

The first “osteolepiform” tetrapodomorph (Sarcopterygii) from the Paleozoic sequences of the Moravian Karst (Czech Republic)

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The first tetrapodomorph specimen from the Paleozoic sequences of the Moravian Karst (Moravo-Silesian Basin, Bohemian Massif, Czech Republic) is described. The well-preserved, cosmine-covered lateral extrascapular bone comes from the Upper Devonian (Famennian) hemipelagic Křtiny Limestone of the Lišeň Formation. The affinity to the “osteolepiforms” is inferred from the cosmine histology and morphological features of the bone. Assignment to the Megalichthyiformes seems most probable. The associated fauna, e.g., clymenids, orthocone nautiloids, thin shelled bivalves, trilobites and crinoids, clearly demonstrate a marine environment.

Key words: Tetrapodomorpha, “Osteolepiformes”, cosmine, Famennian, Moravo-Silesian Basin, Moravian Karst.

INTRODUCTION

Sarcopterygian fish are especially interesting because of their close relation to the tetrapods (Rosen et al., 1981; Thomson, 1993; Cloutier and Ahlberg, 1996; Ahlberg and Johanson, 1998; Long and Gordon, 2004; Clack, 2006). The integumentary skeleton of the sarcopterygians is plesiomorphically characterized by cosmine (e.g., Sire et al., 2009). This unique tissue complex consists of a canal system enclosed in an enamel/enameloid-coated single layer of odontodes (Gross, 1956; Thomson, 1975, 1977; Meinke, 1984; Zhu et al., 2006) and an uppermost part of spongy bone (Thomson, 1975, 1977; Borgen, 1992). Flask-shaped pore-canals, which open to the surface by minute pores, are connected by mesh-canals to each other and by cross-canals to the pulp cavities (Gross, 1956; Thomson, 1975, 1977; Meinke, 1984). The canal system is continuous with the vascular canals of the underlying spongiosa (Thomson, 1977; Borgen, 1992) and is supposed to possess vascular functions involved in the deposition of dentine and enamel/enameloid (Bemis and Northcutt, 1992; Borgen, 1992; Zhu et al., 2006). The cosmine cover in crown sarcopterygians is significant for its uniphase deposition (Zhu et al., 2006, 2010). Seasonal resorption and redeposition of this special tissue complex is supposed to allow growth of the animal (e.g., Westoll, 1936; Ørvig, 1969; Thomson, 1975, 1977; Borgen, 1989, 1992; Fox et al., 1995).

To date, the Devonian and Lower Carboniferous sequences of the Moravian Karst (Moravo-Silesian Basin, Bohemian Massif, Czech Republic; see Figs. 1A, B and 2) have provided poor evidence of sarcopterygian fish comprising onychodontiforms only (see Ginter, 1991; Smutná, 1994, 1996; Kumpan, 2013).

Recently, a cosmine-covered dermal bone was obtained from a small abandoned quarry situated in the southern part of the Moravian Karst near the road connecting Brno-Líšeň and Ochoz at Brno (Fig. 1C). This quarry might correspond to a fossil site described by Rzehak (1910). A section about two metres thick is composed of the Famennian hemipelagic Křtiny Limestone of the Lišeň Formation (Weiner and Kalvoda, 2013). This strongly condensed succession (Weiner and Kalvoda, 2016) corresponds to the Hostěnice facies development (Rez et al., 2011). The bone comes from a darker grey bioclastic limestone (Fig. 3) developed closely above the black limestone lenses of the Lower *Annulata* Event (Upper *Palmatolepis rugosa trachytera* conodont Zone, see Weiner and Kalvoda, 2016). The presence of *Polygnathus styriacus* Hinde, 1900 in the grey bioclastic limestone (microfacies F *sensu* Weiner and Kalvoda, 2016) might indicate the base of the Lower *Palmatolepis perlobata postera* conodont Zone (e.g., Hartenfels, 2011; Weiner and Kalvoda, 2016). Conodonts indicate the palmatolepid-polygnathid biofacies (Weiner, 2013; Weiner and Kalvoda, 2016), which is generally supposed to occupy the upper to middle part of a basin slope environment (e.g., Kalvoda et al., 1999: 144; Fig. 3). The microfacies corresponding to wackestone to packstone was interpreted as deposited above or slightly below storm wave base (microfacies F *sensu* Weiner and Kalvoda, 2016). The layer contains a rich fauna including ammonoids, orthocone nautiloids, thin-shelled bivalves, ostracods, crinoids and trilobites (Weiner and Kalvoda, 2013,

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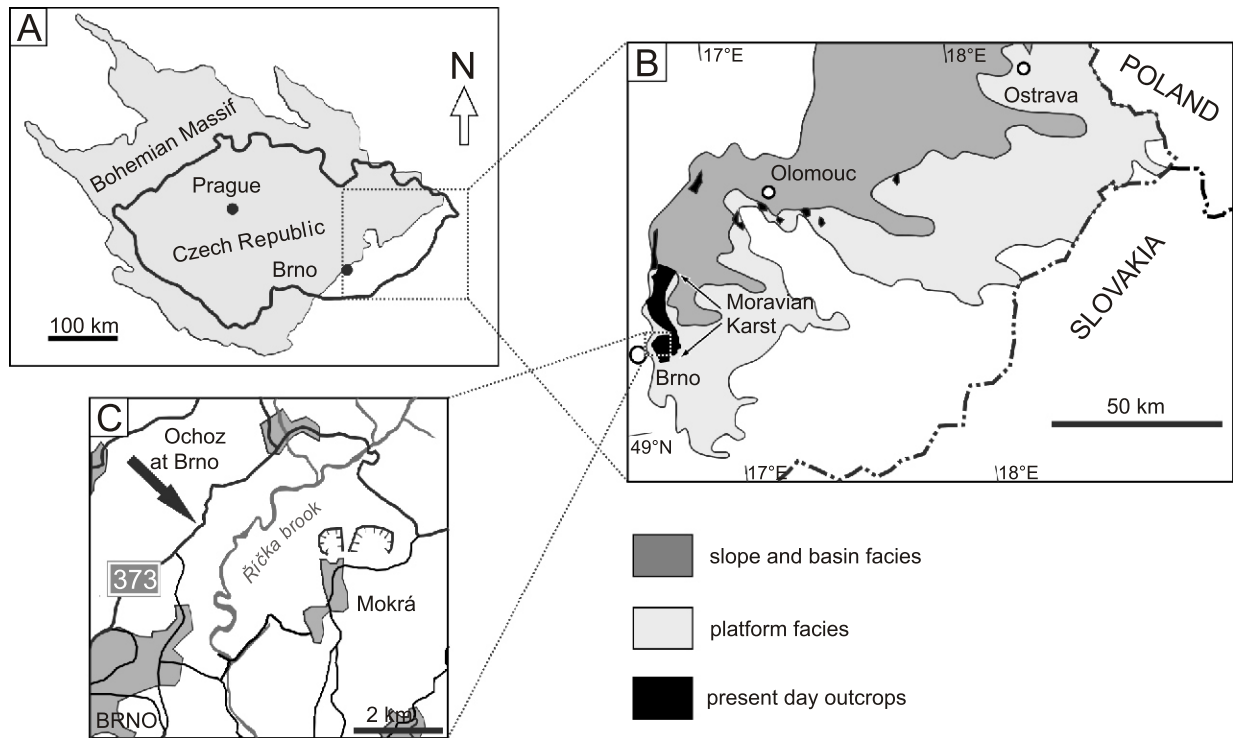


Fig. 1A – position of the area studied in the Czech Republic and the Bohemian Massif; B – simplified map of the Upper Devonian carbonate platform of the Moravo-Silesian Basin in the subsurface and at outcrop, modified after [Bábek et al. \(2007\)](#); C – geographic position of the locality studied (marked by a black arrow)

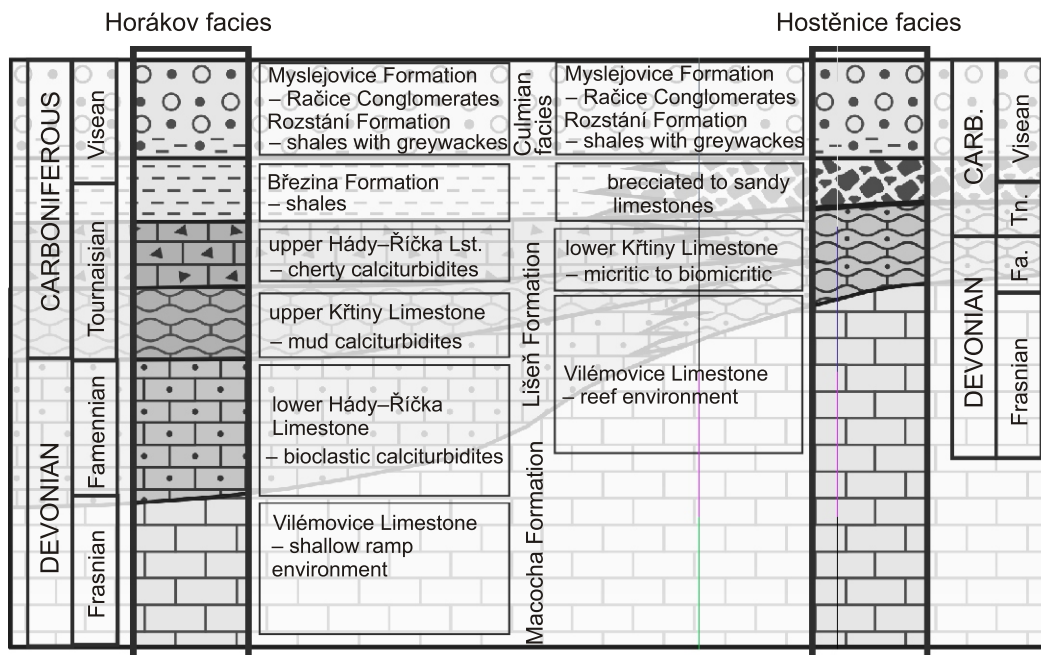


Fig. 2. Stratigraphic scheme of the southern part of the Moravian Karst (after [Kalvoda, 1996 in Rez et al., 2011](#))

Lst. – limestone, Fa. – Famennian, Tn. – Tournaisian

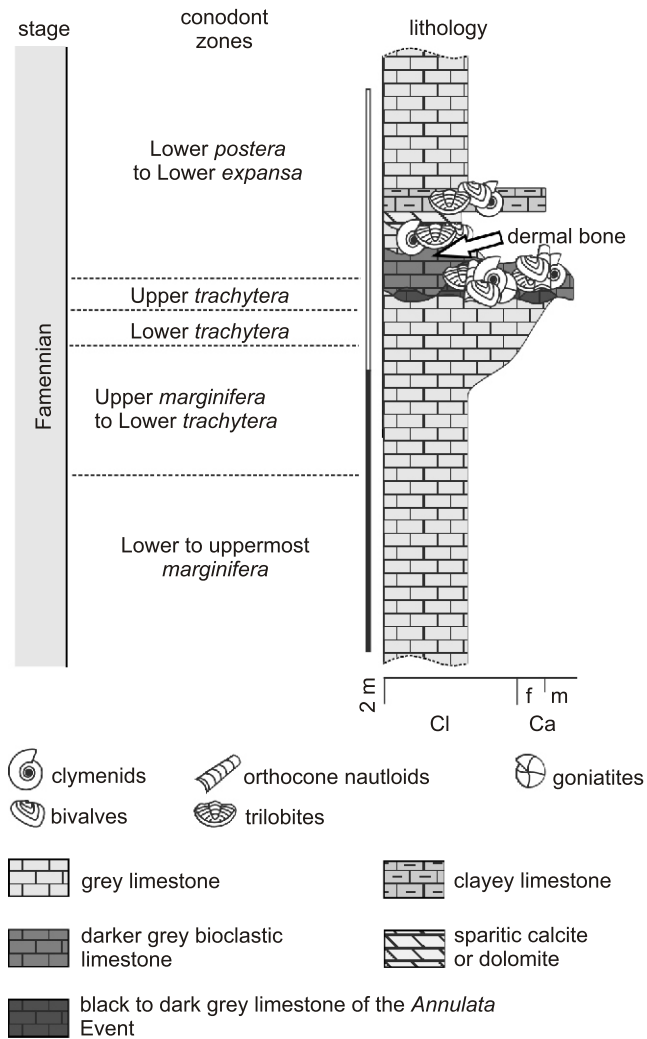


Fig. 3. Lithostratigraphy and biostratigraphy of the section

The stratigraphic position of the “osteolepiform” dermal bone is marked by an arrow; Cl – calcilitite, Ca – calcarenite, f – fine grained, m – medium grained; modified after [Weiner and Kalvoda \(2016\)](#)

2016). The insoluble residuum also yielded fish remains belonging mostly to chondrichthyans and “palaeoniscids”.

The cosmine-covered bone is housed in the Collections of the Czech Geological Survey, Prague, inventory numbers HP108a and HP108b.

GEOLOGICAL SETTING

The Middle Devonian to Lower Carboniferous sequences of the Moravian Karst were deposited in the Moravo-Silesian Basin at the southern margin of Laurussia (e.g., [Kalvoda et al., 2002, 2008](#)). In a regional geological context, these sequences belong to the Moravo-Silesian zone of the Bohemian massif ([Finger et al., 2000](#)) and correspond to the Rhenohercynian zone of the Central European Variscides ([Hladil et al., 1999](#)). The Moravian Karst facies development represents one of several pre-flysch facies domains in the Moravo-Silesian Basin (e.g., [Zukalová and Chlupáč, 1982; Hladil, 1992; Kalvoda et al., 2002, 2008](#)). The carbonate platform (Macocho Formation) of the Moravian Karst development began to be progressively tectonically disintegrated

and drowned during the Frasnian to Late Famennian interval, and this was connected to the onset of the halfgraben sedimentation of the Lišeň Formation ([Kalvoda and Melichar, 1999; Bábek et al., 2007; Kalvoda et al., 2008](#)). In the Famennian interval, two facies developments of the Lišeň Formation may be roughly distinguished in the southern part of the Moravian Karst ([Fig. 2](#)): the Horákov facies development is characterized by relatively thick sequences of calciturbidites (Hády–Říčka Limestone), which were deposited in deeper parts of the slope and basin, whereas the Hostěnice facies development comprises condensed successions of nodular hemipelagites (Křtiny Limestone), representing a shallower environment on the bypass slope ([Kalvoda et al., 1996; Rez et al., 2011](#)).

MATERIAL AND METHODS

The cosmine-covered dermal bone is preserved together with indeterminable fish remains in the same sample. The bone is well-preserved but the cosmine surface especially is affected by numerous microcracks.

The bone, broken in the field into two parts, was mechanically prepared using a pneumatic engraving pen and subsequently chemically treated with dilute acetic acid. The small area at the crack dividing the bone into two parts was polished. Detailed photographs were taken using a *Nikon SMZ 1500* binocular microscope with a *Nikon DXM* digital camera and *NIS-Elements* software. In some cases, the sample was submerged in water for better results, and in others, a coating of ammonium chloride was applied. Detailed measurements were taken using *JMicroVision* software (Nicolas Roduit, Switzerland). A coating of gold was applied to a small area of the cosmine surface before using scanning electron microscopy.

SYSTEMATIC PART

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Rhipidistia Cope, 1887 *sensu* Cloutier and Ahlberg, 1996

Tetrapodomorpha Ahlberg, 1991

“Osteolepiformes” indet.

([Figs. 4A, 5 and 6](#))

Material. – One cosmine-covered right lateral extrascapular from the Křtiny Limestone of the Lišeň Formation; Famennian (the span of the Lower *postera* to Lower *expansa* conodont Zones); “Ochoz section” (*sensu* [Weiner and Kalvoda, 2016](#)) between Brno and Ochoz at Brno.

Description. – The right lateral extrascapular has a subtriangular outline and is about 2 cm in size. Three slightly concave overlapped areas are developed at its anterior margin. The main sensory canal passes through the middle of them. Other margins lack overlapped areas. The corner between the slightly convex lateral to posterolateral margin and the concave posteromedial margin is rounded, without a notch. The medial margin is straight to very slightly concave ([Fig. 4A](#)).

The external surface of the bone bears numerous openings for tubes leading to the main and supratemporal commissural sensory canals. The even distribution of these openings does not allow one to trace the course of the sensory canals from the bone’s external surface ([Fig. 4A](#)). Nevertheless, these sensory canals with a diameter of about 0.6 mm are visible at a crack

going through the bone. A short pit-line with foramina reaching approximately 57 μm in diameter is developed (Figs. 4A and 5F). The cosmine cover is devoid of Westoll lines.

A layer approximately 0.4 mm thick of lamellar bone is overlain by a layer about 1.3 mm thick of spongy bone. Buried odontodes are absent. The enamel/enameloid coated dentine layer is about 0.14 mm thick and encloses the pore-canal network (Fig. 5E). The enamel/enameloid does not enter the

pore-canals. The shape of the pore-canals is reminiscent of an oast-house chimney. These canals reach a height of around 137 μm (Fig. 5A, B, E), and their surface openings are shaped like wide funnels. The diameter of these openings reaches on average 16 μm at the top (based on 70 measurements), but it can be reduced to 5 μm at the base of the funnel. The distance between openings is about 153 μm (140 measurements were taken). The mesh-canals reach their greatest diameter at their contact with the pore-canals, but their thickness often significantly decreases in their central part (Fig. 5B). The lower mesh-canals are missing. Bundles of roughly radially arranged dentine tubules are developed between the flask-shaped pore-canals. The orange colour of the dentine tubules might be caused by iron oxides/oxyhydroxides. The cosmine cover is brown, and its transparency enables one to observe the distribution of the pore-canals and dentine tubules, especially when the specimen is submerged in water (Fig. 5A, D, F). Using an optical microscope, a very fine pattern at the cosmine surface is apparent (Fig. 5C); nevertheless, this pattern was not clearly observed using the scanning electron microscope (see Fig. 6 showing also the details of the sensory tube opening). The partial absence of cosmine is probably caused by damage rather than by resorption.

DISCUSSION

The cosmine histology in various groups of sarcopterygian fish has been discussed e.g., by Gross (1956), Rosen et al. (1981), Meinke (1984), Schultze (1986), Chang and Smith (1992), Sire et al. (2009) and Zhu et al. (2010). The Moravian specimen possesses the combination of cosmine features including the absence of Westoll lines and buried odontodes, the enamel/enameloid not extending into the pore-canals, and the shape of the pore- and mesh-canals, which matches the conditions common in “osteolepiforms” (see Rosen et al., 1981; Meinke, 1984; Chang and Smith, 1992). The specimen also lacks the lower mesh-canals known in the Middle Devonian “osteolepiforms” such as *Osteolepis* Agassiz, 1835 and many early dipnoans (e.g., *Dipterus* Sedgwick and Murchison, 1829), which is usual in younger forms of “osteolepiform” tetrapodomorphs, e.g., *Megalichthys* Agassiz, 1935 or *Ectosteorhachis* Cope, 1880 (see Thomson, 1977). A similar shape of pore- and mesh-canals was recorded especially in *Cladrosymblema* Fox et al., 1995 and *Megalichthys* Agassiz, 1935 (see Fox et al., 1995; Gross, 1956). The diameter of the pore-canal openings in the Moravian specimen is close to the average of 10 μm recorded in the “osteolepiforms” by Thomson (1977). The height of the pore-canals and their spacing also

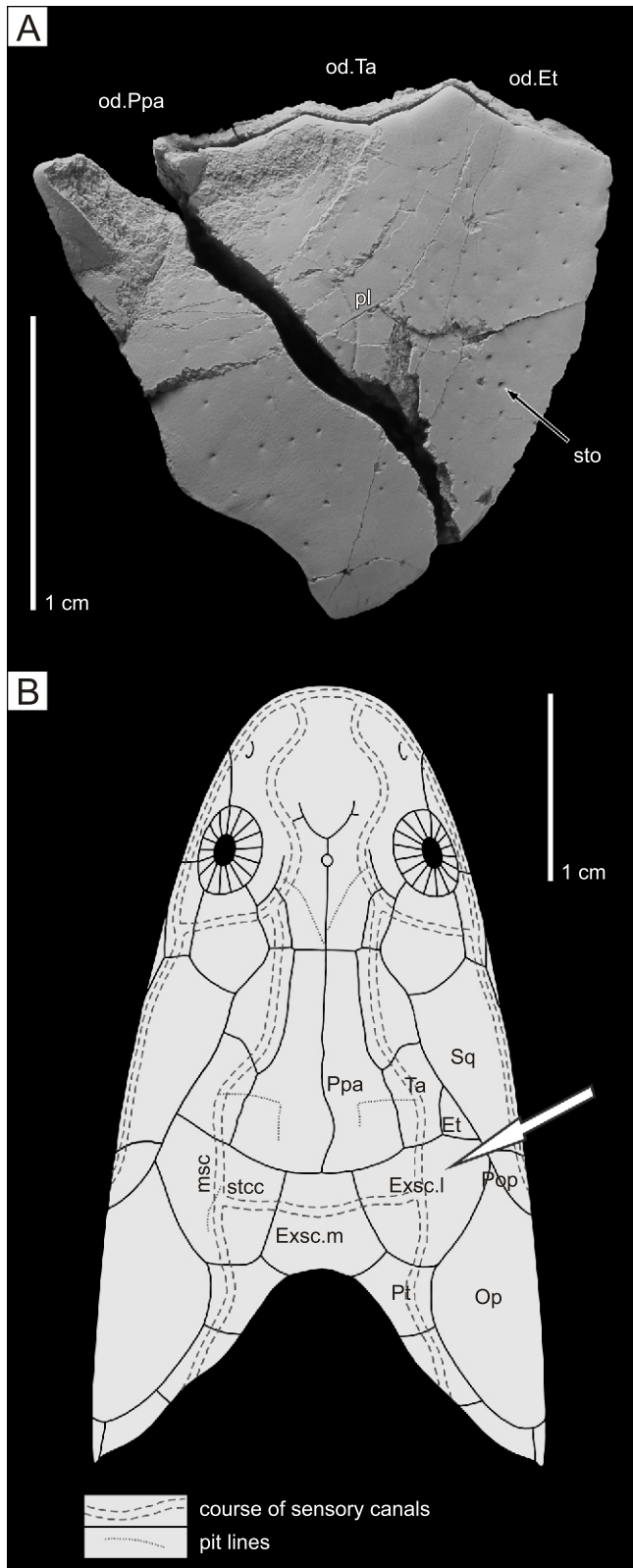


Fig. 4A – right lateral extrascapular of “osteolepiform” tetrapodomorph from the Moravian Karst; the specimen was coated with ammonium chloride; **B** – position of right lateral extrascapular (arrowed) on the skull and exoskeletal shoulder girdle reconstruction of an “osteolepiform” fish (*Osteolepis macrolepidotus* Agassiz, 1835), modified after Jarvik (1948)

Anatomical abbreviations: Et – extratemporal, Exsc.l. – lateral extrascapular, Exsc.m. – median extrascapular, msc – main sensory canal, od.Et – area on lateral extrascapular overlapped by extratemporal, od.Ppa – area on lateral extrascapular overlapped by postparietal, od.Ta – area on lateral extrascapular overlapped by tabular, Op – operculum, pl – pit-line, Pop – preoperculum, Ppa – postparietal, Pt – posttemporal, Sq – squamosal, stcc – supratemporal commissural canal, sto – sensory tube opening, Ta – tabular

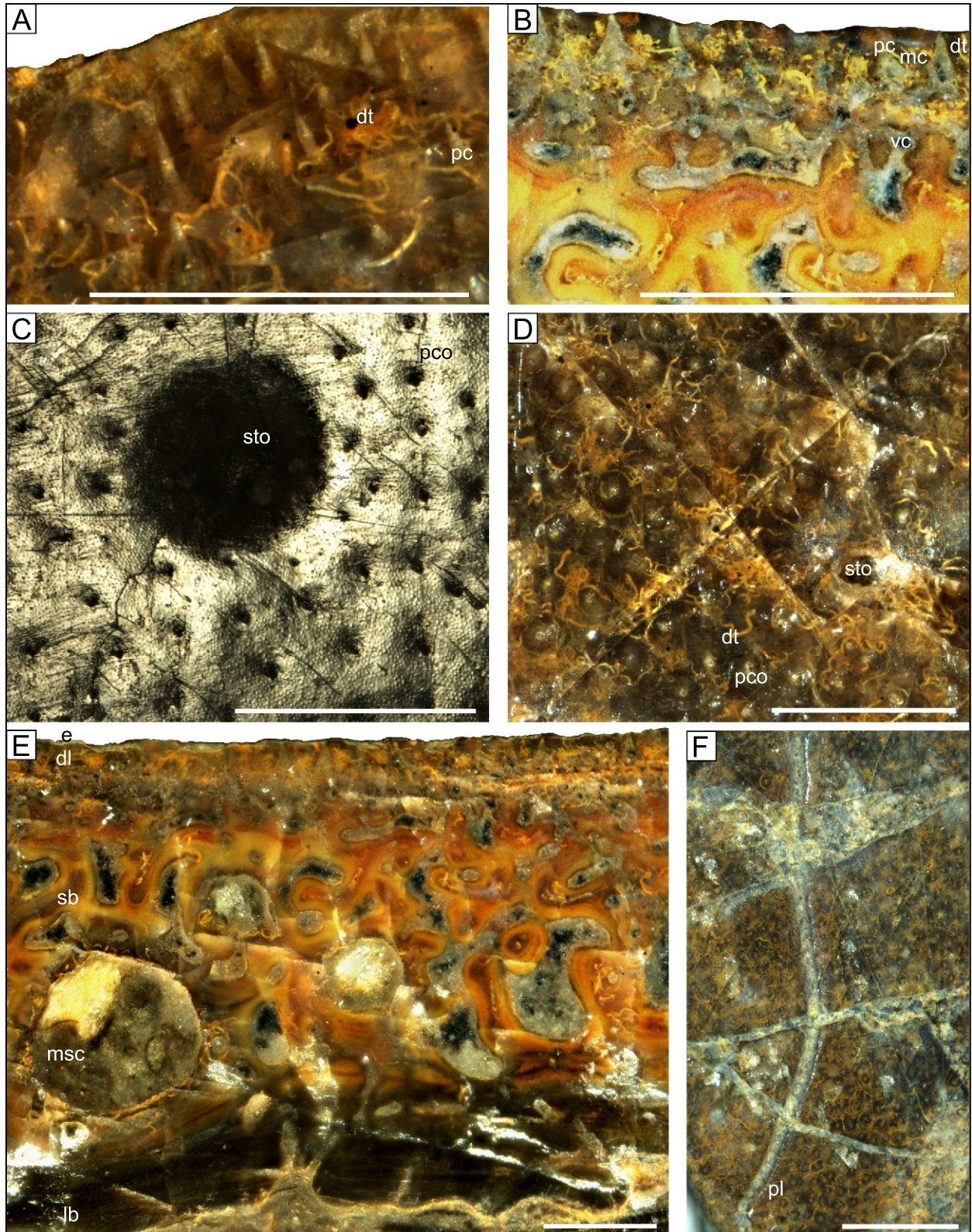


Fig. 5A – detail of the cosmine surface observed at an acute angle; **B** – detail of polished cross-section through the cosmine cover; **C** – detail of the cosmine surface showing very fine granulation; **D** – detail of the cosmine surface; **E** – polished cross-section through the dermal bone with the cosmine cover; **F** – detailed view of the pit-line from the cosmine surface

dl – dentine layer, e – enamel/enameloid, lb – lamellar bone, mc – mesh-canal, msc – main sensory canal, pc – pore-canal, pco – pore-canal opening, pl – pit-line, sb – spongy bone, sto – sensory tube opening, vc – vascular canal

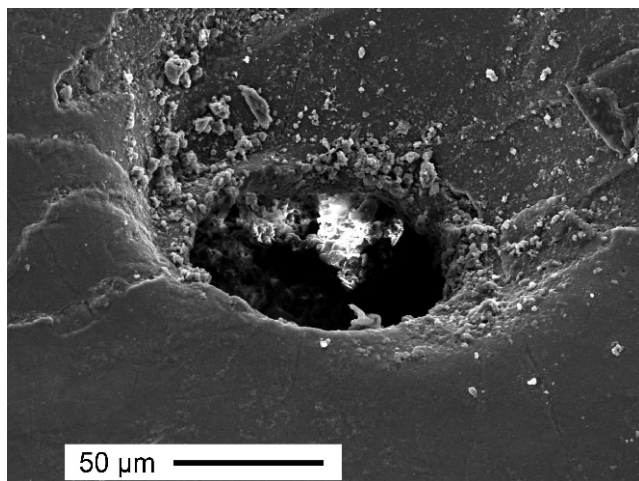


Fig. 6. Scanning electron micrograph of the cosmine surface with the sensory tube opening

correspond to the 150–250 μm measured in “osteolepiforms” (Thomson, 1977). All these values are considerably higher in porolepiforms and dipnoans (Thomson, 1977). The pore-canals of *Porolepis* Woodward, 1891 are approximately 250 μm high, their openings reach 60–70 μm in diameter, and the distance between them is about 300 μm (Thomson, 1977). In the dipnoan genus *Ganorhynchus* Traquair, 1873 the pore-canals are approximately 650 μm high, their openings reach 400 μm in diameter, and the distance between them is about 500 μm (Thomson, 1977). Bemis and Northcutt (1992) recorded the diameter of dipnoan pore-canal openings as follows: 83 μm in *Sunwapta grandiceps* Thomson, 1967; 20–160 μm with an average of 64 μm in *Dipterus valenciennesi* Sedgwick and Murchison, 1829 and the openings as small as 45 μm in *Chirodipterus australis* Miles, 1977.

Few comments have been made on the fine cosmine surface ornamentation between the pores. Chang and Smith (1992) recorded thin scalloped ridges of unknown character anterolateral to the pores in one specimen of *Diabolepis* Chang, 1984. A hexagonal pattern reflecting the arrangement and size of epithelial cells was observed in the dipnoans *Chirodipterus australis* Miles, 1977 (Smith, 1977) and *Dipterus* sp. (Schultze, 1977) using a magnification of 400 to 2000 times. The cosmine surface of the Moravian specimen shows a very fine pattern (Fig. 5C); nevertheless, the scanning electron microscope failed to reveal such a hexagonal pattern using corresponding magnifications (see Fig. 6). S ave-S oderbergh (1941) and Jarvik (1948) described an alternation of dark and light bands in the dentine layer of several (mainly black) specimens of “osteolepiform” tetrapodomorphs, especially if they were submerged in water or alcohol. A brown specimen from the Moravian Karst does not show these bands.

Dermal bones of “osteolepiform” tetrapodomorphs show a uniform overlap pattern (Jarvik, 1980). Overlapped areas at the anterior margin of the lateral extrascapular in the Moravian specimen could have served for articulation with the postparietal, tabular and probably also with the independently developed extratemporal bone (inferred from the tripartite anterior margin, see S ave-S oderbergh, 1933; see Fig. 4). However, bones of the postparietal shield and extrascapular series can vary in development even on both sides of one individual (Jarvik, 1948). A compound character of the lateral extrascapulars was recognized in a specimen of *Osteolepis macrolepidotus* Agassiz, 1835 with an independently devel-

oped posteromedial part of this bone (Jarvik, 1948). On the other hand, a specimen of *Thursius moy-thomasi* Jarvik, 1948 lacking an independently developed median extrascapular is also known (Jarvik, 1948). The medial margin of the Moravian specimen lacks an overlapped area suggesting that the lateral extrascapulars must have overlapped the median extrascapular. This condition is usual in “osteolepiform” tetrapodomorphs (Jarvik, 1980). In porolepiforms, lateral extrascapulars are overlapped by the median one (Jarvik, 1980), and the situation in dipnoans is unclear because of the variability in the number of extrascapulars (Miles, 1977). The variability in shape of “osteolepiform” lateral extrascapulars was clearly demonstrated by S ave-S oderbergh (1933) in Middle Devonian specimens from Scotland. The pit-line can be present or absent in these bones, and this condition can also vary even on both sides of one animal (Jarvik, 1948). Numerous and evenly distributed openings of the main and supratemporal commissural canals in the Moravian specimen represent a feature known especially in younger forms of “osteolepiform” tetrapodomorphs such as *Megalichthys* Agassiz, 1835 or *Eusthenopteron* Whiteaves, 1881 from the Carboniferous and Permian successions (Jarvik, 1948). In Middle Devonian forms such as *Thursius macrolepidotus* (Sedgwick and Murchison, 1829) or *Osteolepis macrolepidotus* Agassiz, 1835, the branching of tubes rising from these canals is weak, and the tubule openings are often arranged in a single row (Jarvik, 1948). An intermediate condition was recorded e.g., in the lowermost Upper Devonian *Latvius grewingki* (Gross, 1933) with tubule openings arranged in double to triple rows (Jarvik, 1948).

“Osteolepiform” tetrapodomorphs have been obtained from freshwater and brackish water as well as marine strata, and the possibility of their anadromy has been discussed (see Thomson, 1969, 1980). According to Long et al. (1997), the sensory pore groups, which are distinctly developed mainly in specimens from freshwater deposits and absent in the marine *Gogonassus andrewsae* Long, 1985 could indicate salinity. The specimen from the Moravian Karst derives from a relatively deeper water environment with clearly marine fauna. Unfortunately, the lateral extrascapulars seem not to be suitable for diagnosis of the presence of sensory pore groups, so the suggestion by Long et al. (1997) cannot be confirmed nor disproved. Moreover, many “osteolepiforms” were obtained from red bed facies, the interpretation of which as regards salinity is still problematic (Laurin and Soler-Gij on, 2010).

The “osteolepiforms” have been subjected to numerous analyses (e.g., Long, 1985a, b; Ahlberg, 1991; Young et al., 1992; Ahlberg and Johanson, 1998; Coates and Friedman, 2010; Swartz, 2012; Witzmann and Schoch, 2012; Holland, 2013) leading to different interpretations of relationships within this group. Swartz (2012) used the term “osteolepiform” to encapsulate the grade of tetrapodomorphs, including the stem-based Canowindridae, Megalichthyiformes and Tristichopteridae.

Cosmine cover is completely absent in tristichopterids (e.g., Snitting, 2008), and canowindrids are supposed to be a Gondwanan group (Young et al., 1992). It is probable that the specimen from the Moravian Karst belongs to the megalichthyiforms *sensu* Swartz (2012). Young et al. (1992) described the shape of lateral extrascapulars in various “osteolepiform” groups (the character “C2: equilateral shape of extrascapulars” in their cladistic analysis). The condition of three-sided lateral extrascapulars almost meeting in the midline in canowindrids and megalichthyids vs. four-sided lateral extrascapulars well separated in the anterior midline in tristichopterids and “osteolepidids” such as *Osteolepis* Agassiz, 1835 or *Gyroptychius* M’Coy, 1848 was later discussed by

Johanson and Ahlberg (1997). These authors pointed out that the lateral extrascapulars of the megalichthyid *Cladrosymblema* Fox et al., 1955 are four-sided and not three-sided as should be expected, and they revealed some contradiction between the descriptions and real shapes of these bones in some other genera. Johanson and Ahlberg (1997: p. 49) divided the character into two: “three sided lateral extrascapulars” and “lateral extrascapulars almost meeting in midline” and recommended further consideration. In this respect, the shape of the lateral extrascapular of the Moravian specimen is closer to megalichthyids than “osteolepidids”. Nevertheless, it is necessary to treat such an assignment with caution. The distance between lateral extrascapulars in the Moravian specimen is not known. In addition, these features are generally rather problematic. Both groups are closely related (see Janvier et al., 2007) and comprise megalichthyiforms according to Swartz (2012).

The specimen described in this paper is the first recorded “osteolepiform” tetrapodomorph from the Paleozoic sequences of the Moravian Karst. Worldwide, other known Famennian cosmine-bearing “osteolepiforms” include e.g., *Megapomus* Vorobyeva, 1977 and *Cryptolepis* Vorobyeva, 1975 (Baltica Province), *Megistolepis* Obruchev, 1955 (Siberia Province) and *Sterropterygion* Thomson, 1972 (Laurentia Province) (see Lebedev and Zakharenko, 2010). A Famennian or possibly a Tournaisian age is also supposed for *Medoevia lata* Lebedev, 1995 which is from an unknown locality (Lebedev, 1995). Although these genera could also possess numerous and evenly distributed openings of sensory canals, we avoid assigning the Moravian specimen to any of them because the material comprises only one bone, and the lateral extrascapulars are known for their shape variability (see Säve-Söderbergh, 1933).

Its position at the Laurussian continental margin (Kalvoda and Bábek, 2010) and its presumed origin in a relatively deeper water environment on the bypass slope (see Weiner and Kalvoda, 2016) suggest assignment of this Moravian “osteolepiform” accompanied by chondrichthyans and “palaeoniscids” to the continental margin assemblage of the Baltica Province periphery *sensu* Lebedev et al. (2010). However, there is still a lack of detailed data on the fish fauna from the Ochoz section or from other Moravian Karst localities representing a similar mid Famennian environment. From the Czech Republic, remains of “osteolepiform” fish have been reported from limnic Upper Carboniferous and Lower Permian deposits (Zajíc, 2000, 2008; Štamberg and Zajíc, 2008). Isolated remains of *Megalichthys nitens* Fritsch, 1889 were recorded from the Carboniferous Kounov Member of the Slaný Formation of the Kladno–Rakovník Basin (Fritsch, 1889, 1893; Romer, 1945; Štamberg and Zajíc, 2008). Remains assigned to “Osteolepiformes” indet. are known from the Carboniferous Kounov Member of the Slaný Formation in the Mšeno–Roudnice

and Kladno–Rakovník basins, the Klobouky Horizon of the Lině Formation in the Kladno–Rakovník Basin and the Permian Kalná Horizon of the Prosečné Formation in the Krkonoše Piedmont Basin (Štamberg and Zajíc, 2008).

CONCLUSIONS

To date, Devonian and Carboniferous deposits of the Moravian Karst (Moravo-Silesian Basin, Bohemian Massif) have yielded poor material of sarcopterygian fish, comprising only onychodontiforms (see Ginter, 1991; Smutná, 1994, 1996; Kumpan, 2013). The newly recorded subtriangular cosmine-covered right lateral extrascapular comes from the predominantly hemipelagic succession of the Famennian Křtiny Limestone of the Lišeň Formation. The combination of cosmine histological features including an absence of Westoll lines and buried odontodes, enamel/enameloid not extending into the pore-canals, pore-canals in a shape reminiscent of oast-house chimneys and the diameter of the pore-canal openings demonstrate an “osteolepiform” affinity. This assignment is supported by the lack of an overlapped area at the medial bone margin. The bone bears numerous evenly distributed openings of the sensory canals as is usual in stratigraphically later forms of “osteolepiform” tetrapodomorphs (Jarvik, 1948), and it lacks the lower mesh-canals present especially in some Middle Devonian forms (Thomson, 1977). The assignment to the “Megalichthyiformes” *sensu* Swartz (2012) seems to be most probable.

The associated fauna has a clearly marine character and contains e.g., clymenids, orthocone nautiloids, thin-shelled bivalves, trilobites, crinoids, conodonts, ostracods, chondrichthyans and “palaeoniscids”. Compared to numerous “osteolepiforms” from red bed sequences, the Moravian specimen originates from the relatively deeper-water environment of the bypass slope (see Weiner and Kalvoda, 2016).

“Osteolepiforms” are recorded in the Paleozoic sequences of the Moravian Karst for the first time. In the Czech Republic, the remains of these tetrapodomorphs have previously only been reported from the Carboniferous and Permian limnic basins (Štamberg and Zajíc, 2008).

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