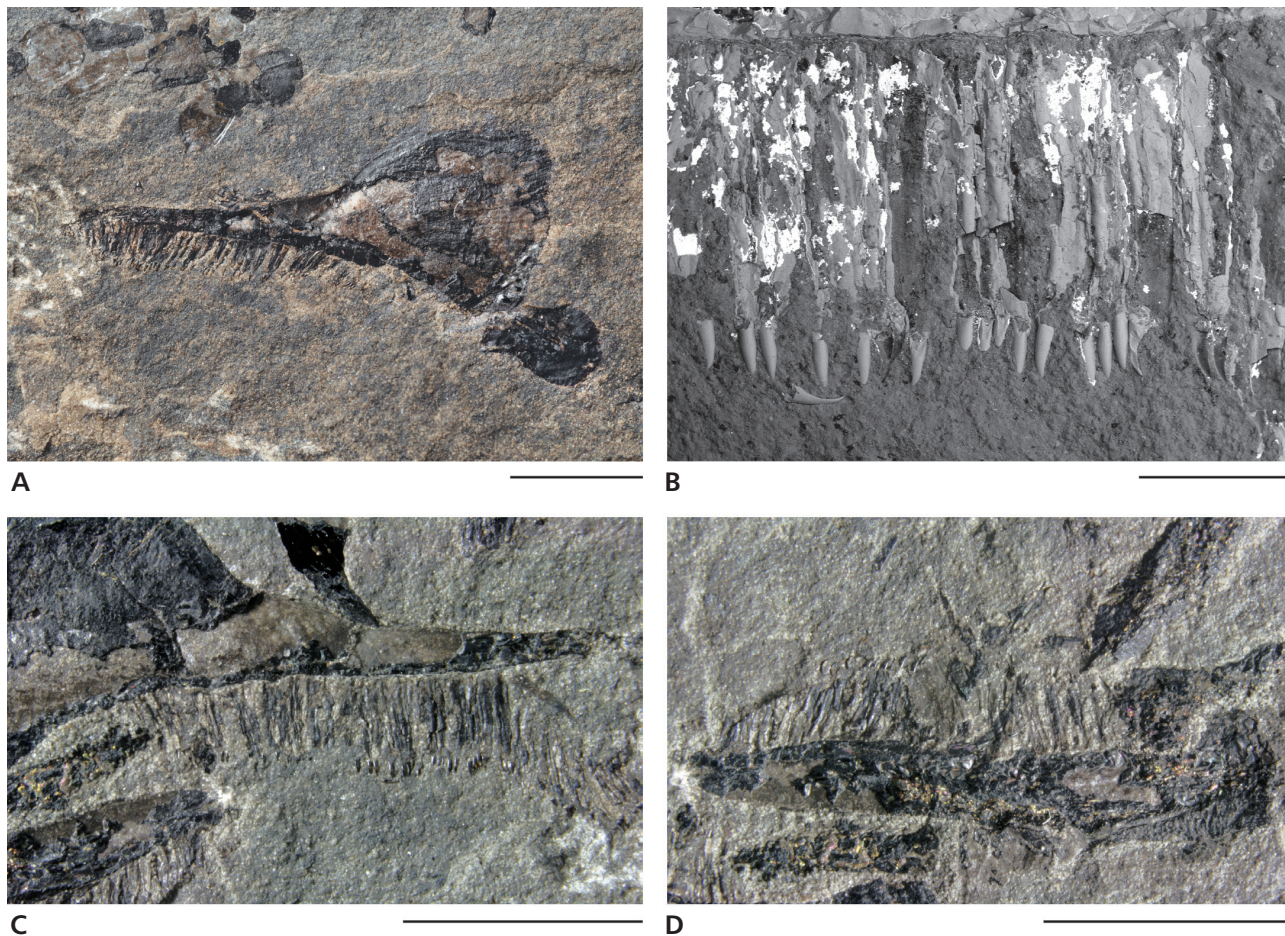
and upper jaws with teeth give a very good idea of the dental structure (Fig. 10). Dentition is very similar to that of *Paramblypterus* sp. from the Boskovice Basin. Specimen P 27571 exhibits a 16 mm long maxilla with tubular teeth. The tubules together with the acrodin apices

are 2 mm long. The length of the acrodin apex is 0.3 mm. The conical apices of the teeth are slimmer than those on the teeth of *Paramblypterus* sp. from the Boskovice Basin. An isolated maxilla (Fig. 8C) shows dentition partly separated from the jaws but the teeth are not scattered. This



**Figure 9.** *Paramblypterus* cf. *rohani*. Lower Permian (Asselian), Vrchlabí Formation, Rudník Horizon, Krkonoše Piedmont Basin. The length of teeth increases during gradual growth of the individuals. Arrows indicate *directio cranialis*; A – right maxilla 12 mm long with marginal teeth. P 81434, scale bar = 500  $\mu$ m; B – right lower jaw 13 mm long with marginal teeth. P 82523, scale bar = 500  $\mu$ m; C – left lower jaw 14 mm long with marginal teeth. P 80154, scale bar = 500  $\mu$ m; D – right maxilla 17 mm long with marginal teeth. Small white frame indicates the portion of the dentition magnified in E of this figure. P 64823, scale bar = 1 mm; E – detail of marginal teeth on right maxilla. P 64823, scale bar = 500  $\mu$ m; F – tubular teeth on left maxilla 23 mm long. Long tubules are terminated by sharply pointed acrodin apices, which in the anterior part of the jaw are more slender and curved posteriorly. P 70046, scale bar = 1 mm.





**Figure 10.** *Paramblypterus* sp. Lower Permian (Asselian), Prosečné Formation, Krkonoše Piedmont Basin. Adult specimen with length of the maxilla 16 mm. Very long tubular teeth on right and left maxilla and lower jaw. P25571; A – right maxilla, scale bar = 5 mm; B – tubular teeth on right maxilla, scale bar = 1 mm; C – left maxilla with tubular teeth partly separated from the jaw anteriorly, scale bar = 5 mm; D – left lower jaw with tubular teeth, scale bar = 5 mm.

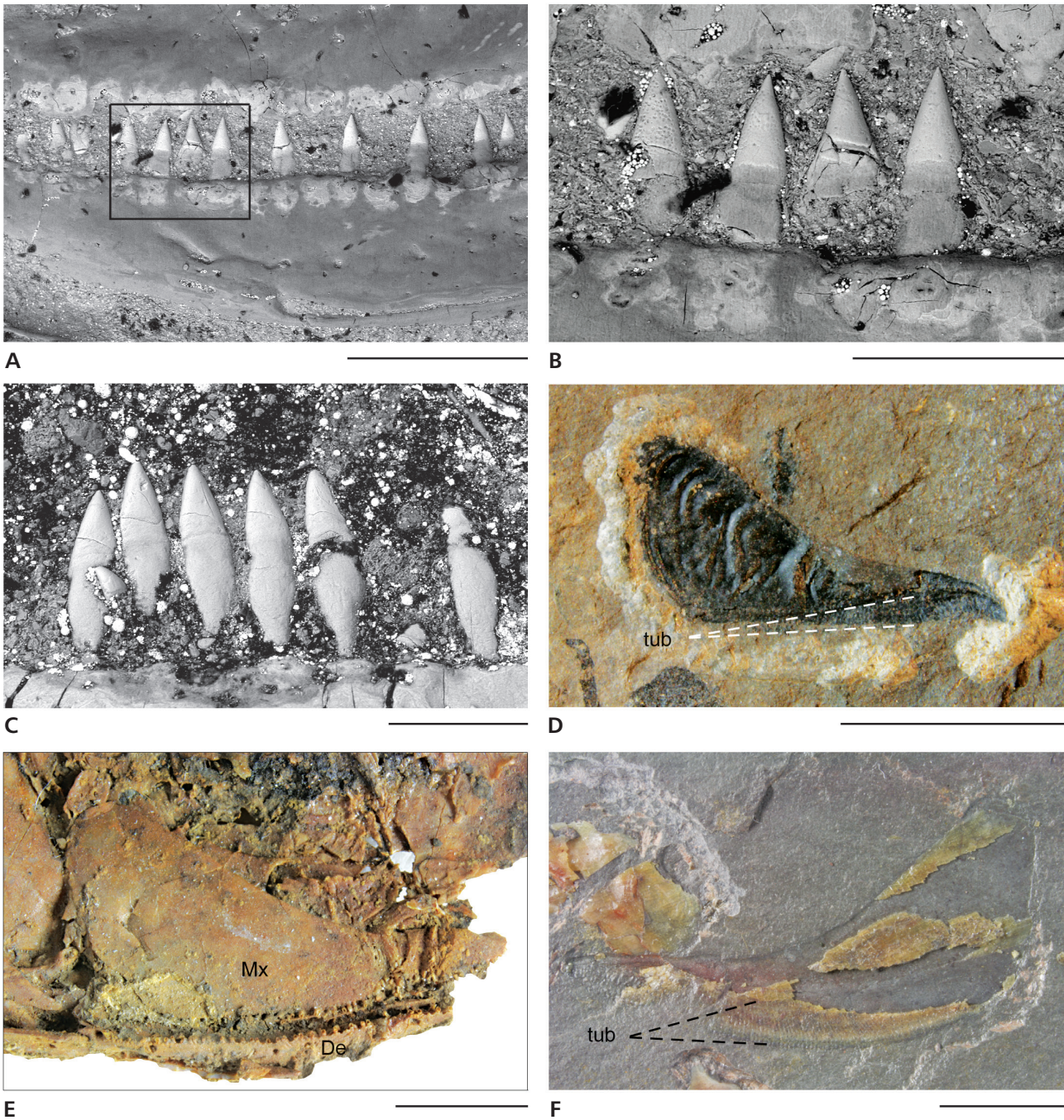
is the advantage of continuity between the tubular bases in the basal lamina and lateral lamina. We find a significant difference if we compare the dentition of this individual and the dentition on the maxilla of the same length on the specimens of *Paramblypterus* cf. *rohani* described above (Fig. 9B–E). The teeth of *Paramblypterus* cf. *rohani* are prolonged but they still retain their conical shape in the described stage of ontogenesis, while specimen P 27571 on Fig. 10 already has tubular teeth with a long tubule and clearly distinguishable acrodin apex. The above described specimen P 27571 also belongs to *Paramblypterus*, but it differs from *Paramblypterus* cf. *rohani* and is closer to *Paramblypterus* sp. from the Boskovice Basin.

A similar maxilla with teeth in *Paramblypterus* sp. is figured by Heyler (2000, fig. 1) from the beds of Igornay (Autun Basin, France).

Tubular teeth are one of the diagnostic features of the family Amblypteridae. This was confirmed in *Amblypterus latus* Agassiz, 1833 and *Amblypterus lateralis* Agassiz,

1833 from the Saar Basin, Germany (Heyler 1976, 2000; Dietze 2000; Štamberg 2013), *Paramblypterus decorus* (Egerton, 1850) from the Stephanian of Commentry, France (Blot 1966, Dietze 2000), *Paramblypterus gaudryi* (Sauvage, 1890), *Paramblypterus rohani* (Heckel & Kner, 1861) and other species of the genus *Paramblypterus* from the Autun Basin, France (Heyler 1969, 1971), from *Paramblypterus duvernoyi* (Agassiz, 1833) and *Paramblypterus gelberti* (Goldfuss, 1847) from the lower Permian of Germany (Boy 1976, Gad 1988, Dietze 2000), and from *Paramblypterus rohani* and other species of *Paramblypterus* of the lower Permian of the Bohemian Massif (Štamberg 1976, 2013). Tubular teeth were also developed in Aeduellidae, as discussed below, in the species *Charleuxia autunensis* Heyler, 2000 from the Autun Basin, France (Heyler 1969) which Heyler (2000) placed in the family Charleuxiidae. I believe that this species, if it is valid, should be placed within the genus *Paramblypterus*.





**Figure 11.** A–C – *Neslovicella elongata* Štamberg, 2010. Lower Permian (Asselian), Krkonoše Piedmont Basin; A – a juvenile specimen 40 mm in total body length. Small teeth on the lower jaw are in one row, very short with basal tubule terminating in a pointed cap. Small black frame indicate the portions of the dentition magnified in B of this figure. DP 3223, scale bar = 500 µm; B – tubular teeth in detail. DP 3223, scale bar = 200 µm; C – a lower jaw of the specimen 45 mm in total body length. The teeth are in one row close to each other but the tubules are a little longer than on the specimen DP 3223 in previous figures A, B. P 64786, scale bar = 200 µm. • D – *Neslovicella rzehaki* Štamberg, 2007. Lower Permian (Asselian), Boskovice Basin. Right maxilla of adult specimen with a strip of long tubular teeth overlain by lateral lamella (white lines define the length of tubular teeth) with minute acrodin caps terminating the tubules. The tubular teeth appear as vertically arranged ridges along the ventral margin of the maxilla. P 64348, scale bar = 5 mm. • E – *Bourbonnella hirsuta* Štamberg, 2007. Lower Permian (Asselian); E – from the Boskovice Basin. Right maxilla and the dentalosplenial of adult specimen in lateral view. Tubules of tubular teeth on the maxilla are completely covered with the lateral lamella and only small acrodin apices shortly protrude along ventral edge of the maxilla. P 63858, scale bar = 5 mm; F – from the Krkonoše Piedmont Basin. Left maxilla in lateral view. Tubular teeth appear as vertically arranged ridges along the ventral margin of the maxilla (black lines dashed define the length of tubular teeth). Small acrodin apices are observable along the strip of tubules. P 62441, scale bar = 5 mm. Abbreviations: Mx – maxilla; tub – tubular teeth.



The marginal tubular teeth could serve only to catch food, but the robust teeth in the mouth cavity could hold the prey and crush it. The relative proportions of these teeth are clearly shown in Fig. 7B. In addition, the ventral side of the corpus parasphenoidis carries short sharp pointed teeth which are slightly smaller than those on the coronoids and bones of the palate. All known species of the genus *Paramblypterus* occur not only in the basins of the Bohemian Massif, but also in the basins of France and Germany in sediments rich in Conchostraca. These benthic forms could have been the main food component of above described species of the genus *Paramblypterus*. The conclusions drawn by Dietze (2001) who studied locomotor capability of *Paramblypterus duvernoyi* also support this type of diet. Dietze (2001) considered this fish to have been a bottom dwelling species with moderate steady swimming speeds and suction as the mode of food capture, with food being composed of small planktonic or benthic invertebrate organisms.

The marginal tubular teeth appear to be very weak, but are complimented by very stout short teeth covering the coronoids and the bones of the palate. Strong teeth on the coronoids and the medial surface of the palatoquadrate certainly contributed significantly to holding prey and deformation of the conchostracan valves.

#### Family Aeduellidae Romer, 1945

##### Figure 11

The family Aeduellidae is represented by four species in the Permo–Carboniferous basins of the Bohemian Massif. Species *Spinarachthys dispersus* (Fritsch, 1895) occurs in the upper Carboniferous (Kasimovian, Gzhelian) sediments of the basins in the Central and Western Bohemia Area and in the Krkonoše Piedmont Basin. *Neslovicella rzehaki* Štamberg, 2007 occurs in the lower Permian (Asselian) of the Boskovice Basin, and *Neslovicella elongata* Štamberg, 2010 in the lower Permian (Asselian) of the Krkonoše Piedmont Basin. *Bourbonnella hirsuta* Štamberg, 2007 occurs rarely in the lower Permian of the Boskovice Basin and recently more abundant finds of this species were discovered in the lower Permian of the Krkonoše Piedmont Basin and Intra-Sudetic Basin. The tubular dentition, similar to that in *Paramblypterus*, is developed in all members of Aeduellidae. The tubular tooth is, as in Amblypteridae, a long tubule with an acute acrodin cap on the top of the tubule. Tubular teeth are numerous and arranged very close to each other on the dentalosplenial and maxilla. Unlike the teeth in *Paramblypterus* they are arranged in one row only. They are covered with lateral lamella on both the lower jaw and the maxilla. Only the acrodin caps on the tops of the tubules overlay the lateral lamella. Tubular teeth are documented in *Spinarachthys dispersus*

and *Bourbonnella hirsuta*, but due to the larger size of the material they are more frequently described in *Neslovicella elongata* and *Neslovicella rzehaki*.

*Neslovicella rzehaki* is a minute fish up to 10 cm long, and it is abundant in the lower Permian of the southern part of the Boskovice Basin (Štamberg 2007). The tubular teeth overlain by lateral lamella from a lateral view appear on the maxilla as vertically arranged ridges along the ventral margin of the maxilla (Fig. 11D). The strip of tubules along the ventral margin of the maxilla is deeper in the anterior region of the maxilla, posteriorly lowers, depending on the shortening of the tubules. The acrodin cap on the top of each tubule is very short, and in adult specimens accounts for only  $\frac{1}{10}$  of the total tooth length.

*Neslovicella elongata* is also a very small fish not exceeding 10 cm in length. The fish occurs in the lower Permian (Asselian) of the Krkonoše Piedmont Basin (Štamberg 2010, 2016). The dentition is the same as in *Neslovicella rzehaki*. The tubular teeth are in one row and close together. Approximately 40 tubular teeth are on the maxilla (Štamberg 2010). Numerous finds of *Neslovicella elongata* made it possible to follow the development of the dentition during ontogenesis. A specimen DP 3223 40 mm in total body length is the most juvenile found. The lower jaw bears very small teeth arranged in one row with a small space between them (Fig. 11A, B). The teeth are very short with a short basal tubule terminating in a pointed acrodin cap. The acrodin cap forms nearly half the tooth length. A 45 mm long specimen P 64786 exhibits cylindrical teeth elongated to the previous piece on the lower jaw (Fig. 11C). The teeth are arranged in one row close to each other but the tubule is a little longer than in the juvenile specimen DP 3223. The acrodin cap forms one-third to one quarter of the total tooth length. An adult specimen 95 mm long has long tubules with a minute acrodin cap which forms approximately  $\frac{1}{10}$  of the tooth length.

*Bourbonnella hirsuta* reaches 15 cm of the total body length, and only the findings of adults are known. Specimen P 63858 shows tubules of tubular teeth on the maxilla completely covered by lateral lamella and only small acrodin apices shortly protrude along the ventral edge of the maxilla (Fig. 11E). A maxilla (P 62441) of the same species from the Krkonoše Piedmont Basin has tubular teeth covered by lateral lamella but the tubules appear in lateral view as vertically arranged ridges along the ventral margin of the maxilla (Fig. 11F).

Tubular teeth of Aeduellidae from the Autun Basin (Massif Central, France) were first described by Heyler (1969). They are also well preserved in *Aeduellia blainvillei* from the site Buxières-les-Mines in the Bourbon-l'Archambault Basin (Massif Central). Numerous specimens of *Aeduellia blainvillei* from this locality made it possible to compare teeth from different



stages of ontogenetic development (Štamberg 2018), and they demonstrate a significant lengthening of the tubules during ontogenesis.

As far as food is concerned, Conchostraca, can be assumed to be the main component in the diet of Aeduellidae. Aeduellidae, similar to *Paramblypterus*, in the basins of the Bohemian Massif and the basins of the Massif Central in France are often accompanied by these small crustaceans.

## Conclusions

Permo–Carboniferous actinopterygians from the Bohemian Massif demonstrate a wide variety of marginal teeth. They are diversified in their morphology, size and location. Three basic types can be distinguished among the described dentition. The first type is characterized by teeth in two rows with numerous small teeth in the outer row and with large and less numerous teeth in the inner row. Species *Progyrolepis speciosus*, *Elonichthys krejcii*, *Letovichthys tuberculatus* and *Letovichthys multidentatus* belong to this group. Carnivorous predatory fish, such as *Progyrolepis speciosus* and *Elonichthys krejcii*, which were powerful swimmers and actively hunted nektonic vertebrates, have large conical teeth in the inner row which are 4–5 times longer than the teeth in the outer row. In species such as *Letovichthys tuberculatus* and *L. multidentatus* there were no large differences between the teeth of the outer and inner rows, but in *L. multidentatus* the large teeth in the inner row are very numerous.

Numerous sharply pointed teeth arranged in a single row characterize the second dental condition. Species such as *Sceletophorus biserialis*, *Sceletophorus verrucosus* and *Sphaerolepis kounoviensis* from the upper Carboniferous and *Igornichthys bohemicus* from the lower Permian compose the group with this second type of dentition *Sceletophorus biserialis*, *S. verrucosus* and *Sphaerolepis kounoviensis* have slender teeth in one row complemented also by irregularly distributed teeth medially from the outer row. The teeth of *Igornichthys bohemicus*, however, are arranged in one row and are not slender but have a wide base.

The third type of dentition is characterized by specialised tubular teeth. This condition is characteristic of the Aeduellidae (*Spinrichthys dispersus*, *Bourbonnella hirsuta*, *Neslovicella elongata*, *Neslovicella rzehaki*) and Amblypteridae (*Paramblypterus* cf. *rohani*, *Paramblypterus zeidleri*, *Paramblypterus vratislaviensis*, *Paramblypterus kablikae*, *Paramblypterus feistmanteli* and *Paramblypterus* sp.). A large number of jaws with teeth from the Boskovice Basin document the construction of tubular teeth as already described by Blot & Heyler (1963). In addition, the connection between the tubules

and the jaw and their connection with the lateral lamella are also elucidated. It appears that the teeth covering the dermal bones on the inner surface of the lower jaw and palatoquadratum and on the ventral side of the parasphenoid are important for food capture and retention. These short strong teeth played an important role during chewing when they lacerated and perforated the integument of the food item, and could cause internal damage to the chitinous valves of conchostracans. As thin sections of the dental structures show, the dentition on the dermal bones of the mouth cavity are made up of both teeth with a dental cavity and teeth in the odontodes stage.

*Paramblypterus* sp. from the Permian sediments of the Boskovice Basin show well developed tubular teeth with long tubules already present in juvenile specimens of length 50 mm.

The growth of tubular teeth during ontogenesis has been demonstrated in *Paramblypterus* cf. *rohani* individuals from the Rudník Horizon of the Krkonoše Piedmont Basin, ranging from 50 mm to 200 mm in total body length. Tubular teeth in juvenile specimens have conical shape with very wide base and most of the tooth length is formed of the acrodin apical cap. During growth of the individual, the tube lengthens and the acrodin cap becomes shorter in proportion to the length of the whole tooth. Similarly, juvenile specimens of *Neslovicella elongata* have very short tubules with large acrodin caps, which form nearly half the length of the tooth. The tubules lengthen during growth and in adult specimens the acrodin cap forms only  $\frac{1}{10}$  of the tooth length. Monitoring of teeth morphology, arrangement and changes during ontogenesis also showed differences in tubular dentition in fishes of the same size of *Paramblypterus* cf. *rohani* from Vrchlabí Formation (Rudník Horizon), a specimen of *Paramblypterus* sp. from Prosečné Formation of the Krkonoše Piedmont Basin and *Paramblypterus* sp. from the Boskovice Basin.

The results of the present study show a great diversity in dentition of “primitive” Permo–Carboniferous actinopterygians. It can be assumed that the development of dentition did not have to start only with predatory lifestyle (Schaeffer & Rosen 1961) and teeth arrange in two rows (Poplin & Heyler 1993). More likely, the type of dentition evolved from the beginning according to the type of food and the lifestyle.

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