Akademie věd
České republiky

Příloha B

Teze disertace
k získání vědeckého titulu "doktor věd"
ve skupině geologických věd

Exceptionally preserved Cambrian and Ordovician fossils in the Barrandian area

Komise pro obhajoby doktorských disertací v oboru geologických věd

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Praha, 22. září 2022

CONTENTS

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Abstract of the DSc. Thesis

1. Introduction

Exceptionally preserved fossils play an important role in reconstruction and understanding of the past. Such fossils commonly provide decisive information on morphology of hard, but also on soft parts of diverse organisms. Detailed study of exceptionally preserved fossil remains makes it possible to find the proper systematic position of a given organism. However, it also provides data for the understanding of the functional morphology and helps to reconstruct trophic relations between organisms in the past. For places with exceptionally preserved fossils, the term *Lagerstätten* (from German meaning place of storage, singular *Lagerstätte*) was proposed nearly fifty year ago (Seilacher 1970).

Fossil Lagerstätten have been documented from all continents from Precambrian to Quaternary. Outcrops with exceptionally preserved Cambrian and Ordovician fossils have been intensively studied at number of continents, like North America (*e.g.*, Canada – Burgess Lagerstätte), U.S.A. (*e.g.*, Wheeler, Marjum and Conasauga Lagerstätten), Greenland (Sirius Passet Lagerstätte), Asia (*e.g.*, China – Chengjiang and Kaili Lagerstätten), Russia (Sinsk Lagerstätte), Australia (Kangaroo Island, Emu Bay Shale Lagerstätte), Africa (Morocco, Fezouata and Tafilalt Lagerstätten), South Africa (Soom Shale Lagerstätte), Europe (Sweden, Orsten Lagerstätte). The extraordinary preservation of both plant and animal remains is most often explained by a rapid burial in an oxygen depleted environment.

2. Types of exceptional preservation of fossils

The analysis of a rich record of non-biomineralizing fossils includes a variety of taphonomic modes; Butterfield (2003) proposed to classify Lagerstätten based on taphonomic processes into six major types, particularly into:

(1) *Bitter Springs-type preservation* explained by permineralization by silica,

(2) *Doushantuo-type preservation* explained by mineralization by phosphate in shallow marine environment,

(3) *Ediacaran-type preservation* explained as casts and moulds on and in sandstones,

(4) *Burgess Shale-type preservation* explained as carbonaceous compressions in shales,

(5) *Orsten-type preservation* explained by phosphate mineralization within carbonate concretions,

(6) *Beecher's Trilobite-type preservation* explained by pyritization in shales.

More recently, dozen papers describing exceptionally preserved fossils from the Silurian locality Herefordshire (Wales) were published (*e.g.*, Siveter 2008; Siveter *et al.* 2012); the fossil material is preserved as calcite in-fills within nodules entombed in volcaniclastic rocks. Such highly specific fossilisation processes (= taphonomic pathway) is possible to designate as the *Herefordshire-type preservation*.

The aim of this thesis is to summarize the state of art in study and understanding of Cambrian and Ordovician exceptionally preserved fossils in the Barrandian area (*Figure 1*) and to show possible direction for their research in future.

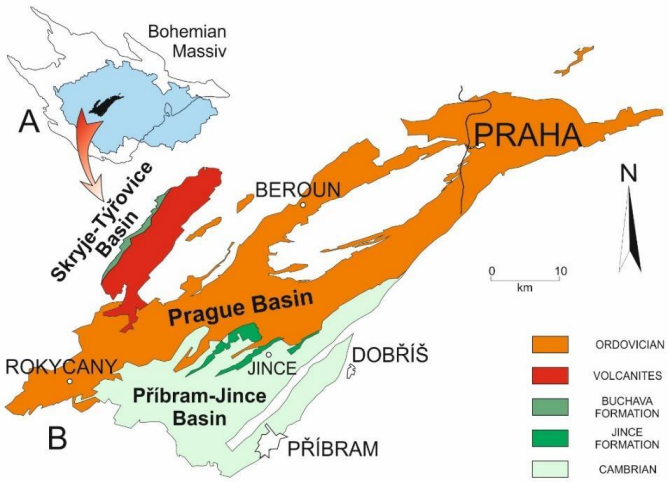

Figure 1. Distribution of Cambrian and Ordovician rocks in the Barrandian area.

Since the paper of Seilacher (1970), the interest of palaeontologists in the study of exceptionally preserved fossils is continuously growing. In the Barrandian area, palaeontological research has been focussed primarily on description and systematic classification of abundant skeletal fossils. Numerous species of trilobites, cephalopods,

graptolites, conodonts and chitinozoans show an apparent restriction in stratigraphical range and such kind of distribution led directly to the application for stratigraphic subdivision. Exceptionally well-preserved fossils, like remains of soft tissue, were occasionally registered and described, but possible Lagerstätten (both Konzentrat and Konservat) were generally overlooked and unstudied in detail.

3. Exceptionally preserved fossils in the Barrandian area

Articulated Cambrian and Ordovician fossils have been studied for a long time (see higher) and numerous trilobites, echinoderms, hyoliths and other invertebrates represent exceptionally preserved fossils. Such samples have been established in the following three Cambrian and five Ordovician units:

- Cambrian; (1) Paseky Shale (2) Jince Formation (3) Buchava Formation.
- Ordovician; (1) Mílina, (2) Šárka, (3) Dobrotivá, (4) Letná and (5) Bohdalec formations (*Figure 2*).

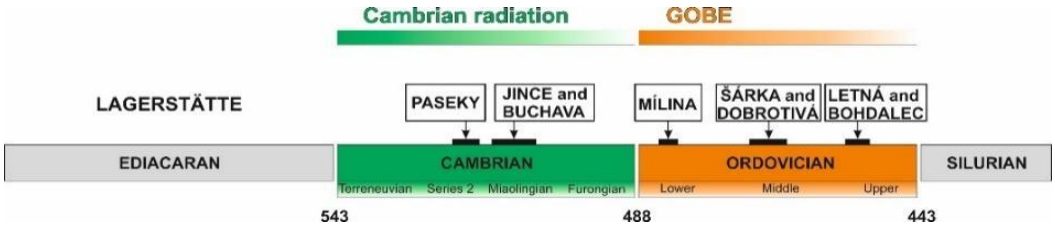

Figure 2. Stratigraphical levels which contain exceptionally preserved fossils in Cambrian and Ordovician of the Barrandian area (after Fatka *et al.* 2011).

In the last 30 years, very intensive collecting of fossils at numerous outcrops in the Příbram-Jince, Skryje-Týřovice and Prague basins provided numerous exquisitely preserved samples, including new taxa as well as remains of several earlier unknown groups of invertebrates. A compressive census of the extensive materials housed in official institutions in the Czech Republic (like National Museum Prague, Czech Geological Survey Prague, regional musea) and in other countries (Germany, France, Austria, Britain, U.S.A.) in combination with the recently gathered samples made possible re-discovery and study of a large set of exceptionally preserved fossils.

In the following chapter, major groups of publications dealing with exceptionally preserved fossils from Cambrian and Ordovician sediments of the Barrandian area are briefly

assessed. The stratigraphic position of specimens used for individual publications included in the DSc. Thesis are shown in *Figure 3*.

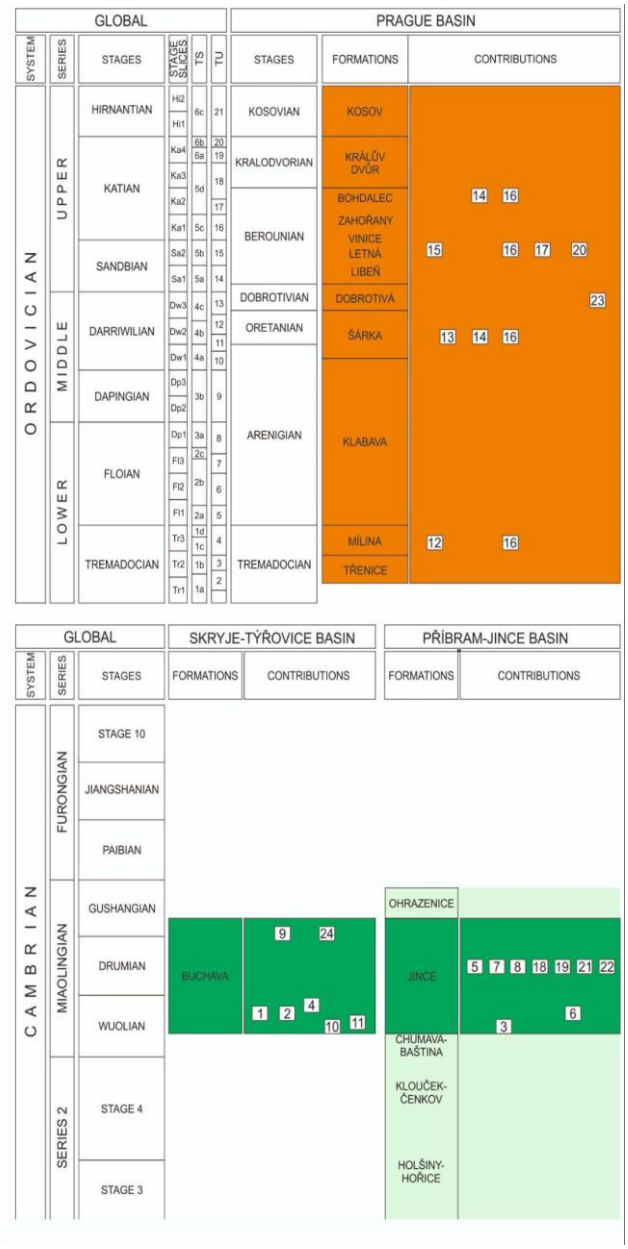

Figure 3. Stratigraphic position of specimens used for individual publications included in the DSc. Thesis. Numbers correspond to the numbering of publications (*original figure*).

1. VALENT, **FATKA** & MAREK (2019). **2.** VALENT, **FATKA** & MAREK (2017A). **3.** VALENT, **FATKA** & SZABAD (2018). **4. FATKA**, KRAFT & SZABAD (2012). **5. FATKA** & KORDULE (1985). **6. FATKA** & SZABAD (2014). **7.** NOHEJLOVÁ & **FATKA** (2016). **8.** NOHEJLOVÁ & **FATKA** (2017). **9. FATKA** & HERYNK (2016). **10. FATKA**, KRAFT & SZABAD (2011). **11.** MIKULÁŠ & **FATKA** (2017). **12. FATKA**, BUDIL & MERGL (2013a). **13. FATKA** & BUDIL (2018). **14. FATKA**, BUDIL & DAVID (2015). **15. FATKA**, LEROSEY AUBRIL, BUDIL & RAK (2013b). **16.** BUDIL & **FATKA** (2022). **17. FATKA** & BUDIL (2021). **18. FATKA**, SZABAD & BUDIL (2009). **19. FATKA**, BUDIL & GRIGAR (2015). **20. FATKA**, BUDIL & ZICHA (2021). **21. FATKA** & SZABAD (2011). **22. FATKA** & KOZÁK (2014). **23. FATKA** & BUDIL (2014). **24. FATKA** & SZABAD (2011).

4. List of publications included in the thesis

Publications included in the thesis are arranged in six groups, each dealing with a specific type of exceptionally preserved fossils from Cambrian of the Příbram-Jince and Skryje-Týřovice basins and the Ordovician of the Prague Basin, all in the Barrandian area:

4. 1. *Conical skeletal fossils* (publications No. 1 to 4).

4. 2. *Echinoderms* (publications No. 5 to 8).

4. 3. *Burgess-type preservation* (publications No. 9 and 10) and *Ediacaran-type preservation* (publication No. 11).

4. 4. *Preservation of soft parts in trilobites* (publications No. 12 to 17).

4. 5. *Wounded agnostids and trilobites* (publications No. 18 and 20).

4. 6. *Examples of frozen behaviour* (publications No. 21 to 24).

4.1. *Conical skeletal fossils*

In the first four papers, morphologically diverse conical skeletal fossils are systematically treated. Finds of both calcium carbonate hyoliths and organo-phosphatic sphenothallids are generally uncommon in Cambrian. The new hyolith species and genus, *Alfaites romeo* was documented from the Drumian Buchava Formation (Skryje-Týřovice Basin) in the publication No. 1. A new hyolithid family Slapylitidae, erected in the publication No. 2, includes two genera *Slapylites* and *Nevadalites* ranging from the Miaolingian to Furongian of West Gondwana, Baltica and Laurentia; one species of this family was established also in Middle Devonian of West Gondwana. Hyoliths from lower stratigraphic levels of the Jince Formation were for the first time comprehensively treated in the contribution No. 3. In the publication No. 4, the first specimens of organo-phosphatic fossils classified as two separate species of the Paleozoic genus *Sphenothallus* Hall, 1847 are described from Wuliuan to Drumian Jince Formation (Příbram-Jince Basin); this material represents a notable widening of geographic distribution of this genus.

4. 2. *Echinoderms*

Articulated thecae of Cambrian echinoderms are usually rare. In the publication No. 5, the presence of the echinoderm class Ctenocystoidea was for the first reported outside of Laurentia. Since that time, diverse species of this class were established in France, Britain,

Spain, Poland, Morocco and Australia. In the contribution No. 6, a complete specimen and disarticulated thecal plates of the family Dibrachicystidae were reported from Cambrian sediments of Central Europe for the first time. This occurrence represents a third report of these rare rhombiferan echinoderms world-wide. A detailed study of the eocrinoid genus *Akadocrinus* Prokop, 1962 provided in the publication No. 7, represents only a second study of eocrinoid ontogeny in the world; this study made possible to revise some of spectacular echinoderm remains as demonstrated in the publication No. 8.

4. 3. *Burgess-type* and *Ediacaran-type of preservation*

In the publication No. 9, the first occurrence of the Burgess Shale-type fauna, particularly the bivalved arthropod *Tuzoia* Walcott, 1912 was reported from the Drumian Buchava Formation (Skryje–Týřovice Basin); this is only a second occurrence of this genus from West Gondwana. Tiny isolated sclerites described from shale interlayers in lower levels of late Wuliuan (Maolingian) Buchava Formation (Skryje–Týřovice Basin) proved the occurrence of non-mineralized genus *Wiwaxia* Walcott, 1911 in Europe for the first time (publication No. 10). This contribution includes a detailed analysis of palaeogeographical distribution of this fossil genus which shows an apparent latitudinal restriction of *Wiwaxia* to the tropical belt. A new study of the imperfectly preserved original specimen of the problematic fossil classified as *Medusites* cf. *radiatus* by Pompeckj (1896) and of one more complete topotype specimen made possible to affiliate this material to the pineapple-shaped ichnogenus *Astropolichnus* Crimes and Anderson, 1985 (publication No. 11).

4. 4. *Preservation of soft parts in trilobites*

In a series of four studies, extraordinarily rare remains of digestive system were described from several levels of Ordovician sequence in the Prague Basin in the following trilobite specimens: (a) in the holotype of the rare harpidid trilobite *Harpides grimmi* Barrande, 1852 from the Lower Ordovician Mílina Formation (publication No. 12), (b) in Middle Ordovician bathycheilid trilobite *Prionocheilus vokovicensis* (Šnajdr, 1956) from the Šárka Formation (publication No. 13), (c) in the common calymenid trilobite *Colpocoryphe bohemica* (Vaněk, 1965) also from the Šárka Formation and in *Flexicalymene* (*Flexicalymene*) *pragensis* Vaněk & Vokáč, 1997 collected from the Upper Ordovician Bohdalec Formation (publication No.

14), and (d) in Upper Ordovician *Selenopeltis buchi* (Barrande, 1846) and *Birmanites ingens* (Barrande, 1852), both from the Letná Formation (publication No. 15).

In these papers, undoubted remain of digestive structures were for the first time established in four trilobite families, particularly in Harpididae Whittington, 1950 - in *Harpides*, Odontopleurida Burmeister, 1843 - in *Selenopeltis* Hawle & Corda, 1847), Calymenidae Burmeister, 1843 - in *Colpocoryphe* Novák in Perner, 1918 and *Flexicalymene* Shirley, 1936, Bathycheilidae Přibyl, 1953 - in *Prionocheilus* Rouault, 1847. A review of all currently known Ordovician trilobites with soft parts described or figured from West Gondwana, European peri-Gondwana and Avalonia shows remains of the digestive system in 19 species, including nine species from the Barrandian area (publication No. 16). Rarely preserved frontal auxiliary impressions (FAIs) are described in twelve exceptionally preserved cephalic shields of holaspid specimens of the trilobite *Dalmanitina socialis* Barrande, 1846 from the Upper Ordovician Letná Formation (publication No. 17).

4. 5. *Wounded agnostids and trilobites*

A high level of exoskeletal regeneration was documented in the small agnostid *Phalagnostus prantli* Šnajdr, 1957 (publication No. 18) as well as in the trilobite *Conocoryphe sulzeri* (Schlotheim, 1823) (publication No. 19), both collected from Drumian sediments of the Jince Formation of the Příbram-Jince Basin. A substantial reduction of the eye surface associated with changes in morphology and surface structure in a cephalon of *Dalmanitina* Reed, 1905 is interpreted as a healed injury after an unsuccessful predatory attack (publication No. 20).

4. 6. *Examples of frozen behaviour*

The last four included studies document rare examples of the so-called frozen behaviour. Finds of articulated agnostid exoskeletons of the abundant species *Peronopsis integra* (Beyrich, 1845) entombed under and inside carcasses of paradoxidid trilobites (publication No. 21) and inside of hyolithid conchs (publication No. 22) are described from the Jince Formation. Rare example of sheltered gregarious behaviour of the harpetid trilobite *Eoharpes benignesis* (Barrande, 1872) is documented from the Middle Ordovician Dobrotivá Formation in publication No. 23. The last publication No. 24 shows an ichno-fossil associated with its

assumed *in situ* preserved maker, a holaspid specimen of the trilobite *Agraulos ceticephalus* (Barrande, 1846); this find comes from the Buchava Formation (Skryje–Týřovice Basin).

5. Abstracts of publications included in the DSc. thesis

(1) Valent, M., **Fatka, O.** & Marek, L. (2019): *Alfaites romeo* gen. et sp. nov., a new Hyolitha from the Cambrian of Skryje-Týřovice Basin (Czech Republic). *European Journal of Taxonomy* **491**, 1–10.

Abstract. The rare hyolith *Alfaites romeo* gen. et sp. nov. is described from the lower half of the mid-Cambrian (Drumian) Buchava Formation of the Skryje-Týřovice Basin in the Barrandian area of the Czech Republic. This new taxon is based on excellently preserved external and internal moulds of three opercula and several conchs collected from carbonate nodules and shale. This rare species has been established at three separate outcrops in lower part of the *Paradoxides* (*Eccaparadoxides*) *pusillus* Biozone. Morphology of conch and both external and internal surface of operculum are well known. However, specific morphology excludes assignment to any of predescribed hyolithid family.

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(2) Valent, M., **Fatka, O.** & Marek, L. (2017): Slapylitidae: a new family of hyolithids (Cambrian - ?Devonian; Laurentia, Gondwana) *Paläontologische Zeitschrift* **91** (4), 497–505.

Abstract. Hyoliths are usually preserved as isolated skeletal elements consisting of conch, operculum, and helens. The occurrence of a conch associated with an operculum is ordinarily exceptional, and the co-occurrence of helens with other skeletal parts is a great rarity. The extraordinary finds of hyolithid conchs associated with opercula in situ are relatively abundant in the Cambrian and Ordovician clastic sediments of the Barrandian area in the Czech Republic. The platyclaviculate operculum with clavicles divided by longitudinal walls into channels characterizes members of the newly established family Slapylitidae fam. nov., which includes two genera: *Slapylites* Marek, 1980 known from the mid-Cambrian of West Gondwana and Baltica and *Nevadalites* Marek, 1976 documented from the Late Cambrian of Laurentia. To this family most probably belongs also an operculum from the Cambrian Series 2–Series 3 boundary of North Greenland and poorly known material from the Middle Devonian of Bolivia.

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(3) Valent, M., **Fatka, O.** & Szabad, M. (2018): The oldest hyolith fauna of the Jince Formation (mid-Cambrian, Barrandian area, Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie* **289** (3), 281–291.

Abstract. The mid-Cambrian Jince Formation of the Barrandian area is globally renowned as a classical repository of exceptionally diverse and well preserved hyoliths. However, our knowledge about hyoliths of the mid-Cambrian Jince Formation of the Příbram-Jince Basin is quite incomplete and the locally abundant and well preserved hyolith specimens are not adequately studied. The hyolith association studied herein consists of three hyolithids and three orthothecids from the lower stratigraphic levels of the Jince Formation and constitutes a considerable increase of our knowledge. The studied material is preserved as internal and external moulds in calcareous nodules, fine greywackes and shales. Except for one taxon, *Maxilites* sp., the other five hyolith species, *Oboedalites oboediens* Marek, 1981, *Slehoferites slehoferi* Marek, 2011, *Circotheca* sp., *Gracilitheca triangularis* Valent et al., 2013, and *Probactrotheca briketa* Marek, 2012 are new for the Příbram-Jince Basin; previously these species have been known exclusively from the Buchava Formation of the Skryje-Týřovice Basin of the Barrandian area.

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(4) Fatka, O., Kraft, P. & Szabad, M. (2012): A first report of *Sphenothallus* Hall, 1847 in Cambrian of Europe. *C. R. Palevol* **11** (6), 539–547.

Ten specimens of two phosphatic fossils have been recently discovered in lower and middle portions of mid-Cambrian Jince Formation in the Czech Republic. They are attributed to the genus *Sphenothallus* Hall, 1847 and described as two separate species; comparatively small conchs are described as *S. kozaki* sp. nov., the much larger specimens characterized by its smooth and partly flexible organo-phosphatic walls of shell are determined as ?*S. kordulei* sp. nov. *Sphenothallus* is known to range from Cambrian to Permian and accommodates numerous species. However, its Cambrian distribution is considerably restricted. Generally rare specimens have been described from Lower to Middle Cambrian of Laurentia and from the Lower Cambrian of Gondwana and peri-Gondwana. The new record of *Sphenothallus* from the Jince Biota represents a notable extension of their geographic range.

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(5) Fatka, O. & Kordule, V. (1985): *Etoctenocystis bohemica* gen. et sp. nov. - new Ctenocystoid from Czechoslovakia (Echinodermata, Middle Cambrian). *Věstník Ústředního ústavu geologického* **60** (4), 225–229.

Abstract. *Etoctenocystis*, a common enigmatic echinoderm from the Jince Formation of Bohemia is closely related to the genus *Ctenocystis* Robison and Sprinkle described from the Spence Shale of Northern Utah. Structure of the inferior surface is the only conspicuous difference between these genera of mid-Cambrian age.

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(6) Fatka, O. & Szabad, M. (2014): Family Dibrachicystidae from the "middle" Cambrian of the Barrandian area (Rhombifera, Echinodermata, Czech Republic). *Paläontologische Zeitschrift* **88** (2), 159–166.

Abstract. A slightly crushed but otherwise nearly complete specimen of the recently described rhombiferan echinoderm genus *Vizcainoia* Zamora and Smith, 2012 is documented from the ‘‘Middle’’ Cambrian Jince Formation of the Příbram–Jince Basin of the Czech Republic. Isolated thecal plates, earlier determined as calyx plates of the eocrinoid *Acanthocystites briareus* Barrande, 1887 and/or as eocrinoid sp., occurring in diverse levels of the Jince Formation are reassigned to Dibrachicystidae gen. et sp. indet. Similarly, isolated thecal plates collected from the Buchava Formation of the Skryje–Týřovice Basin could be classified as Dibrachicystidae gen. et sp. indet. Specimens from the Barrandian area are the first records of the family Dibrachicystidae outside of southwestern Europe, of the family otherwise known only from the Languedocian of Montagne Noire of France and from the Caesaraugustian and Languedocian of Iberian Chains of northern Spain.

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(7) Nohejlová, M. & **Fatka, O.** (2016): Ontogeny and morphology of Cambrian eocrinoid *Akadocrinus* (Barrandian area, Czech Republic). *Bulletin of Geosciences* **91** (1), 141–153.

Abstract. The gogiid eocrinoid *Akadocrinus jani* Prokop, 1962 is known from the middle Cambrian (Drumian) Jince Formation of the Příbram–Jince Basin (Barrandian area, Czech Republic). Seven well- to excellently-preserved juvenile specimens of this species are described for the first time. Detailed comparison of juvenile specimens makes it possible to establish changes in morphology during the early ontogenetic sequence. Juvenile specimens differ considerably from adult specimens in (1) a lower number of thecal plates, (2) a

complete absence of epispires, (3) comparatively shorter brachioles, comprising a small number of brachial plates, (4) a comparatively shorter stem, comprising a small number of columnals and (5) a relatively large attachment disc. Study of the Jince material makes it possible to establish two basic phases in the development of *Akadocrinus*: the pre-epispire bearing phase and the epispire bearing phase.

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(8) Nohejlová, M. & **Fatka, O.** (2017): Revision of the Barrande's specimen "Tige d'une Cystidée indéterminée" (Cambrian, Echinodermata, Eocrinoidea). *Carnets de Géologie (Notebooks on Geology)* **17** (8), 153–160.

Abstract. Reexamination of the type specimen described by Barrande in 1887 as *"Tige d'une Cystidée indéterminée"* shows that this unique specimen represents an articulated but incomplete remnant of the gogiid eocrinoid *Akadocrinus jani* Prokop. The specimen is preserved as an external mould in shale from the mid-Cambrian Jince Formation, and comprises a proximal part of a stem associated with a slightly disarticulated distal portion of a theca, composed of over twenty polygonal plates. With the exception of the basal-most plates, all other preserved thecal plates bear ellipsoidal marginal epispires, and substantiate assignment of this specimen to the epispire-bearing phase in ontogenetic development of *Akadocrinus*.

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(9) Fatka, O. & Herynk, J. (2016): The first occurrence of bivalved arthropod *Tuzoia* from the Skryje–Týřovice Basin (Barrandian area, Czech Republic). *Annales de Paleontologie* **102** (4), 219–224.

Abstract. A fragment of a Burgess Shale-type fossil, bivalved arthropod *Tuzoia* Walcott, 1912, is described from shales of the mid-Cambrian Buchava Formation in the Skryje–Týřovice Basin, Central Bohemia, Czech Republic. It is the second recorded find of *Tuzoia* from West Gondwana. Uncrushed and uncoloured preservation of the tuzoiid valve is consistent with the very thin non-mineralised cuticle described for this taxon. This new occurrence of the genus *Tuzoia*, as well as the earlier described genera *Wiwaxia* and *Hurdia*, indicate the presence of a Burgess Shale-type fauna in several stratigraphical levels of Cambrian sequence of the Skryje–Týřovice Basin. Distribution of other exceptionally

preserved specimens established in the Buchava Formation is briefly summarized and discussed.

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(10) Fatka, O., Kraft, P. & Szabad, M. (2011): *Wiwaxia* Walcott, 1911 from the middle Cambrian of the Barrandian area (Czech Republic). *Acta Palaeontologica Polonica* **56** (4), 871–875.

Abstract. Isolated sclerites of the genus *Wiwaxia* Walcott, 1911 are reported from shale interlayers in lower levels of middle Cambrian (unnamed 3rd Series of Cambrian) Buchava Formation in the Skryje–Týřovice Basin in the Czech Republic. Geographic distribution of *Wiwaxia* indicates latitudinal control as all occurrences are obviously restricted to tropical belt.

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(11) Mikuláš, R. & **Fatka, O.** (2017): Ichnogenus *Astropolichnus* in Cambrian of the Barrandian area, Czech Republic. *Ichnos* **24** (4), 283–290.

Imperfectly preserved specimen of a supposed hydrozoan *Medusites* cf. *radiatus* Linnars., originally described by Pompeckj (1896) from the "Pod trním" locality near Týřovice (Slapnice Member of the Buchava Formation, Skryje–Týřovice Basin) is revised. Recent study of the original specimen and a more complete topotype specimen testify the affiliation to the pineapple-shaped ichnogenus *Astropolichnus* Crimes and Anderson, 1985. A new ichnospecies *A. bohemicus* is established on the material from the Buchava Formation. This material is the first occurrence of *Astropolichnus* in the middle Cambrian as well as the first report of this ichnogenus in the Barrandian area of Czech Republic.

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(12) Fatka, O., Budil, P. & Mergl, M. (2013): Preservation of the digestive structures in *Harpides* (Trilobita) from the Lower Ordovician of the Barrandian area (Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **270** (1), 55–67.

Abstract. Remains of the digestive system are described in the holotype of the rare harpidid trilobite *Harpides grimmi* Barrande, 1852 collected from the Lower Ordovician Mílina Formation of the Prague Basin. The intestine (post-stomach alimentary canal) starts just behind the glabellar posterior margin and extends through the narrow axial region in all nineteen thoracic segments of this exceptionally preserved specimen. The anterior-most part

of the digestive system is masked by the in situ hypostome preserved under the missing glabella. Similarly, also the posterior-most part of the post-stomach alimentary canal is absent, as the pygidium is not preserved. This specimen constitutes the first example of preserved digestive structures in the family Harpididae. Earlier finds of digestive system in Ordovician trilobites are briefly assessed.

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(13) Fatka, O. & Budil, P. (2018): Digestive structures in Middle Ordovician trilobite *Prionocheilus* Rouault, 1847 from the Barrandian area of Czech Republic. *Geologica Acta* **16** (1), 65–73.

Abstract. Remains of digestive system preserved in a slightly damaged articulated specimen of comparatively rare bathycheilid trilobite *Prionocheilus vokovicensis* (Šnajdr, 1956) are described for the first time. The specimen comes from the Middle Ordovician Šárka Formation of the Prague Basin and contains a post-stomach part of alimentary canal preserved through the axial region of glabella and six anterior thoracic segments. The anterior-most part of digestive system is unknown as the anterior glabellar lobes are not preserved in the studied specimen. In the cephalic shield, remains of two pairs of posterior glabellar gut diverticulae are seen in the glabella. Remains of five pairs of small cavities developed in axis of the first six thoracic segments represent remains of thoracic gut diverticulae. The discussed specimen possesses the first undoubted remain of digestive structures established within the family Bathycheilidae Přibyl, 1953.

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(14) Fatka, O., Budil, P. & David, M. (2015): Digestive structures in Ordovician trilobites *Colpocoryphe* and *Flexicalymene* from the Barrandian area of Czech Republic. *Estonian Journal of Earth Sciences* **64** (4), 255–266.

Abstract. Two recently discovered specimens of abundant calymenoid trilobite *Colpocoryphe* Novák in Perner, 1918 from the Middle Ordovician Šárka Formation and one specimen of *Flexicalymene* (*Flexicalymene*) *pragensis* Vaněk & Vokáč, 1997 from the Upper Ordovician Bohdalec Formation, all from the Prague Basin, contain remains of the digestive system. In *Colpocoryphe*, an internal mould of articulated exoskeleton contains a post-stomach part of alimentary canal preserved through the narrow axial region of occipital ring, all thoracic segments as well as in axial part of pygidial shield. The anterior part of digestive system is

poorly known as the specimen shows hypostome preserved *in situ* and the space between glabella and hypostome is represented by an empty cavity associated with probable rests of gut diverticulae in both sides of cephalon. The second, incomplete specimen includes five posterior thoracic segments articulated with pygidium; axial region of this specimen preserves well discernible segmented intestine which terminates at the rhachidial tip and then bends ventrally. In enrolled specimen of *Flexicalymene pragensis*, supposed remains of alimentary tract are comparatively poorly preserved but discernible in middle and posterior part of the thoracic axis and in anterior part of pygidial axis. Discussed specimens constitute the first undoubted examples of digestive structures within the family Calymenidae. Earlier findings of digestive system in Ordovician trilobites of the Barrandian area are briefly assessed.

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(15) Fatka. O., Lerosey Aubril, R., Budil, P. & Rak, Š. (2013): Fossilised guts in trilobites from the Upper Ordovician Letná Formation (Prague Basin, Czech Republic). *Bulletin of Geosciences* **87** (1), 95–104.

Abstract. The preservation of digestive structures of trilobites is extremely rare. Here we describe two new examples of trilobites from the Upper Ordovician Letná Formation (Prague Basin, Czech Republic), which display remains of the digestive system. The first specimen, assigned to *Selenopeltis buchi* (Barrande, 1846), exhibits cavities under the posterior part of the glabella and the axis of most thoracic segments. These cavities are interpreted as remains of metamerically paired digestive caeca and constitute the first example of preserved digestive structures in the order Odontopleurida. The second specimen belongs to *Birmanites ingens* (Barrande, 1852) and displays a tube-like structure, filled with a finely-grained material, that runs under the axial lobe of the entire trunk. We interpret this structure as a gut infilling similar to that repeatedly observed in the Moroccan *Basilicus calzadai*. These specimens confirm that the depositional environment of the Letná Formation was favourable to soft-tissue preservation. They also further document the presence of two different types of digestive systems in trilobites. The possibility that different processes might have been involved in the preservation of different parts of the trilobite gut is discussed, and several criteria to differentiate genuine gut remains from scavenger burrows are proposed.

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(16) Budil, P. & **Fatka, O.** (2022): Ordovician trilobites with soft-parts in African West Gondwana and European peri-Gondwana: a review. In: Hunter, A.W., Álvaro, J.J., Lefebvre, B., van Roy, P. & Zamora, S. (eds.): The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco. Geological Society, London, Special Publications **485**, 139–152.

Abstract. A review of all currently known Ordovician trilobites with soft parts described or figured from West Gondwana, European peri-Gondwana and Avalonia shows remains of the digestive system in 19 species. In comparison, remains of antennae and/or walking legs are known only in five species. Soft parts are known in Asaphidae, Bathycheilidae, Calymenidae, Cheiruridae, Dalmanitidae, Harpidae, Lichidae, Nileidae, Odontopleuridae and Trinucleidae. Exceptionally preserved trilobites originate from the Late Tremadocian Mílina Formation and Fezouata Shale, Middle Darriwilian Šárka and Llanfallteg formations, early Sandbian Tafilalt and Letná Konservat-Lagerstätten and Katian Bohdalec Formation. Levels containing exceptionally preserved trilobites in these units are characterized by prevailing fine-grained sediments with the exception of the Early Sandbian Lower Tafilalt and Letná Lagerstätten.

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(17) Fatka, O. & Budil, P. (2021): Frontal Auxiliary Impressions in Ordovician trilobite genus *Dalmanitina* Reed, 1905 from the Barrandian area (Czech Republic). *Bulletin of Geosciences* **96** (4), 481–491.

Abstract. Fossils preserved in Cambrian to Devonian sediments of the Barrandian area (Czech Republic) have contributed significantly to our knowledge of numerous invertebrate groups. With respect to trilobites, important data has been discovered on the construction of eyes, healing of exoskeletal injuries, as well as on the morphology of soft parts. The generally rarely preserved frontal auxiliary impressions (FAIs) on the glabellar surface of trilobites were first described in Devonian examples from this area in the mid-nineteenth century by Barrande. Such impressions have only rarely been documented in a few trilobite species in the Lower Palaeozoic of the Barrandian area. Here we describe twelve exceptionally preserved holaspid cephalic shields of *Dalmanitina socialis* Barrande, 1846. These specimens are internal moulds and were collected at three localities in the Upper Ordovician Letná Formation. This material documents a high level of variability in the disposition of FAIs within the glabella. However, the FAIs show a common pattern at the anterior glabellar margin and are arranged in two pairs around a medial impression and are also associated with

a third pair situated more posterolaterally. This current study is the first to focus on the distribution of FAIs within the Dalmanitidae. *Dalmanitina socialis* specimens with FAIs from the Letná Formation indicate that the depositional environment at the several localities in that unit was favourable to exceptional preservation. Excellently preserved cephalic shields of *Dalmanitina* demonstrate the presence of the posterior median impression (pmi) of Eldredge (1972) and enable new terminology to be proposed for other FAIs.

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(18) Fatka, O., Szabad, M. & Budil, P. (2009): Malformed agnostids from the Middle Cambrian Jince Formation of the Příbram–Jince Basin, Czech Republic. *Bulletin of Geosciences* **83** (1), 121–126.

Abstract. Two agnostids from Cambrian of the Barrandian area bear different types of skeletal malformations. The tiny pathological exoskeleton of *Hypagnostus parvifrons* (Linnarsson, 1869) has asymmetrically developed pygidial axis, while the posterior pygidial rim in the larger *Phalagnostus prantli* Šnajdr, 1957 has an irregular outline.

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(19) Fatka, O., Budil, P. & Grigar, L. (2015): A unique case of healed injury in a Cambrian trilobite. *Annales de Paléontologie* **101** (4), 295–299.

Abstract. The middle Cambrian Jince Formation of the Příbram–Jince Basin is globally renowned as a classical repository of well-preserved skeletal marine fauna, including abundant remains of trilobites. An exceptionally preserved articulated exoskeleton of middle Cambrian trilobite *Conocoryphe sulzeri* (Schlotheim, 1823) exhibits a prominent palaeopathological anomaly interpreted here as a healed traumatic injury. We suggest to attribute the extensive damage of the right side of the cephalon and three anterior-most right thoracic pleurae to a failed predatory attack. The anomalocaridid genus *Hurdia* and the large bivalved arthropod *Tuzoia* represent two potential candidates for durophagous predators responsible for the described trilobite injury. The large size of healed injury demonstrates a high level of exoskeletal regeneration in trilobites.

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(20) Fatka, O., Budil, P. & Zicha, O. (2021): Exoskeletal and eye repair in *Dalmanitina socialis* (Trilobita, Ordovician). *International Journal of Paleopathology* **34**, 113–121.

Abstract. To analyze anomalies of a biomineralized exoskeleton of a trilobite. A specimen of *Dalmanitina socialis* from the Upper Ordovician Letná Formation at Veselá near Beroun, Czech Republic, curated at the Czech Geological Survey in Prague. The internal mold and external mold and latex casts were coated with ammonium chloride sublimate and photographed. A substantial reduction of the eye surface associated with changes in morphology and surface structure was noted. The anomaly is believed to be the result of a healed injury after an unsuccessful predatory attack. Based on the presumed mechanism of injury, a 'large arthropod' is proposed to be the potential attacker. The low incidence of sublethal attack to cephala in collections of Cambrian to Carboniferous trilobites implies that most such attacks were fatal, rendering this specimen unique and capable of providing insight into healing processes. Post-mortem damage rendered analysis difficult. Exploration of other cases of healed trauma in order to understand Ordovician ecosystems.

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(21) Fatka, O. & Szabad, M. (2011): Agnostid entombed under exoskeletons of paradoxidid trilobites. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **259** (2), 207–215.

Abstract. Occurrence of three entirely preserved articulated exoskeletons of holaspid specimens of the agnostid *Peronopsis integra* (Beyrich, 1845) entombed under and/or within different parts of carapaces of the large polymerid trilobite species *Paradoxides* (*Hydrocephalus*) *minor* (Boeck, 1827) are described from the Jince Formation (Drumian) of the Příbram-Jince Basin. Conchicolous habit and/or feeding of the tiny *Peronopsis* on deteriorating soft parts of large carcasses of are *Paradoxides* proposed as two plausible explanations for entombment of the agnostid specimen. Both these hypotheses support a mode for the agnostid *Peronopsis*, and perhaps for all agnostids.

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(22) Fatka, O. & Kozák, V. (2014): A new type of entombment of *Peronopsis* (Agnostida) in a hyolithid conch. *Carnets de Géologie [Notebooks on Geology]* **14** (10), 191–198.

Abstract. An enrolled exoskeleton of the holaspid specimen of a tiny agnostid *Peronopsis integra* (Beyrich, 1845) entombed inside a conch of the hyolithid ?*Buchavalites* sp. is described from the mid-Cambrian (Drumian) Jince Formation of the Příbram-Jince Basin (Czech Republic). The agnostid is associated with an ichnofossil of the feeding trace classified

as *Arachnostega*-type behaviour. The enrolled attitude of the agnostid exoskeleton suggests that the specimen is a carcass rather than moult. Either the storm disturbance and/or well-protected source of food hypothesis could explain the entombed agnostid. This additional example supports a benthic mode of life in the agnostid *P. integra*. The studied association of feeding tunnels of an unknown *Arachnostega*-strategist and *Peronopsis* preserved inside a hyolithid conch is a case of "frozen" behaviour.

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(23) Fatka, O. & Budil, P. (2014): Sheltered gregarious behavior of Middle Ordovician harpetid trilobites. *Palaios* **29** (9), 495–500.

Abstract. The presence of six articulated exoskeletons of late holaspid specimens of the rare harpetid *Eoharpes benignesis* (Barrande, 1872) entombed under a pygidial shield of the large asaphid trilobite *Nobiliasaphus repulsus* Přibyl and Vaněk, 1968 from the Middle Ordovician Dobrotivá Formation of the Prague Basin, Czech Republic is interpreted as a unimodal monotaxic trilobite cluster. The sheltered preservation of the trilobites is briefly discussed; it could be explained as hiding behavior associated with predation pressure, storm disturbance or molting associated with feeding. It is obvious, that holaspid specimens of Middle Ordovician trilobites deliberately entered the restricted space under large isolated shields of asaphid trilobites to find a refuge and shared the space within restricted shelters with conspecifics. The completeness of all specimens of the rare *Eoharpes* combined with the presence of more than one individual in virtually restricted space under the pygidial shield of *Nobiliasaphus* excludes the possibility of transportation by bottom currents. This exceptional find represents an example of "frozen behavior" and provides a new insight in the life strategy of Middle Ordovician benthic trilobites. Attack abatement, *e.g.*, avoidance and dilution effects are for the first time proposed as a possible explanation for the sheltered gregarious behavior in trilobites.

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(24) Fatka, O. & Szabad, M. (2011): Burrowing trilobite caught in the act. *Paläontologische Zeitschrift* **85** (4), 465–470.

Abstract. A trace fossil associated with its assumed in situ maker, a holaspid specimen of the trilobite *Agraulos ceticephalus* (Barrande, 1846) is reported from the mid-Cambrian Buchava Formation (Drumian Stage) of the Skryje–Týřovice Basin, Czech Republic. The ichnofossil is

preserved on the surface of a mudstone, behind the posterior part of the intact trilobite exoskeleton; this natural association is interpreted as mortichnia. Possible mode of life and feeding strategy of the trilobite genus *Agraulos* are discussed. For the association of a fodichnion with its producer preserved *in situ* (atop, in, or at the end of its trace fossil) is proposed the designation fodichnial association.

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6. Conclusions and future outlook

The above presented census of Cambrian and Ordovician fossils of the Barrandian area approved the occurrence of EPF in numerous levels of two lithostratigraphic units of the Příbram-Jince Basin, in one unit of the Skryje-Týřovice Basin and in four units of the Prague Basin.

In the future, the following topics are to be further developed:

- detailed studies of skeletal, lightly mineralized and non-mineralized fossils, like the anomalocaridid *Hurdia*, lobopodians *Onychodictyon, Hallucigenia,* newly discovered articulated sponges, echinoderms, diverse Ordovician arthropods, etc.
- wider application of methods, like electron microscopy, documentation using optical microscopy (*e.g.*, Keyence), microtomography;
- development of new laboratory methods (*e.g.*, study of SCF);
- search for EPF at other outcrops of Cambrian and Ordovician rocks, as well in still understudied stratigraphic levels (*e.g.*, Silurian and Devonian);

Such research has an eminent potential to bring new data for a more comprehensive reconstruction of global, as well as local extinctions, including better understanding of rejuvenation of trophic relations of the Paleozoic ecosystem.

Acknowledgements.

I would like to express my sincere thanks to all those who participated in the studies underlying this thesis. I would like to gratefully acknowledge the financial support of this study *via* grants from the following agencies:

- Czech Science Foundation through the projects No. 205/06/0395, No. 205/09/1521, and No.18-14575S,
- Ministry of Education, Youth and Sports of the Czech Republic through the projects MSM 0021620855 (Material flow mechanisms in the upper spheres of the Earth),

- CEZ J13/98:113100006, Prvouk P44, Progres Q45, Cooperatio GEOL.

Large part of my research activities are contributions to the following International Geoscience Programs, particularly to:

- IGCP 410 “The Great Ordovician Biodiversification Event”,
- IGCP 503 “The impact of the changing palaeogeography and palaeoclimate on the major biotic changes through the Ordovician (Ordovician biodiversification, end-Ordovician extinction, Silurian radiation)”,
- IGCP 653 “Filling the gap between the Cambrian Explosion and the GOBE”
- IGCP 591, “The Early to Middle Palaeozoic Revolution”.

I would like to thank to my family, spouse Renata and both daughters, Monika and Lucka for their continuous support and understanding.

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