Actinopterygian fishes from the new Lower Permian locality of the Krkonoše Piedmont Basin

Paprskoploutvé ryby z nové spodnopermské lokality podkrkonošské pánve

(10 figs)

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Scales, bones and fragments of actinopterygians were collected from two horizons of grey, reddish, mauve and greenish laminated calcareous mudstones in an outcrop of the Prosečné Formation (Lower Permian) at Klášterská Lhota. Genera *Paramblypterus, Amblypterus* and *Aeduella* were distinguished among the new material. Several specimens of *Aeduella* represent the first described finds of this genus from the Permo-Carboniferous of the Bohemian Massif. Besides the maxilla, frontal, parietal, operculum, suboperculum and cleithrum, which are characteristic of *Aeduella*, also an isolated clavicle was described. The latter differs from the clavicle of *Paramblypterus* and *Amblypterus* and has been unknown till this time in *Aeduella.* A small, slender specimen close to *Paramblypterus* and *Amblypterus* but differing in some anatomical features is described separately as Type A.

Key words: Actinopterygii, Lower Permian, Krkonoše Piedmont Basin, Bohemia

Introduction

A number of palaeontological localities with actinopterygian fishes are known from the Rudník Horizon (Lower Permian, Vrchlabí Formation) and Kalná Horizon (Lower Permian, Prosečné Formation) of the Krkonoše Piedmont Basin. Some of them were cited already in the papers from the end of the 19th century. These were usually outcrops exposed during the exploitation of limestone, coal and organic rich claystone. Additional localities were discovered in the course of the geological mapping in the middle of the last century. It is surprising that the impressive outcrop of the Lower Permian strata along the left bank of the Labe River at the village of Klášterská Lhota (NE Bohemia) escaped the attention of palaeontologists until recently. A steep wall with exposed beds of the Prosečné Formation (Lower Permian) lines the left bank of the Labe River along the distance of two kilometres and is about 20 metres high. The section is largely formed by reddish brown sandstones, conglomerates and siltstones with no fossils. Thin beds of fine-grained calcareous mudstones not more than 10 cm thick with fragments of actinopterygian fishes are exposed at several levels of the section only. In these beds, fossils are very rare. This is probably the reason why no fossils were described from this section during the past several decades of study of the Krkonoše Piedmont Basin.

The first bones and scales of actinopterygian fishes were found by J. Drábková in the course of a detailed study at the locality, and a list of the findings was published by Zajíc (1997) in the final report of the Grant Project 205/94/0692. The author of this paper was studying the conspicuous beds at Klášterská Lhota for the last three years and obtained relatively abundant palaeontological material, in addition to data on stratigraphy of some part of the section. Finds of actinopterygians come exclusively from grey, reddish, mauve and greenish laminated calcareous mudstones. The bed richest in actinopterygians was encountered in the section opposite to house No. 33 at Klášterská Lhota, 4 metres above the river level; the second richest bed was found at the same place, 10 metres above the river level. Fossiliferous strata form close overlying rock of the Kalná Horizon. Besides actinopterygians, the fossil remains also include isolated teeth of sharks (probably *Xenacanthus decheni*) and a hitherto indetermined spine of shark and footprints of tetrapods.

All specimens are deposited in the collection of the Department of Natural History, Muzeum Hradec Králové.

Actinopterygii

Osteological remains of actinopterygians are very fragmentary. Unluckily, no complete specimen was found. Bones and fragments of bodies of actinopterygian fishes can be divided to the orders Paramblypteriformes and Aeduelliformes.

Paramblypteriformes Heyler, 1969

Most specimens from the locality of Klášterská Lhota belong to the family Amblypteridae. A definition of this family of Dietze (2000) is followed, with the genera *Amblypterus* and *Paramblypterus*. According to the revision of Dietze (2000), only some of the bones of *Amblypterus* and *Paramblypterus* can be distinguished, but most of the bones of these genera are indeterminable as they are identical in their morphology as well as sculpture. One specimen shows features close to both genera with the exception of some anatomical details and is therefore described separately as Type A.

Most of the bones and fragments show features shared by both genera, *Amblypterus* and *Paramblypterus*. The most abundant bone is a maxilla (Nos. MHK 62431,

MHK 62437, MHK 62442 and others). Maxilla has a typical short and high maxillary plate (Fig. 1). No teeth were found. Isolated lower jaws are relatively weak, bearing a large projection dorsocaudally. Frequent bones also include supracleithrum and cleithrum, sporadically posttemporal, clavicle and parasphenoid. Parasphenoid is preserved in dorsal view on specimens MHK 62444 and MHK 62425. Parasphenoid on specimen MHK 62425 (Fig. 2) bears corpus parasphenoidis not posteriorly elongated but terminating immediatelly behind the lateral process caudally. The bucco-hypophysial foramen passes through the centre of ossification. Besides the parasphenoid, specimen MHK 62425 also shows a cleithrum, clavicle, supracleithrum, maxilla and postrostral. The postrostral is slightly elongated orocaudally, its length is about 1.5 times its width. The postrostral is anteriorly narrow and the oral margin is provided with a bend for the anterior nasal opening.

Isolated opercular bone on MHK 62454 is relatively large, oblong, 14 mm high and 11 mm wide, its corners are round.

Paramblypterus Blot, 1966

The relatively most completely preserved specimen is MHK 62438/1–2. Most of the trunk is preserved but oral part of the trunk and head are missing (Fig. 3). The whole specimen was probably 125 mm long. Trunk is dorsally arched, highest at the level above the ventral fin. Dorsal and anal fins are large, the length of the anterior margins of both fins is 17 mm, length of the base of the anal fin is 15 mm. The dorsal fin begins above the space between ventral and anal fins. Three large ridge scales are developed in front of the dorsal fin, two large scales are developed in front of the anal fin. Anterior margins of all fins are provided with fulcral scales. The exact scale count cannot be determined due to the absence of scales in front of the ventral fin. Scales behind the ventral fin are well preserved and the scale count may be as follows:

$$\frac{x+19}{x \quad x+13 \quad x+27 \quad x+31}.$$

This indicates that it is not *Aeduella,* but the scale count and the trunk shape suggest *Paramblypterus rohani*. The vertical scale row immediately anterior to the anal fin consists of 8 scales above the lateral line and 11 scales below the lateral line. Scales on flanks are smooth and relatively thick and large, posterior scale margins are broken off with the exception of scales in the rows behind ventral fin. Scales of the fifth row posterior to the ventral fin bear 4 denticles on their caudal margins. The denticles are observed as far as to the eighth row behind the ventral fin (scales bearing 2 denticles). Scales lying fur-

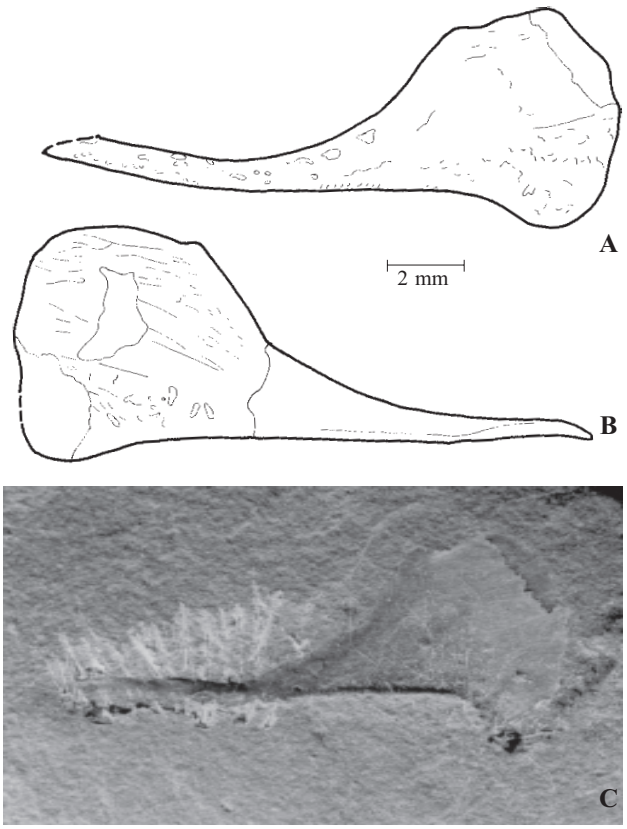

Fig. 1 Maxillae of paramblypterid type. Scale bar 2 mm. a – left maxilla in lateral view. MHK 62431, b – right maxilla in lateral view. MHK 62427/l, c – photo of the left maxilla in lateral view. MHK 62431.

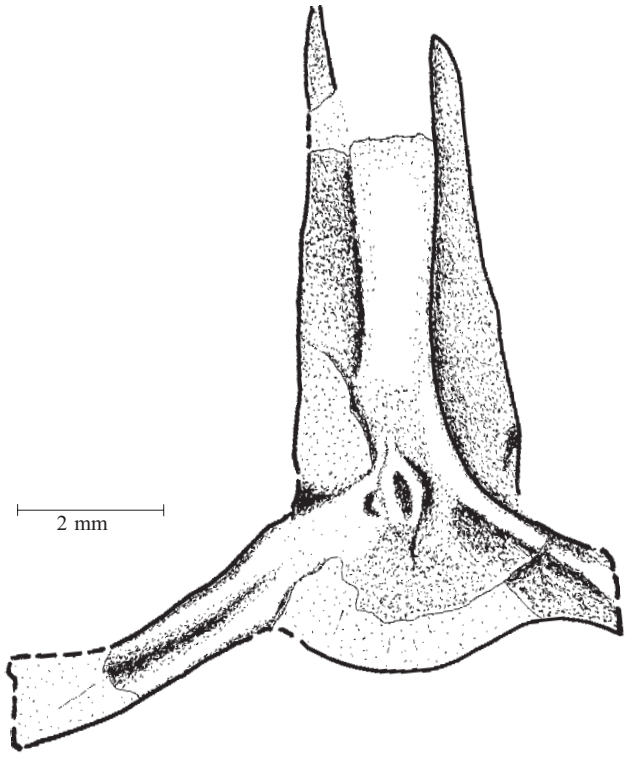

Fig. 2 Parasphenoid of paramblypterid type in dorsal view. MHK 62425/1. Scale bar 2 mm.

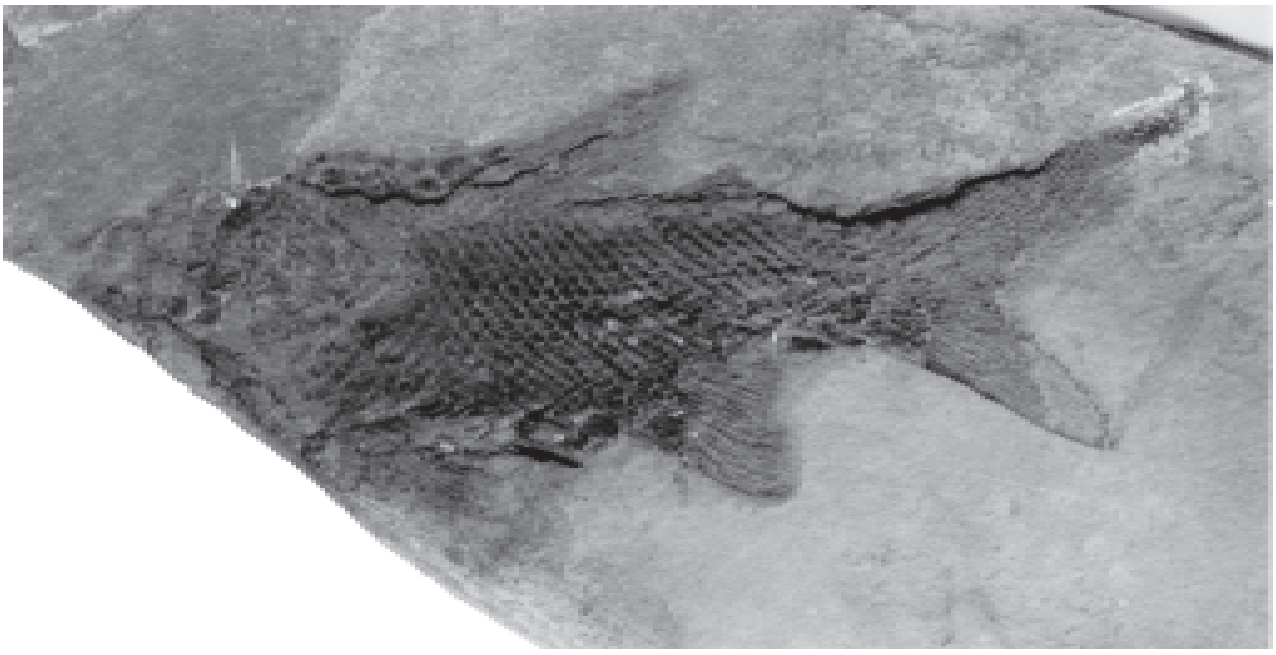

Fig. 3 The most complete specimen of *Paramblypterus*. MHK 62438/1, x 1.5.

ther posteriorly have straight posterior margins with no denticles. The scales form a strong cover, resulting from their thickness, well-developed peg and socket articulation and their mutual overlapping by one half.

The second specimen MHK 62429 is represented by fragments of the oral part of the trunk; its head indicates a relatively large specimen of about 20 cm in total length. Maxilla has a typical large maxillary plate. Left frontal bears a lateral process projected between the dermopterotic and dermosphenotic. Operculum is of oblong shape. The scales in anterior region of the trunk are thick, their caudal margins are denticulated. Seven denticles can be found on the caudal margins of the scales.

Amblypterus Agassiz, 1833

Specimen MHK 62430 yielded several dermal bones and a part of the scaly cover which range this specimen to the genus *Amblypterus*. Well preserved are the bones of the skull roof (Fig. 4). The frontal is of oblong shape with lateral process in caudal third of its lateral margin. Triangular dermosphenotic is relatively large (maximum width 5 mm, length along lateral margin 9 mm). Several pores in one line across the central part of the bone form the rest of the infraorbital canal. The bone is ornamented by tubercles.

Dermopterotic is also well preserved, approximately oblong, 10.5 mm long and 4.5 mm wide. The lateral process and fold in the middle part of the lateral margin of the bone is a very important feature. Sculpture on the bone is plain, formed by flat tubercles and mounds.

The parietal is missing, but two postparietals are distinct. The medial one is 1.5 mm wide, the lateral one is twice as wide.

Lateral extrascapular lies caudally from the postparietals and is partly turned. Rests of the sensory canal are present along its caudal margin. Medial extrascapular in front of the posttemporal also shows rests of the sensory canal along its caudal margin. The posttemporal of oval shape with strong orolateral process is situated posteriorly on the skull.

The bones of the rostral part are not preserved besides the fragment of the postrostral.

Bones of the opercular apparatus are represented only by an operculum which is 11 mm high and 8 mm long. Scales are thick, with no sculpture. Posterior margins of scales are straight, not denticulated, as far as they are preserved.

The above described specimen has a dermopterotic with a lateral process. This feature distinguishes specimen MHK 62430 from the genus *Paramblypterus* and ranges it within the genus *Amblypterus* in the sense of Dietze (2000).

Type A

Specimen MHK 62439/1–2 is a small specimen approximately 10 cm in total length. It is imperfectly preserved but shows several anatomical features which distinguish it from the genera *Paramblypterus* and *Amblypterus*.

Scales show no sculpture, and the posterior margins of scales, as far as preserved, are not denticulated. Several bones of the skull roof are relatively well preserved (Fig. 5). Frontal is oblong, with a small lateral process at the boundary between the dermopterotic and dermosphenotic. Supraorbital sensory canal passes across the frontal along its lateral margin toward the parietal. The sculpture on the frontal is formed by flat, short moulds

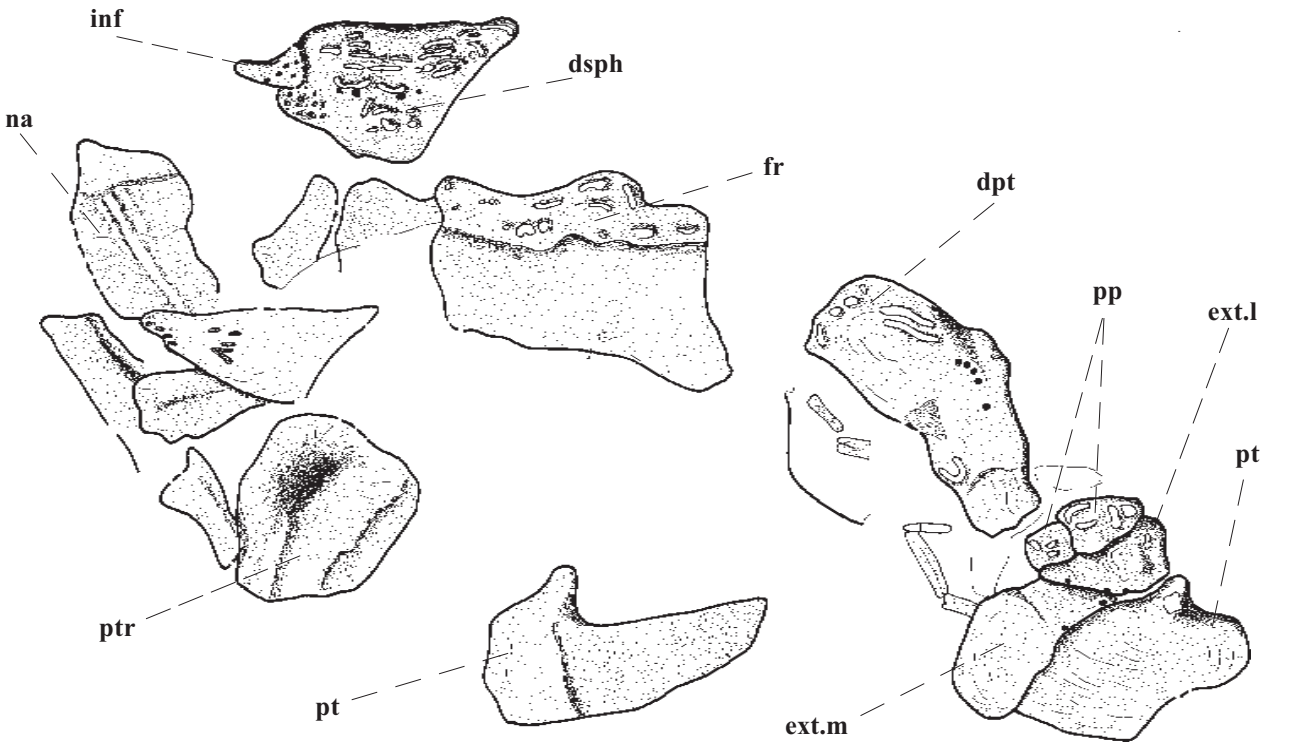

Fig. 4 Dermal bones of the skull roof, rostral region and shoulder girdle of the genus *Amblypterus*. dpt – dermopterotic, dsph – dermosphenotic, ext. l. – extrascapular lateral, ext. m. – extrascapular medial, fr – frontal, inf – infraorbital, na – nasal, pp – postparietal, pt – posttemporal, ptr – postrostral. MHK 62430/1, x 3.7.

and tubercles. Parietal is approximately square in shape, 4 mm long and 3.5 mm wide. Lateral region of the oral margin forms a process partly covering the frontal in the region of passage of the supraorbital sensory canal from the frontal to the parietal. Pit lines are visible on caudolateral region of the bone. The sculpture is the same as on the frontal.

Dermosphenotic is oblong, conspicuously orocaudally elongated, 6 mm long and 1.6 mm wide. Oral margin of the bone is pointed, medially bordered by the frontal and laterally by the nasal. Medial margin of the dermosphenotic is in contact with the frontal as far as to the lateral process of the frontal. The dermosphenotic is bordered by the dermopterotic caudally of this process. Lateral margin of the dermosphenotic probably borders the orbit and contacts the infraorbital caudally. Lateral margin forms a lateral process caudally. The sculpture on the bone is plain, with flat moulds arranged mostly orocaudally. Rests of the infraorbital sensory canal are preserved as three pores in one line running across the central region of the bone. The shape of the dermosphenotic is completely dissimilar to the same bone on *Paramblypterus rohani* from the Krkonoše Piedmont Basin (Štamberg 1976). The dermosphenotic of *Paramblypterus rohani* is more or less of triangular while that in this specimen is conspicuously orocaudally elongated.

The dermopterotic is also distinctively orocaudally elongated, 7 mm long. Oral part is narrow, round and reaches up to the lateral process of the frontal. One-third of the medial margin is in contact with the frontal, two-thirds of the caudal part of the medial margin contact the parietal. It borders the dermosphenotic orally and partly laterally. The sculpture is the same as on the dermosphenotic. Rests of the infraorbital sensory canal are preserved as pores in a line along lateral margin of the bone.

Operculum is oblong, its height twice its length. The suboperculum is only partly preserved, oroventrally elongated. Maxilla bears only partly preserved maxillary plate.

Aeduelliformes Heyler, 1969
Aeduellidae Romer, 1945
Aeduella Westoll, 1937

M a t e r i a l : Isolated bones and fragments Nos. MHK 62425, MHK 62426, MHK 62428, MHK 62440, MHK 62441, MHK 62458. Actinopterygians of the genus *Aeduella* have not been described from the Permo-Carboniferous basins of Bohemia yet, and it is therefore surprising to find isolated bones of six specimens at the locality of Klášterská Lhota.

Description

Among the bones of the skull roof, the frontal of specimen MHK 62428 and the parietal of MHK 62425 are preserved. The frontal is oblong, nearly twice as long as wide. Medial margin of the bone is straight, with no conspicuous curves or processes. Lateral margin is convex

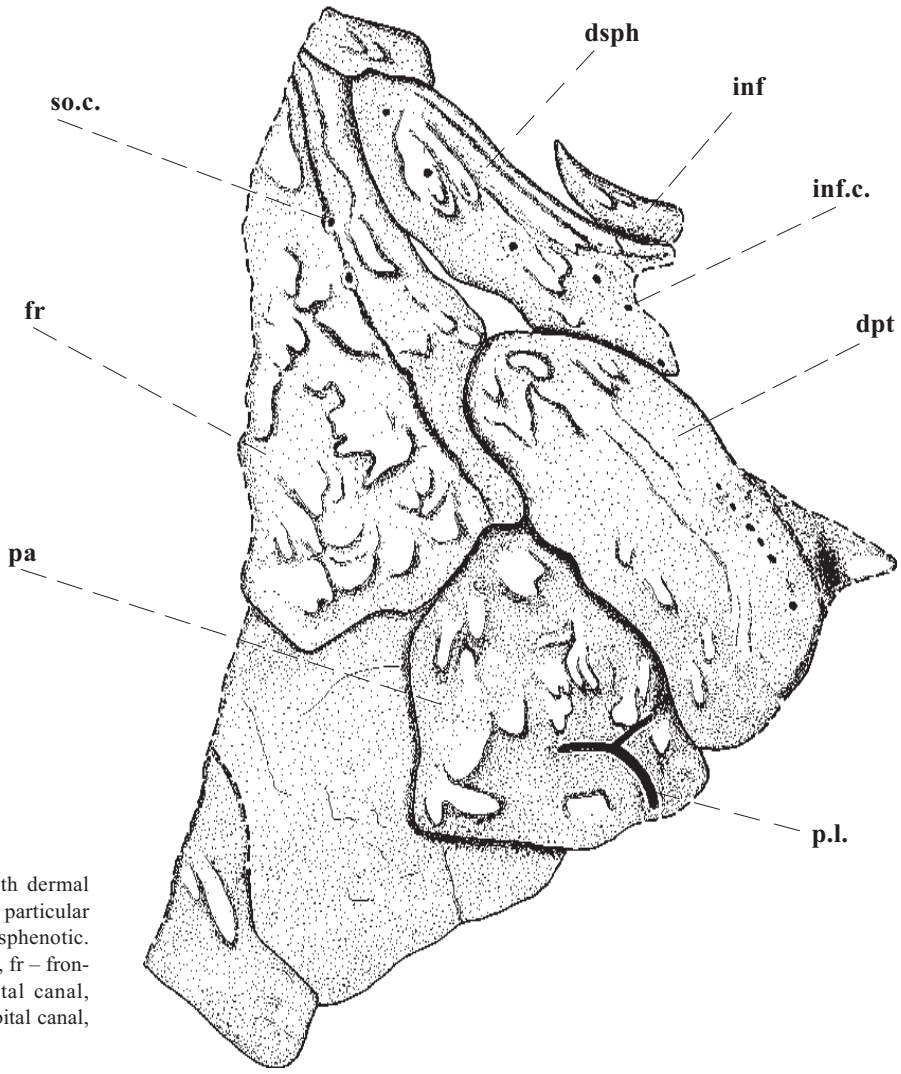

Fig. 5 Specimen described as Type A with dermal bones of the skull roof in dorsal view. Of particular importance is the narrow and long desmosphenotic. dpt – dermopterotic, dsph – dermosphenotic, fr – frontal, inf – infraorbital, inf. c. – infraorbital canal, pa – parietal, p. l. – pit line, so. c. – supraorbital canal, MHK 62439/1, x 10.0.

(Fig. 6a). Supraorbital sensory canal runs parallel to the lateral margin and probably does not pass to the parietal. Sculpture on the dorsal surface of the bone is formed by conspicuous tubercles and very flat moulds. The parietal has irregular shape close to a square. Lateral margin forms curves. Two pit lines can be distinguished. One of them runs orolaterally and one can be assumed to pass to the dermopterotic. The second pit line runs laterocaudally. Conspicuous sculpture is developed on the parietal, especially along the caudal border of the bone, and several moulds are present on the lateral third of the bone.

Maxilla (Fig. 7) belongs to the most typical bones of *Aeduella*. Well preserved isolated maxilla in lateral view is preserved in MHK 62441/1. It is 20 mm long, narrow orally, gradually increasing in height caudally. It is 8.5 mm high in its caudal region. The maxillary plate, which is typical for *Paramblypterus*, is missing. Ventral margin of the maxilla is provided with minute conical teeth embedded in tubules. The teeth are clearly distinct in oral region of the maxilla. The tubules are approxi-

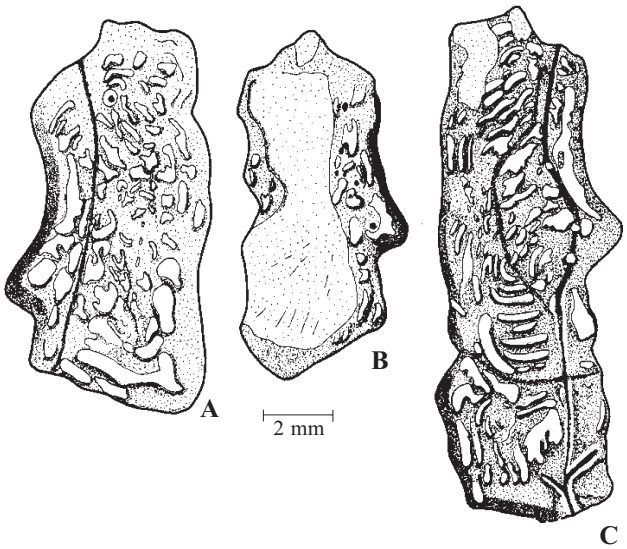

Fig. 6 Frontal bones in dorsal view. Scale bar 2 mm. A – left frontal of *Aeduella,* MHK 62428/1, B – right frontal of paramblypterid type, MHK 62433, C – right frontal and parietal of paramblypterid type with supraorbital canal and pit lines, MHK 62432.

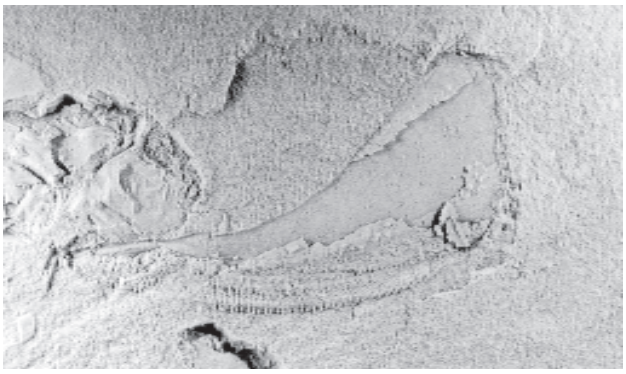

Fig. 7 Left maxilla of *Aeduella* in lateral view with tubular teeth along ventral margin. MHK 62441/1, x 3.0.

mately 1.5 mm long and border the whole ventral margin of the maxilla. Laterally, they are overlapped by a thin and flat bone. Isolated fragments of aeduellid operculum, suboperculum and axonost are preserved in the same specimen as the maxilla.

The operculum and suboperculum of the bones of the opercular series also belong among typical bones of *Aeduella*. They are preserved in specimens MHK 62440, MHK 62426 and MHK 62428. The operculum in MHK 62428 is twice as high as long, dorsally partly bent anteriorly (Fig. 8). The centre of ossification is located immediately next to the oral margin, approximately at one-half of the bone height. The suboperculum is trapeziform, with very bevelled dorsal margin. The height of the suboperculum in its caudal region is nearly twice that in the oral region. The centre of ossification lies in the oroventral corner of the bone. Lateral gular is orocaudally elongated, the left one is preserved in ventral view in specimen MHK 62428. A conspicuous pit line on the gular lies in the centre of ventral surface of the bone, and distinctive moulds and tubercles radiate out of the pit line. Caudal region of the bone is narrow, medial margin is without sculpture and is bent dorsally (Fig. 10).

Cleithrum and clavicle belong to the dermal bones of shoulder girdle and are diagnostic for *Aeduella.* Cleithrum is preserved in MHK 62425 and MHK 62440 and differs from the same bone of *Paramblypterus* in its broadly elliptical shape. Clavicle is preserved in the same specimens; by this time, it has not been described from *Aeduella* from the basins of the Massif Central. It consists from two branches: oral and dorsal (Fig. 9). Oral branch is relatively short, orocaudally elongated and its ventral margin is bent medially. Dorsal branch is more narrow and substantially extends in dorsoventral direction. Dorsal branch is 1.6 times higher than is the length of the oral branch. The shape of clavicle, namely the ratio between oral and dorsal branches, distinguishes it from that of Paramblypteriformes.

Specimen MHK 62428 shows, besides typical aeduellid bones such as operculum, subopercular, lateral gular and frontal, also the lower jaw. Lower jaw on this specimen is relatively weak, with large dorsocaudal process formed by the articular. The shape of the bone is the same as in genus *Paramblypterus*. In view of the fact that the bones are isolated and the fragments could have got mixed, it is not clear whether the lower jaw belongs to *Aeduella* or *Paramblypterus*. *Paramblypterus* and *Aeduella* occupied the same environment and frequently fossilized together, which is the case of specimen MHK 62425 showing bones of *Aeduella* (cleithrum, parietal and clavicle) and numerous paramblypterid bones including maxilla.

Discussion

Genus *Aeduella* is very abundant in the Permo-Carboniferous basins of French Massif Central (Heyler 1969, 1980, 1999, Heyler, Poplin 1983, 1990). The occurrence of *Aeduella* in the Permo-Carboniferous basins of the

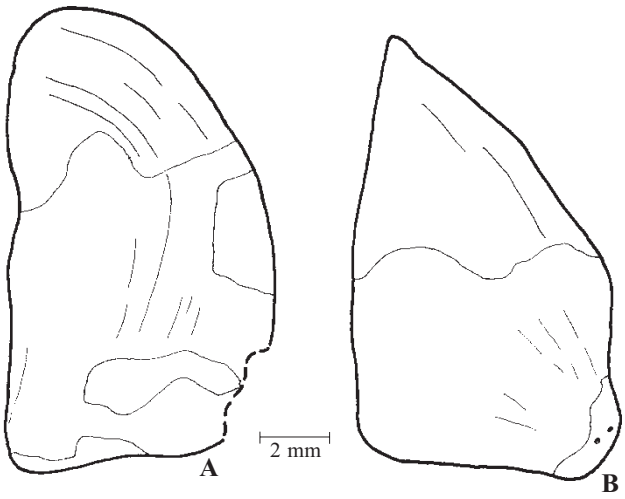

Fig. 8 Operculum and suboperculum of *Aeduella.* Scale bar 2 mm, A – left operculum in lateral view. MHK 62428, B – right suboperculum in lateral view. MHK 62426.

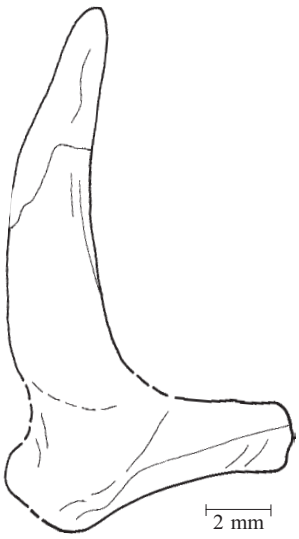

Fig. 9 Right clavicle of *Aeduella* in lateral view with very high dorsal branch and short oral branch. MHK 62440. Scale bar 2 mm.

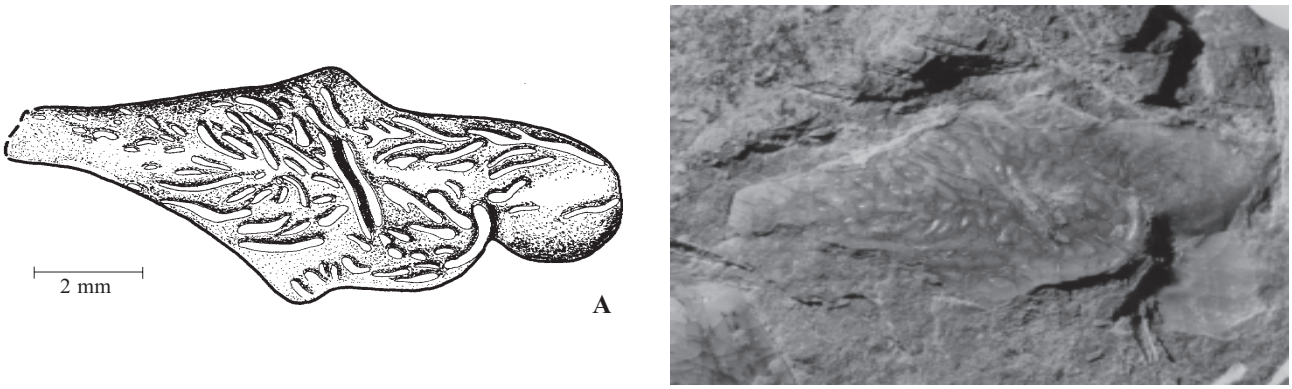

Fig. 10 Drawing (A) and photo (B) of the left gular lateral of *Aeduella* in ventral view with the pit line in central region of the bone. MHK 62428/1, x 6.2. Scale bar 2 mm.

Bohemian Massif was expected already by Heyler (1969) but doubtless bones of *Aeduella* were described only now. The occurence of *Aeduella* in the Lower Permian of the Krkonoše Piedmont Basin, but in younger horizons where acanthodians are missing, is surprising. The finds from Klášterská Lhota provide evidence for a considerable enlargement of areal and stratigraphical range of *Aeduella* occurrences. The wide stratigraphical range of *Aeduella* is somewhat frustrating from biostratigraphical point of view. This genus, which is clearly distinguishable by several bones and scale count, could have become an important taxon for biostratigraphy and a more precise definition of some Lower Permian horizons, much like the present use of the genus *Acanthodes* (Zajíc 2000).

Genus *Paramblypterus*, which is known from a number of localities of the Krkonoše Piedmont Basin, lived in the same environment as *Aeduella*. The above described specimen of *Paramblypterus* (MHK 62438/1-2) has preserved shape of the body and squamation. It differs from *Ambylpterus* in the sense of Dietze (2000) in the dentition on the caudal margin of scales and in the number of scales above and below the lateral sensory line.

Many more features must be compared in specimen MHK 62430, which is herein attributed to *Amblypterus* on the basis of the presence of a ventrolateral process on the dermopterotic. This process is not developed in the species of *Paramblypterus* from the Krkonoše Piedmont Basin, but Dietze (2000) consideres it to be diagnostic for *Ambylpterus*. Besides this feature, the above specimen possesses a large dermosphenotic of triangular shape whereas the same bone in *Amblypterus* (dermosphenotic 1, Dietze 2000) is small and orocaudally elongated. The location of the lateral process on the frontal in posterior one-third of the lateral margin of the bone and not in the middle, as seen in *Paramblypterus* (Štamberg 1976) or *Amblypterus* (Dietze 2000), corresponds to the large triangular dermosphenotic in our specimen MHK 62430. The shift of the lateral process on the frontal posteriorly makes space for a larger dermosphenotic. Specimen MHK 62430 was ranged to *Amblypterus* on the premise of a wide variation in the shape of the skull roof bones. Alternatively, the ventrolateral process on the dermopterotic together with the large dermosphenotic and a shift of the lateral process on the frontal posteriorly may pose features of a different species.

Specimen MHK 62439/1-2 is described separately as Type A. At Klášterská Lhota, it occurs together with *Paramblypterus* and *Amblypterus*. This fish is small, slender, its dermosphenotic is neither triangular as in *Parambylpterus rohani* nor oblong, but is considerably elongated orocaudally. Also the operculum is much higher than in the genera *Amblypterus* and *Paramblypterus.*

Conclusion

Scales, bones and fragments of actinopterygians were collected from two horizons of grey, reddish, mauve and greenish laminated calcareous mudstones in an outcrop of the Prosečné Formation (Lower Permian) at Klášterská Lhota. Genera *Paramblypterus, Amblypterus* and *Aeduella* were distinguished among the new material. Several specimens of *Aeduella* represent the first described finds of this genus from the Permo–Carboniferous of the Bohemian Massif. Besides the maxilla, frontal, parietal, operculum, suboperculum and cleithrum, which are characteristic of *Aeduella*, also an isolated clavicle was described. The latter differs from the clavicle of *Paramblypterus* and *Amblypterus* and has been unknown till this time in *Aeduella.* A small, slender specimen close to *Paramblypterus* and *Amblypterus* but differing in some anatomical features is described separately as Type A.

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Paprskoploutvé ryby z nové spodnopermské lokality podkrkonošské pánve

V rozsáhlém odkryvu spodního permu v Klášterské Lhotě (prosečenské souvrství) v podkrkonošské pánvi byly ve dvou polohách šedých, červenavých, fialových a nazelenalých laminovaných vápnitých prachovců nalezeny šupiny, kosti a fragmenty těl paprskoploutvých ryb. V nově objeveném osteologickém materiálu byly rozeznány rody *Paramblypterus, Amblypterus* a *Aeduella*. Rod *Aeduella* je poprvé popsán z permokarbonu Českého masívu, a to hned v několika jedincích. Kromě kostí, jako jsou maxila, frontale, parietale, operkulare, suboperkulare a kleithrum, které jsou velice charakteristické pro rod *Aeduella*, byla nalezena též izolovaná klavikula. Tato kost, která byla dosud u rodu *Aeduella* neznámá, je svým tvarem značně odlišná od téže kosti rodu *Paramblypterus*. Jeden malý jedinec, který je blízký rodům *Paramblypterus* a *Amblypterus*, je vzhledem ke svým některým anatomickým odlišnostem popsán samostatně jako Typ A.