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Studijní program: Geologie



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**Conodont platform elements from selected sections of Devonian and their
application in biostratigraphic correlation**

Konodontové platformní elementy z vybraných profilů devonu a jejich
aplikace v biostratigrafické korelaci

Disertační práce

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Praha, 2022

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Abstrakt

Předkládaná práce se skládá ze tří samostatných článků, které byly publikovány v odborných recenzovaných časopisech. Publikované studie shrnují a zpřesňují dosavadní znalosti o vybraných konodontových faunách devonu se zaměřením na P1 elementy a na jejich potenciál v rámci biostratigrafie. Disertační práce se člení na tři hlavní části. První část je koncipována jako úvod, shrnutí cílů předkládané práce a použitých metodik při odběru a práci s konodontovými vzorky a výbrusy na mikrofaciální studium. Druhá část práce slouží jako obecný přehled problematiky konodontových elementů a jejich aplikace v biostratigrafii devonu, charakterizuje a popisuje geologické podmínky a paleogeografický vývoj oblastí, ze kterých studované elementy pocházejí. Třetí část následně shrnuje výsledky, rozvíjí diskusi k publikovaným článkům a obsahuje závěrečné slovo ke zkoumané problematice. Publikované studie, ze kterých tato práce vychází, jsou zaměřeny na platformní elementy ozarkodiniidů a icriodontidů, jejichž globální rozšíření v čase i prostoru přináší možnosti jejich studia v odlišných prostředích a stratigrafických úrovních. Kromě toho je zde diskutována také mikrofaciální charakteristika studovaných profilů a problematika konodontové biostratigrafie v devonu. Celkově bylo odebráno a zpracováno 38 nových konodontových vzorků a 39 vzorků pro mikrofaciální analýzu z profilů Na Požárech, Praha-Radotín (pražská synforma, Česká republika) a Hushoot Shiveetiin gol (terán Baruunhuurai, Mongolsko). Dále pak byly do prací zahrnuty studie konodontového materiálu z muzejních sbírek prof. O. Wallisera z University v Göttingen, kde byl hlavní důraz kladen na vzorky ze stratigrafických řezů Cellon (Karnské Alpy, Rakousko-Italská hranice) a Atrous 3 (Anti Atlas, Maroko). Ve vzorcích z profilu Na Požárech bylo popsáno 13 konodontových taxonů a 18 ve vzorcích odebraných z lokality Praha-Radotín. Složení konodontových faun bylo z hlediska rodů a druhů v obou lokalitách srovnatelné. Z obou profilů byl popsán výskyt nového druhu *Zieglerodina petrea*, který byl později nalezen i ve vzorcích z lokality Cellon, což potvrdilo jeho výskyt v rámci peri-Gondwany. Tento taxon má velký potenciál pro biostratigrafické určení báze devonu, zejména pak v profilech, kde není zachycen výskyt druhu *Icriodus hesperius* nebo graptolitů druhu *Uncinatograptus uniformis uniformis*. Na základě morfologie nově popsaného druhu *Zieglerodina petrea* byl zkoumán jeho fylogenetický vztah k taxonu *Zieglerodina paucidentata*, který se také vyskytuje při bázi devonu a je globálně rozšířen. Na základě společného morfologického trendu redukce zubů a vzniku mezery v dentikulaci v posteriorní části platformního elementu bylo navrženo rozdělení do

několika morfologických podskupin, které bude základem pro další práce týkající se systematiky těchto druhů a zpřesnění jejich využití pro globální biostratigrafii. Mikrofaciální analýza potvrdila rozdílné sedimentační podmínky při hranici silur/devon v profilech Na Požárech a Praha-Radotín. I přes přítomnost Syphocrinitového horizontu jsou karbonátové sedimenty na lokalitě Na Požárech při bázi devonu z mělčího mořského prostředí, zatímco na lokalitě Praha-Radotín pocházejí z o něco hlubšího prostředí. V odebraných vzorcích z lokality Hushoot Shiveetin gol bylo popsáno 30 konodontových taxonů, včetně nového taxonu *Ancyrognathus minjini*. Součástí studia mongolských vzorků byl také popis konodontových biofacií, ve kterých bylo nalezeno několik kosmopolitních druhů a dva endemické druhy (včetně nově popsaného taxonu). Mikrofaciální analýza poukázala na převahu siliciklastických sedimentů. Sedimentační prostředí lokality Hushoot Shiveetiin gol bylo ve famennu zjevně ovlivněno vulkanickou aktivitou. Výsledky předkládaných výzkumů a publikací jsou důležité nejen pro využití v konodontové biostratigrafii v globálním měřítku, ale mohou být použity také při rekonstrukci paleoekologických podmínek a paleoprostředí, zejména v kombinaci se sedimentárními a mikrofaciálními analýzami.

Abstract

The presented work consists of three separate papers that have been published in peer-reviewed journals. The published studies summarize and refine the existing knowledge about some conodont faunas of the Devonian with a primary focus on P1 elements and their potential in biostratigraphy. The dissertation thesis consists of three main parts. The first part is designed as an introduction, a summary of the objectives of the presented work, and methodologies used during the conodont sampling and sample processing and samples for thin sections. The second part of the work presents a general overview of the problems of conodont elements in biostratigraphy of the Devonian, characterizes the geological conditions and paleogeographic development of the areas from which the studied elements come from. The third part summarizes the results, brings a discussion on the herein presented data published in articles and contains the final word on the researched issues. The published studies on which this work is based are focused on platform elements of ozarkodinids and icriodontids, whose global distribution in time and space enables their study in different environments and stratigraphic levels. The microfacial characteristics of the studied sections and the issue of conodont biostratigraphy in the Devonian are discussed as well. A total of 38 conodont samples and 39 samples for microfacial analysis were collected and processed from sections Na Požárech, Praha-Radotín (Prague Synform, Czech Republic) and Hushoot Shiveetiin gol section (Baruunhuurai Terrane, Mongolia). Part of the work was also study of conodont material from the museum collections of prof. O. Walliser at the University of Göttingen with the main focus on samples from Cellon section (Carnic Alps, Austrian-Italian border) and Atrous 3 section (Anti Atlas, Morocco). A total of 13 conodont taxa were reported from samples from the Na Požárech section and 18 from samples taken from the Praha-Radotín section. Also, a new species *Zieglerodina petrea* was described from the base of the Devonian in both Bohemian sections. This taxon was found also in samples from the Cellon section, which confirms its occurrence within the peri-Gondwana. The newly described taxon has a great potential for biostratigraphic correlation of the basal Devonian boundary, especially in sections where the conodont species *Icriodus hesperius* or graptolite species *Uncinatograptus uniformis uniformis* are missing. The morphology of the newly described species *Zieglerodina petrea* and its phylogenetic relationship to the taxon *Zieglerodina paucidentata*, which also occurs at the base of Devonian and is widespread worldwide, were studied. Based on similar trend of denticulation in both taxa

and the presence of a gap between the denticles in the posterior part of the platform element, a subdivision into several morphological subgroups was proposed. This proposal would be a basis for follow-up studies on the systematics of these taxa in order to refine their potential in biostratigraphy. Microfacies analysis confirmed diverse sedimentary environments at the Silurian/Devonian boundary in the Na Požárech section and Praha-Radotín section. Despite the presence of the *Syphocrinites* Horizon, the Na Požárech section represents an area with relatively shallow water sedimentation close to the Silurian/Devonian boundary, while in the Paha-Radotín section represents slightly deeper water environment. All together, 30 conodont taxa were described in the samples from the Hushoot Shiveetiin gol section. Also, a new species *Ancyrognathus minjini* was described. The study of Mongolian conodont samples also included a description of conodont biofacies, in which several cosmopolitan species and two endemic species (including the newly described taxon) were found. Microfacial analysis indicated a predominance of siliciclastic sediments. The sedimentary environment of the Hushoot Shiveetiin gol section was apparently affected by volcanic activity in Famennian. The results of the presented research and publications are important not only for the conodont biostratigraphy on a global scale but can also be used in the reconstruction of paleoecological conditions and paleoenvironment, especially in combination with sedimentary and microfacial analysis.

Acknowledgements

In the first place I would like to thank my supervisor RNDr. Ladislav Slavík, CSc. for help and support during my doctoral studies and during my previous master's and bachelor degree. I thank him for passing on all the knowledge, for his patience, understanding and for being able to bring my studies to a successful end. Very special thanks belong to my co-supervisor prof. RNDr. Katarína Holcová, CSc. for all encouragement and support. I am also very grateful to Dr. Markus Aretz and Dr. Frédéric Christophoul for their kind guidance, help and constructive discussions during my half-year internship at Université Paul Sabatier Toulouse. I thank very much to Dr. Helga Groos-Uffenorde and Dr. Alexander Gehler from the University of Göttingen for access to the museum's collections and providing conodont material from the collection of prof. Otto H. Walliser. I also thank to my colleagues, mainly to Pavel Lisý for his assistance in laboratory and RNDr. Zuzana Korbelová for the help and guidance with the SEM photography. Also, I would like to thank to my close colleagues Mgr. Andrea Svobodová, Ph.D., Mgr. Ondřej Kohout, Mgr. Veronika Veselá, Mgr. Lucie Kunstmüllerová, Mgr. Jana Čepičková, Mgr. Alexandra Chernomorets, Mgr. Jakub Vodička, Mgr. Kateřina Němečková, Bc. Adéla Šoobová, Bc. Renata Hánová, and the rest of current students of Geobiology programme for their neverending enthusiasm, encouragement and cheering conversations during the light and dark moments of my (student) life. I would like to thank the Institute of Geology and Palaeontology, Charles University and the Institute of Geology of the Czech Academy of Sciences for creating a suitable work environment to prepare research, publications and also this thesis. My biggest thanks also go to my beloved husband Ing. Petr Formáček, two fluffy cat ladies Angie and Eevee, all members of my family, and my friends for their constant support throughout my studies.

This research was financially supported by student projects of the Charles University GAUK No. 1698119 “*Zieglerodina petrea* sp. nov. and *Zieglerodina paucidentata*: phylogenetic models and their application in the global stratigraphy of the Silurian/Devonian boundary” and GAUK No. 922216 “Family Spathognathodontidae (Conodonts) from the Silurian/Devonian boundary and its biostratigraphic correlation (Na Požárech and Praha-Radotín sections; Prague Synform)”, the Czech Science Foundation No. GA17-06700S, and by the Research plan of the Institute of Geology of the Czech Academy of Sciences RVO 67985831. The PhD. study was also founded by the Center For Geosphere Dynamics (UNCE/SCI/006).

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1. Introduction

Conodonts are an extinct group of marine organisms which were widespread during the Palaeozoic era. Till today, there are few discoveries of the soft tissues of these animals (e.g., Aldridge et al., 1993; Gabbott et al., 1995; Liu et al., 2006; von Bitter et al., 2007), but their systematic position within zoological taxonomy remains unclear. Nevertheless, the study continues because their phosphatic fossil elements of their feeding apparatus are frequent in carbonate sediments and shales from the Cambrian to the Upper Triassic strata all over the world.

Conodont elements are used for various applied approaches like paleoecology, thermal and burial reconstruction of thermal sedimentary history using CAI - Conodont Colour Alteration Index (e.g., Golding and McMillan, 2021), palaeoenvironmental reconstructions using conodont geochemistry (mainly REEs and oxygen isotope $\delta^{18}\text{O}$ composition of conodont elements), paleogeographic reconstructions due to tracking of palaeogeographic distribution of taxa during specific time intervals and/or reconstruction of faunal provinces in paleogeographical areas. But above all, they are most commonly used for the global biostratigraphic correlation and relative dating of sedimentary rocks - biostratigraphy. The biostratigraphic approach is also utilized as a basal framework for chronostratigraphic methods (e.g., radiometric dating) and other chemo-physical proxies (e.g., gamma spectrometry, magnetic susceptibility) and could be helpful to other geochemical studies (e.g., Husson et al., 2016; Oborny et al., 2020). Conodonts are very commonly represented as index fossils for various stratigraphic units due to the rapid and, in some cases, easily recognizable morphological changes in the conodont elements in time. The conodont biostratigraphic scale for most of the Palaeozoic is constantly being refined and contributes significantly to the International Chronostratigraphic Chart. The presented thesis and the related papers are especially focused on the biostratigraphy of specific parts of Devonian period and possibilities of biostratigraphic refinements.

Despite the fact that the index fossil for the base of the Lochkovian (and base of Devonian) is the graptolite *Uncinatograptus uniformis uniformis* (Přibyl, 1940) as was defined in Chlupáč et al. (1972), the rest of the Devonian biostratigraphy is based mainly on conodonts and cephalopods. This is mainly due to paleogeographic conditions and increased carbonate sedimentation, where conodonts and cephalopods are stratigraphically more important.

Many recent studies have used Devonian conodonts for stratigraphical, paleoecological and paleogeographical interpretations (e.g., Schönlaub et al., 2017; Vacek et al., 2018; Over et al., 2019; Zhang et al., 2019; Corradini et al., 2020; Girard et al., 2020; Kaiser et al., 2020; Slavík and Hladil, 2020; Barrick et al., 2021; Suttner et al., 2021; Zhang et al., 2021; Ferretti et al., 2022). This work presents studies of selected Devonian sections from different paleoenvironmental conditions and stratigraphic positions - Na Požárech section and Praha-Radotín section (mainly **study II.**) and Hushoot Shiveetiin gol section (**study III.**). From all these three sections conodont samples and also samples for microfacies analysis were taken. Comparative conodont material comes from previously unpublished material from the Cellon section and Atrous 3 section (**study I.**), which were collected and processed by prof. Otto H. Walliser and his students. Nowadays, this material is deposited in museum collections in Georg-August-Universität at Göttingen.

1.1 List of publications

This dissertation thesis is based on the following articles, which are marked in Roman numerals (from newest to oldest):

I. Hušková, A., & Slavík, L., 2021. Morphologically distinct P1 elements of *Zieglerodina* (Conodonts) at the Silurian–Devonian boundary: review and correlation. *Bulletin of Geosciences*, 96(3), 327–340.

- <https://doi.org/10.3140/bull.geosci.1822>

II. Hušková, A., & Slavík, L., 2020. In search of Silurian/Devonian boundary conodont markers in carbonate environments of the Prague Synform (Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109126: 1–17.

- <https://doi.org/10.1016/j.palaeo.2019.03.027>

III. Suttner, T. J., Kido, E., Ariunchimeg, Y., Sersmaa, G., Waters, J. A., Carmichael, S. K., Batchelor, C. J., Ariuntogos M., Hušková, A., Slavík, L., Valenzuela-Ríos, J. I., Liao, J.-C., & Gatovsky, Y. A., 2020. Conodonts from Late Devonian island arc settings

(Baruunhuurai Terrane, western Mongolia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109099.

- <https://doi.org/10.1016/j.palaeo.2019.03.001>

Publication on related topic but not included in this thesis:

Slavík, L., Valenzuela-Ríos, J. I., Hladil, J., Chadimová, L., Liao, J. C., **Hušková, A.**, Calvo, H., & Hrstka, T., 2016. Warming or cooling in the Pragian? Sedimentary record and petrophysical logs across the Lochkovian–Pragian boundary in the Spanish Central Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 449, 300–320.

- <https://doi.org/10.1016/j.palaeo.2016.02.018>

Valenzuela-Ríos, J. I., Slavík, L., Liao, J. C., Calvo, H., **Hušková, A.**, & Chadimová, L., 2015. The middle and upper Lochkovian (Lower Devonian) conodont successions in key peri-Gondwana localities (Spanish Central Pyrenees and Prague Synform) and their relevance for global correlations. *Terra Nova*, 27(6), 409–415.

- <https://doi.org/10.1111/ter.12172>

1.2 Focus of studies included

Study I.: Morphologically distinct P1 elements of *Zieglerodina* (Conodonta) at the Silurian–Devonian boundary: review and correlation.

This study is focused mainly on P1 elements of the ozarkodinids from family Spathognathodontidae, mainly of the genus *Zieglerodina* and its species *Zieglerodina petrea*, *Zieglerodina paucidentata* and morphologically close forms to these taxa which share similar morphological trend – a gap in denticulation of the posterior part of P1 element. Research compares new conodont material from the Na Požárech and Praha-Radotín sections (Prague Synform), Cellon section (Carnic Alps) and Atrous section (Morocco) with the revision of the previously described conodont material and shows ambiguities in the classification of these species. Based on the worldwide paleogeographic distribution of these taxa in early Devonian, these two species have potential for the improvement of the global conodont biostratigraphy of the

Silurian/Devonian boundary. Therefore, the study proposes a preliminary concept of subdivision of *Z. paucidentata* and *Z. petrea* into different morphological groups with respect to the phylogenetic trend of morphological changes within these taxa, which can lead to more accurate identification and utilization of these species as the biostratigraphic markers for the base of Devonian.

Study II.: In search of Silurian/Devonian boundary conodont markers in carbonate environments of the Prague Synform (Czech Republic).

This study deals with distribution of conodont faunas in two sections across the Silurian/Devonian boundary from the Barrandian area (Prague Synform) with different depositional settings: Praha-Radotín and Na Požárech. The Praha-Radotín section represents deeper-water carbonate sedimentation, while the Na Požárech section could be considered as relatively shallower close to the Silurian-Devonian boundary. The study included microfacies study (thin sections), but research is mostly focused on conodonts. Abundant conodont material from both sections showed relatively high diversity and disparity. Most common conodont elements belong to ozarkodinids of the family Spathognathodontidae, a little rarer were elements of icriodontids. Species *Icriodus hesperius*, which is a current conodont biostratigraphic marker of the base of Devonian, was obtained from both studied sections. Moreover, the occurrence of the *I. hesperius* at the same bedding couplet with graptolite *Uncinatograptus u. uniformis* (current marker for the Silurian/Devonian boundary) confirms *I. hesperius* as the most reliable conodont biostratigraphic index for the Silurian/Devonian boundary at global scale. Study also presents a newly described conodont species *Zieglerodina petrea*, which has a great potential to become a promising conodont biostratigraphic marker for the base of the Devonian among spathognathodontids.

Study III.: Conodonts from Late Devonian island arc settings (Baruunhuurai Terrane, western Mongolia).

This study represents a detailed biostratigraphy and biofacies analysis of the conodonts from the Hushoot Shiveetiin gol section in Baruunhuurai Terrane in the western part of Mongolia. All together, twenty species mostly from the family Palmatolepidae, Spathognathodontidae, Polygnathidae and Icriodontidae were identified and ten more

taxa were left in open nomenclature. A new conodont species *Ancyrognathus minjini* was described. Compared to the worldwide conodont distribution at the Upper Devonian, conodont biodiversity of localities within the northern-hemisphere island arc complex, where the Baruunhuurai Terrane belongs, is relatively low. Apart from the occurrence of several cosmopolitan taxa, only endemic representatives of conodont genus *Ancyrognathus* sp. and *Icriodus* sp. show slightly higher diversity. Genus *Pelekysgnathus* and several commonly globally distributed species are absent in all samples, probably due to siliciclastic-dominated sedimentation in the Hushoot Shiveetiin gol section during the early Famennian. Results from conodont biofacies and microfacies analyses also suggest slight changes in bathymetric conditions. Analysis of conodont biofacies indicates a polygnathid-palmatolepid conodont assemblage that dominates the sequence. Their dominance is interrupted only by a short change to an icriodontid-polygnathid biofacies just before the beginning of the *Palmatolepis rhomboidea* Biozone.

Summary of the published papers and link among them:

The presented studies are based on modern micropaleontological taxonomic classification with the focus on comparison of conodont biodiversity and disparity in selected Devonian sections from two stratigraphically important areas of the world. Research combines the biostratigraphic methods based on platform elements of ozarkodinid and icriodontid conodonts and approaches examining sedimentary conditions, such as study of thin sections and microfacies interpretation. Specification of the marine sedimentary environment points out the geological history of the studied areas, which could facilitate the interpretation of the changes in species diversity and fluctuation in paleogeographic distribution of the conodont faunas. These data and knowledge are the key for the most important goal of the work – application of the ozarkodinid and icriodontid elements in global or local biostratigraphy. Overall, the most important data were obtained due to study of conodont diversity and biofacies in contrasting areas by means of degree of exploration. On one hand, there is the Prague Synform where the biostratigraphical studies date back to the early half of 19th century, and the western Mongolian Baruunhuurai Terrane where the biostratigraphic studies started relatively recently, i.e., 20 years ago. Irrespective the number of previous studies, new conodont taxa were described in both areas, e.g., *Ancyrognathus minjini*, that is an important local marker for paleoecology and biostratigraphy in the western Mongolia and *Zieglerodina petrea*,

which could play the fundamental role among spathognathodontids in the distinction of base of the Devonian in global point of view.

1.3 Conference contributions

Preliminary results and final outcomes of the research related to this thesis were presented at the following conferences and congresses:

Hušková, A., & Slavík, L., 2017. Konodonti čeledi Spathognathodontidae z intervalu hranice Silur/Devon z Pražské synformy. Paleozoikum 2017, Brno. Sborník abstraktů, *Masarykova univerzita*, ISBN 978-80-210-8479-7, p. 7.

Hušková, A., & Slavík, L., 2017. Conodonts of family Spathognathodontidae from the Silurian/Devonian boundary, Prague synform. The International Conodont Symposium, “Progress On Conodont Investigation”, Valencia. Abstract volume, *Instituto Geológico y Minero de España, Madrid*, ISBN: 978-84-9138-031-3, p. 115-118.

Hušková, A., & Slavík, L., 2018. Konodonti z hraničního intervalu Přídolí/Lochkov z Pražské synformy. Paleozoikum 2018, Olomouc. Sborník abstraktů, *Univerzita Palackého v Olomouci*, p. 11-12.

Hušková, A., & Slavík, L., 2018. Conodont diversity from the Silurian/Devonian boundary interval from Praha-Radotín section. 1st Palaeontological Virtual Congress, online. Abstract book, *Palaeontology in Virtual era*, ISBN: 978-84-09-07386-3, p. 112.

Hušková, A., & Slavík, L., 2018. Diversity of the Lower Devonian icriodontids from the Prague Synform. 5th International Palaeontological Congress, Paris. The fossil week Abstract volume, *5th International Palaeontological Congress*, p. 795.

Hušková, A., & Slavík, L., 2019. Discussion on phylogeny of biostratigraphic markers among Spathognathodontidae (Conodonta) around the Silurian/Devonian boundary. 3rd International Congress on Stratigraphy, Milano. Abstract volume, *Società Geologica Italiana*, DOI: 10.3301/ABSGI.2019.04, p. 186.

Hušková, A., 2020. Diversity of the Lower Devonian conodonts from the Prague Synform (Czech Republic). *Progressive Palaeontology 2020*, online. Abstract booklet, *University of Leeds*, p. 46.

1.4 Aims of the thesis and problem definition

Conodonts are fundamental faunal group for detailed biostratigraphy of the Devonian period. Accordingly, further studies are still necessary in order to improve and refine the current state of Devonian conodont biozonation at regional or global scale. Therefore, this thesis is focused mainly on morphological changes on conodont platform elements during Devonian and its implications for global biostratigraphy. Specifically, the main objectives of the thesis are following:

- complex study of conodont elements from different stratigraphic levels in Devonian and their application in global biostratigraphy
- biostratigraphic evaluation, based on taxonomic revision of selected taxa from the families Spathognathodontidae, Polygnathidae, Palmatolepidae and Icriodontidae
- correlation of studied conodont material and its diversity and disparity from the sections in the Prague Synform (Czech Republic), Carnic Alps (Austrian-Italian borders), Anti-Atlas (Morocco) and Baruuhanuurai Terrane (Mongolia)
- in the scope of multidisciplinary research using of conodonts and sedimentological analysis specify paleoenvironmental characteristics and understand geological processes and distinct changes in the studied areas
- discussion on newly proposed biostratigraphic markers among the ozarkodinids and icriodontids

2. Material and Methods

2.1 Material

Each paper presents conodont material from sections situated in different areas. Main material studied in **paper I** comes from Na Požárech section, Praha-Radotín section (Prague Synform, Czech Republic), Cellon section (Carnic Alps, Italy) and Atrous 3 section (Anti-Atlas, Morocco). Additional material used in **paper II** was collected from the Na Požárech section and Praha-Radotín section (Prague Synform, Czech Republic). Material used in **paper III** comes from the Hushoot Shiveetiin gol section (Baruunhuurai Terrane, Mongolia).

Altogether, nine conodont samples were taken from the section Na Požárech, thirteen conodont samples were taken from the Praha-Radotín section and sixteen conodont rock samples for conodonts were collected from the Hushoot Shiveetiin gol section. Another samples for the microfacies analysis were taken from the sections: ten samples from the section Na Požárech, thirteen samples from the section Praha-Radotín and sixteen samples from the Hushoot Shiveetiin gol section.

Conodonts were found in all samples from the Na Požárech section, in twelve out of thirteen samples from Praha-Radotín section and in ten out of sixteen samples from Hushoot Shiveetiin gol section. In most of the samples were also found representatives of other faunal groups (e.g., small or fragmented valves of brachiopods, bivalves, bryozoans, ostracods, gastropods and crinoid debris).

The rest of studied material came from older, previously mostly unpublished conodont collections. In particular, it is conodont material from the Cellon section and Atrous 3 section, which was collected and separated by prof. O. H. Walliser and his students.

Published material is deposited in the different collections. Conodont elements from the Na Požárech section and Praha-Radotín section are deposited at the Institute of Geology of the Czech Academy of Sciences (Prague, Czech Republic). Material from the Cellon section and Atrous 3 section is stored in the Georg-August-Universität (Göttingen, Germany) and conodonts from the Hushoot Shiveetiin gol section are deposited at the Mongolian Paleontological Center of the Mongolian Academy of Sciences (Ulaanbaatar, Mongolia).

2.2 Methods

The approximate weight of each rock sample for conodonts was around 2 – 3 kg. The separation of conodont elements from limestone samples followed standard published processing methods (Jeppsson and Anehus, 1995). Because of the various limestone lithology were used carboxylic acids: For dissolving of limestones from the Prague Synform (mostly limestones with shale interbeds) was used the 8% solution of acetic acid (**study I. and II.**), meanwhile for the samples from Barunhurai Terrane (limestones alternated with calcareous sandstones) was used 5% solution of formic acid (**study III.**). The process of dissolving and exchanging of the solution was repeated every three weeks until all carbonate samples were dissolved and conodonts and other insoluble residues were extracted. The insoluble residues of the samples were then dried and subsequently concentrated by separation in heavy liquids (sodium polytungstate or tribromomethane). After that, the obtained conodont material was studied under stereomicroscopes (Leica MZ75 microscope and Intraco Micro STM721 microscope) and selected conodont elements were photographed using a scanning electron microscope (**study I., II. and III.**).

3. Conodonts and their general characteristics

Conodonts are microscopic, denticulated elements of 0.3 mm to 3 mm in length. These elements formed a bilaterally symmetrical feeding apparatus, which was located in the head part of a conodont animal. According to the latest studies, conodont animals were active predators and scavengers (Balter et al., 2019; Leonhard et al., 2020; Murdock et Smith, 2021). Each conodont element had exact position within the apparatus. Movements of the elements and cooperation of each element within the apparatus are still subject of many recent studies (e.g., Goudemand et al., 2011; Agematsu et al., 2017; Sun et al., 2020). Each conodont animal had a certain number of elements with various morphology (for more details see chapter 3.1).

The chemical composition of the elements corresponds to carbonate fluorapatite, which is close in chemical formula to mineral francolite $\text{Ca}_5\text{Na}_{0.14}(\text{PO}_4)_3.01(\text{CO}_3)_{0.016}\text{F}_{0.73}(\text{H}_2\text{O})_{0.85}$ (Pietzner et al., 1968). However, this composition is only approximate, because there are often alterations and replacements of individual chemical elements as strontium, neodymium, uranium, thorium and other rare earth elements, which can also be incorporated into the conodont mineralised tissues (summarized in Trotter and Eggins, 2006). Due to this trace element contents in carbonate fluorapatite are conodont elements still in interest of many geochemical studies (e.g., Maslov et al., 2019; Zhuravlev et al., 2020; Žigaitė et al., 2020; Medici et al., 2021).

3.1 Taxonomy of Conodonta

The position of conodonts in the current phylogenetic systems is still unclear and thus, their classification is not united. There are two main classifications that could be followed. One of the prevailing views is that conodonts could be classified as the separate phylum Conodonta, which is subdivided into two classes: Cavidonti and Conodonti (Clark et al., 1981, later modified by Sweet, 1988). Other opinion sees Conodonts as a class that belongs to the phylum Chordata (e.g., Aldridge and Purnell, 1996; Janvier, 2015; etc.). Conodonta (class) includes five orders: Protopanderodontida, Panderodontida, Prioniodinida, Prioniodontida (which includes, inter alia, the family Icriodontidae Müller and Müller, 1957) and Ozarkodinida (this contains, inter alia, the family Spathognathodontidae Hass, 1959; Polygnathidae Bassler, 1925; and Palmatolepidae, Sweet, 1988) (classification according to Dzik, 1976, later modified by Sweet and

Donoghue, 2001; Armstrong and Braiser, 2013). Representatives of Ozarkodinida dominate conodont faunas in diversity and abundance for most of the Palaeozoic (Purnell and Donoghue, 1997), but other mentioned orders are also important for understanding the evolution of conodonts and for the biostratigraphy. However, the conodont classification and phylogeny remain the subject of many studies (e.g., Donoghue et al., 2000; Donoghue, 2001; Donoghue et al., 2008; Wickström et Donoghue, 2005; Blicek et al., 2010; Turner et al., 2010; Murdock et al., 2013; Mazza and Martínez-Pérez, 2016; Sallan et al., 2018; Karádi et al., 2020).

The representatives of the order Prioniodontida (mainly the family Icriodontidae) and Ozarkodinida (mainly families Spathognathodontidae, Polygnathidae and Palmatolepidae), which were represented by several genera and species, were the main focus of the presented studies (**studies I., II. and III.**). Each of the order and family have their own specification about the paleogeographic distribution, morphology of the platform elements and species diversity. Key for these studies are conodont biofacies models, which refer to different tolerances to the environment in individual genera or families (Clark et al., 1984) – e.g., according to Sandberg and Dreesen (1984), the family Spathognathodontidae seems to be significantly more tolerant to various factors (especially bathymetry and changes in temperatures), than the family Icriodontidae. Although spathognathodontids were more widespread during Devonian, this family is often underestimated due to more subtle and less significant morphological changes of its elements.

3.2 Classification of conodont elements

Conodont elements are classified according to several basic features. Each element consists of a crown in the upper part and basal cavity in the lower part, which was filled with soft tissue during the animal's lifetime (Sweet, 1988). In terms of morphology there can be distinguished three different groups of elements according to Sweet (1981). For the three types of element see Fig. 1. The first type are coniform elements, which are simple, conical forms with relatively stable morphology in the course of time. The second type are ramiform elements that have an elongated blade with antero-posterior orientation and distinctive denticulation on the upper part. The third type are platform (also referred as pectiniform) elements with a relatively low blade and denticulation. Their most

distinctive feature is widening edges of the basal cavity at the bottom of the element, which is called a platform.

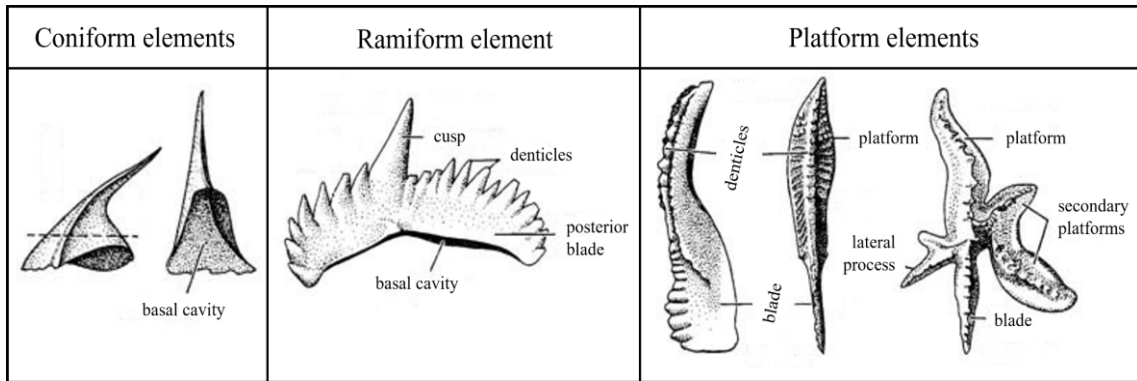


Fig. 1: Conodont elements classification according to the morphology (modified according to Armstrong and Brasier, 2013).

Due to the fast morphological evolutionary changes in time, these elements are the most common conodonts that are used in biostratigraphy and they are also essential for this work. Moreover, platform elements of the spathognathodontids, palmatolepids, polygnathids and icriodontids are markedly different (see Fig. 2). While Spathognathodontidae have mostly simple platform element with strong main blade and oval shape of basal cavity (Fig. 2A), for Polygnathidae is typical the strong main blade and wide open basal platform from the central to posterior part of element (Fig. 2B). Platform element of Palmatolepidae has also very open basal platform, but this opening goes from the interior to posterior part of element and could also have lateral process (Fig. 2C). For Icriodontidae are often typical platform elements where could be distinguished the main central blade (also called primary process), and secondary process, which branch from the main blade at different angles and may carry denticulation or other kind of ornamentation (Fig. 2D). The primary process carries the widening of the basal cavity and the specific main denticle.

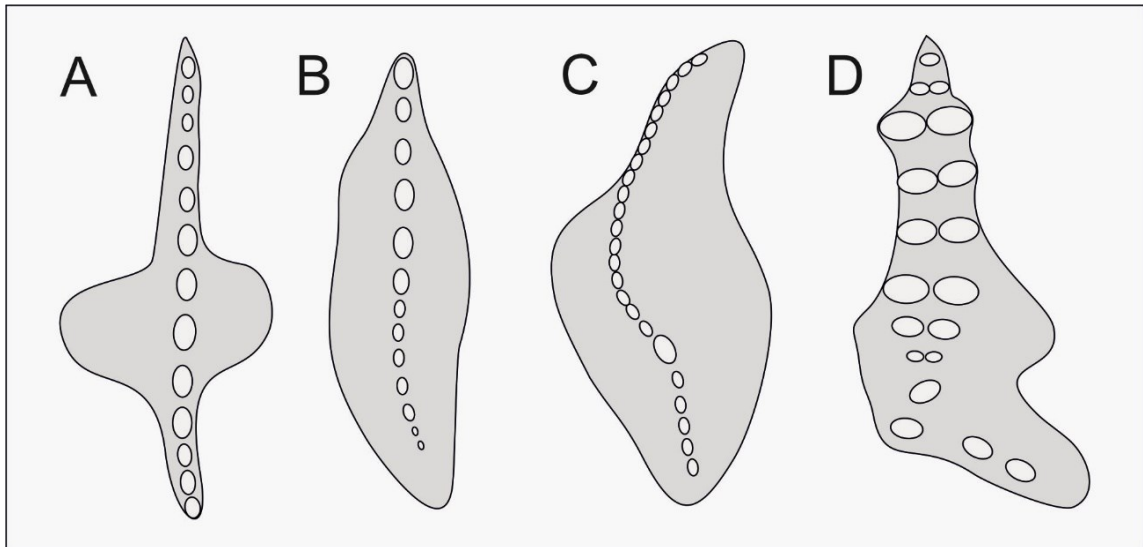


Fig. 2: Examples of different types of conodont platform elements (upper view). Simplified drawings of A: platform element of *Ozarkodina* sp. (family Spathognathodontidae), B: platform element of *Polygnathus* sp. (family Polygnathidae), C: platform element of *Palmatolepis* sp. (family Palmatolepidae), D: platform element of *Icriodus* sp. (family Icriodontidae). Drawing by Formáčková for this thesis.

It is also very important to identify the anterior and posterior part of the element. These parts can be determined according to the proportions of the element, the direction of inclination of the denticles or especially according to inclination of the main denticle, which is also referred as the cusp. The cusp is usually the largest denticle and is located above the basal cavity. Another important characteristics of conodont element are overall proportions, such as the size of the whole element, the number of denticles and their shape, blade width, openness and shape of the basal cavity, gaps between individual denticles or their fusion or absence.

3.3 Position of elements in conodont apparatus

In modern classification of conodont elements it is also important to pay attention to their position within the conodont feeding apparatus. Although the conodont apparatus differs among the conodont orders and families, all elements could be divided into four groups: “S”, “M”, “C” and “P”. Each group could be divided into subtypes, which can be distinguished by the letters – for example Sa, Sb, Sc, Sd, etc. (according to Sweet, 1988)

or by the numbers, e.g., S0, S1, S2, S3, S4, etc. (according to Purnell et al., 2000). This thesis follows the latter classification because it is commonly used.

3.3.1 Apparatus of icriodontids

The icriodontids has a relatively simple apparatus consisting of only the “C” and “P” type of elements (for reconstruction of the apparatus see Fig. 3). The number of these elements have been part of many studies and hypotheses (e.g., Lange, 1968; Nicoll, 1982; Serpagli, 1983; etc.). Whereas the older data present apparatus which is composed of one pair of platform (“P”) elements and five pairs of coniform (“C”) elements (e.g., Serpagli, 1983), newest data supposed that the incriodontid apparatus consists of twenty “C” type elements and two “P” elements (Suttner et al., 2018). The “C” type are coniform elements, typical with their conical shape, which can differ a little in each subtype. Depending on the number of elements, “C” types could be divided into five subtypes C1, C2, C3, C4 and C5 according to their place in apparatus and morphology. Some of the conic elements could be simple, slightly curved, without denticulation or other ornamentation, while others could bear a striate surface ornamentation. In Murphy (2016) are the simple conic elements with widely open basal cavity classified as “F” elements (= flared elements), while the conic elements with denticulation are described as “D” elements (= denticulate element). All the “C” elements are always situated in pairs. The “P” type is a platform (pectiniform) element with a wide open platform, which could bear one or more lateral processes, usually with denticles or ornamentation. Main blade is thick with one or two rows of denticles that could be flat or fused. This specific “P” element is often called as “I” like icriodontid or icriodontan element (Nicoll, 1982; Serpagli, 1983). The “P” or “I” type is a pair of opposed elements and the position of these elements and the “C” elements shows bilateral symmetry of the whole icriodontid apparatus (Dzik, 2015; Suttner et al., 2018).

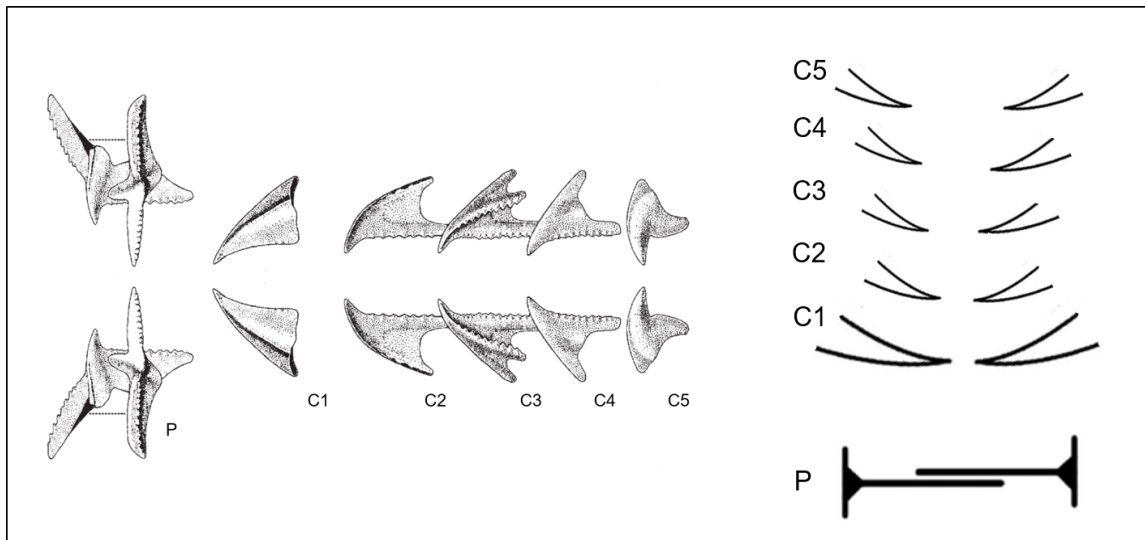


Fig. 3: Element classification according to the position in the conodont apparatus of icriodontids (modified according to Dzik, 2015; Suttner, 2018; and Jain, 2020).

3.3.2 Apparatus of ozarkodinids

General ozarkodinid apparatus consists of 15 elements (Purnell and Donoghue, 1997). All these elements could be divided into three groups: “S”, “M” or “P”, the “C” type of elements are completely missing (for reconstruction of the apparatus see Fig. 4). The “S” type are long narrow ramiform elements with numerous sharp denticles. Their shape could be represented by different degrees of curvature. These “S” elements are often present in pairs with distinctive left and right symmetry that mirror each other and are usually classified as the S1, S2, S3 and S4 element. Non-paired type of “S” element is marked as the S0 element and is bilaterally symmetrical with a shape like an open horseshoe. S0 element is usually supplemented with a long, straight and narrow denticulated posterior process. This single type of element is mostly located in the middle of the rest of “S” and “M” elements. The “M” type are also long ramiform elements with pick-like shape, accompanied by numerous thin denticles along the whole element. “M” elements of ozarkodinids are usually single and non-paired, that is why they are not subdivided into subtypes in contrast with the “S” and “P” type of element (Sweet, 1981). The “P” type are platform (pectiniform) elements which vary among the ozarkodinids (see Fig. 2). Most prominent character of this type is a strong central blade and wide platform, lateral processes with or without denticulation could be present as well. The “P” elements are situated in pairs, but due to a relatively flat shape and minimum of

differences it is not always possible to recognise left elements from right elements. The P1 elements are usually used for identification of species or subspecies, because of well recognizable changes in morphology and variability in time (Peavey, 2013).

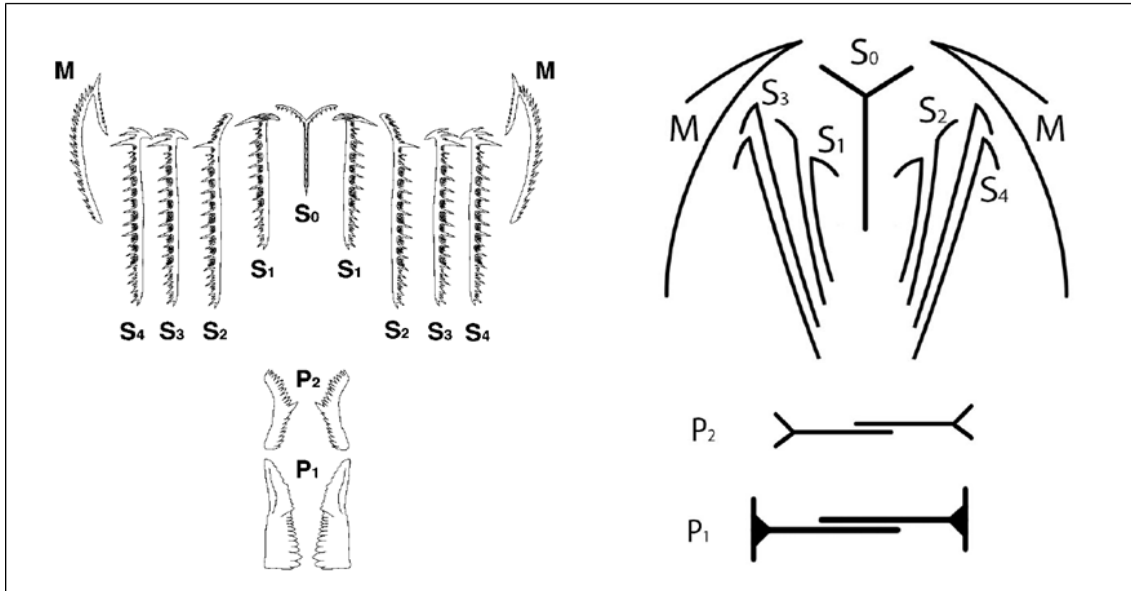


Fig. 4: Element classification according to the position in the conodont apparatus of ozarkodinids (modified according to Sweet and Donoghue, 2001; Peavey, 2013; and Jain, 2020).

According to the reconstructions of the conodont apparatuses, it is supposed that elongate “S” and “M” elements were situated in clusters near the mouth opening, whereas “P” elements were positioned in the back of the mouth (Aldridge et al., 1993). These studies are supported by the data from discoveries of elements that have been imposed in the soft tissues of conodont animals (e.g., Briggs et al., 1983; Liu et al., 2006; Aldridge et al., 2012).

3.4 Morphology of conodont elements and taxonomy

Even though conodont taxonomy should be based on the morphology of the elements and the reconstruction of the whole apparatus, there is still not enough data for apparatus models of every species. Therefore, most of the classification is based mainly on the morphology of the elements and their description. It is important to pay attention to detailed morphology of specific element, because some taxa may have more slightly

different varieties. All elements of the apparatus change over time – some only a little (e.g., element loses or gain few denticles, blade becomes wider or thinner, basal cavity could be more open or closed, the blade can be detorted and/or other characters change), and some with more distinctive changes. The morphological changes and evolution of individual elements in conodont feeding apparatus is mosaic, i.e., there is a different pace of changes in individual types elements of the apparatus. On the other hand, morphology of some elements may not fit exactly to the definition of species and therefore remain in open nomenclature (e.g., *Ozarkodina* sp., *Lanea* sp., *Zieglerodina* sp. in **paper II.**; *Ancyrognathus* sp., *Pelekysgnathus* sp., *Mehlina* sp. in **paper III.**) waiting for further taxonomic studies. Also, there are still many conodont elements which remain unclassified, often due to damage and fragmentation. Description of a new species is always necessary for conodont elements, which have a potential in global biostratigraphy, or which could be important also for the local biostratigraphy or paleoecology (for example as the taxa determining conodont biofacies models). Therefore, only two new species have been described in our studies. First of them is *Zieglerodina petrea* (described in **paper II.**, follow-up study in **paper I.**), which seems to have a great potential in the global biostratigraphy of the base of the Devonian. The second is *Ancyrognathus minjini* (described in **paper III.**), that is obviously an endemic species of the western Mongolia and could be used in local biostratigraphy and paleoecology (for more detailed information see chapter “Newly described species”).

4. Geological setting in Devonian

Geological development in Devonian was mostly affected by the ongoing assembly of supercontinent Pangea (Kidder and Worsley, 2004). While Gondwana was moving north, Euamerica was moving south and the narrow Rheic Ocean between them was closing. As a result, Eovariscan tectonic movements occurred lately in the Devonian. The continents are thus distributed mainly around the equator and on the southern hemisphere for the most part of Devonian. They are surrounded by the Panthalassia Ocean and Paleo-Thetys Ocean, whose sea-level stand is exceptionally high compared to other Paleozoic periods (Becker et al., 2020). It is one of the reasons why the climatic situation during Devonian is relatively warm and stable. Another reason is because of the decrease of the CO₂ level due to the spreading of vascular land plants (Algeo et al., 2001). Therefore, the Devonian is a period of greatest carbonate production, large representation of biogenous reef growth and high diversity of marine fauna (Kiessling et al., 2000; Joachimski et al., 2009). The cooling came just before the end of the Devonian and glaciations occurred in the south polar areas of Gondwana (especially in Central Africa, South Africa and South America), but there is also evidence for mountain glaciers in tropical latitudes (in North America), which appeared only for a limited time (Isaacson et al., 2008; Wicander et al., 2011; Carmichael et al., 2016).

Due to this contemporary glaciation were continental shelves uncovered and exposed to the subaerial influences (Song et al., 2017). This cooling trend is also reflected by the conodont faunas, where the visible gradual evidence could be observed from the Famennian (Girard et al., 2020). The cooling trend then continued and later led to a large carbon glaciation. However, life in the Devonian was also influenced by other factors. Marine ecosystems were mostly affected by the geochemical anomalies, eustatic fluctuation, faunal blooms and extinctions and the anoxic events associated with that. Important role also had the CO₂ concentration in the atmosphere, its changes during the Devonian and active volcanism episodes (Golonka et al., 2012; Qie et al., 2019). The atmospheric, ecological and climatic changes in the Devonian brought two mass extinction events – Lower and Upper Kellwasser Crisis at the Frasnian/Famennian boundary and the Hangenberg Crisis at the end of the Devonian, which affected most representatives of fossil groups and whole marine ecosystems. Also, other less significant extinction events occurred in Devonian: the Silurian/Devonian Boundary Event (also referred as “Klonk Event”) at the base of the Devonian; *Atopus* Event, basal Zlichov

Event, Chebbi Event, Basal and Upper Zlíčov Event and Daleje Event in the Emsian; Choteč Event, Bakoven Event, Stony Hollow Event and Kačák Event in the Eifelian; Taghanic Event and Geneseo Event in Givetian; Frasnian Events, Genundewa Event and Middlesex Event (also referred as *Punctata* Event) in Frasnian; Condroz Event, *Annulata* Event and Dasberg Event in Famennian (see the summary in Becker et al., 2020). These events had an impact on many taxonomic groups and caused disappearance of some previously widespread species or even genera. On the other hand, in the Devonian are also few events, which are characterised by a spread and radiation of the taxa rather than their extinction: e.g., the *Icriodus* Event in the Lower Devonian, the *Pumilio* Events in Givetian, Timan Event, Rhinestreet Event and *Semichatovae* Event in Frasnian, and Nehden Event in Famennian (Walliser, 1996; Sandberg et al., 2002; Racki, 2005; Becker et al., 2016; Becker et al., 2020; Slavík and Hladil, 2020).

4.1 Geology of the studied sections

The studied sections differ both in geographical location and stratigraphy. Therefore, a brief characteristic of each selected section is provided below.

4.1.1 Na Požárech section

The Na Požárech section is situated in Prague Synform (in sense of Melichar, 2004; Knížek et al., 2010) in eastern part of Teplá-Barrandian Unit, which contains the unmetamorphosed Lower Palaeozoic volcanosedimentary rocks (Cháb et al., 2008). The Teplá-Barrandian Unit is located in the central part of the Bohemian Massif in Czech Republic. The **study I.** and **study II.** are focused on the quarry Na Požárech (N 50°01'41"; E 14°19'28"), which is situated in the southwestern edge of Prague. This locality represents an area with relatively shallow water sedimentation at the Silurian/Devonian boundary. Přídolí is represented by an alternation of bioclastic and biomicrite limestones typical for the Požáry Formation (beds 96 to 158). From bed 150 onwards, more massive light grey limestones predominate. The beginning of the Devonian is defined here by the first occurrence of the conodont taxon *Icriodus hesperius* Klapper et Murphy, 1974 in bed 159 (Carls et al., 2007). The lowermost Devonian part of the section is represented by light grey bioclastic (especially crinoid) and biomicritic limestones, which are called Kotýs Limestone (defined by Chlupáč, 1953, 1981). Equivalent limestones rich in crinoid

detritus from *Scyphocrinites* taxa are often called “*Scyphocrinites* horizon beds” and could be also found in other sections all over the world (e.g., Buggisch and Mann, 2004; Donovan and Lewis, 2009; Klug et al., 2013; Corrigan et al., 2014a; Donovan et al., 2018; Ferreti et al., 2022). However, silty limestones between layers 158 and 159, 160 and 161 also appear here. The studies of the sedimentary record (Koptíková et al., 2010; Vacek et al., 2010; Gocke et al., 2013; Bábek et al., 2018) also point out to the presence of turbidites in several beds in Silurian and Devonian parts of the section. The limestones in the section are rich in diverse fauna, mainly crinoids, conodonts, brachiopods, cephalopods and trilobites. For more details on fauna of this section see for example Kříž et al (1986); Kříž (1992); Chlupáč (1993); or Čáp et al. (2003).

4.1.2 Praha-Radotín section

The section Praha-Radotín (N 49°59'33.9"; E 14°20'46.4") is situated, as the section Na Požárech, in the Prague Synform in eastern part of Teplá-Barrandian Unit (Bohemian Massif, Czech Republic) and the **study I.** and **study II.** are focused on this locality. Unlike the previous section, the section Praha Radotín lies in the road notch on the left bank of the Radotín brook on the southern edge of Prague. For the uppermost Silurian are typical dark grey micritic bituminous limestones of the Požáry Formation, alternating with grey to grey-brown calcareous shales (beds 1 to 8). The “*Scyphocrinites* horizon can be recognized” around the Silurian/Devonian boundary (beds 8 and 9) and is characterized by abundant remnants of crinoids of the genus *Scyphocrinites*. The beginning of Devonian is defined by the first occurrence of the graptolite taxon *Uncinatograptus uniformis uniformis* in the bed 9 (Čáp et al., 2003). Lower part of Lochkovian is represented by the Radotín Limestone facies, i.e., alternation of dark micritic limestones and calcareous shales (beds 9 - 12). The overlying beds form fine-grained, bioclastic limestones typical for the Kosoř Limestones facies (as defined by Chlupáč, 1953) (beds 12 - 14). The studies of the sedimentary record also point out to the presence of turbidites (Čáp et al., 2003; Manda, 2003). The most common fauna in this section contains mainly graptolites, cephalopods and bivalves (for more details on fauna in this section see for example Kříž, 1999; or Manda, 2003).

4.1.3 Cellon section

The Cellon section (N 46°36'32"; E 12°56'31") is located near the village Plöcken Pass in the Carnic Alps close to the Italian-Austrian border. The section is exposed in the eastern part of Mt. Cellon in a narrow avalanche gorge and represents succession of Ordovician to Devonian marine sediments. A shallower deposition environment is typical for the uppermost Silurian part. Light grey limestones in this stratigraphic level are rich in fossils of cephalopods, bryozoans and brachiopods. The base of Devonian is located in the bed 47B according to the first occurrence of conodont species *Icriodus hesperius* (Corradini et al., 2015). The presence of the graptolite marker of the Silurian/Devonian boundary *Uncinatograptus uniformis uniformis* is documented in bed 50 (Jaeger, 1975), which lies approximately 1.5 m above in shale interbeds. Lowermost Devonian part is characterized by dark grey to black limestones accompanied by black shales to marl interbeds. The limestones in this section are rich in diverse fauna, mainly bivalves, acritarchs, brachiopods, cephalopods, conodonts, chitinozoans, corals, ostracods, graptolites, foraminifers and trilobites (for more details on fauna of this section see for example Walliser, 1964; Priewalder, 1987; Priewalder, 1997; Pickett, 2007; Histon, 2012; Corradini et al., 2015; Corrigan et al., 2016; Corradini et al., 2020). The **study II** includes conodont data from this locality.

4.1.4 Atrous 3 section

The Atrous 3 section (N31°00'50.2"; W4°05'22.7") is located in the southern Tafilalt, northwest of Taouz, Morocco. The section represents an area with relatively shallow water marine sediments of uppermost Silurian and lowermost Devonian. The sediments from the Přídolí are dark micritic limestones with abundant faunal remains, mainly from orthoceratid cephalopods, bivalves and gastropods. They are often referred to as “*Orthoceras* limestones” or “*Temperoceras* limestones” (according to Kröger, 2008). Sedimentation changes around the Silurian/Devonian boundary, where the thick beds of the “*Scyphocrinites* limestones” appear. These light grey limestones are coarse-grained with predominant component of crinoidal detritus or even well-preserved crowns and loboliths (Haude and Walliser, 1998; Corrigan et al., 2014a). The base of the Devonian is located in the bed 25 according to the first occurrence of conodont *Icriodus hesperius* (Corrigan et al., 2014b). Due to the predominance of limestones, there is no evidence of

graptolites around the Silurian/Devonian boundary. Sedimentation continues by the onset of grey to brownish micritic limestones in the upper beds. Main fossil remains in these limestones are represented by cephalopods and crinoids, but their occurrence is not as rich as in the previous types of limestones. For more details according to the fauna of this section see for example Hollard, 1977; Haude and Walliser, 1998; Kröger, 2008; Corrigan et al., 2014a; Corrigan et al., 2014b; Corrigan and Corradini, 2019; Klug et al., 2019. Mainly the **study II** is focused on several conodont taxa from this locality.

4.1.5 Hushoot Shiveetiin gol section

The Hushoot Shiveetiin gol section (N 45°16'16"; E 91°03'11") lies in the Baruunhuurai Terrane, which belongs to the Central Asian Orogenic Belt. This Central Asian Orogenic Belt is situated in the Gobi fold megazone in western Mongolia (Tomurtoogoo, 2014). From north to south, the Baruunhuurain Terrane is subdivided into the four subterrane: Baaran, Ulaanus, Baitag and Olonbulag (according to Badarch et al., 1998). The **study III** is focused mainly on the Ulaanus and Olonbulag Subterrane. Both subterrane contain volcanosedimentary rocks of the Devonian and Carboniferous age. The Devonian rocks are represented mainly by the epiclastic sediments, limestones, tuffs and tuffites. In the Carboniferous part of the section predominate flysch (in Ulaanus subterrane) and flysch alternating with tuff and limestone sedimentation (in Olonbulag subterrane).

The study in the Ulaanus and Olonbulag subterrane is focused mainly on the Samnuuruul Formation, which contains the Late Devonian (Famennian) sediments - fossiliferous limestones, gravel stones with limestone beds, reddish brown conglomerates, grey to greenish grey sandstones, siltstones and tuffites. For more details according to the sedimentology see Munkhjargal et al., 2021. The most common fauna in this section contains conodonts, trilobites, brachiopods, bivalves, bryozoans, ostracods and also the plant remains (for more details on fauna of this section see Crônier et al., 2021; Nazik et al., 2021; Roelofs et al., 2021).

4.2 Paleogeographic position of the studied areas during Devonian

The Devonian palaeogeography (Fig. 5) is affected by several significant events. In the Lower Devonian, the continents Laurentia and Baltica, which are situated in a tropical zone around the equator, collide together. The result of this collision is the emergence of

Laurussia (also often called the "Old Red Continent"). This collision is accompanied by caledonian orogeny. The Gondwana continent, which is located in the southern hemisphere, is moving towards the north through all Devonian. The Pacific Ocean, which was situated between the new continent Laurussia and Gondwana, begins to close in the Middle Devonian. These movements lead to the ongoing assembly of a supercontinent Pangea. The origin of the supercontinent Pangea is accompanied by the Variscan (Hercynian) orogeny. The overall trend in distribution of continents on Earth should be described as the successive moving of continents to tropical and subtropical zones. Only the southern part of Gondwana remained in temperate zone (for more detailed information see McKerrow and Scotese, 1990; Scotese et al., 1999; or Becker et al., 2020).

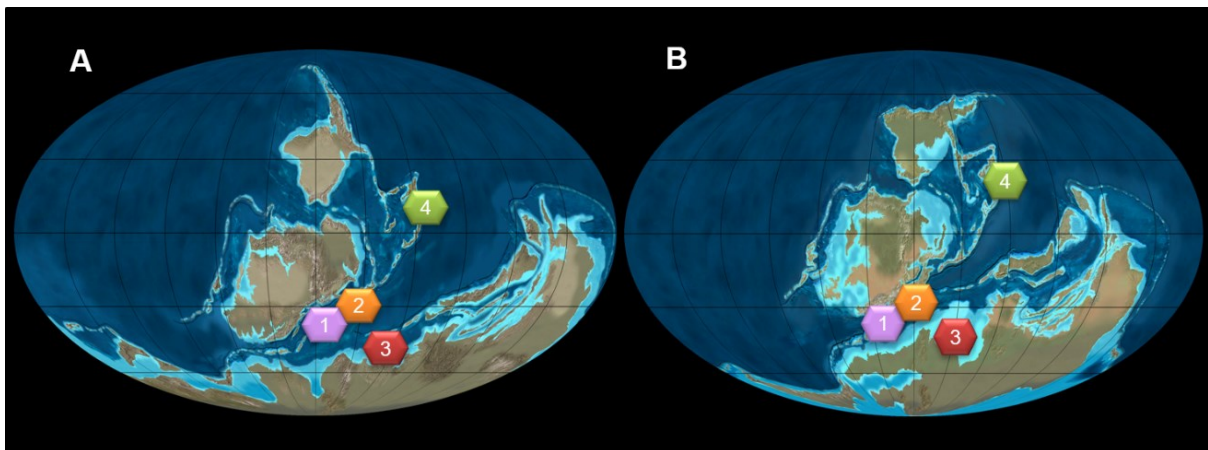


Fig. 5: Paleogeographic location of the studied sections. A: Early Devonian (400 Ma) map with marked sections: 1 – Carnic Alps (Cellon section), 2 – Bohemian Massif (Na Požárech and Praha-Radotín section), 3 – Tafilalt (Atrous 3 section), 4 – Baruunhuurai Terrane (Hushoot Shiveetiin gol section). B: Late Devonian (370 Ma) map with marked sections: 1 – Carnic Alps (Cellon section), 2 – Bohemian Massif (Na Požárech and Praha-Radotín section), 3 – Tafilalt (Atrous 3 section), 4 – Baruunhuurai Terrane (Hushoot Shiveetiin gol section). Map adapted from Blakey, 2008 and Golonka, 2020.

During the latest Silurian and lowermost Devonian, the Teplá-Barrandian Unit (including sections in the Prague Synform – Praha-Radotín and Na Požárech) was located in the small microcontinent so-called Perunica (Havlíček et al., 1994; Torsvik and Cocks, 2004; Fatka and Mergl, 2009), which was situated in the northern edge of Gondwana (in sense of Cháb et al., 2008). Later on, during the Devonian, Perunica moved towards the north

due to the rifting of the Paleotethys Ocean (according to Torsvik and Cocks, 2013). In connection with these changes and ongoing Variscan orogeny, the unit was lifted up and sedimentation in this area ended in the Middle Devonian.

Similarly as the Teplá-Barrandian Unit in Perunica, the Carnic Alps were situated in the separated peri-Gondwanan terranes. According to recent studies (Stampfli et al., 2013) the Carnic Alps (including the Cellon section) were part of the Galatian terranes during the early Paleozoic. Later, these terranes separated from the northern edge of Gondwana (same as Perunica) and drifted north during the opening of the Paleotethys Ocean (von Raumer and Stampfli, 2008). Since the earliest Devonian, Galatian terranes moved towards Laurussia and all these continents were affected by the later processes of Variscan Orogeny.

During the early Paleozoic, Tafilalt (and Atrous 3 section) was situated in Eastern Anti-Atlas region, on the northern to north-western margin of Gondwana (Baidder et al., 2008). Like the previous sections, also the Eastern Anti-Atlas region was affected by the rifting of the Paleotethys Ocean and subsequent Variscan Orogeny (Michard et al., 2008).

Compared to the previous peri-Gondwanan terranes, the Central Asian Orogenic Belt (including the Baruunhuurai Terrane - Hushoot Shiveetiin gol section) were part of the Island Arc Settings situated on the northern hemisphere. The Central Asian Orogenic Belt was composed of microcontinents and island arcs, which together form a comprehensive accretionary wedge system during the Early Palaeozoic. According to Ruzhentsev et al. (1992), the individual subterrane of the Baruunhuurai Terrane represent different types of environments: Baraan and Olonbulag subterrane are supposed to be an active continental margin, whereas Ulaanus subterrane is interpreted as a back arc basin and the Baitag subterrane as the fore arc zone (according to Li et al., 2019). In Carboniferous, part of the Palaeoasian Ocean is closing and the Central Asian Orogenic Belt is formed into a system of continental fragments and intra oceanic island arc (for more information see Yang et al., 2013; Li et al., 2017; Li et al., 2019; Liu et al., 2021).

5. Conodont application

5.1 Conodont biostratigraphy in Devonian

The base of the Devonian is globally established on the first occurrence of graptolite taxon *Uncinatograptus uniformis uniformis* (def. by Chlupáč et al., 1972, summary in Martinsson et al., 1977), but the biostratigraphic subdivision of the rest of the Devonian is based mostly on conodonts. The Devonian conodont zonation is usually based on the first appearances of taxa but parts of the zonation work well only regionally, because of provincialism and lack of global conodont indexes.

Conodont biostratigraphy has undergone a long development and is constantly being improved and refined into more detail (see Fig. 6). One of the first important comprehensive views of Devonian conodont biozonation was published by Bischoff and Ziegler (1957) and Ziegler (1962). Most changes in **Lower Devonian** biostratigraphy were proposed by Klapper (1977), Ziegler (1979), Ziegler and Sandberg (1984), Jeppsson (1988), Valenzuela-Ríos and Murphy (1997), Murphy and Valenzuela-Ríos (1998), Slavík (2004, 2011), Slavík and Hladil (2004, 2020), Murphy (2005), Carls et al. (2007), Slavík et al. (2007, 2012), Yolkin et al. (2011), Corradini and Corrigan (2012), Valenzuela-Ríos et al. (2015), Schönlaub et al. (2017). Improvements of **Middle Devonian** conodont zonation proposed Bultynck (1985, 1987), Aboussalam (2003), Aboussalam and Becker (2007), Narkiewicz and Bultynck (2010). The **Upper Devonian** zonation was revised and further developed by Ziegler (1962), Sandberg and Ziegler (1973), Ziegler and Sandberg (1984, 1990) (often referred to as the “Late Devonian Standard Conodont Zonation”); Ziegler and Klapper (1985), Klapper et al. (1996, 2004), Klapper and Becker (1999), Schülke (1999), Girard et al. (2005), Klapper (2007a,b), Corradini (2008), Ovantanova and Kononova (2008), Hartenfels et al. (2009), Hartenfels and Becker (2009), Kaiser et al. (2009), Hartenfels (2011), Becker et al. (2012), Spalletta et al. (2017), Becker et al. (2020).

Many studies were also focused on calibration of the conodont biostratigraphy in relation to geochronology (e.g., Kaufmann, 2006; Becker et al., 2012, 2020; Brett et al., 2020; etc.), because the combination of these two approaches is a key for understanding the past phenomena and processes in geological history.

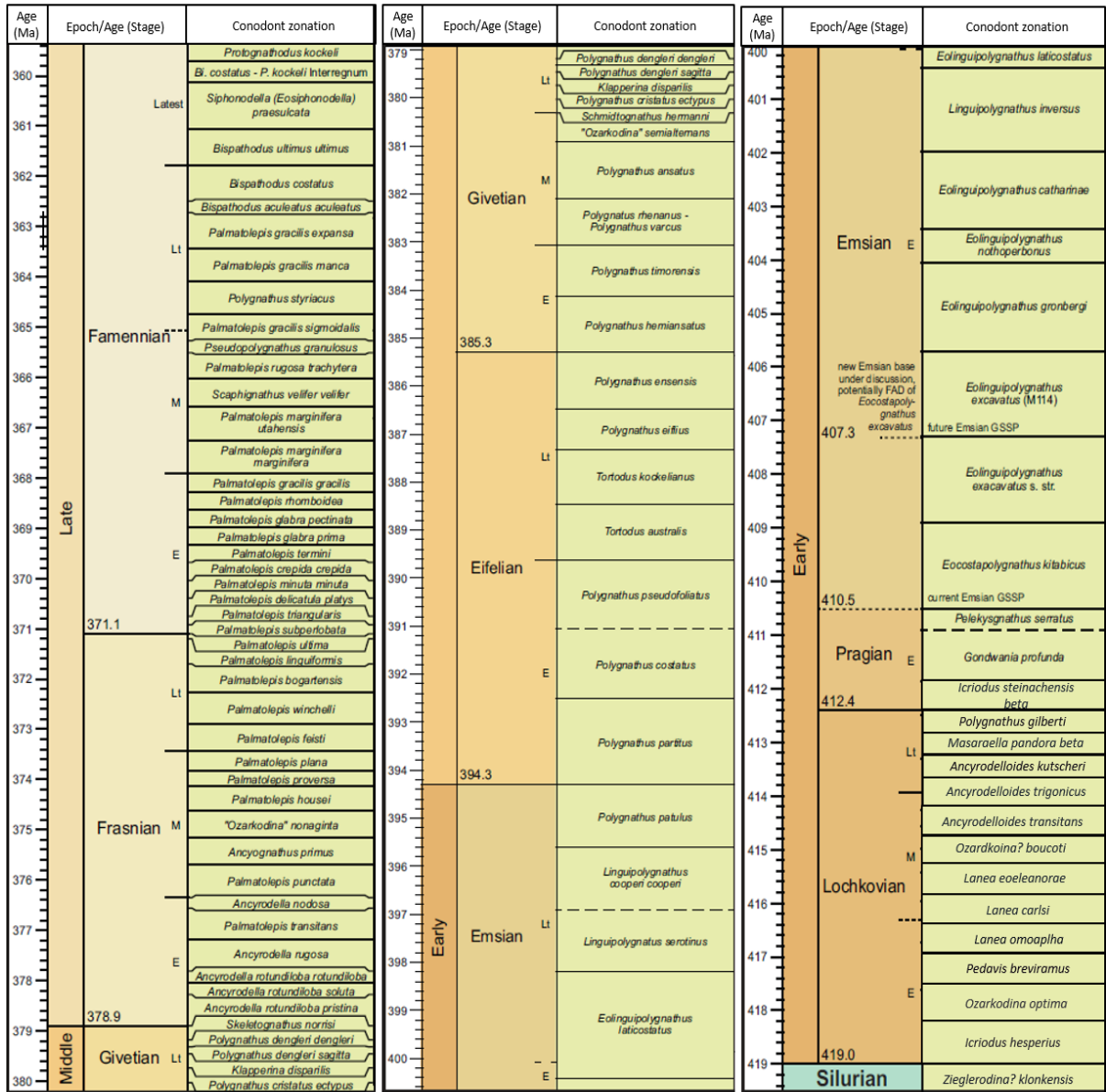


Fig. 6: Conodont zonation of Devonian period (modified according to Becker et al., 2020, Slavík and Hladil, 2020).

5.2 Devonian conodont biofacies

Conodont biofacies are based on changes in the global distribution of conodont taxa. The composition of conodont faunas on site depends on paleoecological limitations of individual taxa in specific paleoenvironmental conditions, such as position in ocean slope, character of sedimentation, bathymetry, salinity, response to biotic factors such as competition or predation, nutrition, and others (Hermann et al., 2015; Lüddecke et al., 2017; Girard et al., 2020). The conodont biofacies models are based on detailed

biostratigraphic studies and the nomenclature of biofacies is then based on predominant taxon or two dominant taxa (e.g., polygnathid-palmatolepid assemblage or icriodontid-polygnathid assemblage). However, it is necessary to take into account the exact percentage when evaluating the composition of biofacies – if the predominance of two taxa does not exceed seventy percent, the sample could be affected by a mixing during transport or other secondary events (as defined Ziegler and Sandberg, 1984). Due to this fact, it is critical to have sedimentological and microfacies data when evaluating the conodont biofacies.

Knowledge of conodont biofacies can provide a basis for further studies in reconstruction of palaeoenvironmental changes (e.g., Söte et al., 2017; Lüddecke et al., 2017; Bahrami et al., 2019). However, it must be taken in account that most taxa have some palaeoecological limitations (Sandberg, 1976; Corradini, 1998; Lüddecke et al., 2017). Accordingly, applicability of conodont facies varies throughout Palaeozoic, as well as in Devonian. In the Lower Devonian, there are only few attempts to work with biofacies models, because conodont provincialism is rather low in the Lochkovian and lower Pragian (Klapper and Johnson, 1980; Flessa and Hardy, 1988). Provincialism slightly increased in the upper Pragian and in the Emsian (Charpentier, 1984). There are several biofacies models for the Middle Devonian (e.g., Seddon and Sweet, 1971; Schumacher, 1976), but they are not universally applicable.

Decrease of sea level due to the cooling in the Upper Devonian influenced conodont distribution and caused increased conodont provinciality (Klapper and Johnson, 1980; Flessa and Hardy, 1988). That is the reason why conodont biofacies models became widely used mostly in the Upper Devonian (e.g., Sandberg and Barnes, 1976; Sandberg and Dreesen, 1984; Dreesen, 1992; Kalvoda et al., 1999; Kaiser et al., 2008; Lüddecke et al., 2017; Bahrami et al., 2019). Accordingly, only the study **III.** deals with the conodont biofacies models.

6. Results and discussion

The most important results and points of discussions of the study are summarized in the following chapters, for more detailed description see the attached articles (**paper I., II. and III.**).

6.1 Conodont biodiversity

Conodont elements were found in all studied sections, but the abundance and preservation differ significantly both among the localities and the samples. Total of five taxa were recognized in the conodont samples of the uppermost Silurian taken from the section Na Požárech (Prague Synform): *Zieglerodina* sp. indet.; *Zieglerodina* cf. *remscheidensis* Ziegler, 1960; *Ozarkodina* sp. indet.; *Ozarkodina typica* Branson and Mehl, 1933; *W eosteinhornensis* s.l. (Walliser, 1964). In the samples taken from the lowest Devonian, the diversity of conodonts was significantly higher: *Zieglerodina* sp. indet.; *Zieglerodina* cf. *remscheidensis* Ziegler, 1960; *Zieglerodina petrea* n. sp. Hušková and Slavík, 2020; *Ozarkodina* sp. indet.; *Ozarkodina typica* Branson and Mehl, 1933; *Ozarkodina* cf. *optima* (Moskalenko, 1966); *Wurmiella* sp. indet.; *W eosteinhornensis* s.l. (Walliser, 1964); *Lanea* sp. indet.; *Lanea planilingua* Murphy and Valenzuela-Ríos, 1998; *Icriodus* sp. indet.; *Icriodus* cf. *w. woschmidti* Ziegler, 1960; *Icriodus hesperius* Klapper and Murphy, 1974. For the detailed distribution of taxa in the section Na Požárech see Fig. 7.

In contrast, the diversity of conodonts in the studied Silurian/Devonian interval at the Praha-Radotín section (Prague Synform) was slightly higher (for details see Fig. 8). In the samples from the uppermost Silurian were identified five taxa: *Zieglerodina* sp. indet.; *Zieglerodina* cf. *zellmeri* Carls et al., 2007; *Zieglerodina* cf. *remscheidensis* Ziegler, 1960; *Wurmiella* sp. indet.; *W eosteinhornensis* s.l. (Walliser, 1964). Diversity of conodont species is increasing just above the base of the Devonian. Following taxa were recognised in the lowermost Devonian: *Zieglerodina* sp. indet.; *Zieglerodina* cf. *zellmeri* Carls et al., 2007; *Zieglerodina* cf. *remscheidensis* Ziegler, 1960; *Zieglerodina petrea* Hušková and Slavík, 2020; *Ozarkodina* sp. indet.; *Ozarkodina typica* Branson and Mehl, 1933; *Ozarkodina* cf. *optima* (Moskalenko, 1966); *Wurmiella* sp. indet.; *Wurmiella excavata* (Branson and Mehl, 1933); *W eosteinhornensis* s.l. (Walliser, 1964); *Lanea* sp. indet.; *Lanea planilingua* Murphy and Valenzuela-Ríos, 1998; *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1998; *Icriodus* sp. indet.; *Icriodus* cf. *w. woschmidti* Ziegler, 1960;

Icriodus hesperius Klapper and Murphy, 1974; *Pedavis* sp. indet.; *Pedavis breviramus* Murphy and Matti, 1982.

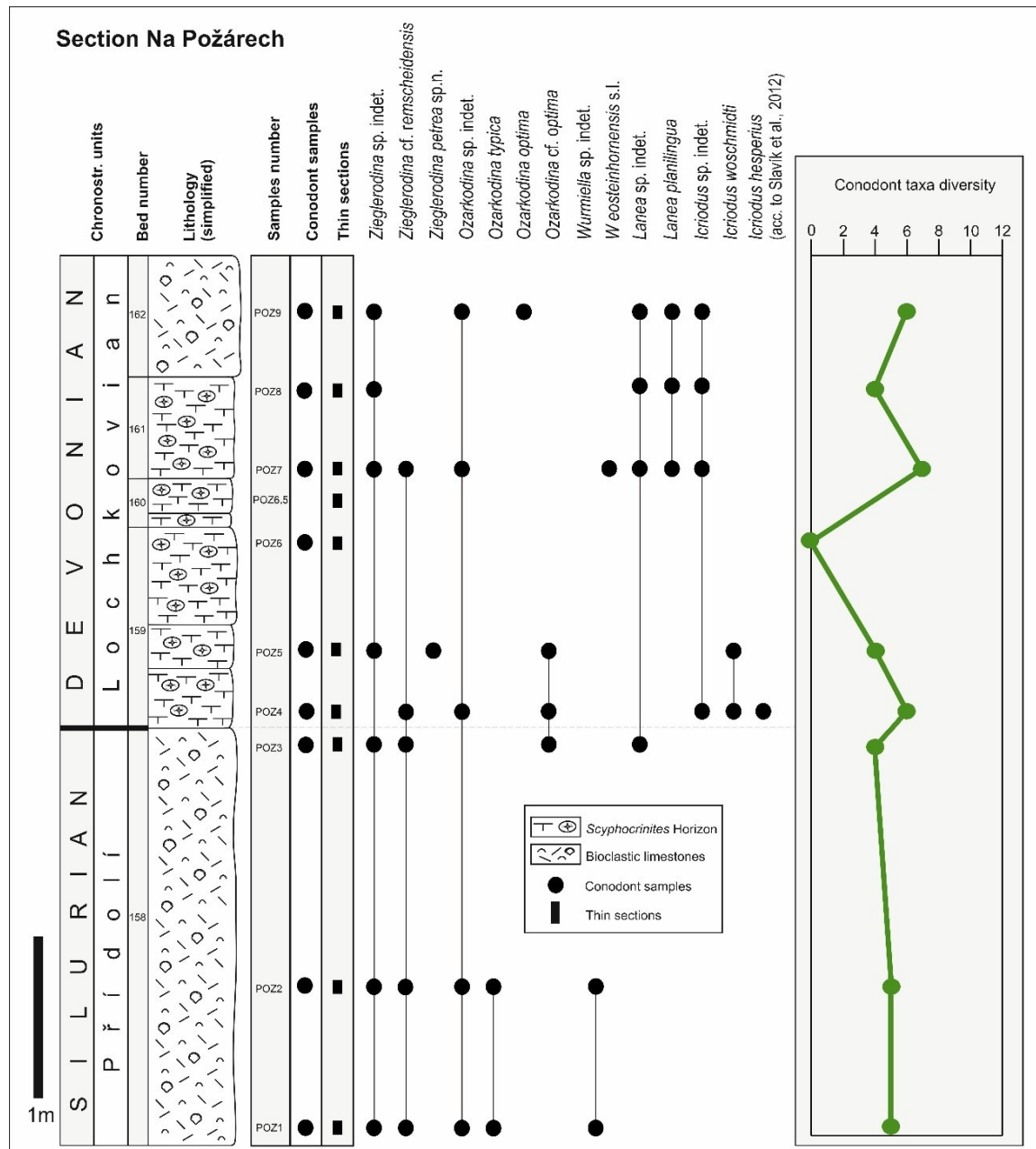


Fig. 7: Distribution of conodont taxa from the uppermost Silurian and lowermost Devonian strata at the Na Požárech section (modified according to Hušková and Slavík, 2020).

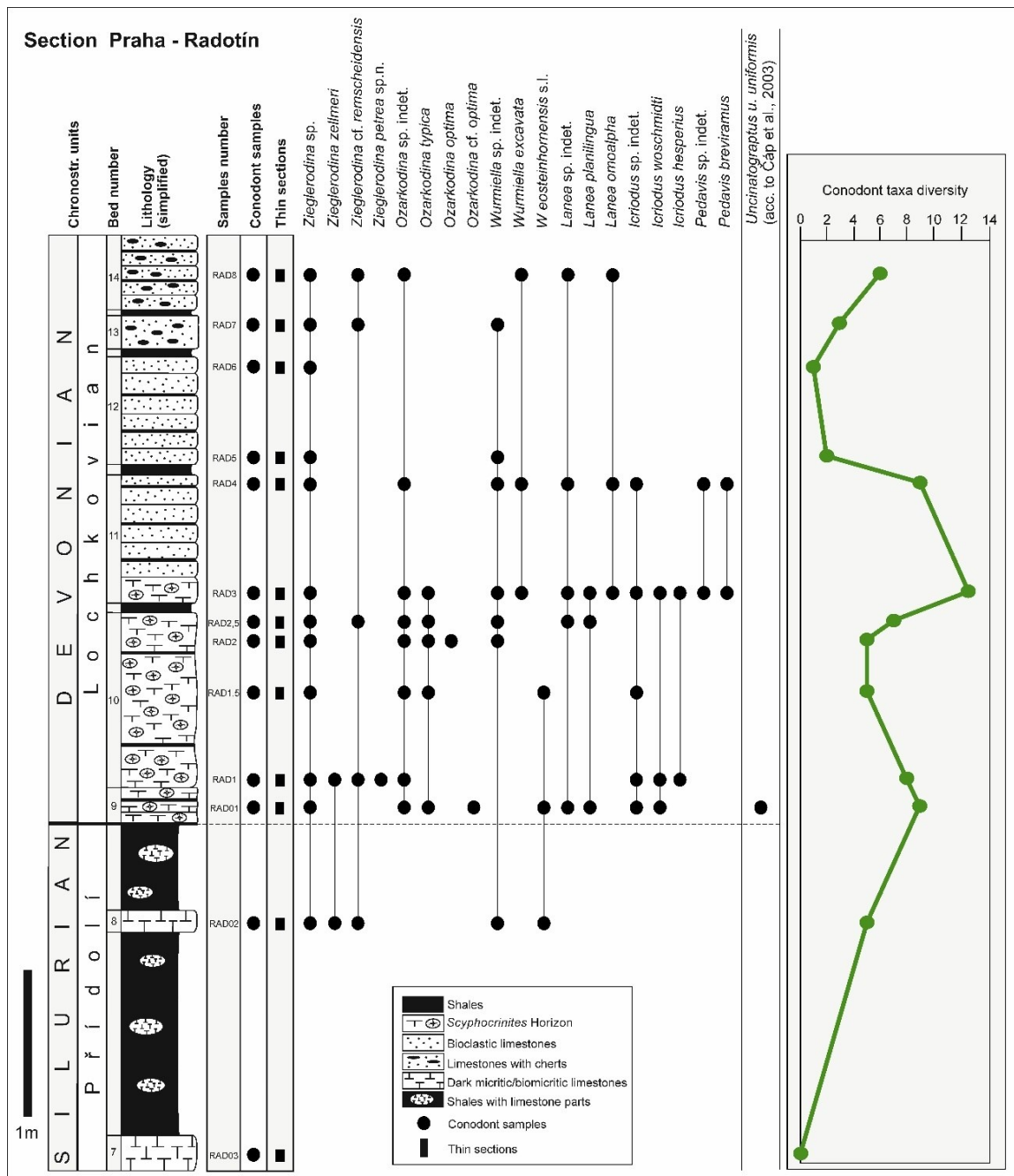


Fig. 8: Distribution of conodont taxa from the uppermost Silurian and lowermost Devonian strata at the Praha-Radotín section (modified according to Hušková and Slavík, 2020).

Thirteen taxa were identified in the Na Požárech section, the Praha-Radotín section was richer in diversity (for detail comparison see Fig. 9). A total of eighteen taxa were identified in samples from the Praha-Radotín section. The Uppermost Silurian part of the studied interval of both sections belong to the latest Silurian *klonkensis* Zone, while the

conodonts obtained from the lowermost Lochkovian belong to the *hesperius-optima* Zone and the *optima-breviramus* Zone. The studied interval at the section Praha-Radotín covers a longer period of time: the Silurian part belongs to the *klonkensis* Zone, then it continues to the *hesperius-optima* Zone and *breviramus-omoalpha* Zone, and, at least part reaches the *omoalpha-carlsi* Zone (for more details see **paper II**).

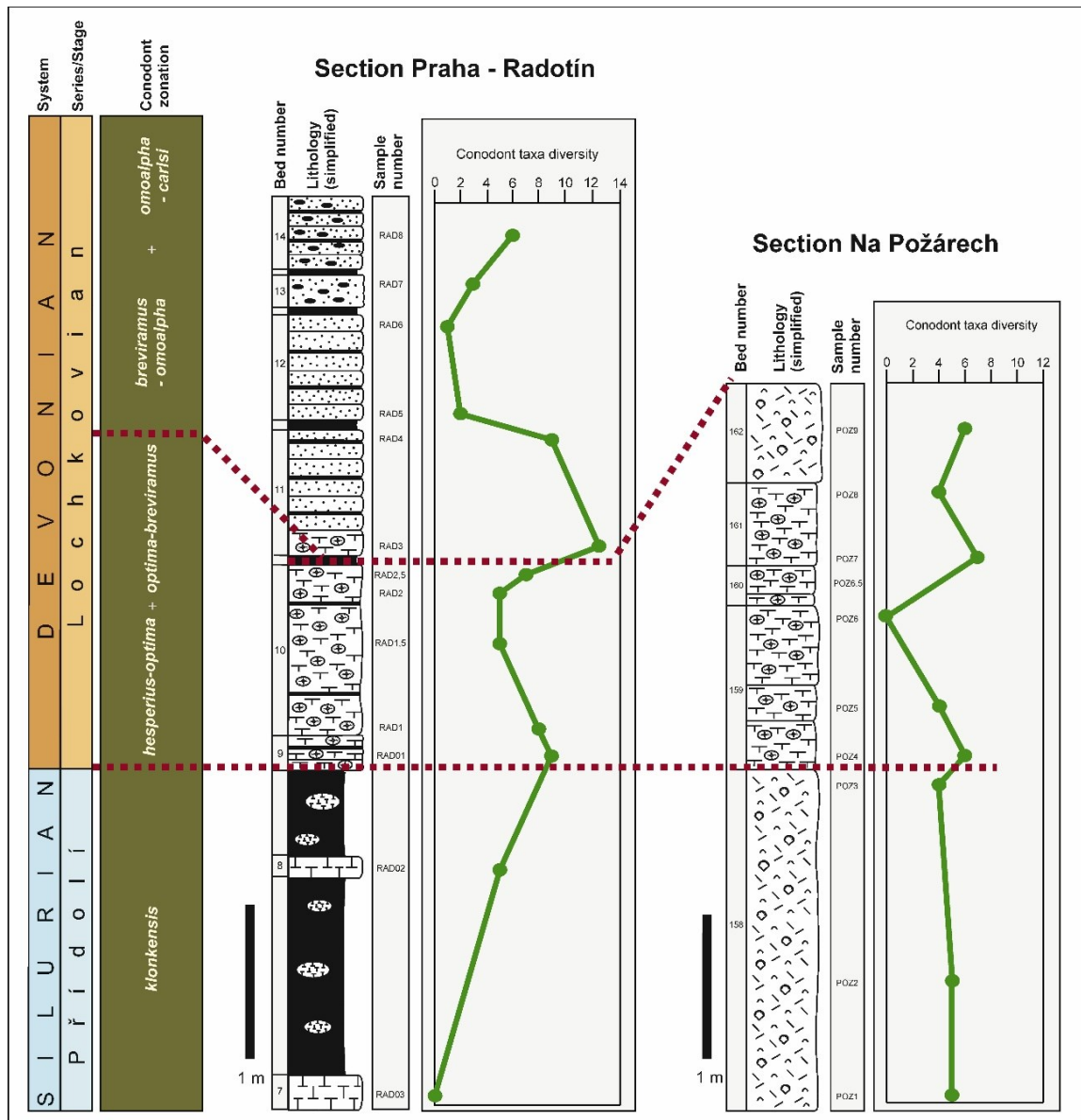


Fig. 9: Correlation of the studied sections Praha-Radotín and Na Požárech, their lithology, conodont diversity and conodont biozonation (modified according to Hušková and Slavík, 2020).

Similarly, as in the previous sections, samples taken at Hushoot Shiveetiin gol section (Baruunhuurai Terrane) point to a diversified community of Famennian conodonts (for details see Fig. 10). All together, 20 species and 10 taxa in open nomenclature were reported from the locality: *Ancyrognathus symmetricus* Branson and Mehl, 1934, *Ancyrognathus minjini* n. sp. Suttner et al., 2020, *Ancyrognathus bifurcatus* (Ulrich and Bassler, 1926), *Icriodus alternatus alternatus* Branson and Mehl, 1934, *Icriodus* cf. *alternatus alternatus* Branson and Mehl, 1934, *Icriodus* sp., *Icriodus plurinodosus* Wang et al., 2016, *Polygnathus praecursor* Mattyja, 1993, *Polygnathus buzmakovi* Kuz'min, 1990, *Polygnathus procerus* Sannemann, 1955, *Polygnathus nodocostatus nodocostatus* Branson and Mehl, 1934, *Polygnathus* sp. 1, *Polygnathus* sp. 2, *Polygnathus* sp. 3, *Polygnathus* sp. 4, *Polygnathus* sp. 5, *Polygnathus* sp. 6, *Polygnathus brevilaminus* Branson and Mehl, 1934, *Polygnathus subnormalis* Vorontsova and Kuz'min, 1984, *Palmatolepis minuta minuta* Branson and Mehl, 1934, *Palmatolepis* cf. *delicatula delicatula* Branson and Mehl, 1934, *Palmatolepis glabra prima* M1 Ziegler and Huddle, 1969, *Palmatolepis glabra prima* M3 Hartenfels, 2011, *Palmatolepis subperlobata* M1 Branson and Mehl, 1934, *Palmatolepis* sp., *Palmatolepis rhomboidea* Sannemann, 1955, *Palmatolepis poolei* Sandberg and Ziegler, 1973, *Palmatolepis quadratinodosalobata* M1 Sandberg and Ziegler, 1973, *Mehlina* sp. 1, *Mehlina strigosa* (Branson and Mehl, 1934). The lowermost part of the section belongs to the *Palmatolepis minuta minuta* Biozone, then the section continues without interruption to the *Palmatolepis crepida* Biozone, *Palmatolepis glabra prima* Biozone and the uppermost part of the section belongs to the *Palmatolepis rhomboidea* Biozone. Taxonomic data together with biostratigraphic and palaeobiogeographic results were then carefully compared with already published data in numerous papers (for more details see Table 2 in **paper III**).

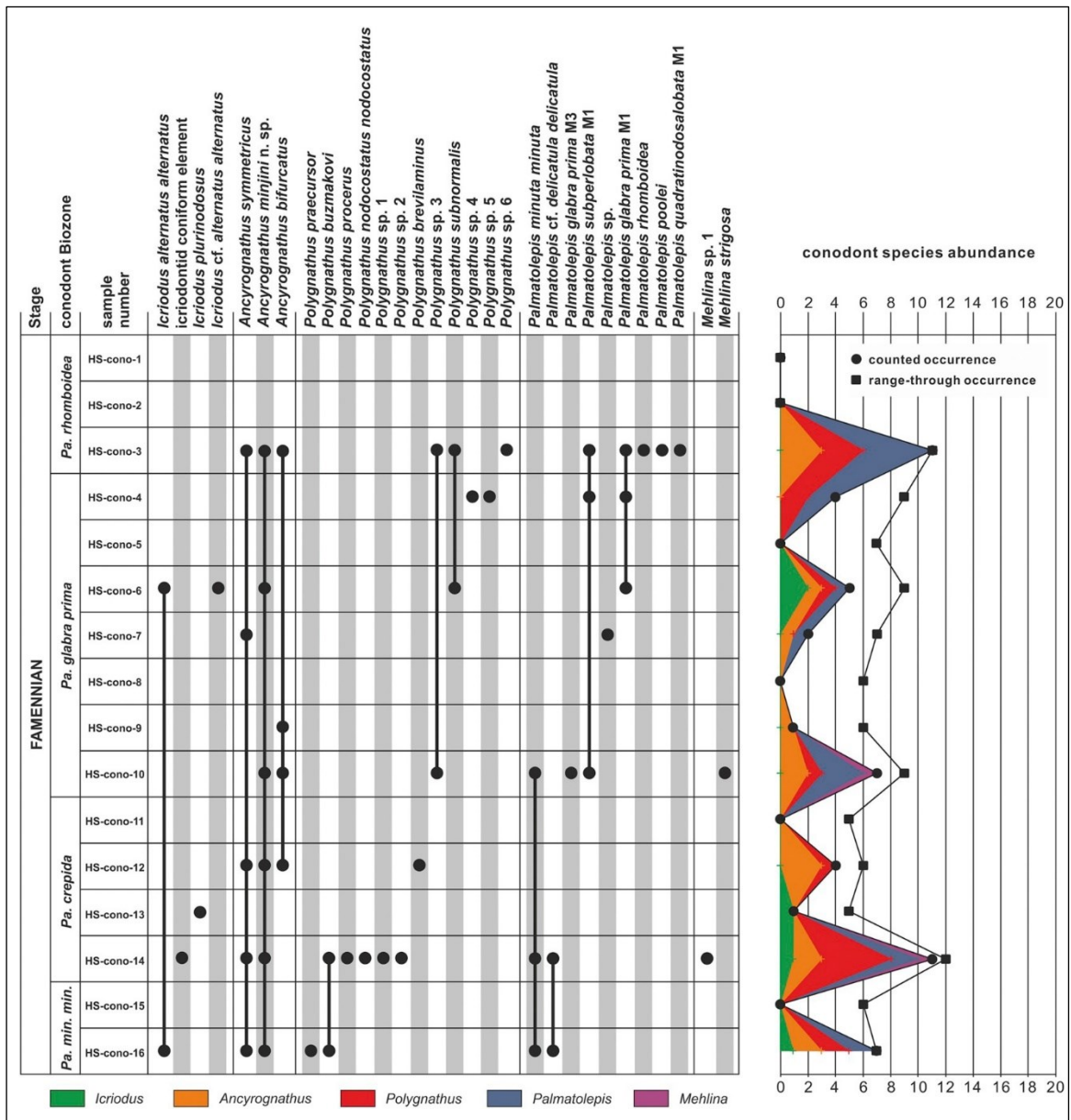


Fig. 10: Detailed distribution of conodont taxa from the Famennian strata at the Hushoot Shiveetiin gol section (modified according to Suttner et al., 2020).

Although the maximum number of total identified taxa is different in each locality, the average diversity within the samples is around 6 taxa in a Devonian sample from the Praha-Radotín section, the Na Požárech section and also the Hushoot Shiveetiin gol section. Slightly higher diversity peaks correlate with the beginning of the conodont biozone. Another similar phenomenon is that both known species and as yet undescribed taxa were found in the samples from all studied sections. In the **study II**, were these potentially new taxa left in open nomenclature: *Icriodus* sp. indet., *Lanea* sp. indet.,

Ozarkodina sp. indet., *Pedavis* sp. indet., *Wurmiella* sp. indet., *Zieglerodina* sp. indet. In the **study III**, the unknown taxa belong mainly to *Polygnathus* sp., *Palmatolepis* sp. and *Mehlina* sp. Further studies are required for description of these new taxa.

6.2 Microfacies analysis

In total, ten samples were collected and processed for petrographic thin sections from section Na Požárech. Samples from the uppermost Silurian part of the section are mostly packstones to grainstones rich in various faunal remains of ostracods, trilobites, brachiopods, gastropods, crinoids and also phosphatic fragments of fishes or conodonts. The inner filling in shells and valves is recrystallized and also the surrounding cement is affected by dolomitization. The amount of skeletal parts of crinoids increases towards the upper beds and also presence of the “*Scyphocrinites* horizon bed” around the Silurian/Devonian boundary is slightly visible in the section. The samples from these beds could be characterized as coarse grained grainstone to rudstones. The prevailing fossil remains belong to crinoids, brachiopods, trilobites, bivalves and corals. The rest of thin sections from the Devonian part of the section are mainly packstones with various bioclasts of crinoids (but in lesser numbers than in previous samples), ostracods, brachiopods, trilobites and fragments of fishes or conodonts. According to the microfacial analysis, the Na Požárech section represents an environment of relatively shallow water sedimentation. This interpretation is also supported by the presence of abundant fauna.

All together, thirteen samples were taken for the microfacial analysis from the Praha-Radotín section. The majority of the samples show calcisiltite-dominant compositions. Compared to the Na Požárech section, samples from the Praha-Radotín section are less rich in diversity of faunal remains. Samples from the Silurian part of the section can be characterized as calcisiltite to packstone with visible structures of recrystallization processes (dolomitization and stylolitization). The crystals of early-formed pyrite or pyrrhotite are also present. The recrystallization is also significant on the bioclasts of prasinophytes and chitinozoans, which are partially fragmented. In the lower Devonian samples, there is a noticeable transition from a relatively deeper calcisiltites to the coarse-grained grainstones to rudstones of the *Scyphocrinites* horizon beds. Samples are full of crinoidal hash, most of them are coated by algae crusts. The number of crinoidal fragments decreases slightly in the upper beds, and other faunal groups also appear in the

samples (mostly ostracods, gastropods, bivalves and phosphatic remains from fish or conodonts). According to the microfacial analysis, the Praha-Radotín section could be interpreted as a transitional environment, which represented pelagic conditions (in Silurian) with the transition to a relatively more shallow water sedimentation (in lowermost Devonian). This interpretation is also confirmed by changes in composition and diversity of the faunal groups. In the first sample, where the pyrite and pyrrhotite is present, the fauna (and also the conodont elements) is totally missing. It points out to the dysoxic or anoxic conditions below the seafloor. Then bioclasts become more abundant and also the sediment is changing to more coarse grained, without the pyrite or pyrrhotite crystals.

In total, sixteen samples were collected for the microfacial analyses from the Hushoot Shiveetiin gol section. The majority of the samples represent predominantly clastic sediment composition with presence of different faunal groups. The lowermost part of the section is characterized by alternation of greenish silty mudstones and ocher brown siltstones to sandstones. Most common bioclasts in these samples belong to brachiopods, crinoids and ostracods. The greenish mudstones to fine grained silty mudstones become prevailing towards the upper beds. In these facies are also present the remains of brachiopods, bryozoans, crinoids, ostracods, rugose corals and trilobites. Several volcanoclastic layers of pyroclastic ashes were also deposited in the section, mainly during the related intra-oceanic arc volcanism episodes. According to the microfacial analysis, in the Hushoot Shiveetiin gol section there are alternation of two environments: more shallow, fine-grained siltstones rich in bioclasts, and more deeper water mudstones or finely layered mudstones to siltstones poorer to fossil remains. This points to a relatively shallow environment close to the base of the section, which is changing to the deeper facies during the *Palmatolepis crepida* Biozone. This deepening is then followed by a recurrent change to shallower environment during the *Palmatolepis glabra pectinata* Biozone. Then again in the *Palmatolepis rhomboidea* Biozone is the onset of another deepening. Despite these slight changes in bathymetric conditions, all samples from the Hushoot Shiveetiin gol section indicate shallow marine nearshore sedimentation close to the volcanically active area.

6.3 Newly described species and their biostratigraphic potential

Two new conodont species were described during the study of conodont material, which was obtained from sections in two geographically distant areas. The first of the newly reported taxon is *Zieglerodina petrea* (Fig. 11-A). This species was documented just above the base of the Devonian in two sections: Praha-Radotín section and Na Požárech section (Prague Synform, Czech Republic) (**study II.**). The studies of additional sections around the Silurian/Devonian boundary proved occurrence of this taxon also in the Cellon section in Carnics Alps (**study I.**). Its distribution in other areas points to a wider occurrence of this species not only around Perunica, but also in other parts of peri-Gondwana. This species might be important for biostratigraphy of the Silurian/Devonian boundary, because it enters in the first bed of Devonian, just at the base of *hesperius-optima* Biozone. Although, the official marker for the Devonian base is the graptolite taxon *Uncinagraptus uniformis uniformis*, graptolites are restricted to deeper marine environments, especially mudstones and dark shales. If the Silurian/Devonian boundary is developed in limestones, a conodont marker is needed. Among stratigraphically important conodonts for the Devonian base, *Icriodus hesperius* is a critical marker, but in many sections this species is missing due to its restriction to shallower environment. Thus, it is necessary to have a reliable substitute taxon or taxa. Accordingly, *Zieglerodina petrea* should play a fundamental role among spathognathodontids as a marker for the base of the Devonian in carbonate environment, where the conodont marker *Icriodus hesperius* and/or graptolite *Uncinagraptus uniformis uniformis* is missing. Also, phylogenetic relations of *Zieglerodina petrea* and other spathognathodontids were studied (mainly in **study I.**).

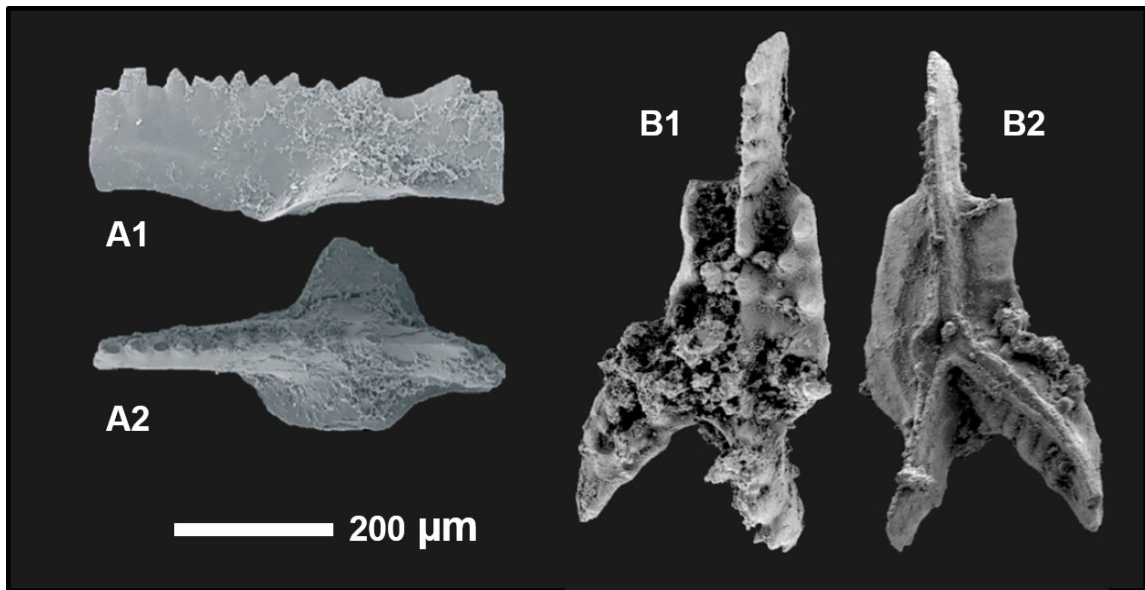


Fig. 11: New species *Zieglerodina petrea* and *Ancyrognathus minjini*. A: *Zieglerodina petrea*, RAD1, RAD-1-001, A1: lateral view, A2: upper view. B: *Ancyrognathus minjini*, HS-cono-12, MPC-Co-15/34, B1: upper view, B2: lower view.

It was pointed out that *Zieglerodina petrea* could have a close relation to *Zieglerodina paucidentata*. Both taxa share similar morphological trend – suppressed denticles in the posterior part of the P1 element and do occur in lower Devonian at close stratigraphic position. As a result, a preliminary concept was established, which shows the phylogenetic trend of gap appearance and its modification from older specimens (which bear and incipient gap only) to younger morphotypes (which are characterised by a significant developed gap) (Fig. 12). Accordingly, six cluster groups of similar morphotypes were distinguished from taxa that belong to *Z. petrea* and *Z. paucidentata* or are morphologically close to these taxa. The first group follows the characteristics of *Z. petrea*, i.e., lower number of denticles (12-13), basal cavity in the posterior part of element, widely open asymmetrical basal lobes and the shape of gap between denticles in the posterior part of element. The second group is represented by elements, which resemble both the *Z. petrea* and *Z. paucidentata* with several characters (e.g., shape of the basal lobes, number of denticles, size and shape of denticles and total proportion of the element). The gap is not less developed, but in the posterior part of the element are reduced denticles. The third group bears rather the characteristics of *Z. petrea* than of *Z. paucidentata*, such as: low number of denticles, asymmetrical basal lobes and two denticles behind the gap in the posterior part of the element. This group also has a few

characteristics that resemble *Z. paucidentata*: denticles are smaller than the cusp and the basal cavity is situated almost in the middle part of the element. The fourth group resembles characteristics of *Z. paucidentata*, like higher number of denticles (around 15), circular widely open basal lobes and basal cavity situated in the central part of the element. The gap is followed by up to four reduced denticles. All these four mentioned groups have representatives in the Lochkovian. The fifth group resembles both *Z. paucidentata* and *Z. petrea*: the gap is situated in the posterior part of the element, but small denticles should be present in the gap, number of denticles is around 10 and the basal cavity is located in the middle part of the element. However, representatives of this group occur in the Pragian. The sixth group is more different from the previous ones and it shares only morphology of the gap between denticles, whereas other parameters are different (such as size of the element, number of denticles, and narrow shape of basal platform. Also, the representatives of this group occur in the Pragian. The morphological trend with the gap between denticles on P1 elements seems to have evolved in more spathognathodontid elements at different stratigraphic levels. Therefore, possibility of splitting the taxa into (sub)species or distinction of the morphotypes should be a next step of the follow-up studies.

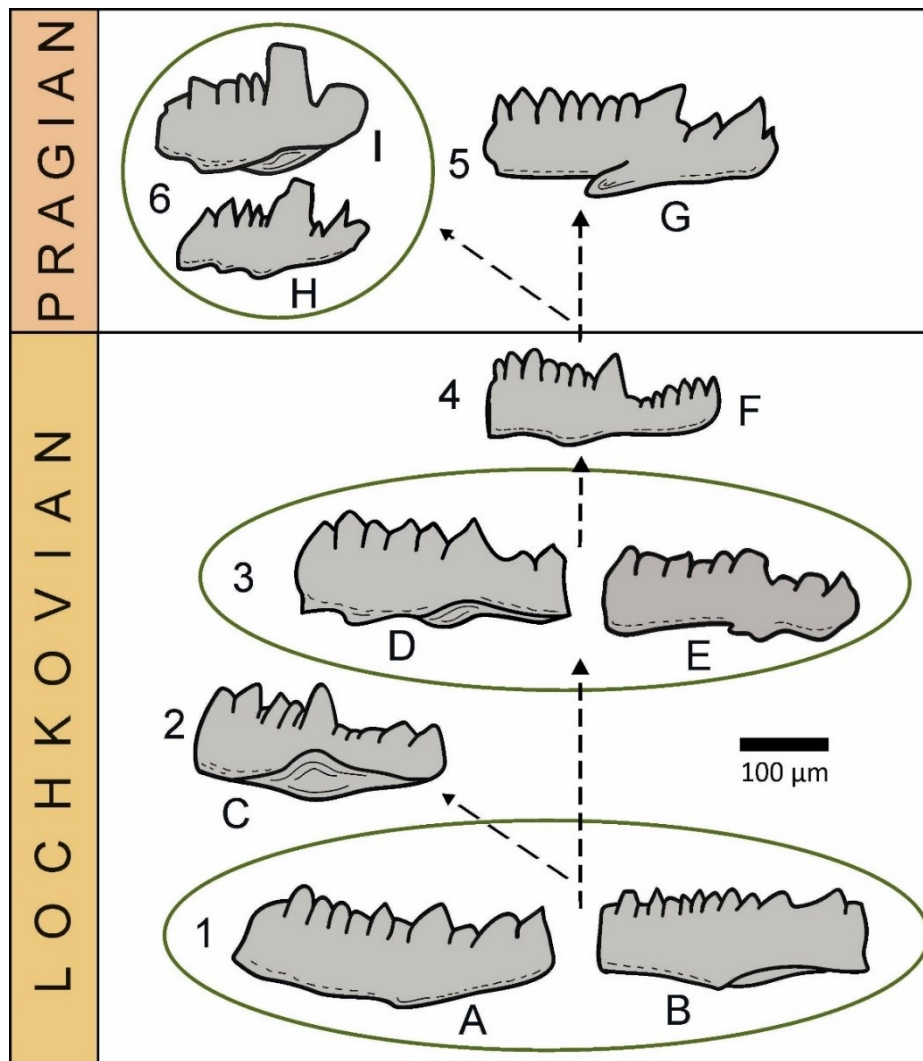


Fig. 12: Drawing of selected P1 elements of *Zieglerodina petrea* and *Zieglerodina paucidentata* clustered into groups according to morphological similarities. Group 1 follows the morphological characteristics of *Z. petrea*. Group 2 and 3 bears the morphological characteristics of both *Z. petrea* and *Z. paucidentata* and occurs in Lower Lochkovian. Group 4 resemble *Z. paucidentata*. Group 5 and 6 bears the characteristics of both *Z. petrea* and *Z. paucidentata* and occurs in the Pragian. A: *Z. petrea* Hušková and Slavík, 2020, Na Požárech section, published in Hušková and Slavík (2021, fig. 3b); B: *Z. petrea* Hušková and Slavík, 2020, Radotín Section, published in Hušková and Slavík (2020, fig. 6e); C: “*Ozarkodina*” aff. *paucidentata* Murphy and Matti, 1982, published in Mavrinskaya and Slavík (2013, fig. 6j), Mindigulovo Section; D: *Ozarkodina* cf. *paucidentata* Murphy and Matti, 1982, published in Mawson et al. (2003, pl. 4, fig. 19), Kandar–Pir Sabak area; E: *Z. cf. paucidentata* Murphy and Matti, 1982, Atrous 3 section, published in Hušková and Slavík (2021, fig. 3f); F: *Z. paucidentata* Murphy and Matti, 1982, published in Murphy and Matti (1982, pl. 1, fig. 25), Coal

Canyon section; G: *Oz. paucidentata* Murphy and Matti, 1982, published in Mathieson et al. (2016, fig. 32i), section western New South Wales – Trundle; H: *Z. cf. paucidentata* Murphy and Matti, 1982, published in Drygant and Szaniawski (2012, fig. 11t), Ivanye Zolote section; I: *Z. cf. paucidentata* Murphy and Matti, 1982, published in Drygant and Szaniawski (2012, fig. 11r), Ivanye Zolote section. Drawing modified according to Hušková and Slavík, 2021.

Another newly described taxon is *Ancyrognathus minjini* (Fig. 11-B). This species was documented from the Hushoot Shiveetiin gol section in Baruunhuurai Terrane in Mongolia (**study III.**). The stratigraphic range of the *Ancyrognathus minjini* is from the early to middle Famennian. The taxon first occurs in the upper part of the *Palmatolepis minuta minuta* Biozone and continues through the *Palmatolepis crepida* Biozone, *Palmatolepis glabra prima* Biozone to the *Palmatolepis rhomboidea* Biozone. Until now, this taxon was described only from this only section. The species seems to be a local marker for paleoecology and biostratigraphy in relation to western Mongolia. Further studies are necessary to prove the endemic provenance of this taxon, or to widen the regional occurrence of the species. Especially a comparison with the closely located sections in Junggar of Xinjiang (Northwest China) would be necessary. A manuscript discussing the paleoecological specifications of this taxon and its relationship to other Famennian conodont species, is already in preparation (by T. Suttner et al., including applicant of this thesis).

6.4 Palaeoecological and paleogeographical evaluation

Results from microfacies analysis and composition of conodont faunas suggest slightly changing bathymetric conditions in specific intervals in the studied sections. In the section Praha-Radotín is visible a change from deeper marine environment to more shallow conditions around the Silurian/Devonian boundary, then another deepening follows. It is similar in the section Na Požárech, but not as marked as in the Praha-Radotín section. Representatives of ozarkodinids and icriodontids were presented in both sections, but ozarkodinids shows higher diversity and abundance. However, this abundance changes in time, probably in connection to the fluctuation in water depth. Also, several new taxa observed in the lowermost Devonian will require systematic classification and

further studies. Most of the representatives of the conodont taxa are cosmopolitan in the lowermost Devonian, mainly due to low geomorphological and ecological barriers. It should be noted that the composition of conodont faunas is biased by a presence calciturbidite deposition both in the Praha-Radotín and Na Požárech sections, where some of the elements could have been transported together with other faunas from the primary shallower to secondary deeper environment. Especially important are conodont data from the Praha-Radotín section, where *Icriodus* cf. *woschmidti woschmidti* co-occurs with the graptolite index taxon *Uncinatograptus uniformis uniformis* in the same bedding couplet, i.e., just below the entry of *Icriodus hesperius*, which is the current conodont biostratigraphic marker of the Silurian/Devonian boundary. This is an example of unique co-occurrence of graptolites and conodonts due to convergent facies that is convenient for both facies-depend faunas.

In addition to that, changes in bathymetry are recorded in the Hushoot Shiveetiin gol section from the *Palmatolepis minuta minuta* to *Palmatolepis rhomboidea* biozones (for more detailed information see chapter Microfacies analysis). In most samples, the polygnathid-palmatolepid assemblage of conodonts predominates, which is, however, interrupted several times by a short change to an icriodontid-polygnathid assemblage. According to biofacial models (Dreesen and Houleberghs, 1980; Dreesen and Thorez, 1980; Dreesen et al., 1986; Dreesen, 1992) this change should indicate a deepening in these intervals. The composition of the conodont fauna also helps to specify the paleobiogeographical and paleoecological reconstruction. Representatives of the cosmopolitan taxa of *Ancyrognathus*, *Icriodus*, *Mehlina*, *Polygnathus* and *Palmatolepis*, show relatively low biodiversity. Slightly higher diversity was observed in endemic representatives of *Ancyrognathus* and *Icriodus*. Representatives of common cosmopolitan taxa *Pelekysgnathus* are completely absent, probably due to the prevailing siliciclastic facies despite carbonates. This composition of conodont taxa points out to the factors that could limit the conodont distribution, such as latitude, temperature, geomorphological barriers and also the ecological barriers. Most of these taxa occur in tropical environments of a low latitude of the northern hemisphere and in the low latitude arid belt of the southern hemisphere. In addition, most taxa are bound to shelf areas, with the predominant limestone facies, but at the Hushoot Shiveetin gol section dominates mostly the silty mudstone to siltstones and sandstones with only low amounts of carbonates.

7. Conclusion

The study of conodont faunas and microfacies analysis were carried out in the Na Požárech, Praha-Radotín and Hushoot Shiveetin gol sections. Additional conodont material from the Cellon section and Atrous 3 section was studied in museum collections at Georg-August-Universität in Göttingen. The study included field work, collection and preparation of conodont elements, their taxonomic classification, biostratigraphic correlation, description of new species, microfacies analysis, interpretation of results. The conclusions resulted in three publications.

All together, 38 samples for conodonts and 39 samples for microfacies analysis were collected and processed. In total, thirteen conodont taxa were described from the section Na Požárech, eighteen from the section Praha-Radotín and thirty from the Hushoot Shiveetiin gol section. According to the similar stratigraphic range from uppermost Silurian to lowermost Devonian, the sections Na Požárech and Praha-Radotín were compared and correlated. Samples from both sections show a high diversity in taxa of families Spathognathodontidae and Icriodontidae. The microfacial analysis and composition of conodont taxa confirm the differences in depositional environments around the Silurian/Devonian boundary, where the characteristic perigondwanan *Scyphocrinites* horizon is present in both sections. The Na Požárech section represents relatively shallow-water marine environment (due to the coarser detrital component, abundance and diversity of fauna and well oxygenated conditions), while the Praha-Radotín section is relatively deeper environment (predominance of micritic component, less abundant fauna, presence of organic matter, pyrite and pyrrhotite). Due to the predominance of cosmopolitan conodont taxa around the Silurian/Devonian boundary, a similar composition of conodont faunas was reported in both sections.

A stratigraphically important new conodont species *Zieglerodina petrea* was described from both Bohemian sections. The occurrence of this taxon was then confirmed by subsequent studies also from the Cellon section. Its occurrence at the same stratigraphic position in these sections proves its importance as a biostratigraphic marker among the ozarkodinids for the Silurian/Devonian boundary, especially in the sections around the peri-Gondwana, which lack both graptolites and the oldest representatives of conodont genus *Icriodus*. Morphology and origin of this promising biostratigraphic marker among lowermost Devonian conodonts was studied in detail, as well as its phylogenetic relations with *Zieglerodina paucidentata* – an early Devonian taxon that shows a close

morphological similarity with *Z. petrea*. The result of this study is a proposal for subdivision into several morphological groups of taxa that belong to *Z. petrea* and *Z. paucidentata*, or are morphologically close to these taxa. The subdivision is based on possible phylogenetic trend that reflects the development of the gap on P1 elements. The proposed phylogeny supposes that the older specimens bear an incipient gap only, and there is a gradual transition into distinct gap in younger specimens. This proposal can be a basis for the follow-up studies leading to a subdivision of these taxa into subspecies or morphotypes. This could be helpful for refinement of conodont biostratigraphy above the Silurian/Devonian boundary.

Another section for the study of conodonts and microfacies was selected in Mongolia. According to the studies of Baruunhuurai Terrane, it is evident that the Hushoot Shiveetin gol section represents shallow-intertidal to open marine environments affected by volcanic activity. The biostratigraphic study of conodont elements and regional correlation confirmed the Famennian age of the Upper Devonian deposits of the section. Some of conodont taxa found belong to cosmopolitan species (e.g., *Icriodus alternatus alternatus* and *Mehlina strigosa*), but also several species are supposed to be endemic (*Ancyrognathus minjini* and *Icriodus plurinodosus*). The conodont distribution in this area is mostly affected by changing of shallower and relatively deeper water environment and siliciclastic-dominated sedimentation during the Famennian. Comparison with other sections from the Central Asian Orogenic Belt is recommended to refine the results according to conodont taxa and paleoenvironment of this region.

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List of Appendices

Appendix 1:

Hušková, A., & Slavík, L., 2021. Morphologically distinct ozarkodinids (Conodonta) at the Silurian-Devonian boundary: review and correlation. *Bulletin of Geosciences*, 96(3), 327–340.

Appendix 2:

Hušková, A., & Slavík, L., 2020. In search of Silurian/Devonian boundary conodont markers in carbonate environments of the Prague Synform (Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109126: 1–17.

Appendix 3:

Suttner, T. J., Kido, E., Ariunchimeg, Y., Sersmaa, G., Waters, J. A., Carmichael, S. K., Batchelor, C. J., Ariuntogos M., Hušková, A., Slavík, L., Valenzuela-Ríos, J. I., Liao, J.-C., & Gatovsky, Y. A., 2020. Conodonts from Late Devonian island arc settings (Baruunhuurai Terrane, western Mongolia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109099: 1–22.

Prohlášení školitele o podílu studenta na publikacích, které jsou součástí doktorské práce

Jako školitel studentky Mgr. Anety Formáčkové prohlašuji, že studentka se podílela na pracích, které byly předloženy jako součást její disertační práce, následujícím podílem:

I. **Hušková, A.**, & Slavík, L., 2021. Morphologically distinct P1 elements of *Zieglerodina* (Conodonta) at the Silurian–Devonian boundary: review and correlation. *Bulletin of Geosciences*, 96(3), 327–340. DOI: <https://doi.org/10.3140/bull.geosci.1822>

- 70% sběr a příprava materiálu, taxonomické zhodnocení, interpretace stratigrafických, paleoekologických dat, kompilace dat, interpretace výsledků, příprava a finalizace rukopisu

II. **Hušková, A.**, & Slavík, L., 2020. In search of Silurian/Devonian boundary conodont markers in carbonate environments of the Prague Synform (Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109126: 1–17. DOI: <https://doi.org/10.1016/j.palaeo.2019.03.027>

- 70% sběr a příprava materiálu, taxonomické zhodnocení, interpretace stratigrafických, paleoekologických dat, kompilace dat, interpretace výsledků, příprava a finalizace rukopisu

III. Suttner, T. J., Kido, E., Ariunchimeg, Y., Sersmaa, G., Waters, J. A., Carmichael, S. K., Batchelor, C. J., Ariuntogos M., **Hušková, A.**, Slavík, L., Valenzuela-Ríos, J. I., Liao, J.-C., & Gatovsky, Y. A., 2020. Conodonts from Late Devonian island arc settings (Baruunhuurai Terrane, western Mongolia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109099. DOI: <https://doi.org/10.1016/j.palaeo.2019.03.001>

- 5% příprava materiálu, interpretace konodontových dat, podíl na přípravě a finalizaci rukopisu

RNDr. Ladislav Slavík, CSc.

školitel

The declaration of the supervisor on the student's participation in publications that are part of the doctoral thesis

As the supervisor of Mgr. Aneta Formáčková I declare her participation in the studies that were submitted as a part of her Ph.D. thesis by the following contribution:

I. **Hušková, A.**, & Slavík, L., 2021. Morphologically distinct P1 elements of *Zieglerodina* (Conodonta) at the Silurian–Devonian boundary: review and correlation. *Bulletin of Geosciences*, 96(3), 327–340. DOI: <https://doi.org/10.3140/bull.geosci.1822>

- 70% collection and preparation of the material, taxonomic classification, stratigraphic and palaeoecological interpretation, data compilation, interpretation of results, preparation, finalization and final editing of the manuscript

II. **Hušková, A.**, & Slavík, L., 2020. In search of Silurian/Devonian boundary conodont markers in carbonate environments of the Prague Synform (Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109126: 1–17. DOI: <https://doi.org/10.1016/j.palaeo.2019.03.027>

- 70% collection and preparation of the material, taxonomic classification, stratigraphic and palaeoecological interpretation, data compilation, interpretation of results, preparation, finalization and final editing of the manuscript

III. Suttner, T. J., Kido, E., Ariunchimeg, Y., Sersmaa, G., Waters, J. A., Carmichael, S. K., Batchelor, C. J., Ariuntogos M., **Hušková, A.**, Slavík, L., Valenzuela-Ríos, J. I., Liao, J.-C., & Gatovsky, Y. A., 2020. Conodonts from Late Devonian island arc settings (Baruunhuurai Terrane, western Mongolia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 549, 109099. DOI: <https://doi.org/10.1016/j.palaeo.2019.03.001>

- 5% preparation of the material, interpretation of conodont data, contribution to the preparation and finalization of the manuscript

RNDr. Ladislav Slavík, CSc.

The Ph.D. supervisor