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The first documented co-occurrence of conodonts and graptolites in Silurian (Telychian) black shales of the Prague Synform, Czech Republic, and its stratigraphical and palaeoecological significance

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Abstract

The Želkovice locality, located in the south-western part of the Prague Synform, is well-known for its exceptionally well-preserved graptolites in black shales. Despite being studied repeatedly by several authors for over 170 years, no record of conodonts has been found until now. Both conodonts and graptolites are significant biostratigraphic groups of Paleozoic fossils. However, papers about their co-occurrence are rare. Their occurrence is tied to distinct lithofacies, which makes direct biozonal correlation difficult. Their partial overlap sheds new light on ecological niches, resilience, and the palaeoecological conditions of the environment. Determined conodonts belong to cosmopolitan taxa with a long range, inhabiting the deeper, distal parts of the shelf or continental slope. A total of 10 conodont species were identified at the same locality, spanning the entire *linnaei* Biozone. The occurrence of the index species *Distomodus staurognathoides*, whose stratigraphic range overlaps with the locally used graptolite *linnaei* Biozone and the internationally used *guerichii* Biozone, is documented. This study also documents rare specimens of pelagic fauna for the first time and discusses hypothetical parasitism and predation in conodonts and graptolites. This is the first study to describe the co-occurrence of both groups within the same lithology (black shale) and stratigraphic level, not only at the Želkovice site, but also elsewhere in the Silurian of the Prague Synform.

Keywords Silurian, Co-occurrence, Conodonts, Graptolites, Barrandian area, Predation, Parasitism

Introduction

Planktonic graptolites and pelagic conodonts are two groups of the most-commonly used fossils for the detailed biostratigraphic subdivision of Paleozoic marine sediments, particularly in offshore environments. The occurrence ranges of some taxa and communities allow biozones to be established on a regional and global scale. The length of individual biozones varies. In the Ordovician and Silurian periods, for example, this ranges from 1.5 million years to, in the best cases, only a few hundred thousand years (Corradini et al., 2024; Goldman et al., 2020; Maletz, 2017; Štorch, 2023; Štorch et al., 2024). However, their potential for

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biostratigraphic use is, in most cases, limited by their occurrence in different facies, because graptolites usually occur in siliciclastic sediments, whereas conodonts occur in biogenic sediments. The 'limits of occurrence' in different lithofacies are influenced by their potential for preservation, which depends on their biochemical composition (e.g., the organic phosphate composition of conodont elements vs. the polysaccharide associated with collagen fibres of graptolite tubaria - see Maletz, 2023; Towe & Urbanek, 1972). This reflects their original preferred niche and lifestyle in the aquatic environment. Consequently, both conodonts and graptolites are also good indicators of environmental conditions.

The limits of occurrence, however, were subject to changes and fluctuations in natural environmental conditions, including the rise and fall of sea levels, changes in water temperature, the formation of glaciers and continents, and changes in the direction and intensity of ocean currents. Moreover, at present, the ‚limits of occurrence' are to some extent emphasised by the research methodology applied to graptolites and, primarily, conodonts. Conodonts were first reported by Pander (1856) and were exclusively described in shales until the 1940s (Perner, 1894; Schmidt, 1934; Scott, 1934; Ulrich & Bassler, 1926, etc.). However, with the publication of the work of Ellison & Graves (1941), which describes conodonts obtained from limestones using organic acids, there was a significant turn of events. Since the 1950s, most publications have described conodonts primarily from limestone facies, although there are exceptions (Albanesi & Ortega, 2016; Barnes & Williams, 1988; Bergström et al., 2017; Loydell et al., 2007, 2009). Graptolites have been found in various types of rock, but they are most commonly found in siliciclastic deposits, particularly in shales. Nevertheless, the most important information regarding their morphology, which helps us better understand their astogeny and biological relationships, is obtained from chemically isolated 3D rhabdosomes from limestones, marls, or clay-rich sediments (Jarochowska et al., 2013; Maletz, 2017).

Despite the general preference for studying both groups from different lithofacies and the overall manner and possibility of their preservation, multiple cases of co-occurrence of graptolites and conodonts in the same lithologies do occur and are described in the fossil record. These cases are not common, but not rare, and are known from both the Ordovician and Silurian (see Bergström, 1971, 1986; Barnes & Williams, 1988; Ferretti et al., 1998, 2009; Pålsson et al., 2002; von Bitter et al., 2007; Loydell et al., 2003, 2007, 2009; Männik et al., 2011; Bergström et al., 2017; Spiridonov et al., 2017).

However, no publication has yet recorded the occurrence of conodonts or other fossil faunas from the Želkovice locality, nor has it addressed the palaeoecological conditions of the environment in which the black shales of the Litohlavy Formation, which correspond to the *linnaei* Biozone, were deposited in any depth. Although Strossová et al. (2024) repeatedly mentioned the presence of conodonts in their descriptions of layers Z0, Z1, and Z2 (see pp. 6, 7, and 11), this important occurrence has not been confirmed or discussed in any way.

The main goals of this paper are: (i) to determine and illustrate conodont elements from the shales of the Litohlavy Formation; (ii) to discuss and interpret the occurrence of conodonts in the facies of local black graptolite shales, as well as the palaeoecological environmental conditions of the Želkovice locality during the deposition of the black shales of the *linnaei* Biozone; (iii) to discuss in a lesser extent the common biostratigraphic overlap of two prominent groups of Paleozoic organisms, on whose distinct facies occurrences detailed biostratigraphy in siliciclastic and biogenic sediments is established.

Finally, the discussion of a hypothetical example of predation and parasitism on graptolites and their potential originators is one of the key goals of the paper.

Geological setting and history of research

The Prague Synform is located in the central part of the Teplá-Barrandian Unit. The central area consists of Silurian and Devonian deposits; the marginal areas are of Ordovician Period (Fig. 1a, b). The area's structural and tectonic development has been described in detail by several authors, including Havlíček (1981), Havlíček et al. (1994), Chlupáč et al. (1998), Melichar (2004), Röhlich (2007), and Vacek and Žák (2017). The Silurian deposits in the Prague Synform consist of shale facies that gradually transition to limestone facies. The deposition of shales and limestones was accompanied by volcanic activity (Kříž, 1992; Štorch, 2006). Currently, these rocks are formally divided into five successive formations: the Želkovice, Litohlavy, Motol, Kopanina, and Požáry.

The Želkovice and Litohlavy formations consist of black silty shales, siliceous shales, clayey shales, silicites, pale-coloured mudstone and claystone (especially in the Litohlavy formation), as well as basal mudstones. There are also exceptional volcanic-carbonate facies containing shelly fauna (Havlíček & Kříž, 1973; Štorch, 2001). Štorch (2023) summarised the precise characteristics of the individual Silurian formations and their correlation within graptolite biozones.

The upper part of the Želkovice Formation and the lower part of the Litohlavy Formation have been reported at the studied locality. These formations are characterised by siliceous shales and black silty shales, as well as black

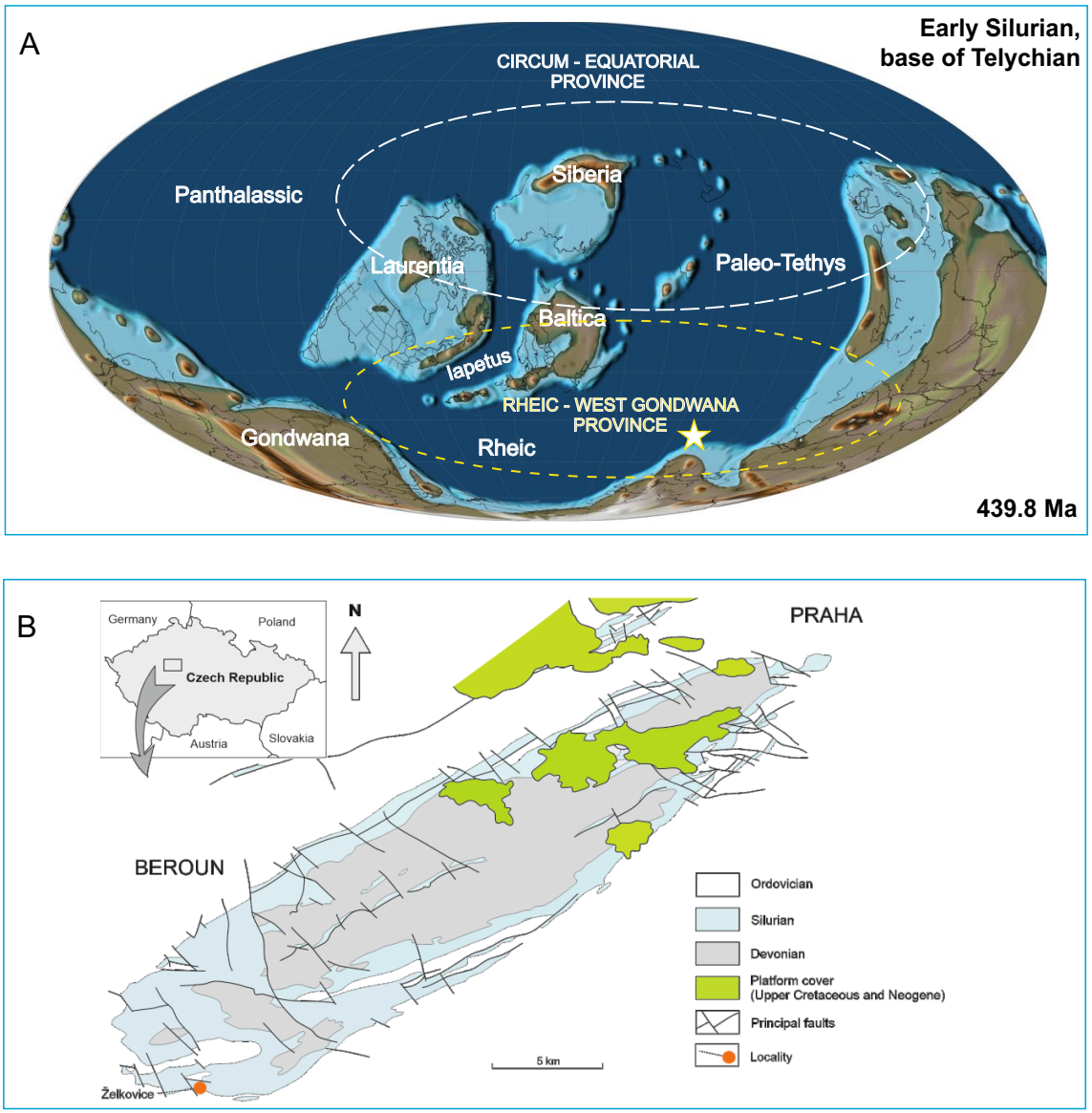

Fig. 1 **A** The Early Silurian (early Llandovery, base of Telychian–439,8 Ma) palaeogeographical map after Scotese (2014), showing presumed location of the study area (marked by a star). **B** Position of Želkovice locality in Prague Synform, highlighted by an orange point. This locality yielded the described conodont and graptolite material. Base map provided by Š. Manda.

silicites. The Litohlavy Formation consists of graptolite-bearing black shales irregularly alternating with pale-coloured mudstones; the latter are devoid of graptolites. The *sedgwickii*, *rastrum*, *linnaei,* and *turriculatus* biozones are found in the southern part of the village of Želkovice.

The boundary between the Aeronian *Lituigraptus rastrum* Biozone and the lower Telychian *Rastrites linnaei* Biozone is described within a pale-coloured mudstone without graptolites.

A basalt sill occurring within it separates the *linnaei* Biozone (see Fig. 2; Štorch, 2023).

The Želkovice locality is historically significant for graptolite research based on unusually favourable preservational conditions. Barrande (1850), Perner (1897), and Bouček and Přibyl (1941) were among the first to describe species from the *Rastrites linnaei* Biozone in Želkovice. Bouček (1953) studied the stratigraphic position and division of the locality and recognised the *sedgwickii* Biozone for the first time. Currently, its upper part belongs to the *Lituigraptus rastrum* Biozone (Štorch, 2023; Štorch & Frýda, 2012), which corresponds to the *Stimulograptus halli* Biozone of Loydell (1991, 1992).

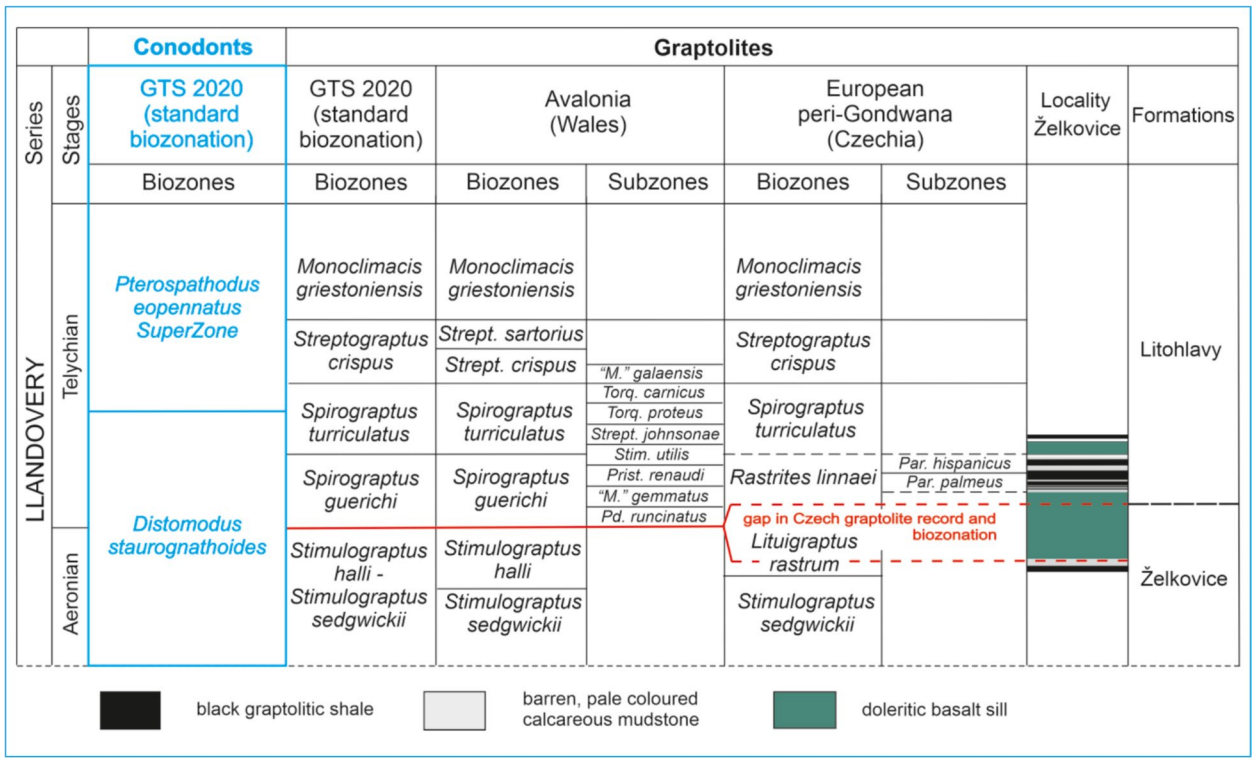

Fig. 2 Stratigraphic-sedimentary chart and biozonation of the key interval at the Želkovice locality. Modified after Strossová et al. (2024) and McAdams et al. (2019).

Bouček (1953) divided the *linnaei* Biozone into the lower *Petalograptus (Parapetalolithus) palme*us and upper *Petalograptus (Parapetalolithus) hispanicus* subzones. Strossová (2024) recently studied *Parapetalolithus* species, including their juvenile stages, and discussed the overall composition of the graptolite community and its fluctuations in a case study (in Strossová et al., 2024).

The Prague Synform area has been the subject of geological and palaeontological study since the 18th Century. Barrande (1850) and Suess (1851) were the first to describe graptolites from the Prague Basin. A pioneer in modern graptolite research, Bouček (1933, 1937) focused primarily on the Ordovician and Silurian sedimentary successions in the same area in the (Bouček, and Přibyl, 1930)s. The first mention about graptolites from the Želkovice locality within the *linnaei* Biozone was published by Barrande (1850), followed by Perner (1897), Bouček (1953), Bouček and Přibyl (1941), Štorch (1994), and, most recently, Strossová (2024) and Strossová et al. (2024). The locality is currently inaccessible, and the most recent material used in this study was obtained during a research rescue operation in the summer of 2021 by the first author. Conodonts in the Prague Synform are important for the stratigraphy of limestone facies. They are essential for understanding the alternating sequences of shale and limestone layers from the Silurian and Devonian periods, where the graptolite record is either incomplete or entirely absent (see Manda et al., 2012, 2019, 2023; Weinerová et al., 2024).

The first report of conodonts in the Prague Basin was made by Perner (1894), but this is questionable. The so-called ‚*Prioniodus barrandei*' originated from Barrande's ‚Lapworth Colony' near Zdice. This site was later rediscovered by Bouček (1930); however, he did not mention the occurrence of any other conodonts. Both Bouček (1930) and Štorch (1994) described a graptolite community from the ‚Lapworth Colony' that corresponds to the *linnaei* and *crispus* biozones in terms of age. Unfortunately, it is not possible to confirm or rule out the identification of this conodont. As Tonarová (2008) and Tonarová et al. (2012) summarised, the deposition of the type material of *P. barrandei* remains unknown.

Over the last 150 years, several papers about graptolites have been published from the Želkovice locality (see, for example, Barrande, 1850; Perner, 1897; Bouček & Přibyl, 1943 ; Bouček, 1953; Štorch, 1994).

Nevertheless, no paper dealing with conodont elements from the eponymous locality has been published. Strossová et al. (2024) mentioned ‚some conodont elements' in the descriptions of the study layers for the first time, but without providing further details.

Material and methods

The conodonts and graptolites were photographed either dry or immersed in ethanol using an Olympus SZX16 and an Olympus SZX10 stereo microscopes fitted with a Canon EOS 2000D camera at the Institute of Geology of the Academy of Sciences in Prague, Czech Republic. Figures containing photos and line drawings were created using Adobe Photoshop and CorelDRAW software. Conodonts are preserved embedded in the pelitic matrix of the rock, and only part of the element are observable, being the rest of the element covered.

Graptolites are mostly preserved as flattened silvery impressions on black shale surfaces, and are rarely partially pyritized and preserved in low relief. The conodonts and graptolites were collected by the first author (ZS) during in situ sampling of the lower Litohlavy Formation at the Želkovice sections. The material is currently temporarily stored at the Institute of Geology, Academy of Sciences of the Czech Republic in Prague, and will later be deposited in the collection of Zuzana Strossová (prefix ZAZ) at the Czech Geological Survey in Prague. The illustrated graptolite specimens and conodont elements with the prefix 'L' are from the collections of the National Museum in Prague (Barrande's type material, Perner, Bouček and Přibyl) and are stored at its Horní Počernice site in Prague.

All determined conodont taxa are mentioned in Table 1. Figure 3 shows the deposition of scattered conodont specimens between individual graptolites on the shale surface. All recognised conodont taxa are illustrated in Figs. 4 and 5. The key, index species of graptolites are shown in Fig. 6. The newly documented, rarely preserved accompanying fauna is illustrated in Fig. 7. All material, which was the subject of this study, comes exclusively from the Želkovice locality in Prague Synform, from black shales of the age *linnaei* Biozone in the base of the Litohlavy Formation (see Fig. 2).

Results

Conodonts

More than 170 conodont elements were discovered on black shales surfaces of the Litohlavy Formation from the Želkovice locality. Of these, 159 of the best preserved conodonts were selected for this study. In general the state of preservation is not good, and the determination of many elements is difficult because they are imbedded in the rock and, therefore, only partially observable (see Figs. 4 and 5 and appendices 1 and 2). As example, the two platform P1 elements (see Fig. 4, element W) collected are exposed in lower and in lower-lateral view, respectively, whereas the main diagnostic features are observable in upper view. We were able to determine only about a half of the fauna, and among those only one fourth tentatively at species level, whereas the rest is left in open nomenclature. The list of taxa discriminated and their abundance is reported in Table 1.

The large majority of the association is represented by genera which apparatuses are composed only by coniform elements (*Dapsilodus*, *Panderodus*, *Pseudooneotodus* and *Walliserodus*), which represent the 68% of the determined association. Platforms and ramiforms elements are less represented and are attributed to genera *Aspelundia*, *Distomodus*, *Ozarkodina*, and *Wurmiella*. *Distomodus staurognathoides* (Walliser, 1964) is the index species for the eponymous biozone that spans the upper Aeronian and lower Telychian (Corradini et al., 2024), and encompass several graptolite biozones, including the *S. guerichi* Biozone (Melchin et al., 2020) that is equivalent to the local Czech *R. linnaei* Biozone (Fig. 6; Štorch et al., 2024), to which is attributed the studied section. The other discriminated taxa has a longer stratigraphic distribution, that includes the *R. linnaei* graptolite Biozone.

Table 1 List of determined conodont taxa and the number of recognized elements of individual elements

Conodont taxa	no. of elements
Aspelundia fluegeli (Walliser, 1964)	5
Aspelundia sp.	12
Dapsilodus obliquicostatus (Branson and Mehl, 1933)	4
Dapsilodus cf. *praecipuus* Barrick, 1977	2
Dapsilodus cf. *sparsus* Barrick, 1977	2
Dapsilodus sp.	17
Distomodus staurognathoides (Walliser, 1964)	8
Distomodus sp.	4
Ozarkodina sp.	2
Panderodus cf. *recurvatus* (Rhodes, 1953)	1
Panderodus sp.	20
Pseudooneotodus beckmanni (Bischoff and Sannemann, 1958)	2
Walliserodus sp.	8
Wurmiella sp.	2

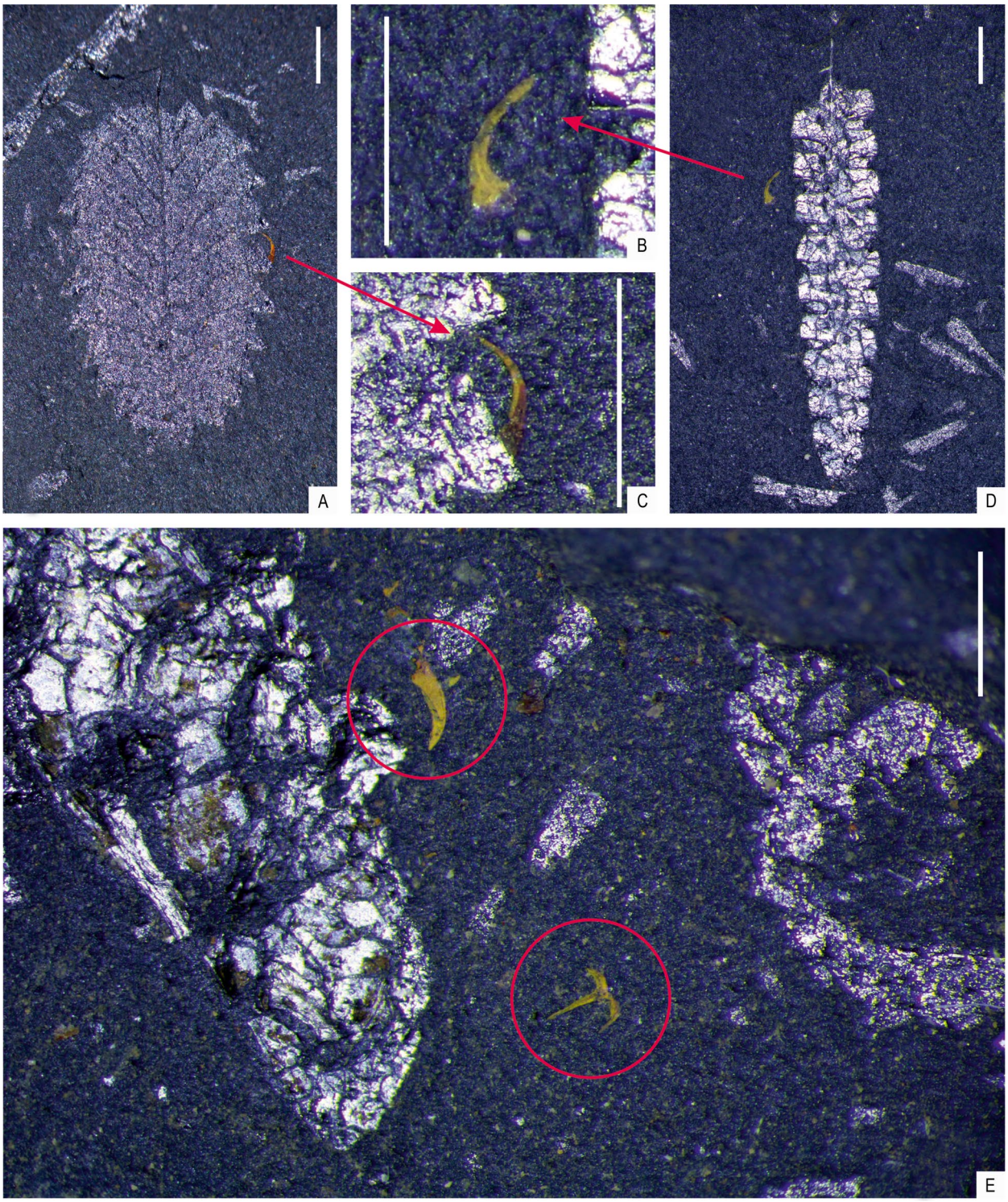

Fig. 3 An example of the preservation and size ratio of scattered conodont elements to graptolite rhabdosomes on the surface of black shales (**A**, **D**, **E**). **B**, **C**—Detail of conodont elements and their positions near (or in) the thecae apertures of the graptolites *Parapetalolithus ovatus* (Barrande, 1850) in figs A, C), specimens no. ZAZ 50 and *Metaclimacograptus asejradi* Legrand, 1993 (in figs. B, D), specimens no. ZAZ 111. **E** The conodont elements are captured in red circles. Conodonts *Walliserodus* sp. (circle above) and *Aspelundia* sp. (circle below) are found near the index graptolite species *Spirograptus guerichii* (right), sample no. ZAZ 136. All illustrated conodont elements and graptolites originate from the *linnaei* Biozone, the lowermost Litohlavy Formation in the Želkovice locality of the Prague Synform. Scale bars represent 1 mm.

(See figure on next page.)

Fig. 4 Conodont taxa identified from surface of black shales. **A** *Dapsilodus* sp., specimen no. ZAZ 122. **B** *Dapsilodus* sp., specimen no. ZAZ 123. **C** *Dapsilodus* cf. *praecipuus* (Barrick, 1977), specimen no. ZAZ 124. **D** *Dapsilodus* cf. *praecipuus* (Barrick, 1977), specimen no. ZAZ 125. **E** *Dapsilodus* cf. *sparsus* (Barrick, 1977); specimen no. ZAZ 126. **F** *Dapsilodus* cf. *sparsus* (Barrick, 1977); specimen no. ZAZ 127. **G** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 128. **H** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 129. **I** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 130. **J** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 131. **K** *Dapsilodus* sp, specimen no. ZAZ 133. **L** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. L 30167 (b). **M** *Pseudooneotodus beckmanni* (Bischoff & Sannemann, 1958), specimen no. L 31470 (b). **N** *Wurmiella* sp., specimen no. L 31470 (c). **O** *Aspelundia fluegeli* (Walliser, 1964), specimen no. ZAZ 135. **P** *Panderodus* sp., specimen no. L 31624 (c). **Q** *Panderodus* cf. *recurvatus* (Rhodes, 1953) specimen no. ZAZ 132. **R** *Aspelundia* sp., element S0, specimen no. ZAZ 136. **S** *Aspelundia* sp., specimen no. ZAZ 137. **T** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 139. **U** fragment of *Distomodus* sp., specimen no. ZAZ 141. **V** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 138. **W** *Distomodus staurognathoides* (Walliser, 1964), P1 element, specimen no. ZAZ 142. **X** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 140. All illustrated conodont elements originate from the *linnaei* Biozone, the lowermost Litohlavy Formation in the Želkovice locality of the Prague Synform. Elements C and J were photographed using the ethanol, the others without. Scale bars represent 1 mm.

Graptolites

The damaged graptolite rhabdosomes are from material from the Želkovice locality, *linnaei* Biozone age, which includes a smaller part of the Petr Štorch collection (obtained in the 1990s) and a larger part of the Zuzana Strossová collection (7180 specimens), obtained during the research rescue operation in the summer of 2021. All the material is stored in the collections of the Czech Geological Survey, prefix ZAZ. In total, more than 9500 graptolite specimens were examined, of which more than 40 showed signs of damage of rhabodosomes, interpreted as a result of predation.

Broken and folded or partially broken and interrupted rhabdosomes have been documented in the uniserial graptolites *Streptograptus* sp. A (14), *Stimulograptus becki* (16), *Pristiograptus dentatus* (4) or *Torquigraptus contor*tus (7) and many specimens from the genus *Rastrites* (several dozen) (see Fig. 8). Especially, in specimens of the genus *Rastrites*, several graptolites have been documented to be broken or bent and twisted after the 2–4 thecae. Due to the delicate morphology of the rhabdosome, the possibility cannot be excluded in some species (e.g. *Rastrites abbreviatus*) that the interruption of the rhabdosome was caused by the fragility of the rhabdosome, and not by the external environment.

No specimens of biserial graptolite species have yet been documented whose rhabdosome disruption could be attributed to predation.

Discussion

Taphonomical view of black shales from Želkovice locality, *linnaei* Biozone

Bouček and Přibyl (1941), Bouček (1953), Štorch (1994) and Strossová et al. (2024) confirmed that the sedimentation of the black shales of the Litohlavy Formation in the *linnaei* Biozone occurred slowly under relatively calm conditions. There is no evidence of turbidites in the black shales derived from distant lands that have ever been observed or described. Black shales are more or less locally ferruginous, with alternating lighter (dysoxic) and darker (anoxic) laminae that are occasionally visible in cross sections. Cavities are filled with iron or iron minerals such as limonite and pyrite. Pyrite occurs as concretions or small crystals, but is usually found in the form of coatings. Sometimes, graptolite rhabdosomes are pyritised. Pyrite probably originated in the early stages of diagenesis, or even prior to its onset during sedimentation (see Berner, 1984; Raiswell, 1997). Secondary precipitated pyrite occurs in the form of pseudomorphs that fill cavities after pyrite crystals, in coatings, or dispersed. Regularly oriented rhabdosome graptolites have been observed locally, but their orientation has never been described within one formation or layer (Bouček, 1953; Štorch, 1994; Strossová et al., 2024).

Based on the unusual occurrence of benthic fauna (see Fig. 7, fig. C) and absence of ichnofossils, as well as the rarity of pelagic taxa (see Fig. 7), we can hypothesise short-term or seasonal fluctuations in sea level. This theory is supported by previous graptolite data, as well as the inclusion of the conodont record. The vertical mixing of oxygenated and non-oxygenated waters close to the sea bottom (e.g. due to upwelling and downwelling) is not very probable; however, we may hypothesise a minimal concentration of dissolved oxygen slightly above the sea bed.

This could lead to the formation of pyrite concretions and crystals, as well as pyritised rhabdosome graptolites, during the deposition of lighter (dysoxic) laminae of black shales. This suggests that horizontal transport post-mortem from the upper portions of the water column, where the conodonts and graptolites died, was less significant. Dead organisms (or ‚lost teeth') gradually sank to the seabed, where they were destroyed by microbiological activity (mainly soft tissues), protected from predators and scavengers due to anoxic conditions.

Conodont elements were observed sporadically on the surface layers of black shales, but never in large numbers. Rhabdosomes of graptolites occur both dispersed and in clusters. Sometimes they are oriented in one direction, probably due to a current (see Strossová et al., 2024). Pyritized rhabdosome graptolites are occasionally found in the lighter layers of black shale. It was counted between a few

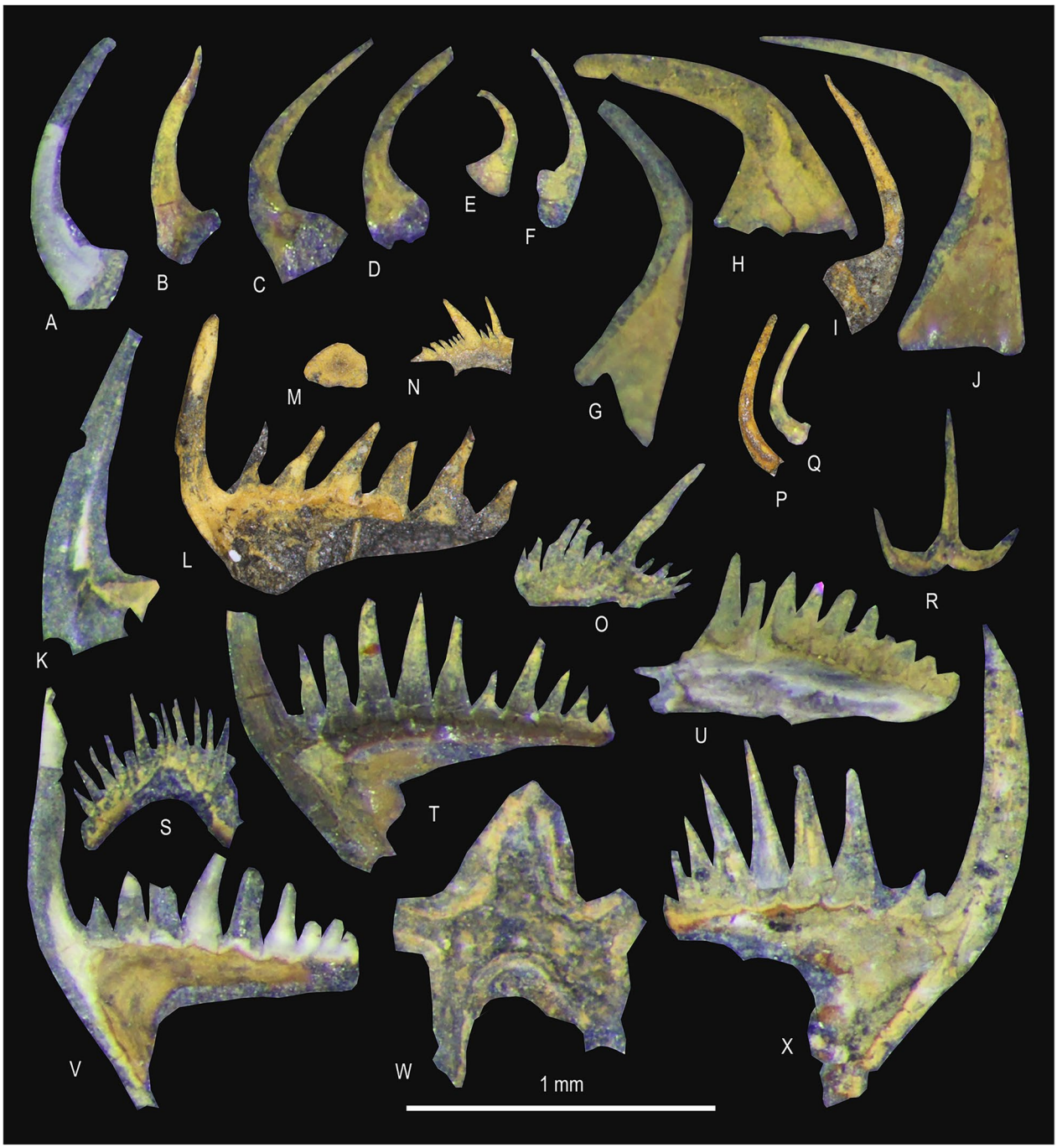

Fig. 4 (See legend on previous page.)

hundred and a few thousand specimens of graptolites on the surface of the black shales, measuring 1 square metre. The specimens can be independent individuals or in undestroyed colonies of different ages (see Strossová, 2024, and Strossová et al., 2024). Colonies of rhabdosomes are excellently preserved as silver-plated impressions. Occasionally, fine, morphologically significant structures can be seen, such as the medium septum, fusselar rings and nematularia, which are typically found in 3D preserved specimens or in secondary, bleached, weathered shales (see Štorch et al., 2024). No impressions of the soft tissues of conodonts or graptolites were observed. However, some elements occur close to the graptolite rhabdosome, and some specimens of graptolites are clearly broken, as discussed below. The origin of pyrite in sediments and pyritised fossils in black shales, and their relationship to taphonomic processes, has been discussed by several authors (Berner, 1984; Feldman, 1989; Díaz & Morse, 1992; Morse & Wang, 1997; Raiswell,

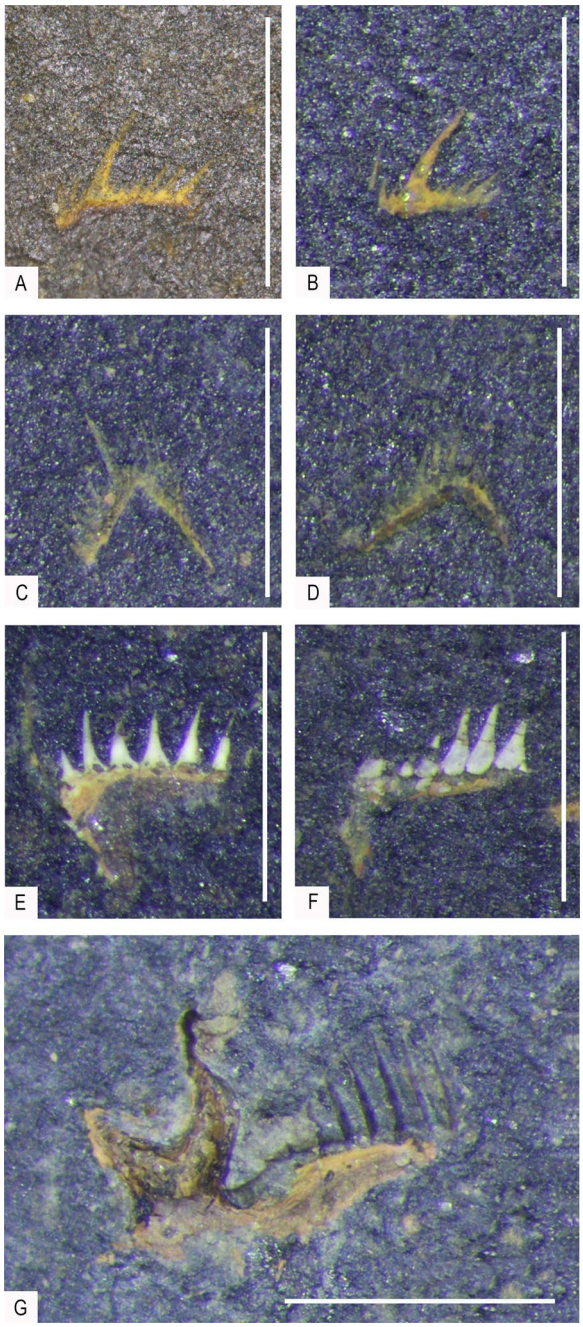

Fig. 5 Conodont taxa identified from the surface of black shales and illustrated in their original state. **A** *Aspelundia fluegeli* (Walliser, 1964), S2 element, specimen no. L 27530 (b). **B** *Aspelundia fluegeli* (Walliser, 1964), S2 element, specimen no. ZAZ 144. **C** *Aspelundia* sp., S2 element specimen no. ZAZ 145. **D** *Aspelundia* sp., S2 element specimen no. ZAZ 146. **E** ?*Distomodus* sp., S2 element, specimens no. ZAZ 147 and ZAZ 148. **F** ?*Distomodus* sp., S2 element, specimens no. ZAZ 147 and ZAZ 148. **G** *Distomodus staurognathoides* (Walliser, 1964), element P1, specimen no. ZAZ 149. All illustrated conodont elements originate from the *linnaei* Biozone, the lowermost Litohlavy Formation in the Želkovice locality of the Prague Synform. All elements were photographed without the use of ethanol. Scale bars represent 1 mm.

1997; Raiswell & Canfield, 1998; Borkow & Babcock, 2003; Schieber, 2003; Liu et al., 2021; Chang et al., 2022).

If we apply the findings and knowledge from the above works to the studied level of black shales from the Želkovice locality, whose conodont and graptolite communities are the subject of this study, we cannot avoid comparison with recent marine euxinic basins, in which black shales are also deposited. Long-term basinal stratification in surface-oxygenated waters and deeper anoxic portions of oceans, where sulfate reduction to sulfide occurs and sulfur is reduced by bacteria, followed by pyritization, are processes that are already known from the Paleozoic era under comparable, perhaps even the same, conditions.

Environment and palaeoecology at the Želkovice locality

Currently, for the Silurian Period, we generally distinguish two main graptolite bioprovinces: the Circumequatorial province and the Rheic-West Gondwana province, as defined by Melchin (1989) and Sun et al. (2022). The Prague Synform, the source of the material studied here, was located in the south-western part of the Rheic-West Gondwana bioprovincial area (see Fig. 1). In comparison with previous Ordovician Period, Silurian graptolites show a lesser degree of a faunal differentiation (see Melchin et al., 2013, Maletz, 2017 and Štorch et al., 2024).

According to Štorch (1998), within the peri-Gondwana European Graptolite Province, three depth-nutrient graptolite assemblages (in the original „subfaunas“) can be recognised in south-western part of the Rhetic-West Gondwana bioprovince (see Fig. 1a):

(i) A low-diversified graptolite assemblage. (ii) A moderately diversified subfauna in deeper environments, still within the shelf and (iii) A rich graptolite subfauna.

The graptolite fauna of the studied level at the Želkovice locality corresponds more to the second last mentioned graptolite community, inhabiting the deeper shelf environment. However, rare or unusual occurrences of the newly documented fauna correspond to the third, deep-water graptolite community, with the occurrence of graptolite index species, where non-graptolite fauna are rare and significant representatives may be absent.

Similar to graptolites, conodonts also exhibit facies-lateral division. The previous concept of communities (see Barnes et al., 1973; Merrill, 1973) was later replaced by the concept of biofacies (see Corradini et al., 2024). Based on the conodont community, we distinguish three general biofacies here: (i) the major marine shelf biofacies, which has a higher species diversity; (ii) the offshore biofacies; and (iii) the

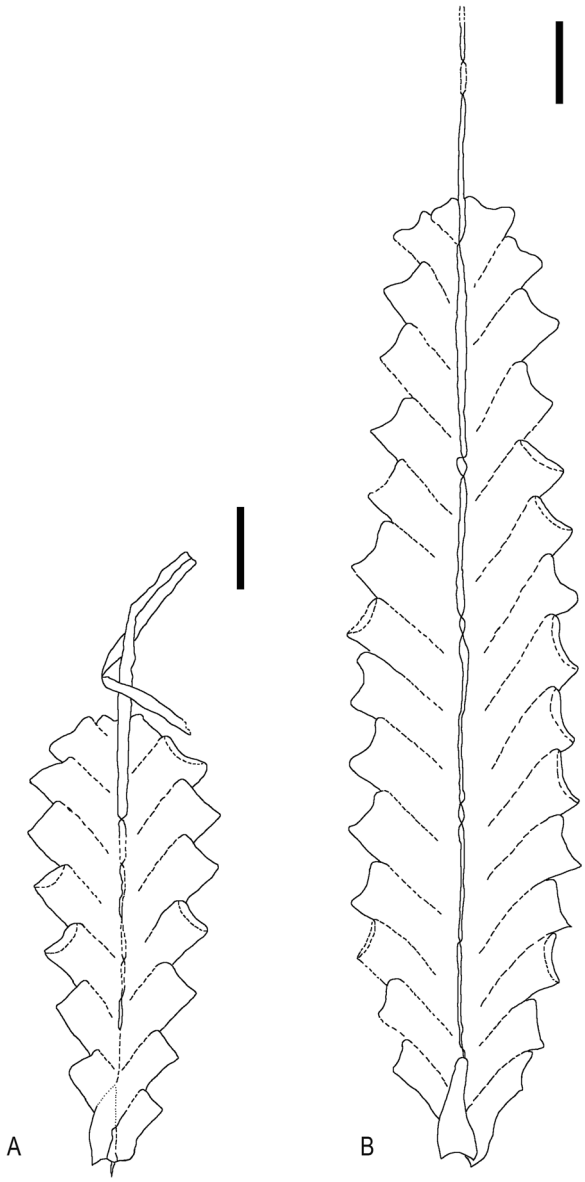

Fig. 6 Index graptolites species of *linnaei* Biozone, *Parapetalolithus palmeus* (Barrande, 1850) and *Parapetalolithus hispanicus* (Haberfelner, 1931), dividing the *linnaei* Biozone into two eponymous subzones; the lower *palmeus* Subzone and the upper *hispanicus* Subzone. **A** *Parapetalolithus hispanicus* (Haberfelner, 1931), specimens no. ZAZ 23. **B** *Parapetalolithus palmeus* (Barrande, 1850), specimens no. ZAZ 12. Scale bars represent 1 mm.

deeper water biofacies, which extends along the shelf margins, slope and basinal settings.

Cosmopolitan species of conodonts are found in offshore and deep-water biofacies, but the species that are most useful for global correlation are found in the offshore biofacies. In contrast, species diversity is low and endemic species occur in the nearshore biofacies. The most diverse conodont assemblages are found in tropical to subtropical regions, with diversity decreasing towards higher latitudes, particularly in areas affected by glacial activity (Corradini et al., 2024).

The identified conodonts of the studied level belong to cosmopolitan, long-ranging taxa, occurring mainly in deep-water environments. However, the use of the concept of conodont biofacies can be sometimes questionable, because during the early Silurian (and early Telychian) conodont diversity was very low globally (see Knell et al. 2012).

However, for example, a comprehensive study by Yan et al., (2022) using multivariate statistical analysis recognized two conodont biofacies within the *Pterosphatodus eopennatus* conodont Biozone on the South China Palaeoplate, namely a deep-water (*Dapsilodus-Decoriconus*) and a shallow-water (*Apsidognathus-Galerodus*) biofacies.

Simultaneously, they provide a detailed description of the abundance of transitional conodont elements between these two biofacies. The identified taxa of conodonts at the Želkovice locality mainly correspond to the characteristics of the deep-water community of the *Dapsilodus-Decoriconus* biofacies, after Yan et al. (2022).

In conclusion, the absence of turbidites, landslides, and traces of storm surges, as well as benthic assemblages, and the presence of an abundant and diverse community of graptolites, cosmopolitan conodonts, rare remains of arthropods, brachiopods and cephalopods, and (see Fig. 7), together with the data of previous authors, support the idea of a deeper marine environment, probably shelfal, with episodic fluctuations in sea level and the possible movement of the thermocline, as well as an indeterminately large mass of oxygenated water. This environment is analogous to today's euxinic basins.

Graptolites–traces of parasitism, predation or degeneration?

The topic of predation on planktonic graptolites is little-studied, but all the more interesting. In the Early Paleozoic food chain, graptolites were probably the main representatives of primary consumers and, simultaneously, a food source for organisms in the higher layers of the food pyramid. It may be hypothesised that predation on graptolites was relatively common. However, there remains a paucity of direct evidence to support this hypothesis. Each new piece of data on predation is significant progress (see Underwood, 1993, Bull, 1996, Loydell et al., 1998, or for a summary see Maletz, 2017).

The research presented herein was focused on new conodont data and disturbed graptolite rhabdosomes (see Fig. 8). The nature of the observed damage or „injury" bears a resemblance to post-predation attacks, as previously described by Loydell et al. (1998). It is imperative to note that significant disruption to the rhabdosome must have originated in the water column, prior to the colony's descent to the seabed. This is predicated on the

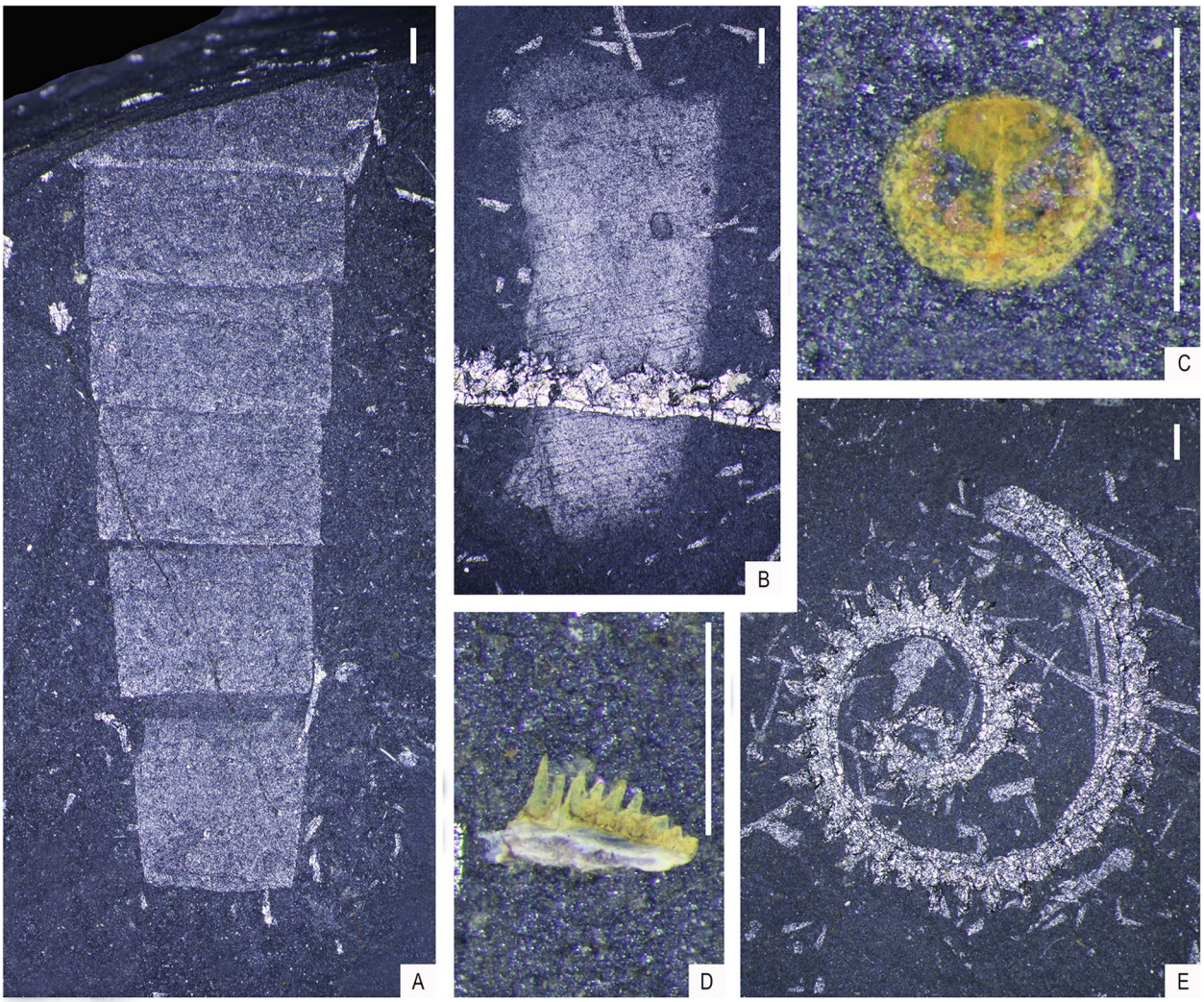

Fig. 7 Overview of the fauna recorded from the Želkovice locality, *linnaei* Biozone. **A** Remain of metasoma part from an Arthropod representative, probably of the order *Eurypterida* or *Chasmataspidida*, specimen no. ZAZ 150. **B** Part of representative by the *Cephalopoda* group, specimen no. ZAZ 151. **C** The acrotretid microbrachiopod *Opsiconidion* sp., brachial valve, specimen no. ZAZ 152. **D** Fragment of *Distomodus* sp., conodont, specimen no. ZAZ 141. **E** *Torquigraptus contortus*, representatives of planktonic graptolites, specimen no. ZAZ 153. Scale bars represent 1 mm.

premise that the absence of subsequent effects from scavengers is indicative of an absence of bioturbation caused by anoxic and dysoxic conditions. Significantly damaged, attacked graptolites (broken or folded rhabdosomes—see Fig. 8, B–G) are not preserved in the so–called „dense, ovoid masses„ and apparently not even faecal pellets sensu Loydell et al. (1998). It is important to note that only uniserial graptolites with this type of rhabdosome damage have been found so far at the Želkovice locality.

There are three hypothetical explanations for broken damagedd rhabdosomes (see Fig. 8): (i) parasitism—activity of some microorganisms would literally decompose damaged areas in rhabdosome or parasitic microorganisms that sucked zooids would intensively break the rhabdosome. This hypothetical explanation is not very probable because we have not any supporting evidence.

(ii) predation—the graptolite was attacked by an hypothetical predator, which „tasted“ rhabdosome and graptolite zooids. Rhabdosome would be significantly damaged (see details in Figure 8 and frames C–E) in this case. Shortly after, the hypothetical predator probably left graptolite colony before ingestion of graptolite rhabsome. Similar examples are discussed by Underwood (1993) and Loydell et al. (1998).

(iii) degeneration—the rhabdosome was broken/fractured without external influence, due to the age of the colony. However, the longest documented graptolite colonies reached a diameter of about 50 cm and a length of up to 145 cm (Bouček, 1957; Loydell & Loveridge, 2001; Maletz, 2017) and the topic of unfinished growth in some graptolite species is still open (Maletz, 2017). Illustrated

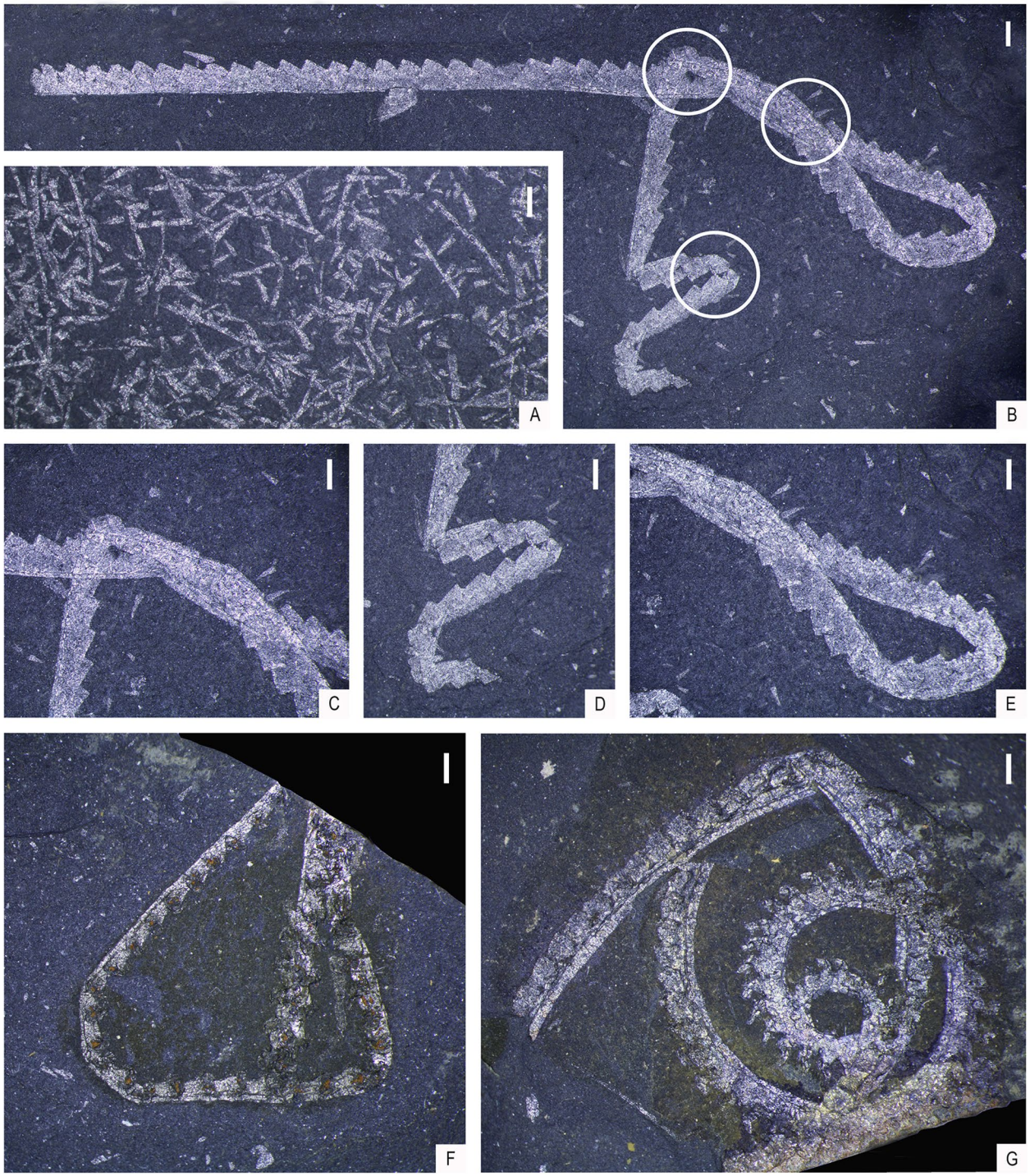

Fig. 8 Traces of injury and probable predation on graptolites rhabdosomes, caused by an unknown (?) predator. **A** Accumulation of broken parts of graptolite rhabdosomes, both monograptid (*Stimulograptus*, *Streptograptus* and *Spirograptus*) and biserial types (*Glyptograptus*), no. ZAZ 154. Occurrences of these accumulations on shales surfaces were not rare. **B** Mature specimen of *Pristiograptus pristinus* Přibyl, (Pander 1940), no. ZAZ 155, with several broken, but unseparated parts of the rhabdosome, highlighted by white circles and re-illustrated at higher magnification in C, D, E. These injuries were probably caused by an unknown predator, possibly a member of the Arthropod family. **C**, **D**, **E** Details of injuries and broken and twisted parts of the rhabdosome by *Pristiograptus pristinus* Přibyl, 1940, no. ZAZ 155. **F** Specimen by *Streptograptus* sp., no. ZAZ 156, with a partially broken rhabdosome. **G** Mature specimen of *Torquigraptus contortus* (Perner, 1897), no. ZAZ 157, with a broken and twisted rhabdosome. All illustrated specimens originate from the *linnaei* Biozone, Litohlavy Formation, location Želkovice. Scale bars represent 1 mm.

specimens of the genera *Pristiograptus* and *Streptograptus* do not reach such dimensions (see Figure 8 and scale).

Disruption-damage of rhabdosome is usually explained (Loydell et al., 1998; Maletz, 2017, 2023; Underwood, 1993) by an attack by predators but such examples of predation of graptolites are very rare.

The following text aims to provide a concise summary of the key points discussed. This study posits that predation, a phenomenon that occurs infrequently among graptolites, serves as the most probable explanation for the observed disruption of rhabdosomes. The identity of the hypothetical predator remains unknown.

The most probable hypothesis is that the unknown predator can belong to the Arthropoda based on the type of disruption and "abnormal cutting" of rhabdosomes of *Streptograptus*, *Stimulograptus* or *Rastrites* specimens after a few thecae (see Fig. 8, A). In this study, we present a new set of specimens (see Fig. 8) from the same geographical location and stratigraphic level.

Conodont elements have been frequently discovered in close proximity to the apertures of rhabdosomal graptolite thecae (see Fig. 3, frames A–D). This phenomenon can be explained by the predatory or parasitic relationship between conodonts and graptolites. As stated by Underwood (1993), the concept was initially proposed as being highly probable, albeit with the caveat that there was an absence of direct evidence to support this assertion.

However, if we take into account the relationship of conodonts to vertebrates (Aldridge et al., 1995; Purnell, 1995) and lampreys living today (class *Cephalaspidomorphi*), whose model organism is *Petromyzon marinus*, it is not difficult to apply the principle of actualism by analogy.

Petromyzon marinus feeds on fishes as adults, sucking their blood and gnawing their flesh. The protective shell of graptolites, the so-called rhabdosome, was probably not attractive to conodonts and other predators (Bates & Kirk, 1986). However, the "soft" zooids essentially offer their nutritional value. In the context of the recent observations of lampreys parasitically sucking blood from fishes, it is pertinent to consider the potential of conodonts to similarly suck zooids from the rhabdosome of graptolites. A comparison of the feeding apparatus of extant lampreys and extinct conodonts reveals a high degree of similarity in their structural design (Aldridge et al., 1995; Yokoyama et al., 2020). Furthermore, in the upper layers of the water column, which were oxygen-depleted, a sufficient source of sustenance was a limiting factor for all organisms, including conodonts.

The presence of a possible low-energy source of nutrients was a pervasive phenomenon, characterised by its substantial abundance, which likely attracted certain *predators.*

Underwood (1993) described damaged specimens of Silurian monograptids in detail and discussed hypothetical modes of predation on graptolites including their potential originators. He distinguished and demonstrated three main modes of attack and damage of graptolites: absorption, crunching and plucking. The third possibility, i.e., the damage to the rhabdomosome thecae, it may even be impossible to demonstrate this in the fossil record. Concurrently, the third possibility of predation may corroborate the hypotheses of Underwood (1993) and Štorch et al. (2014), and others, who proposed variations of thecae and thecae apertures, the occurrence of dorso-ventral spines, and substantial narrowing of the apertures in Silurian uniserial graptolites as a specialized defences against attacks on graptolite zooids. Maletz (2017) noted that this explanation, unfortunately remains speculative, as „the gradational change of thecal styles along the stipes in many monograptids (e.g., „biform" monograptids: Hutt, 1974) may suggest a connection to the lifestyle and feeding mechanism of the graptolites." However, findings from previous works and this study are more inclined to follow Underwood (1993) or Štorch et al. (2014). Predation has been observed in uniserial graptolites with shorter and more open thecae (see Fig. 8).

Interestingly, no case of predation has been observed in biserial taxa (e.g. genera *Parapetalolithus* and *Glyptograptus*) from the Želkovice locality. The explanation could be simple. Biserial graptolites (especially the genus *Parapetalolithus*, see Strossová, 2024) had relatively longer and narrower thecae and thecal apertures. If graptolite zooids were capable of retraction, they may have retracted „deep" into the theca and thus were better protected from attack. Similarly, the biform monograptids discussed by Hutt (1974) may have been specialized. However, this does not explain attacks on biserial graptolites, illustrated by Underwood (1993). Simultaneously, it may be a reason why we still have no have direct evidence in the fossil record concerns feeding interaction between graptolites and conodonts.

Finally, Lidgard (2008) described predation of bryozoans by small predators that attack individual bryozoan zooids. According to Maletz (2017), it would be difficult to compare and imagine this situation in planktonic graptolites within the water column. He wrote, "because one would have to expect that another planktonic or nectic organism would feed on them (graptolites)." Nevertheless, conodonts were probably capable of coordinated, active movement (see Briggs et al., 1983).

Suggested predation remains speculative till the time when somebody provides direct evidence from the fossil record of conodont predation/parasitism on graptolites.

The overlap of conodont and graptolite biofacies, their stratigraphic use, and their potential

If we want to correlate the graptolite and conodont biozones in the Silurian as accurately as possible, we have to take into account the influence of several factors.

Firstly, graptolite and conodont biozones are found in different lithofacies, reflecting their original niches (biofacies). This leads to significant differences in the abundance and diversity of conodont and graptolite taxa. In an environment less favorable for the given group, only the most resistant taxa will survive in the long term, which are usually very few species, but will show a relatively high abundance. In such environments, monospecific assemblages are formed (Corradini et al., 2024; Maletz, 2017). These monospecific assemblages can survive not only locally but also globally if unfavourable conditions persist. The "proven" morphology of these long-lived taxa remains unchanged (see Maletz, 2017; Voldman et al., 2017).

Secondly, global climate change influences the distribution of carbonate platform platform facies and black shale facies, which has a direct impact on conodont and graptolite occurrence. The diversity of conodonts varies repeatedly from the Cambrian to the Triassic, reflecting global environmental changes. Sometimes diversity increased (e.g. in the Ordovician and Devonian periods), while at other times it decreased rapidly (e.g. in the first half of the Silurian and the early Carboniferous; see Knell et al., 2012; Goldman et al., 2020; Corradini et al., 2024).

However, the main problem of Silurian biostratigraphy is the correlation of the graptolite and conodont zonation schemes, due to the very rare localities where the two groups co-exist. Due to taphonomic and palaeonvironmental factors, graptolites are abundant in pelitic facies, and very rarely preserved in limestones. Oppositely, conodonts are well preserved and abundant in calcareous facies, whereas they are rarely reported from black shales. It results that the correlation of the two schemes is mainly based on the few localities where limestone and black shales alternate in the sedimentary record (e.g., Corradini et al., 2015; Manda et al., 2023).

It is important to note that, in the stratigraphically older and younger layers of black shales from the same locality belong to the *sedgwickii* and *turriculatus* biozones, there is still no mention yet or published evidence of other conodonts occurring alongside graptolites.

The collection from Želkovice contains both graptolites and conodonts, and confirms the precise correlation between the *S. guerichi* graptolite Biozone and the *D. staurognathoides* conodont Biozone. It results that the studied section is among the few others Silurian localities in the world where conodonts and graptolites co-occur in the same beds, as, for example, Dob's Linn (Scotland; Barnes & Williams, 1988), El Kachla (Morocco, Männik et al., 2011), Fluminimaggiore (SW Sardinia, Italy; Corradini et al., 2009; Ferretti et al., 1998, 2009), Corral de Calatrava (central Spain; Loydell et al., 2009) and Latvia (Loydell et al., 2003, 2010).

Conclusions

1. Ten conodont taxa are documented for the first time from the Želkovice locality. These are also the first conodonts from black shales at this level in the Prague Synform, and the first reliably verified conodonts in Silurian black shales in the Prague Synform. In addition to conodonts, fossil remains of arthropods, cephalopods and brachiopods were recorded and illustrated for the first time.
2. Coniform conodonts represent the majority of the association, mainly represented by genera *Dapsilodus* and *Panderodus*. However, due to the preservation on bedding plane, only a minor part of the association can be determined at least at genus level, and about 15% at specificic level.
3. The presence of the zonal index conodont species *Distomodus staurognathoides*, allows to attribute the section to the eponymous *D. staurognathoides* Biozone, in good agreement with the age already established on the basis of the graptolite fauna: in fact the *D. staurognathoides* Biozone encompass several graptolite zones of latest Aeronian and early Telychian age, including the *Rastrites linnaei* Biozone.
4. The graptolite community at this site corresponds to a deep-water or deeper shelf environment. Other data (e.g. the absence of benthos, turbidites and storm surges) confirm this idea.
5. The overlap of conodont and graptolite indicates fluctuations in the sea level and may confirm the existence of a vast, oxygenated body of water between the anoxic seabed and the surface of the sea. This allowed pelagic fauna to be present and to migrate. Thus, anoxic conditions could not have occurred across the entire water column up to the sea surface.
6. Available specimens and the overlap of conodonts and graptolites suggest hypothetical parasitic-predatory relationships between them, which could have occurred precisely due to their overlap of facies. However, direct evidence is lacking and this idea remains untested.
7. Finally, new examples of hypothetical predation on graptolites from the same locality and elsewhere in the Prague Basin have been documented. The type of predator is far from certain. However, the way in which the rhabdosome of the graptolites was interrupted (broken) suggests that the predators may have belonged to an arthropod group.

Appendix 1

See Fig. 9.

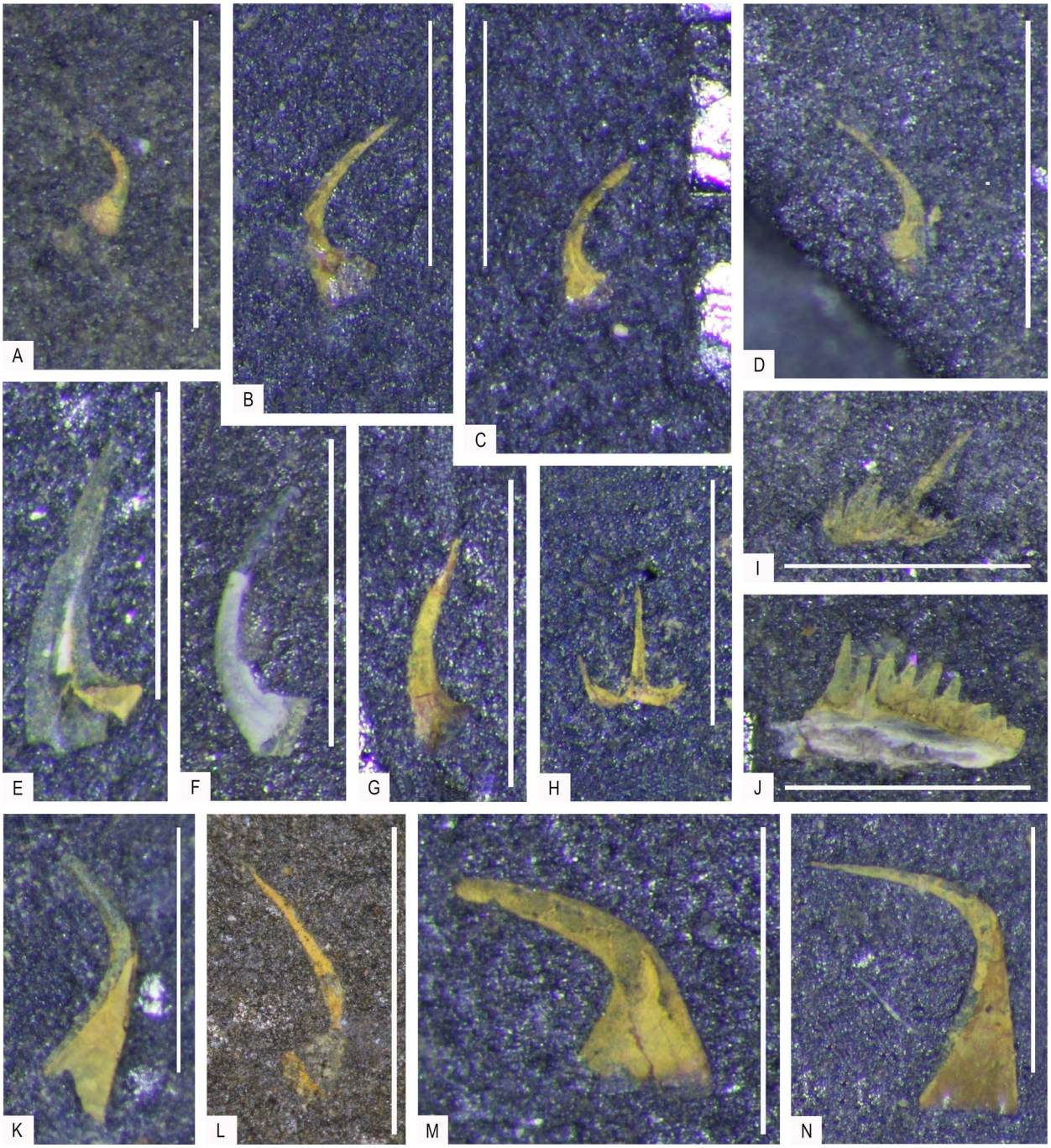

Fig. 9 Conodont taxa identified from surface of black shales and illustrated in their original state, illustrated in Fig. 3. **A** *Dapsilodus* cf. *sparsus* (Barrick, 1977); specimen no. ZAZ 126. **B** *Dapsilodus* cf. *praecipuus* (Barrick, 1977), specimen no. ZAZ 124. **C** *Dapsilodus* cf. *praecipuus* (Barrick, 1977), specimen no. ZAZ 125. **D** *Dapsilodus* cf. *sparsus* (Barrick, 1977); specimen no. ZAZ 127. **E** *Dapsilodus* sp, specimen no. ZAZ 133. **F** *Dapsilodus* sp., specimen no. ZAZ 122. **G** *Dapsilodus* sp., specimen no. ZAZ 123. **H** *Aspelundia* sp., element S0, specimen no. ZAZ 136. **I** *Aspelundia fluegeli* (Walliser, 1964), specimen no. ZAZ 135. **J** fragment of *Distomodus* sp., specimen no. ZAZ 141. **K** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 128. **L** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. L 31624 (b). **M** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 129. **N** *Dapsilodus obliquicostatus* (Branson & Mehl, 1933); specimen no. ZAZ 131. All illustrated conodont elements originate from the *linnaei* Biozone, the lowermost Litohlavy Formation in the Želkovice locality of the Prague Synform. Scale bars represent 1 mm

Appendix 2

See Fig. 10.

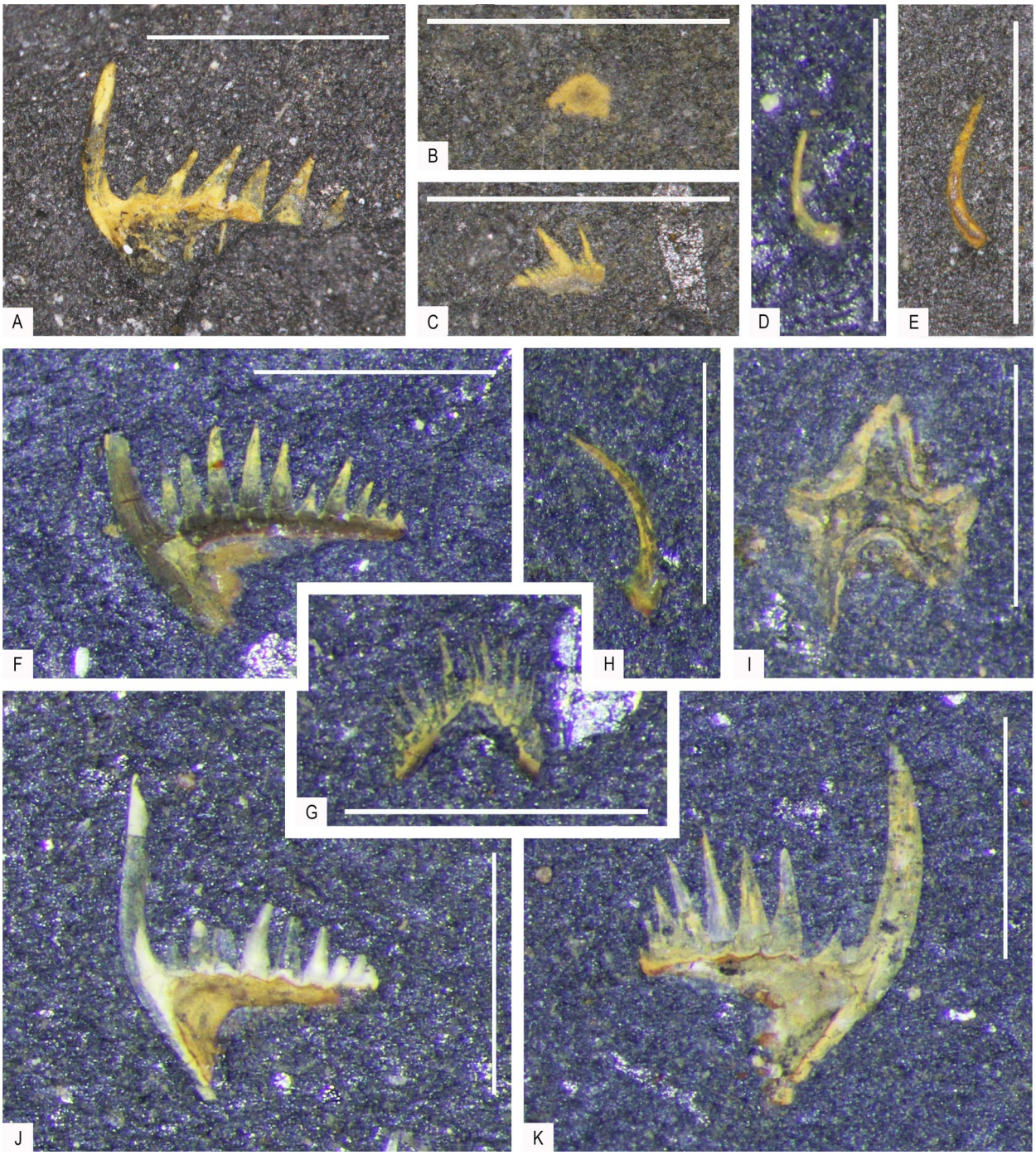

Fig. 10 Conodont taxa identified from surface of black shales and illustrated in their original state, illustrated in Fig. 3—continued. **A** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. L 30167 (b). **B** *Pseudooneotodus beckmanni* (Bischoff & Sannemann, 1958), specimen no. L31470 (b). **C** *Wurmiella* sp., specimen no. L 31470 (c). **D** *Panderodus* cf. *recurvatus* (Rhodes, 1953) specimen no. ZAZ 132. **E** *Panderodus* sp., specimen no. L 31624 (c). **F** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 139. **G** *Aspelundia* sp., specimen no. ZAZ 137. **H** *Distomodus staurognathoides* (Walliser, 1964), S0 element, specimen no. ZAZ 134. **I** *Distomodus staurognathoides* (Walliser, 1964), P1 element, specimen no. ZAZ 142. **J** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 138. **K** *Distomodus staurognathoides* (Walliser, 1964), element S2, specimen no. ZAZ 140. All illustrated conodont elements originate from the *linnaei* Biozone, the lowermost Litohlavy Formation in the Želkovice locality of the Prague Synform. Scale bars represent 1 mm

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Author contributions
Z.S., C.C. and M.G.C. collaborated on the research's conceptualization and investigation. Z.S. dealt with the graptolite material and partly the conodont material, and C.C. with M.G.C. analysed and determined the conodont material. Z.S. and C.C. worked jointly on the original draft preparation. ZS worked on visualization of manuscript.

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Data availability
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
Not applicable.

Competing interests
The authors declare no competing interests.

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