

Response of the Silurian jawed polychaete fauna to environmental changes during the Mid-Ludfordian Glaciation in the Prague Basin, Czech Republic

PETRA TONAROVÁ, JIŘÍ FRÝDA, MICHAL KUBAJKO & OLLE HINTS



Numerous recent studies have revealed that the Ludfordian was an unstable part of the Silurian Period, linked with global climatic changes and glaciation, changes in ocean chemistry, and a distinct perturbation of the carbon cycle expressed by the largest carbon isotope excursion throughout the whole Phanerozoic, the Mid-Ludfordian carbon isotope excursion (MLCIE). These dramatic environmental changes were associated with faunal crises in conodont (Lau conodont Bioevent) and graptolite (Kozlowskii graptolite Bioevent) faunas. The response of other faunal groups to global environmental changes during the mid-Ludfordian has been less thoroughly documented. Here, we present an analysis of the taxonomic composition and stratigraphical distribution of jaw-bearing polychaete worms from the Ludfordian strata of the Prague Basin. Based on more than 5,000 diagnostic posterior maxillae, more than thirty species were recorded from the studied interval. The family Rhytiprionidae was recorded from the peri-Gondwanan region for the first time. During the MLCIE and the Mid-Ludfordian Glaciation interval, the jawed polychaete fauna was disturbed and reorganised but recovered relatively quickly, sooner than, e.g. lingulate brachiopods. The most distinct change was documented at the end of the *Polygnathoides siluricus* Zone marking the beginning of the glaciation. Approximately half of the species showed a continuous range through the event interval, twenty percent of species represented Lazarus taxa, six percent disappeared and 24 percent appeared during or after the event interval in the Kosov section. • Key words: scolecodonts, jawed polychaetes, Silurian, MLCIE, Lau and Kozlowskii bioevents, Prague Basin.

TONAROVÁ, P., FRÝDA, J., KUBAJKO, M. & HINTS, O. 2025. Response of the Silurian jawed polychaete fauna to environmental changes during the Mid-Ludfordian Glaciation in the Prague Basin (Czech Republic). *Bulletin of Geosciences* 100(X), xxx–xxx (9 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received October 27, 2024; accepted in revised form March 19, 2025; published online May 17, 2025; issued Xxxxxx XX, 2025.

Petra Tonarová (corresponding author), Czech Geological Survey, Klárov 3/131, 11821 Praha 1, Czech Republic; petra.tonarova@geology.cz • Jiří Frýda, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Praha 6 – Suchbátka & Czech Geological Survey, Klárov 3/131, 11821 Praha 1, Czech Republic; bellerophon@seznam.cz • Michal Kubajko, Czech Geological Survey, Klárov 3/131, 11821 Praha 1, Czech Republic; michal.kubajko@geology.cz • Olle Hints, Department of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; olle.hints@taltech.ee

The Silurian Period, lasting from 443.8 to 419.2 Ma (Melchin *et al.* 2020), represents a key interval in Earth's history and biological evolution. During this time, vascular plants diversified and colonised the continents during the 'Siluro-Devonian terrestrial radiation' (e.g. Steemans *et al.* 2012, Pšenička *et al.* 2021). The rapid emergence of land plants and the ongoing expansion of terrestrial ecosystems during the mid-Palaeozoic also initiated fundamental changes in the structure of marine ecosystems. Specifically, the mid-Palaeozoic was a time of explosive diversification in marine life, accompanied by increasing predation (e.g. Signor & Brett 1984, Brett & Walker 2002), and the corresponding macro-ecological changes affected almost all groups of marine organisms (see Nützel & Frýda 2003, Clack 2007, Klug *et al.* 2010, Whalen & Briggs 2018).

The dynamic nature of the Silurian Period can be illustrated by the instability of the global carbon cycle, and probably rapid changes in atmospheric pO₂ and pCO₂ (Hayes *et al.* 1999; Berner 2005, 2006, 2009; Berner *et al.* 2003; Schachat *et al.* 2018). At least five global stable carbon isotope ($\delta^{13}\text{C}$) excursions (CIEs) have been recognised during this relatively short period, in the mid-Llandovery, early Wenlock, late Wenlock, late Ludlow, and across the Silurian-Devonian boundary (Munnecke *et al.* 2003, Loydell 2007, Cramer *et al.* 2011, Saltzman & Thomas 2012, Melchin *et al.* 2020).

The Mid-Ludfordian Carbon Isotope Excursion (MLCIE) is the largest magnitude carbon isotope event throughout the whole Phanerozoic and the second largest in Earth history (Munnecke *et al.* 2003, Saltzman & Thomas 2012). Strangely, however, the MLCIE was associated with

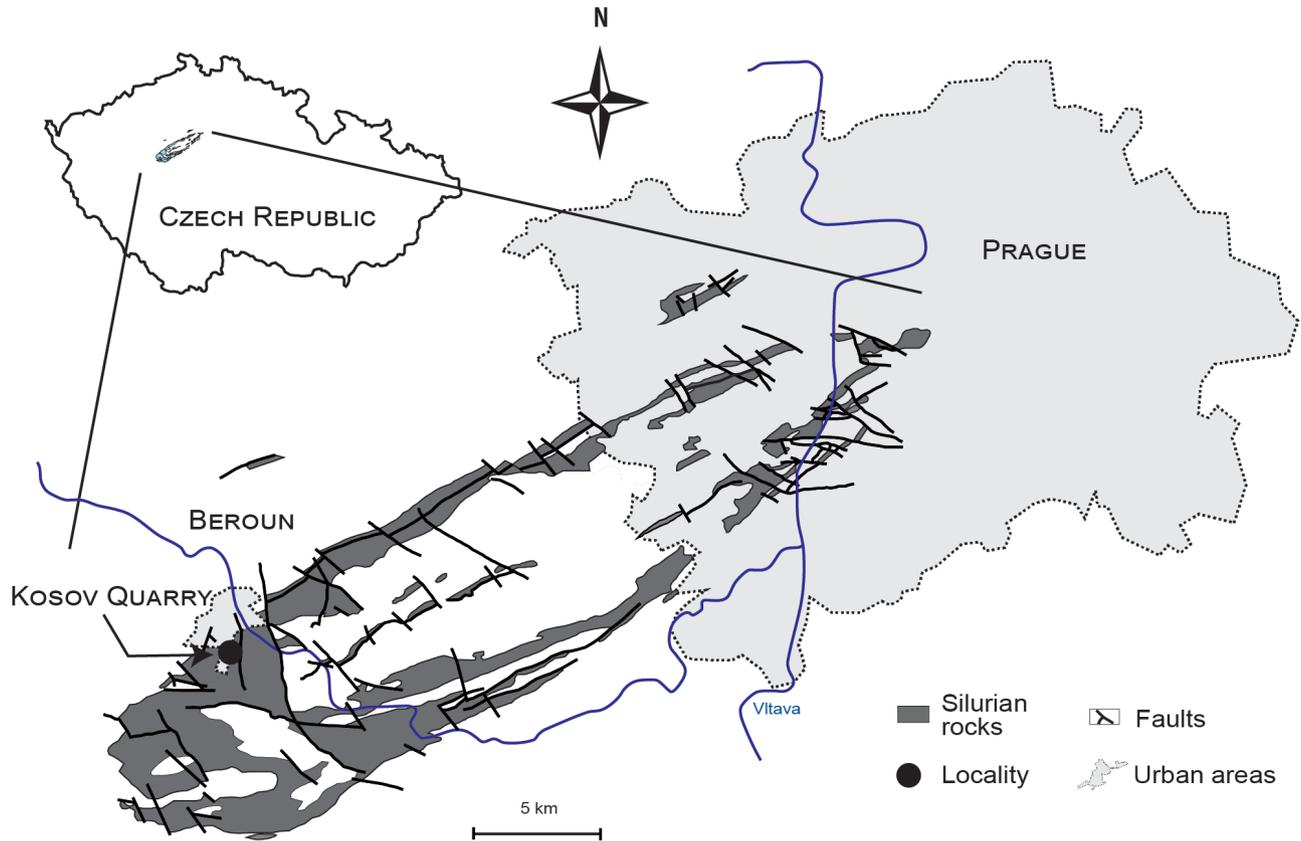


Figure 1. A schematic map with the location of the Czech Republic and the study area. The detailed view shows the distribution of the Silurian rocks of the Prague Basin and location of the Kosov Quarry section.

only moderate faunal crises referred to as the Lau conodont Bioevent (Jeppsson 1987, 1993), and Kozlowskii graptolite Bioevent (Urbanek 1993). Changes in biodiversity have also been recorded for other invertebrate groups such as polychaete worms and brachiopods (Talent *et al.* 1993; Eriksson *et al.* 2004; Tonarová *et al.* 2012; Spiridonov *et al.* 2017, 2020; Mergl *et al.* 2018; Bowman *et al.* 2020) and phytoplankton (Stankevič *et al.* 2024). Distinct extinction events during which large parts of the pre-event fauna were replaced are also documented for marine vertebrates (Märss 1992, Kaljo *et al.* 1995, Eriksson *et al.* 2009). The corresponding changes were often named after some taxa or biostratigraphical intervals (*e.g.* the *Cardiola* Bioevent, *podoliensis* Bioevent, Bioevent 3, C3, *A. hedei* Event, and Pentamerid Event; Jeppsson *et al.* 2007). However, some of these bioevents were described based only on the evaluation of the stratigraphical distribution of individual fossil groups in a limited area or even a single section. None of them represents a single sudden event but rather an interval of gradually decreasing biodiversity. This has made the correlation of individual events challenging (see Kaljo *et al.* 2015, and Frýda *et al.* 2021b, for discussion). Also, the bioevents are often linked to lithological

changes suggesting significant modifications in living and environmental conditions (*e.g.* the Lau conodont Bioevent and the *Cardiola* Bioevent). This raises the question of whether the “extinction” events represent a global extinction or if they only indicate extirpation (*i.e.* a local extinction) of a certain fossil group by a change in environment. For example, in the case of lingulate brachiopods, an invertebrate group with long-ranging species, re-occurrences of taxa after the bioevent, and subsequent mid-Ludfordian carbon isotope anomaly were documented as soon as living conditions returned to the pre-event state (Mergl *et al.* 2018). Therefore, additional quantitative analyses involving different faunal groups from various environments and palaeo-regions are needed.

During the last 15 years, we have been conducting a multidisciplinary study of Silurian carbon isotope anomalies and related bioevents in different environments of the Prague Basin. These studies have accumulated high-resolution geochemical, palaeontological, and sedimentological data (see review in Frýda *et al.* 2021a, b). High resolution sampling (typically with a precision of better than 0.1 m) allows a very detailed analysis of the relationships between environmental and biotic changes.

The response of jawed polychaete assemblage in the aftermath of the MLCIE and associated environmental changes was hitherto studied in detail only using data from the Baltica palaeocontinent (Bergman 1989, Eriksson *et al.* 2004). Until now, only a single preliminary study based on limited data from peri-Gondwana, has been published (Tonarová *et al.* 2012).

The goal of the present paper is to analyse the stratigraphical distribution of the jawed polychaetes and to evaluate their response to environmental changes, including the Mid-Ludfordian Glaciation and carbon isotope event, based on high-resolution data from the Kosov reference section (Fig. 1, no. JF195; see Frýda *et al.* 2021a) in the Prague Basin. The latter represents one of the most complete and best studied MLCIE sections with detailed sedimentological, palaeontological, and biostratigraphical records worldwide (see Frýda *et al.* 2021b).

Early Palaeozoic jawed polychaetes

Polychaete worms represent one of the most common components of benthic invertebrate faunas in modern-day oceans (*e.g.* Hutchings & Fauchald 2000, Díaz-Castañeda & Reish 2009). They play an important role in the functioning of benthic communities (Hutchings 1998), and have been proposed as surrogates for marine biodiversity (Olsgard *et al.* 2003). In addition, they are among the best indicators of large-scale environmental perturbations, as exemplified by, *e.g.* Giangrande *et al.* (2005) and references therein. Polychaete worms are commonly pioneering organisms, important to initial community structuring, colonizing both soft and hard bottoms rapidly after environmental perturbations (Díaz-Castañeda & Reish 2009). The fossil record of polychaetes is mainly evidenced by their jaws – the scolecodonts, which are composed of highly resistant organic matter, enabling preservation in various types of sedimentary rocks. Most Palaeozoic jaw-bearing polychaetes belong to the order Eunicida, representatives of which live today as infaunal burrowers, epifaunal crawlers, tube builders, or inhabitants of reefs and reef-like structures (*e.g.* Paxton 2000). They are found worldwide, from the intertidal zone to great depths. Although some are exclusively carnivorous or herbivorous, most are omnivorous scavengers (Beesley *et al.* 2000).

The fossil record of polychaetes dates back to the middle Cambrian (Conway Morris 1979); however, the oldest undisputed scolecodonts are recorded from the uppermost Cambrian (Williams *et al.* 1999). The abundance of scolecodonts in Early Palaeozoic rocks suggests that polychaete worms were widespread and diverse and already in the Ordovician Period played an essential ecological role (Hints & Eriksson 2007a, b).

The rapid evolution of the group occurred in the early Middle Ordovician, with the highest diversity just before the end-Ordovician mass extinction in the late Katian (Kaljo *et al.* 2011). In the following Silurian Period, the jawed polychaete taxa, similarly to other groups, had a more cosmopolitan biogeographical distribution (Eriksson *et al.* 2013). However, the data available on Palaeozoic scolecodonts are skewed towards the Baltica and Laurentia palaeocontinents (Eriksson *et al.* 2013). It is only during the last decades that new data sets have emerged from other regions (*e.g.* Hints 1998a, b; Hints *et al.* 2016, 2017; Tonarová *et al.* 2012, 2016, 2017, 2019, 2024; Vandenbroucke *et al.* 2019).

Geological background

Mid-Ludfordian environmental changes

Mid-Ludfordian carbon isotope excursion

The MLCIE and the associated faunal turnover have been documented from many palaeocontinents (Fig. 2), in particular from different areas of Laurussia (see Kaljo *et al.* 1996, 1997, 2007, 2014; Eriksson & Calner 2008; Eriksson *et al.* 2009; Barrick *et al.* 2010; Kozłowski & Munnecke 2010; Jeppsson *et al.* 2012; Kozłowski & Sobieñ 2012; Spirodonov *et al.* 2017; Younes *et al.* 2017; Bowman *et al.* 2019, 2020, 2021; Jarochovska *et al.* 2020), Australia (Talent *et al.* 1993; Andrew *et al.* 1994; Jeppsson *et al.* 2007, 2012), Perunica (Lehnert *et al.* 2003, 2007a, b; Slavík *et al.* 2010; Manda *et al.* 2012; Slavík & Carls 2012; Tonarová *et al.* 2012; Vodička 2012; Frýda & Manda 2013; Manda & Frýda 2014; Mergl *et al.* 2018; Frýda *et al.* 2021a, b), Avalonia (Loydell & Frýda 2011), and the Carnic Alps (Wenzel 1997, Histon & Schönlaub 1999, Brett *et al.* 2009). Vecoli *et al.* (2009) recorded a smaller amplitude of the isotopic excursions from Tunisia (Gondwana). Compared to typical MLCIE values which have an average amplitude of 8–9‰ (Frýda & Manda 2013), Vecoli *et al.* (2009) measured only 3‰ $\delta^{13}\text{C}$ which is significantly smaller. A trend towards a basinward decline in the magnitudes of positive $\delta^{13}\text{C}$ excursions has been previously described in the literature (*e.g.* Kaljo *et al.* 1997, Melchin & Holmden 2006), and was discussed more in detail by Loydell (2007) for the early and middle Silurian excursions.

As mentioned above, the MLCIE was documented from many different areas of tropical and moderate palaeolatitudes, mostly based on $\delta^{13}\text{C}_{\text{carb}}$ data. In this context, it is surprising that the carbon isotope fractionation between organic and inorganic carbon pools during one of the largest or probably even the largest Phanerozoic CIE, the MLCIE, was not analysed in detail.

Recently Frýda *et al.* (2021a) analysed $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{carb}}$ records based on high-resolution sampling of the Kosov section JF195 (Prague Basin; peri-Gondwana). The analysis revealed a tight coupling of the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{carb}}$ records, which in turn indicates the photosynthetic origin of the MLCIE_{org} via links to primary production and changing rates of organic carbon burial (Frýda *et al.* 2021a). On the other hand, their new data also revealed a short-term decoupling of the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{carb}}$ records preceding the MLCIE, which may have been related to an increase in atmospheric pCO₂ levels (Kump & Arthur 1999) before the onset of the MLCIE. The peak of the $\Delta^{13}\text{C}$ anomaly ($\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{carb}} - \delta^{13}\text{C}_{\text{org}}$) exactly coincides with a short warming and the Lau/Kozłowski extinction events just before the MLCIE (Frýda *et al.* 2021a) and, therefore, this fact suggests a tight link between the change in marine carbon cycling and the extinction events. However, similar to other Palaeozoic positive carbon isotope anomalies, the causes of the MLCIE are not clear, and numerous conceptual models have been established to offer an explanation.

Changes in marine anoxia during the mid-Ludfordian

Increased marine anoxia together with the potential role of climatic change, glaciation, sea-level changes, enhanced primary productivity, ocean circulation, and variations in Earth's solar insolation induced by orbital changes have been proposed to explain positive CIEs in the Palaeozoic (Jeppsson 1990; Bickert *et al.* 1997; Holmden *et al.* 1998; Kump *et al.* 1999; Panchuk *et al.* 2006; Melchin & Holmden 2006; Cramer & Saltzman 2007; LaPorte *et al.* 2009; Kozłowski & Sobień 2012; Holmden *et al.* 2012; Schrag *et al.* 2013; Kozłowski 2015, 2020; Piszczowska *et al.* 2020; Hartke *et al.* 2021; Sproson *et al.* 2022; Zhang *et al.* 2022; del Rey *et al.* 2023, and references therein).

Positive $\delta^{13}\text{C}$ excursions and the associated extinctions have been linked to increased marine productivity (ocean eutrophication), leading to increased organic carbon burial, and expansion of marine anoxia in shallow continental seas. However, marine redox conditions across the MLCIE were hitherto documented only from Laurussia (Fig. 2, Kozłowski 2015; Bowman *et al.* 2019, 2020, 2021; del Rey *et al.* 2020), peri-Gondwana (Frýda *et al.* 2021a, b; del Rey *et al.* 2023), and eastern Gondwana (del Rey *et al.* 2023). These data include local (pyrite framboids; I/Ca) as well as global ($\epsilon^{205}\text{Tl}$ and $\delta^{238}\text{U}$) redox proxies. Persistent euxinia occurring right before and during the rising limb of the MLCIE were documented from Poland (eastern Laurussia) based on the size-frequency distribution of pyrite framboids (Kozłowski 2015, 2020). Bowman *et al.* (2020) used the I/Ca as a local redox proxy in four successions deposited on the southern Laurussian shelf (Tennessee).

Their data revealed more reducing conditions before and during the MLCIE and well-oxygenated conditions after the MLCIE. Bowman *et al.* (2019) published the first thallium isotope data from the Priekule-20 drill core (Latvia). The elevated $\epsilon^{205}\text{Tl}$ values show two weak peaks, the first before the onset of the $\delta^{13}\text{C}$ anomaly and the second at about the middle part of the falling limb of the MLCIE. Bowman *et al.* (2019) interpreted the $\epsilon^{205}\text{Tl}$ record as evidence for expanding marine deoxygenation in the interval that preceded the MLCIE. Del Rey *et al.* (2020) analysed brachiopod shells and their host carbonate matrices from five different stratigraphical levels across the MLCIE on Gotland. They noted that seawater $\delta^{238}\text{U}$ values were relatively stable but lower than present-day values. These results were interpreted as an indication of a more anoxic ocean state across the MLCIE. Taken together, data from the palaeotropical realm suggested local and probably global anoxia during the MLCIE.

Redox conditions during the MLCIE in the non-tropical realm were characterised recently using local as well as global redox proxies, including redox-sensitive trace elements, and S, Ba and U isotopes (Frýda *et al.* 2021a, b; Zhang *et al.* 2022; del Rey *et al.* 2023). Frýda *et al.* (2021a, b) showed that significant enrichment of Mo, U, V, Co, Ni, Zn, Cr, and Pb recorded in the Prague Basin indicates that the expansion of oxygen-depleted deep waters (*i.e.* oxygen minimum zones – OMZ) from the upper slope/deep shelf onto the carbonate platform peaked just before the MLCIE. Zhang *et al.* (2022) showed that the $\delta^{138}\text{Ba}$ carbonate record from the Kosov section (Czech Republic, peri-Gondwana) forms a large negative excursion, which correlates with the positive shift in $\delta^{13}\text{C}_{\text{carb}}$. They suggested that the observed negative shift in $\delta^{138}\text{Ba}$ to values as low as -0.33 can be best interpreted as the upwelling of isotopically light Ba from deeper waters due to pelagic barite dissolution under euxinic conditions. This hypothesis is also consistent with results from barium concentration data as well as the results from the sulphate mass balance modelling that indicate a contraction in the seawater sulphate reservoir, with seawater sulphate concentrations decreasing from several mM ranges before the Lau CIE to less than 100 μM during Lau CIE. Frýda *et al.* (2021b) noted that available local and global redox proxies from tropical (Laurussia) to temperate (peri-Gondwana) palaeoregions showed that the expansion of reducing waters to shallow-water settings coincides with the level of the Lau/Kozłowski extinctions. According to Frýda *et al.* (2021b), the contemporaneous occurrence of maximal expansion of anoxic waters onto Laurussian and peri-Gondwanan shelves is evidence of the global nature of the anoxic event, which they named the Siluricus Ocean Anoxic Event (Siluricus OAE). In addition, the expansion of anoxic and/or euxinic waters onto the carbonate shelf at the top of the Siluricus OAE could have increased primary bioproductivity and

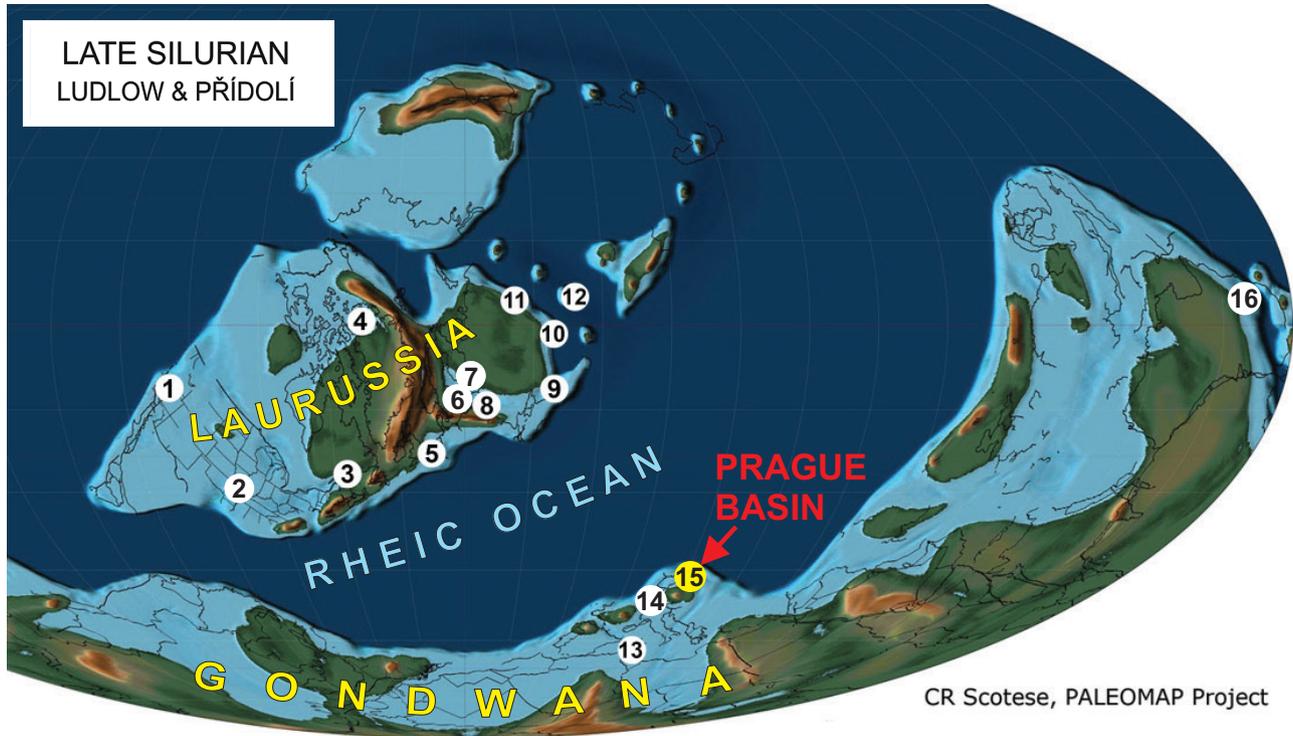


Figure 2. Palaeogeographical distribution of published records of the MLCIE and/or the Lau/Kozłowski Bioevent (palaeogeographical reconstruction after Scotese 2014). Laurentia: 1 – Nevada, USA; 2 – Oklahoma, Missouri and Tennessee, USA; 3 – Quebec, Canada; 4 – Ellesmere Island, Canada; Avalonia: 5 – Ludlow area, England; Baltica: 6 – Gotland; 7 – East Baltic; 8 – Poland; 9 – Podolia; 10 – Chernov Swell; 11 – Subpolar Urals; 12 – Chernyshev Swell; 13 – Tunisia; 14 – Carnic Alps; 15 – Prague Basin; 16 – Queensland, Australia. Modified from Frýda *et al.* (2021b).

enhanced the burial rate and preservation of organic matter. Higher availability of organic matter, as well as anoxia/euxinia, likely increased the intensity of anaerobic respiration of organic matter including microbial sulfate reduction producing H_2S , increasing carbonate alkalinity and pH (Lin *et al.* 2018). Observed high $\delta^{34}S_{py}$ and low $\delta^{44/40}Ca_{carbonate}$ values agree well with a high deposition rate of syngenetic pyrite and rapid calcium carbonate precipitation under carbonate hypersaturation conditions (see Kozłowski 2015; Farkaš *et al.* 2016; Frýda *et al.* 2021a, b). A recent study of $\delta^{238}U$ records (del Rey *et al.* 2023) from temperate (Kosov, peri-Gondwana) and tropical (Broken River, Australia, eastern Gondwana) palaeo-realms demonstrate that an interval of widespread global anoxia occurred before and during the onset of the MLCIE, which is when the extinctions took place. The mid-Ludfordian $\delta^{238}U$ records reveal that expansive ocean anoxia preceded and was contemporaneous with the faunal extinctions of the Lau/Kozłowski Bioevent. Thus, the $\delta^{238}U$ records, as a measure of the ‘global redox state of the oceans’ (Zhang *et al.* 2020) denoted as $\delta^{238}U$, clearly support the global nature of the Siluric Ocean Anoxic Event culminating at the *P. siluricus* Biozone when anoxic and/or euxinic waters expanded onto the carbonate shelf (Frýda *et al.* 2021b).

Mid-Ludfordian Glaciation

Palaeotemperature changes inferred from the oxygen isotope composition of conodont phosphate ($\delta^{18}O_{apatite}$) have not been studied systematically for the mid-Ludfordian except for the interval at the beginning of the CIE and its falling limb (Lehnert *et al.* 2007a, Trotter *et al.* 2016), although early studies on the oxygen isotope composition of brachiopod calcite suggested cooling during the MLCIE (Samtleben *et al.* 1996, Wenzel & Joachimski 1996, Wenzel 1999). Recent analysis of sea-water surface temperature changes (Frýda *et al.* 2021b) using $\delta^{18}O_{phos}$ records from different regions located in temperate (Prague Basin and Carnic Alps) as well as tropical (Gotland) palaeolatitudes revealed significant global cooling during the MLCIE. This climatic perturbation was linked to a distinct sea-level fall recorded on all palaeocontinents (see Frýda *et al.* 2021b, for review). Intensive cooling (inferred from the positive shift in $\delta^{18}O_{apatite}$ of at least 3‰) together with a eustatic sea-level fall was explained by a major glaciation in polar and subpolar Gondwana, named the “Mid-Ludfordian Glaciation” (Frýda *et al.* 2021b). Unfortunately, no evidence of glacial deposits from this period has yet been found. This may be due to the difficulty or even impossibility of accurately dating glacial deposits.

Mid-Ludfordian of the Prague Basin

The Prague Basin is a linear, NE–SW elongated depression (Fig. 1; basin axis trends 065° direction) that contains a continuous sedimentary succession with associated volcanic rocks ranging from the Lower Ordovician (Tremadocian) to the Middle Devonian (Givetian; see Chlupáč *et al.* 1998 for details); the sedimentary rocks overlie the Proterozoic basement called the Barrandian (or Teplá–Barrandian Terrane), the Křivoklát–Rokycany Volcanic Complex, and the Cambrian rocks of the Příbram–Jince Basin.

The present study is based on upper Silurian (Ludfordian) sedimentary rocks of the Kopanina Formation in the Prague Basin. Palaeomagnetic data suggest a palaeoposition between 25 and 30 degrees south of the palaeo-equator during the Ludfordian Age (Tasáryová *et al.* 2014). Facies distribution indicates that shallow water domains were surrounded by deeper and open-marine settings dominated by hemipelagic deposition (Horný 1955a, b; Kříž 1991). Whether the Barrandian formed part of accreted peri-Gondwanan terrains or it was a small isolated crustal block (microcontinent or terrane) often referred to as Perunica (Havlíček *et al.* 1994; Cocks & Torsvik 2002, 2013; Fatka & Mergl 2009; Servais & Sintubin 2009; Franke *et al.* 2017; Torsvik & Cocks 2017; Žák & Sláma 2018) is still under debate. Detailed descriptions of the Ludfordian sedimentary and fossil successions of the Prague Basin, as well as its tectonic development, are well compiled in the summary papers by Horný (1955a, b), Havlíček & Štorch (1990, 1999), Kříž (1991, 1992, 1998a, b) and Manda & Kříž (2006).

Kosov Quarry

Scolecodont samples originate from the upper Silurian of Kosov quarry in a section No. JF195 (49° 56' 12.2" N, 14° 03' 20.1" E), which shows a complete sedimentary record across the MLCIE (see Frýda *et al.* 2021a, b, for review). The Ludfordian sedimentology and palaeontology of the Kosov quarry area were summarised in detail by Kříž (1992). The section is composed of carbonates with marly interbeds (*i.e.* laminated calcareous shales) or shales. The exposed succession consists of a variety of limestone facies, including fine-grained limestones (micritic mudstone, wackestone), thin-bedded skeletal limestones, and crinoidal grainstones (Lehnert *et al.* 2007a, Gocke *et al.* 2012, Frýda & Manda 2013). Analyses of faunal changes across the Lau conodont Bioevent and Kozłowskii graptolite Bioevent, and the MLCIE recorded in the studied section can be found in Kříž (1992), Štorch (1995, 2023), Manda & Kříž (2006), Lehnert *et al.* (2007a, b), Tonarová *et al.* (2012), Frýda & Manda (2013),

Mergl *et al.* (2018), and Vokáč *et al.* (2019). Published geochemical studies from the Kosov section include high-resolution $\delta^7\text{Li}$, $\delta^{13}\text{C}_{\text{carb}}$, $\delta^{13}\text{C}_{\text{org}}$, $\delta^{18}\text{O}_{\text{apatite}}$, $\delta^{34}\text{S}_{\text{py}}$, $\delta^{44/40}\text{Ca}$, $^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{88/87}\text{Sr}$, $\delta^{138}\text{Ba}$, $^{187}\text{Os}/^{188}\text{Os}$, $\delta^{238}\text{U}$ and redox-sensitive trace element records (Lehnert *et al.* 2007a, b; Frýda & Manda 2013; Farkaš *et al.* 2016; Frýda *et al.* 2021a, b; Sproson *et al.* 2022; Zhang *et al.* 2022; del Rey *et al.* 2023; Farkaš *et al.* 2024).

The Kosov quarry succession studied for scolecodonts was divided into three sequence stratigraphical intervals (Fig. 3; Frýda *et al.* 2021a, fig. 4) to summarise and understand the dynamics of the jawed polychaete faunas across the MLCIE. These intervals represent different palaeoenvironments and are characterised by distinct faunas as shown by previous studies (see summary in Frýda *et al.* 2021b). A recent analysis of the influence of the mid-Ludfordian environmental changes on the evolution of lingulate brachiopod faunas also revealed the robustness of this subdivision (Mergl *et al.* 2018).

Interval I is below the level L1, where the $\delta^{13}\text{C}_{\text{org}}$ values increase abruptly from about -31‰ to about -25‰ . It is assumed to have been a pre-glacial period, bearing the *Opsiconidion ephemerus* (Mergl, 1982) lingulate brachiopod Community which disappears in the limestone bed with the LAD of *Polygnathoides siluricus* Branson & Mehl, 1933, *i.e.* at the end of the *P. siluricus* conodont Biozone and slightly below the top of the *Neocucullograptus kozłowskii* graptolite Biozone. High U_{EF} and Mo_{EF} values suggest mostly anoxic conditions and deposition in an unrestricted marine system. The most distinct perturbation in redox conditions was found in the Kosov section in the short stratigraphical interval starting about 0.5 m below level L1 and ending at this reference level. This shale interval is characterised by high concentrations of U, Mo, V, Co, Cr, Cu, Zn, Ni, Pb, total sulphur, and organic carbon. The values of the authigenic fractions, as well as the enrichment factors of the above-mentioned trace elements, also indicate a significant trace metal enrichment (Frýda *et al.* 2021b, Fig. 6).

Samples from Interval II (between reference levels LI and LII) *sensu* Frýda *et al.* 2021a (glacial period) show no or only a weak enrichment in U and a moderate to high enrichment in Mo, arguing for deposition under suboxic to weakly anoxic conditions. However, water depth on the carbonate platform was likely much lower during this period (lowstand) than during Interval I, as documented by sedimentological features (*e.g.* Lehnert *et al.* 2007b). Therefore, higher seawater oxygenation could be related only to the shallower environment and not necessarily redox changes in the deeper part of the shelf. The monospecific *Kosoidea fissurella* brachiopod Community occurs in Interval II, also bearing the *Kosovopeltis–Scharyia–Metaplasia* trilobite Community. Interval II corresponds to the highest $\delta^{13}\text{C}$ values, varying between

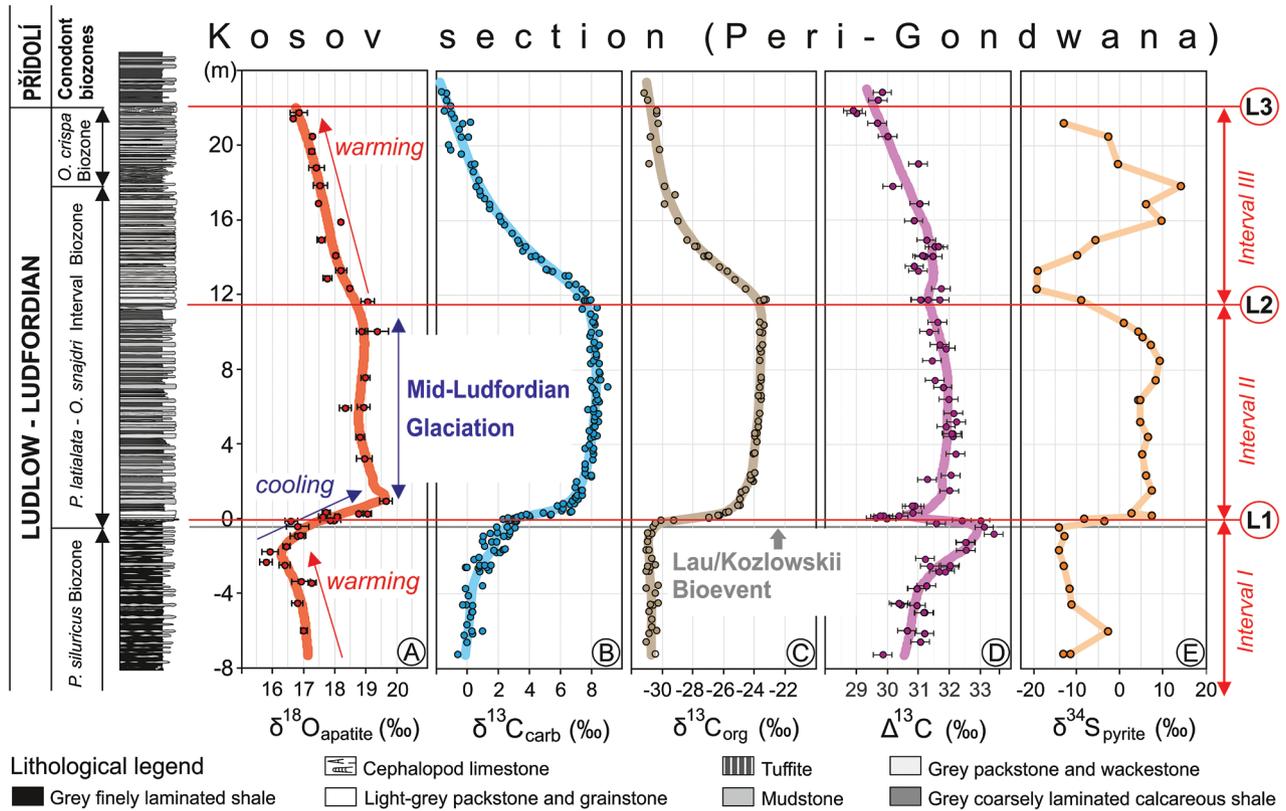


Figure 3. Kosov section. Stratigraphical variations of $\delta^{18}\text{O}_{\text{apatite}}$, $\delta^{13}\text{C}_{\text{carb}}$, $\delta^{13}\text{C}_{\text{org}}$, $\Delta^{13}\text{C}$, and $\delta^{34}\text{S}_{\text{pyrite}}$ values based on Frýda *et al.* (2021a, b). The Kosov section was subdivided into three stratigraphic intervals with different sedimentary regimes. Each interval is bounded by sequence boundaries L1, L2, and L3 (for details see Frýda *et al.* 2021a, b). Conodont zonation *ex* Frýda *et al.* (2021b).

−24.4 to −23.4‰ ($\delta^{13}\text{C}_{\text{org}}$), and around 8‰ ($\delta^{13}\text{C}_{\text{cab}}$) record (Fig. 3).

Interval III includes the falling limb of the MLCIE and bears the *Opsiconidion parephemerus–Kosagittella clara* Community, *Ananaspis fecunda–Cyrtia postera* Community and *Prionopeltis archiaci–Atrypoidea modesta* Community. Interval III ends at the base of the Požáry Formation (Přídolí). The warming trend and decrease in $\delta^{34}\text{S}_{\text{py}}$ starts at stratigraphical level L2 just before a distinct transgression which resulted in the gradual flooding of the entire previously exposed carbonate shelf. The transgression coincides with the onset of decreasing $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$ values, as well as an increase in $\delta^{44/40}\text{Ca}$. These changes in seawater chemistry or carbonate isotope composition are also linked to distinct faunal changes and the gradual appearance of highly diversified faunal communities (Havlíček & Štorch 1990, 1999; Kříž 1992; Manda & Frýda 2014; Mergl *et al.* 2018; and references therein). The decrease in $\delta^{34}\text{S}_{\text{py}}$ could reflect a temporary influx of better-oxygenated ocean waters into a partly restricted epeiric basin during the transgression (Frýda *et al.* 2021a, b). Above reference level L2, within interval III, the $\delta^{34}\text{S}_{\text{py}}$ record, in contrast to the $\delta^{13}\text{C}_{\text{carb}}$, $\delta^{13}\text{C}_{\text{org}}$, and

$\delta^{44/40}\text{Ca}$ records, shows an additional positive anomaly (Fig. 3), which may point to a persisting high pyrite burial in the basin (Frýda *et al.* 2021a, b).

Material and methods

The samples used for this study were collected from the lower Ludfordian to the lowermost Přídolí of the Kosov section JF195, corresponding to the uppermost part of the *Polygnathoides siluricus* to *Ozarkodina crispa* conodont biozones (Figs 3, 4). Thirty samples were dissolved to collect micro- and mesofossils, primarily conodonts and lingulate brachiopods, but the residues yielded also scolecodonts, chitinozoans, prasinophytes and acritarchs, sometimes accompanied by sponge spicules, crinoid columnals, ostracods, juvenile gastropods and bivalves, mazuelloids, hyoliths, graptoloids, palaeoscolecids, conulariids, vertebrate microremains and unidentifiable organic fragments.

The initial bulk samples of 1–2 kg were treated with 6% acetic acid. After dissolution, the residues were gently rinsed through 80, 50, and 10 μm sieves. For scolecodonts,

the wet samples were handpicked from Petri dishes under a stereomicroscope, using a micropipette or an eyelash (a wet technique *sensu* Kielan-Jaworowska 1966). The specimens are stored in small plastic containers filled with glycerine. The abundance of scolecodonts was derived by counting from 250 g subsamples dissolved separately. The number of specimens of each species in a sample was inferred from the number of the more common maxilla (usually left or right MI). The specimens were photographed using a FEG-SEM Tescan Mira 3GMU Scanning Electron Microscope of the Czech Geological Survey, Prague. The samples are stored in the collections of the Czech Geological Survey (Prague), under the collection numbers PT125–155.

Results

Taxonomic composition of the Kosov polychaete fauna

The Kosov scolecodont collection documented herein contains approximately 5000 jaws identified at the species or genus level. These are mostly the posterior maxillae (= first maxillae, MI) or second maxillae (MII), for details on apparatus structure see Kielan-Jaworowska (1966). Altogether, at least 30 species belonging to 19 genera were documented. This number of species remains a conservative estimate due to poor preservation, a too-small number of specimens (for instance, kalloprionids and atraktopronids are commonly represented by only a few specimens per sample), or the lack of diagnostic features that would allow unambiguous reconstruction of jaw apparatuses from isolated scolecodonts. The number of species per sample reaches 22, but usually varies between 11 and 20 (Fig. 4). Individual taxa are further discussed below.

Polychaetaspidae Kielan-Jaworowska, 1966

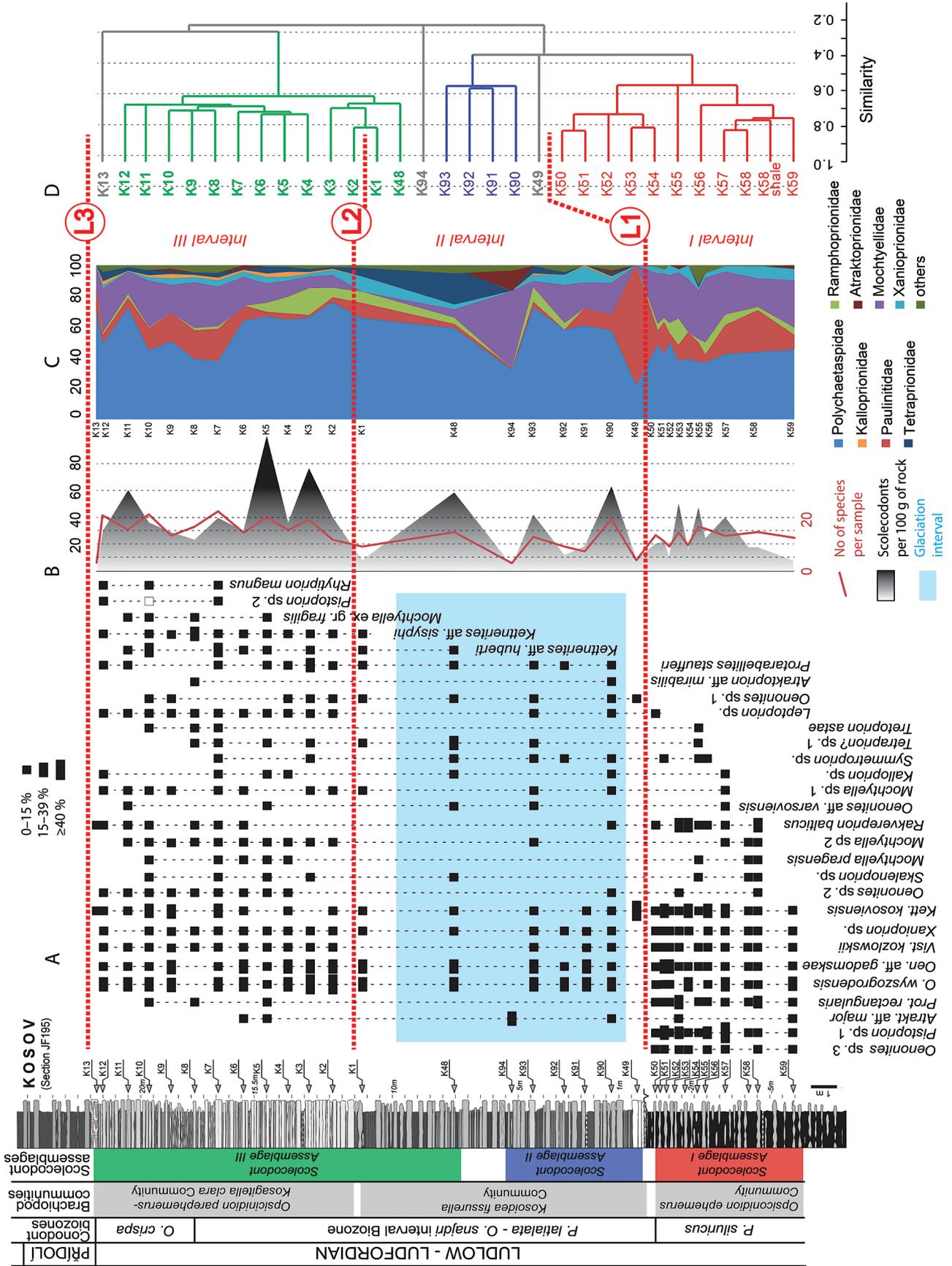
The most diverse and abundant family is Polychaetaspidae, although represented by a single genus *Oenonites* Hinde, 1879. Polychaetaspids represent approximately 50% of the scolecodonts in the Kosov section (Fig. 4). At least eight species can be distinguished, but most are only tentatively identified or kept under open nomenclature (Figs 5H, M, P–R, T; 6I–K, M, P, R, AA; 7X–Z). The most common

are *O. aff. gadomskae* (Kielan-Jaworowska, 1966) (Figs 6N, Q; 7N, O) and *O. ex gr. wyszogrodensis* (Kozłowski, 1956) (Figs 5K, L, S; 7P, Q, W), which are present in most samples. The latter morphotype is also common in the Ordovician (Kielan-Jaworowska 1966); it has a short, pointed ramus in the right MI, a long inner wing in the left MI, and a slender appearance of both posterior maxillae. *Oenonites aff. gadomskae* has a typical left MI with a triangular and pointed outer face of the left MI, and the right MI with a wide ramus, extending half the length of the maxilla. There are three distinct morphologies that cannot be affiliated with previously described species: *Oenonites* sp. 1 (Fig. 6L, S) has large and sturdy posterior maxillae compared to the rest of the *Oenonites* species in the Kosov samples. A very long and sturdy ramus in the right MI that extends more than two-thirds of the jaw length is typical for this taxon. *Oenonites* sp. 2 (Figs 5I, J; 7L, M, U, V) is somewhat similar to *O. olavi* Eriksson, 1997 from Gotland and *Oenonites* sp. A *sensu* Hints *et al.* (2006); it has a wide and prominent ramus with a square-shaped extension in the right MI; the left MI has a long inner wing ($4/5$ of the jaw length) and a very wide anterior end and outer face. *Oenonites* sp. 3 (Fig. 5N, O) has a short and pointed ramus in the right MI; its left MI has a prominent extension in the posterior end of the inner wing. A prominent ramus with an extension in the right MI is also a common feature in the Kosov section. *Oenonites aff. varsoviensis* (Figs 6O, T; 7R–T) has a patchy occurrence throughout the section. It is very similar to *O. varsoviensis* (Kielan-Jaworowska, 1966), which has a long ramus on the right MI and a very short inner wing in the left MI. The left maxillae of the genus *Oenonites* could not be matched to the right MI in many cases; these specimens were attributed to *Oenonites* spp.

Mochtyellidae Kielan-Jaworowska, 1966

The second most common family, Mochtyellidae, is represented by three genera: *Vistulella* Kielan-Jaworowska, 1961, *Mochtyella* Kielan-Jaworowska, 1961, and *Pistoprion* Kielan-Jaworowska, 1966. In most samples, the family represents more than 20% of the assemblage (Fig. 4). *Vistulella kozłowskii* Kielan-Jaworowska, 1961 (Fig. 8L, M, O, P, AA) is present in most samples. It is a notably long-ranging species first appearing in the Middle Ordovician (Hints 2000). *Mochtyella* has a patchy occurrence, with at least three species recorded in the Kosov section. *Mochtyella pragensis* Tonarová, Eriksson

Figure 4. Simplified section with distribution of selected scolecodont taxa. Plots depict: A – stratigraphic ranges of scolecodont species in the Kosov section. B – abundance of scolecodonts per 100 g of rock and number of species per sample. C – distribution of scolecodont families in the samples. D – the dendrogram based on stratigraphically constrained clustering using unweighted pair-group average algorithm and Dice similarity showing the similarity of the jawed polychaete assemblages. Abbreviations used: *Oen.*, *O.* – *Oenonites*; *Kett.* – *Ketnerites*; *Vist.* – *Vistulella*; *Atrakt.* – *Atraktopron*; *Prot.* – *Protarabellites*.



& Hints, 2012 (Fig. 8I, J) has short compound maxillae; the Prague Basin is its type region. *Mochtyella* ex gr. *fragilis* (Fig. 8Q) is rare in the Kosov section. Its morphology is closer to *M. pragensis* than typical *M. fragilis* Szaniawski, 1970, known from coeval strata. *Mochtyella* sp. 1 (Fig. 8C, D, E) is a distinct species with very short compound posterior maxillae only 1.5 times longer than wide. It was previously recorded from the Telychian of the Viki drill core as *Mochtyella* sp. C (Tonarová *et al.* 2014). *Mochtyella* sp. 2 (Fig. 8F, H, T) was previously described as *Mochtyella* sp. A by Hints *et al.* 2006, it belongs to the *M. cristata* group. The maxillae are slender, and the anterior ridge in the right MI is very short, equipped with just three or four denticles.

The genus *Pistoprion* is represented by two species, here treated as *P.* sp. 1 (Fig. 5Z, AA) and *P.* sp. 2 (Fig. 8N, W). Tonarová *et al.* (2012) assumed that there is a relationship between the Ludfordian *Pistoprion* species from the Prague Basin with *Eunicites serrula* Hinde, 1880, but it seems that *Pistoprion* sp. 1 is a different species. Its left MI has a pointed extension of the outer margin, and the inner wing of the right MI is shorter than in the type species *P. transitans* Kielan-Jaworowska, 1966. The general shape is, however, very similar both to *P. transitans* from the Hirnantian of Anticosti Island, Canada (Hints *et al.* 2016), but *P.* sp. 1 lacks the anterior fold on the left MI, and *Pistoprion* sp. 1. reported from the Ludlow of Japan (Vandenbroucke *et al.* 2019, fig. 8.6). This species may be conspecific with an undescribed *Pistoprion* that occurs in the Llandovery to Ludlow of Baltoscandia (Bergman 1979, Hints *et al.* 2006), Arctic Canada (Hints *et al.* 2000) and Siberia (Männil & Zaslavskaya 1985). *Pistoprion* sp. 2 is very rare in the Kosov section. Its left MI does not have an extension of the posterior outer margin, and it looks more similar to *Vistulella*. *Pistoprion* has been shown to be strongly facies controlled, preferring shallow-shelf settings (Hints 2000, 2001), and events like volcanic ash-falls have affected this genus severely (Hints *et al.* 2003). In the Kosov section, it is more common in the lowermost part of the succession, and the abundance rises with the shallowing of the basin.

Paulinitidae Lange, 1947

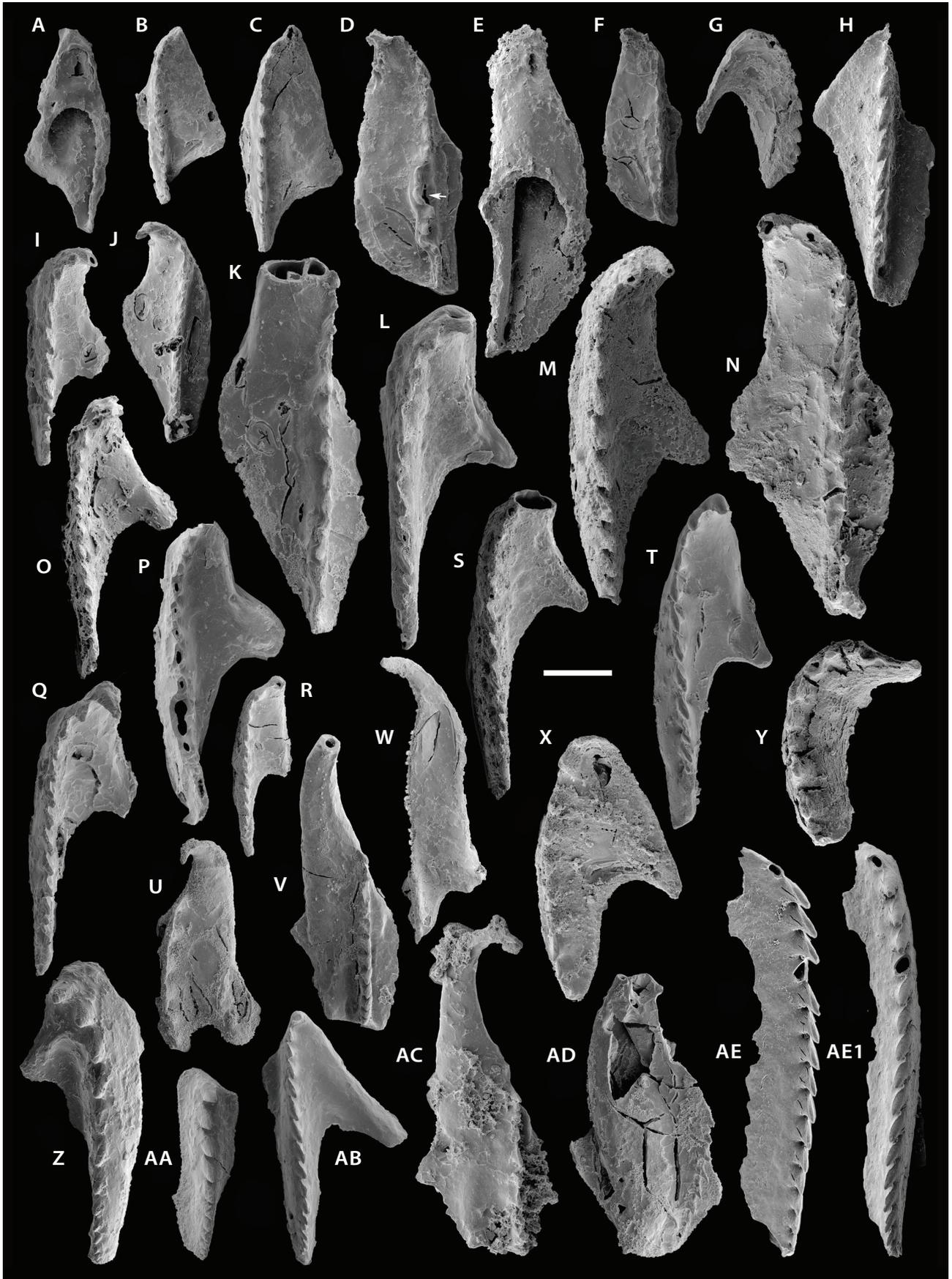
Paulinitids are the third most common family in the Kosov polychaete fauna. They are represented by at least three species of the genus *Kettnerites* Žebera, 1935 and occur in all productive samples. The other common paulinitid genera known from coeval strata in other regions, such as *Hindenites* Bergman, 1987 and *Lanceolatites* Bergman, 1987, have not been recorded in the Kosov section. However, *Hindenites* does occur in the Lower Devonian of the Prague basin (Tonarová *et al.* 2017).

The most common paulinitid is *K. kosoviensis* Žebera, 1935 (Figs 5W, X; 6U–Y; 7AK, AL), which was found in almost all Kosov section samples. So far, this species has been identified with certainty only from the Prague Basin (Tonarová *et al.* 2012). The diagnostic right MII of *K. kosoviensis* has a prominent pre-cuspidal denticle, the left MII has no pre-cuspidal denticle, and both second maxillae have pointed denticles whose size grows posteriorly and the biggest denticles are in the lower half of the maxillae. It has typically prominent inner wings in the first maxillae that are protruding posteriorly even below the lower margin, the MIs have a slender appearance, usually with a prominent spur in the lower outer margin. The size of the jaws may exceed 2 mm, being very large compared to other scolecodonts in the Kosov section, which are usually around 0.3–0.5 mm.

Another species co-occurring with *K. kosoviensis* is referred to here as *Kettnerites* aff. *sisyphi* (Fig. 7AB, AD, AE, AJ). Its outer ligament of the MIs forms a pronounced outer wing in the posterior area of the jaws. The pre-cuspidal denticle is less prominent than in *K. kosoviensis*. *K.* aff. *sisyphi* first appeared in sample K1; however, Tonarová *et al.* (2012) reported this species also from the *siluricus* Biozone of the Prague Basin. The two species are difficult to distinguish in cases of poor preservation of the diagnostic right MII.

In the upper part of the interval II (sample K48), another species of *Kettnerites* appears, having two pre-cuspidal denticles in right MII, assigned here to *K.* aff. *huberti* (Fig. 7AA, AC, AF–AI). This species was recorded in the upper

Figure 5. Scanning electron micrographs of selected scolecodonts from Assemblage I. The scale bar corresponds to 100 µm (except for figures A, C, E, F, G, H, R, S, V, W, Y, AA, AB, AE where it represents 200 µm). All specimens are in dorsal view, if not stated otherwise. • A–G – *Protarabellites* cf. *rectangularis*; A – right MI, ventral view, sample K57, specimen PT128.9; B – right MI, sample K53, PT132.6; C – right MI, sample K57, PT128.3; D – left MI. Note arrow that points to the malformed dentary, sample K53, PT132.10; E – left MI, ventral view, sample K50, PT135.3; F – left MI, sample K57, PT128.4; G – left MII, sample K7, PT128.6. • H, M, P–R, T – *Oeononites* sp., left MI, sample K50, PT135.2; M – right MI, sample K50, PT135.1; P – right MI, sample K57, PT128.7; Q – right MI, sample K57, PT128.8; R – right MI, sample K53, PT132.3; T – right MI, sample K57, PT128.1. • I, J – *Oeononites* sp. 2; I – right MI, sample K53, PT132.9; J – left MI, sample K53, PT132.8. • K, L, S – *Oeononites* ex gr. *wyszogrodensis*; K – left MI, sample K57, PT128.5; L – right MI, sample K59, PT125.1; S – right MI, sample K50, PT135.4. • N, O – *Oeononites* sp. 3; N – left MI, sample K50, PT135.8; O – right MI, sample K50, PT135.6. • U, V, AC – *Atraktoprion* aff. *major*; U – right MI, sample K53, PT132.5; V – left MI, sample K59, PT125.2; AC – left MI, sample K53, PT132.4. • W, X – *Kettnerites kosoviensis* Žebera, 1935; W – right MI, sample K53, PT132.1; X – right MII, sample K53, PT132.2. • Y – *Xanioprion* sp., right MII, sample K50, PT135.7. • Z, AA – *Pistoprion* sp. 1; Z – left MI, sample K57, PT128.10; AA – right MI, sample K57, PT128.11. • AB – *Kalloprion* sp., right MI, sample K57, PT128.2. • AD – *Atraktoprion* sp., left MI, sample K53, PT132.7. • AE, AE1 – *Rakveprion*, specimen is slightly broken, sample K50, PT135.5; AE – lateral view; AE1 – dorsal view.



Ludlow of the Mielnik borehole, Poland (Szaniawski 1970) and from the Wenlock and Ludlow of Gotland, Sweden, and the Ludlow of the Welsh Borderland (Bergman 1989).

Rhytiprionidae Kielan-Jaworowska, 1966

Rhytiprion Kielan-Jaworowska, 1966, represented by *Rhytiprion magnus* Kielan-Jaworowska, 1966 (Fig. 8R, S) is reported from the Prague Basin and entire peri-Gondwana region for the first time. This is also the youngest record of the genus, with the previously youngest finds coming from the lower Ludlow of Gotland (Bergman *et al.* 2003). The transversal ridges in the jaws of *Rhytiprion* may have been useful for crushing and/or grinding food or grazing rather than grasping or penetrating prey. It is believed that *Rhytiprion* preferred deeper water muddy-bottom conditions (Bergman *et al.* 2003). In the Kosov section, only one or two maxillae per sample were recorded.

Ramphoprionidae Kielan-Jaworowska, 1966

Even though the average abundance of the Ramphoprionidae is *ca.* 5%, and reaches 17% at maximum (sample K3), it shows changes within the stratigraphical succession. The family is represented by two species, both belonging to *Protarabellites* Stauffer, 1933. Usually, only a single species is present per sample. *Ramphoprion* Kielan-Jaworowska, 1962 was not found in the Kosov section. However, a single poorly preserved MI possibly belonging to this genus was reported by Tonařová *et al.* (2012), and by Šnajdr in the Ludlow of the Lišči Quarry (Šnajdr 1951, restudied by Tonařová 2012). The indisputable occurrence of *Ramphoprion* in the Prague Basin comes from the Upper Ordovician of the Levín section (Tonařová *et al.* 2023).

The first ramphoprionid species *P. cf. rectangularis* (Figs 5A–G; 7G–K), is transitional between *P. rectangularis* Eriksson, 2001 and *P. triangularis* Eriksson, 2001. Typical for this morphotype is the straight outer margin of left MI, without bending in the middle part as in *P. rectangularis*. The anterior part of the posterior maxillae is often strongly corroded, similarly as observed in *P. triangularis*

by Eriksson (2001), which was explained as a corrosion of the iron-enriched area of the maxilla. The triangular ramus of the first right maxilla is pointed. Some malformed left maxillae *P. cf. rectangularis* were observed in sample K53 (Fig. 5D). The dentary is crooked, and several denticles are dislocated from the normal position. Until now, malformation has been observed only for this single species in the Kosov section. The second species is *P. staufferi* Eriksson, 2001 (Figs 6A–H; 7A–F), which is almost indistinguishable from the type species. Originally, *P. rectangularis* and *P. staufferi* were considered the least stenotopic among the genus (Eriksson 2001).

Tretoprionidae Hints, 1999

The tretoprionid species *Tretoprion astae* Hints, 1999 (Figs 4; 7AM, AN) was also recorded in the section. The genus has appeared in the Late Ordovician (Hints 1999). It usually occurs in small numbers, but thanks to its distinctive morphology is easy to identify. Its morphology seems to be quite conservative up to the upper Silurian.

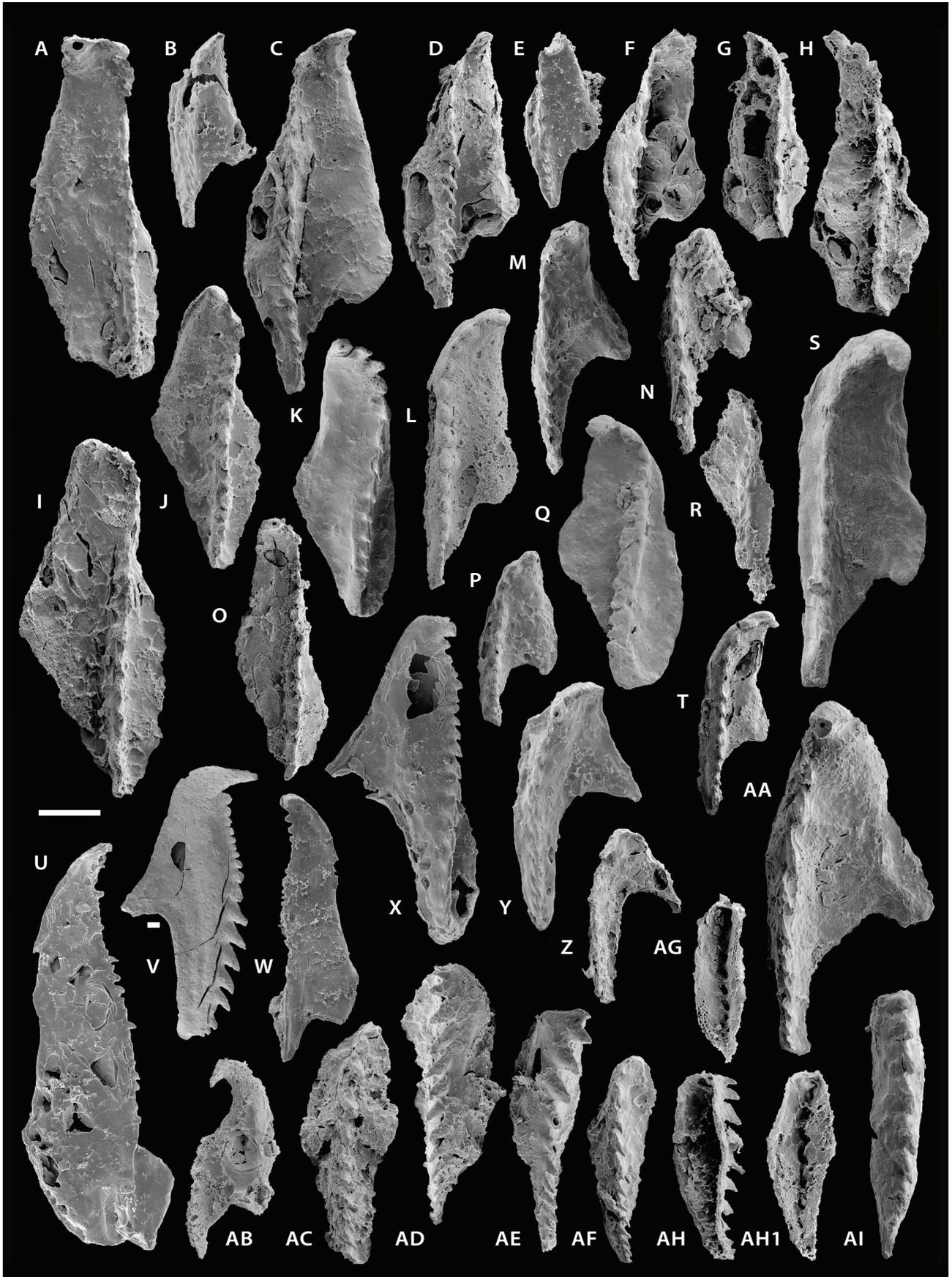
Kallopriionidae Kielan-Jaworowska, 1966

Two kallopriionid genera were recorded in the Kosov section, both appearing during the CIE interval. Tonařová *et al.* (2012) reported kallopriionids also from the *kozłowski* Biozone. *Kallopriion* sp. (Figs 5AB; 8Y, Z) has a very similar morphology to Ordovician species, e.g. *Kallopriion ovalis* Kielan-Jaworowska, 1962 from Baltica (Szaniawski 1970). Compared to other *Kallopriion* Kielan-Jaworowska, 1962 species, it has delicate and densely packed denticles. *Leptoprion* sp. (Fig. 8AG–AI), includes both slender and broad morphotypes in the Kosov assemblage, but due to the small number of specimens, they are treated under a generic designation only.

Atraktoprionidae Kielan-Jaworowska, 1966

Atraktoprionids are represented by at least two species of *Atraktoprion* Kielan-Jaworowska, 1962 in the samples

Figure 6. Scanning electron micrographs of selected scolecodonts from assemblages II and III. The scale bar corresponds to 100 μm (except for figures K, L, O, P, S, T, AI where it corresponds to 200 μm and figure V where it represents 500 μm). All specimens are in dorsal view, if not stated otherwise. • A–H – *Protarabellites staufferi* Eriksson, 2001; A – left MI, sample K93, PT140.8; B – right MI, sample K1, PT143.2; C – right MI, sample K48, PT142.3; D – right MI, sample K93, PT140.4; E – right MI, sample K1, PT143.7; F – right MI, sample K48, PT142.2; G – left MI, sample K48, PT142.6; H – left MI, sample K 48, PT142.11. • I–K, M, P, R, AA – *Oeononites* sp.; I – left MI, sample K48, PT142.12; J – left MI, sample K93, PT140.6; K – left MI, sample K48, PT142.7; M – right MI, sample K93, PT140.7; P – right MI, note the resemblance of the specimen to *Dubichaetaspis*, sample K90, PT137.5; R – left MI, sample K1, PT143.8; AA – right MI, sample K 48, PT142.5. • L, S – *Oeononites* sp. 1; L – right MI, sample K90, PT137.1; S – right MI, sample K1, PT143.1. • N, Q – *Oeononites* aff. *gadomskae*; N – right MI, sample K93, PT140.1; Q – left MI, sample K90, PT137.3. • O, T – *Oeononites* aff. *varsoviensis*; O – left MI, sample K93, PT140.2; T – right MI, sample K48, PT142.8. • U–Y – *Kettnerites kosoviensis* Žebera, 1935; U – left MI, sample K1, PT143.6; V – right MII, sample K90, PT137.2; W – right MI, sample K1, PT143.4; X – left MII, sample K1, PT143.5; Y – right MII, sample K1, PT143.3. • Z – *Kettnerites* sp., right MII, sample K48, PT142.1. • AB – *Atraktoprion* aff. *mirabilis*, right MI, sample K90, PT137.4. • AC–AH, AH1 – *Tetraprion?* sp. 1; AC – sample K93, PT140.5; AD – sample K48, PT142.13; AE – sample K48, PT142.4; AF – sample K48, PT142.14; AG – ventral view, sample K48, PT142.9; AH, AH1 – ventral view, sample K48, PT142.10. • AI – *Xantoprion* sp., sample K93, PT140.3.



studied. The first, present in two samples (K90, K8), has a long hook similar to *A. mirabilis* Kielan-Jaworowska, 1966. It is referred to as *A. aff. mirabilis* (Fig. 6A, B) in this study. The second one is similar to *A. major* Kielan-Jaworowska, 1966, and is referred to as *A. aff. major* (Figs 5U, V, AC; 8AJ). It has shorter hook, a prominent rectangular extension of the ramus, and a longer dentary than *A. aff. mirabilis*. Some of the maxillae were only assigned to the family without generic determination (Figs 5AD; 8AE, AF).

Xanioprionidae Kielan-Jaworowska, 1962

The abundance of xanioprionids varies between 3% and 10% of the assemblage. The maxillae have the appearance of long comb-like ridges that tend to break apart, hampering determination. Therefore, undisputable xanioprionids are treated here as *Xanioprion* sp. (Figs 5Y; 6AI; 8A, G) and some of the incomplete maxillae are left in a generic group “Placognatha” (Fig. 4).

Tetraprionidae Kielan-Jaworowska, 1962

Tetraprionidae is represented by at least two species. A yet undescribed species, is here referred to as *Tetraprion?* sp. 1 (Fig. 6AC–AH). A very similar form was previously described as *Tetraprion?* sp. by Szaniawski (1970). *Tetraprion* sp. 2 (Fig. 8K), is closer to *Tetraprion* sp. A *sensu* Hints *et al.*, 2006 from the Llandovery of Estonia, and to the type species of the genus, *Tetraprion pozaryskae* Kielan-Jaworowska, 1966.

Skalenoprionidae Kielan-Jaworowska, 1966

Several skalenoprionid maxillae occur in the Kosov section. They are rare, and most probably of a single species, *Skalenoprion* sp. (Fig. 8AB–AD, length approx. 270 µm), characterised by relatively small maxillae, with

the dentary occupying $\frac{3}{5}$ of the jaw length. The maxillae resemble *Skalenoprion bugensis* Szaniawski, 1970 from the Wenlock of Estonia (Hints *et al.* 2006), but the hook is shorter and sturdier.

Symmetropionidae Kielan-Jaworowska, 1966

Symmetropionids are rare in the Kosov section, represented by up to five maxillae per sample. They are treated as *Symmetropion* sp. herein (Fig. 8U). Bergman (1995) assumed that *Symmetropion spatiosus* (Hinde, 1882), the type species of the genus, is a facies-dependent taxon preferring reef environments where it can occur in higher numbers.

Polychaeturidae Kielan-Jaworowska, 1966

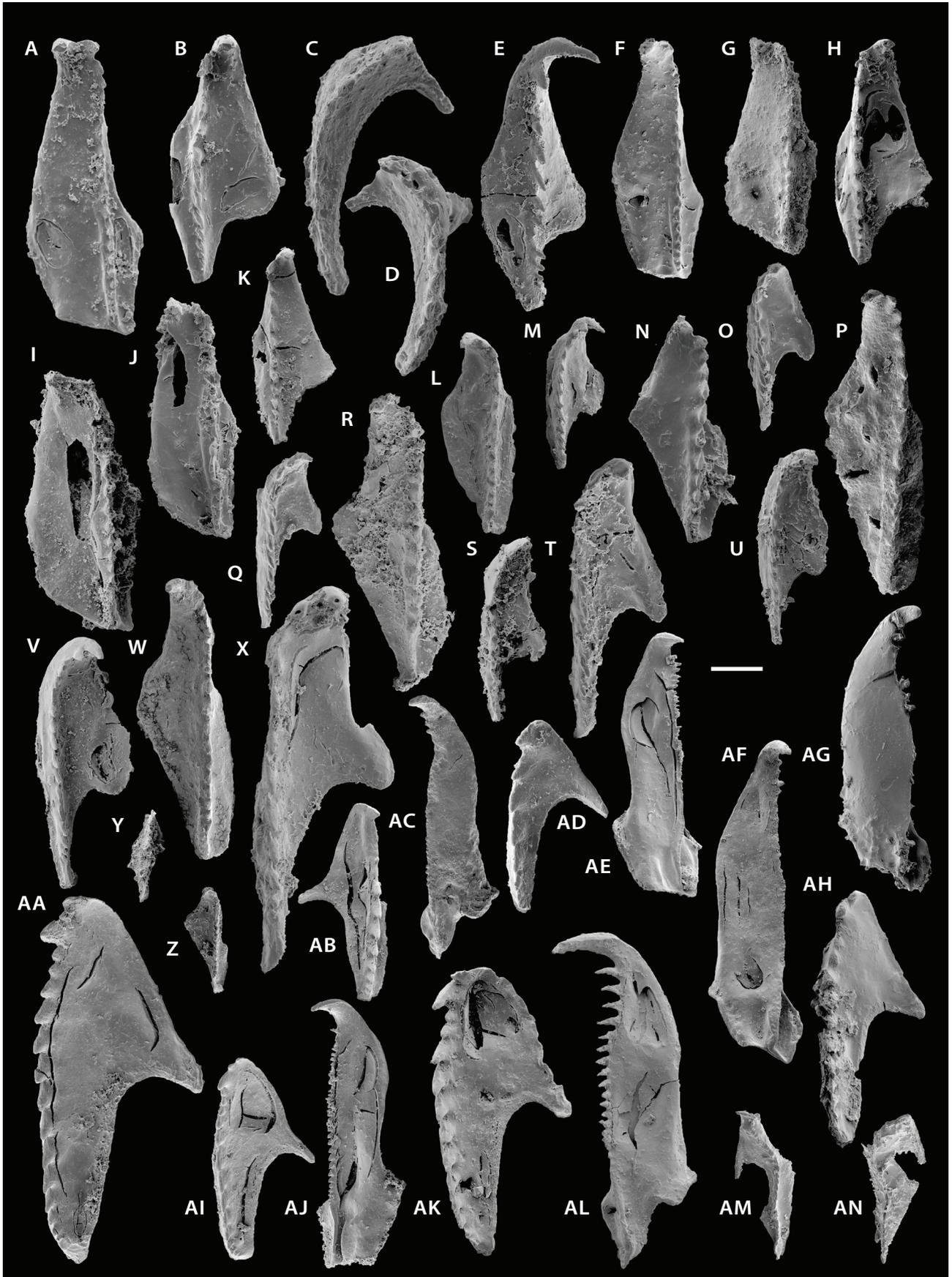
In Tonarová *et al.* (2012, Fig. 5ad), a questionable polychaeturid *Pteropelta?* sp. was described. In our samples, some further questionable specimens also occur, but the more diagnostic left maxilla has not yet been found and thus the presence of the family in the Prague Basin remains tentative only.

Other taxa

A relatively common component of the assemblage is the genus *Rakvereprion* Mierzejewski, 1978, whose family-level affinities are uncertain. In the Kosov section, it is most common in the lowermost and uppermost parts of the section. *Rakvereprion balticus* (Eisenack, 1975) (Figs 5AE, 8B) is a common species since the Ordovician, most characteristic of deeper-water environments (Hints 2000).

A second species of uncertain family-level affinity is *Lunoprionella symmetrica* Eisenack, 1975 (Fig. 8V, X). Its maxillae are fragile and delicate occurring throughout the Ordovician and Silurian.

Figure 7. Scanning electron micrographs of selected scolecodonts from Assemblage III. The scale bar corresponds to 100 µm (except for figures W, AA, AB, AC, AE, AF, AH, AI, AJ where it corresponds to 200 µm). All specimens are in dorsal view. • A–F – *Protarabellites stauferi* Eriksson, 2001; A – left MI, sample K3, PT145.3; B – right MI, sample K3, PT145.1; C – right MII, sample K2, PT144.1; D – left MII, sample K2, PT144.3; E – right MI, sample K3, PT145.4; F – left MI, sample K3, PT145.9. • G–K – *Protarabellites cf. rectangularis* Eriksson, 2001; G – left MI, sample K5, PT147.2; H – right MI, sample K5, PT147.7; I – left MI, sample K5, PT147.8; J – left MI, sample K3, PT145.8; K – right MI, sample K5, PT147.4. • L, M, U, V – *Oeononites* sp. 2; L – left MI, sample K7, PT149.9; M – right MI, sample K7, PT149.7; U – right MI, sample K6, PT148.2; V – right MI, sample K5, PT147.7. • N, O – *Oeononites aff. gadomskae*; N – left MI, sample K6, PT148.5; O – right MI, sample K6, PT148.1. • P, Q, W – *Oeononites* ex gr. *wyszogrodensis*; P – sample K10, PT152.2; Q – sample K2, PT144.2; W – left MI, sample K5, PT147.1. • R–T – *Oeononites aff. varsoviensis*; R – sample K5, PT147.5; S – sample K3, PT145.5; T – sample K5, PT147.6. • X–Z – *Oeononites* sp.; X – sample K3, PT145.2; Y – right MI, sample K3, PT145.7; Z – left MI, sample K3, PT145.6. • AA, AG–AI – *Kettnerites aff. huberti*; AA – right MII, sample K7, PT149.3; AG – left MI, sample K6, PT148.8; AH – right MII, sample K11, PT153.1; AI – right MII, sample K7, PT149.2. • AB, AD, AE, AJ – *Kettnerites aff. sisyphi*; AB – left MII, sample K7, PT149.4; AD – right MII, sample K6, PT148.10; AE – left MI, sample K7, PT149.5; AJ – right MI, sample K7, PT149.1. • AC, AF – *Kettnerites aff. huberti?*; AC – right MI, sample K10, PT152.6; AF – left MI, sample K10, PT152.7. • AK, AL – *Kettnerites kosoviensis* Žebera, 1935; AK – right MII, sample K10, PT152.8; AL – right MI, sample K6, PT148.7. • AM, AN – *Tretopriion astae* Hints, 1999; AM – left MI, sample K7, PT149.18; AN – right MI with fused basal plate, sample K7, PT149.17.



Jawed polychaete faunal assemblages

The composition of the jawed polychaete fauna from the Kosov section shows similar trends to coeval strata elsewhere (Eriksson *et al.* 2004): the most common family in the section as a whole is Polychaetaspidae (Fig. 4), followed by Paulinitidae and Mochtyellidae.

The evenness of the polychaete fauna varies between 0.7 and 0.89 in most samples, *i.e.* the assemblages are quite well balanced, with no dominant species, except in few cases, where the value decreases to 0.5 and 0.6 (samples K49 and K3, respectively). Stratigraphically constrained clustering using unweighted pair-group average algorithm and Dice similarity revealed three distinct clusters interpreted here as scolecodont assemblages – Assemblage I occurring in Interval I, Assemblage II occurring in the lower part of Interval II, and Assemblage III occurring in the upper part of Interval II and in Interval III (Fig. 4).

Assemblage I (samples K59–K50, Fig. 5)

The most common families are Polychaetaspidae, followed by Mochtyellidae and Paulinitidae. Altogether, polychaetaspids represent approximately half of the assemblage with at least six species present (Figs 4, 5).

There are several characteristic species: *Kettnerites kosoviensis* (Fig. 5W, X), *Protarabellites* cf. *rectangularis* (Fig. 5A–G), *Pistoprion* sp. 1 (Fig. 5Z, AA), *Oeononites* aff. *gadomskae*, *O.* sp. 3 (Fig. 5N, O), *Mochtyella pragensis*, and *Rakvereprion balticus* (Fig. 5AE). *Pistoprion* sp. 1 represents 5–35% of the assemblage, occurring only in this interval. Among mochttyellids, *Vistulella* is very common and *Mochtyella* is rare, represented only by *M. pragensis*, which is viewed as an environmentally sensitive species (previously described as “*Mochtyella*” sp. D *sensu* Hints *et al.* 2006). Its record is from the lower Telychian of the Baltic palaeobasin, where it is typical for the Velise Formation in Estonia (Hints *et al.* 2006, Tona-

rová *et al.* 2014). Atraktoprionids (Fig. 5U, V, AC, AD), symmetropionids, tretoprionids, xanioprionids (Fig. 5Y), and kallopionids (Fig. 5AB) are rather rare in this interval.

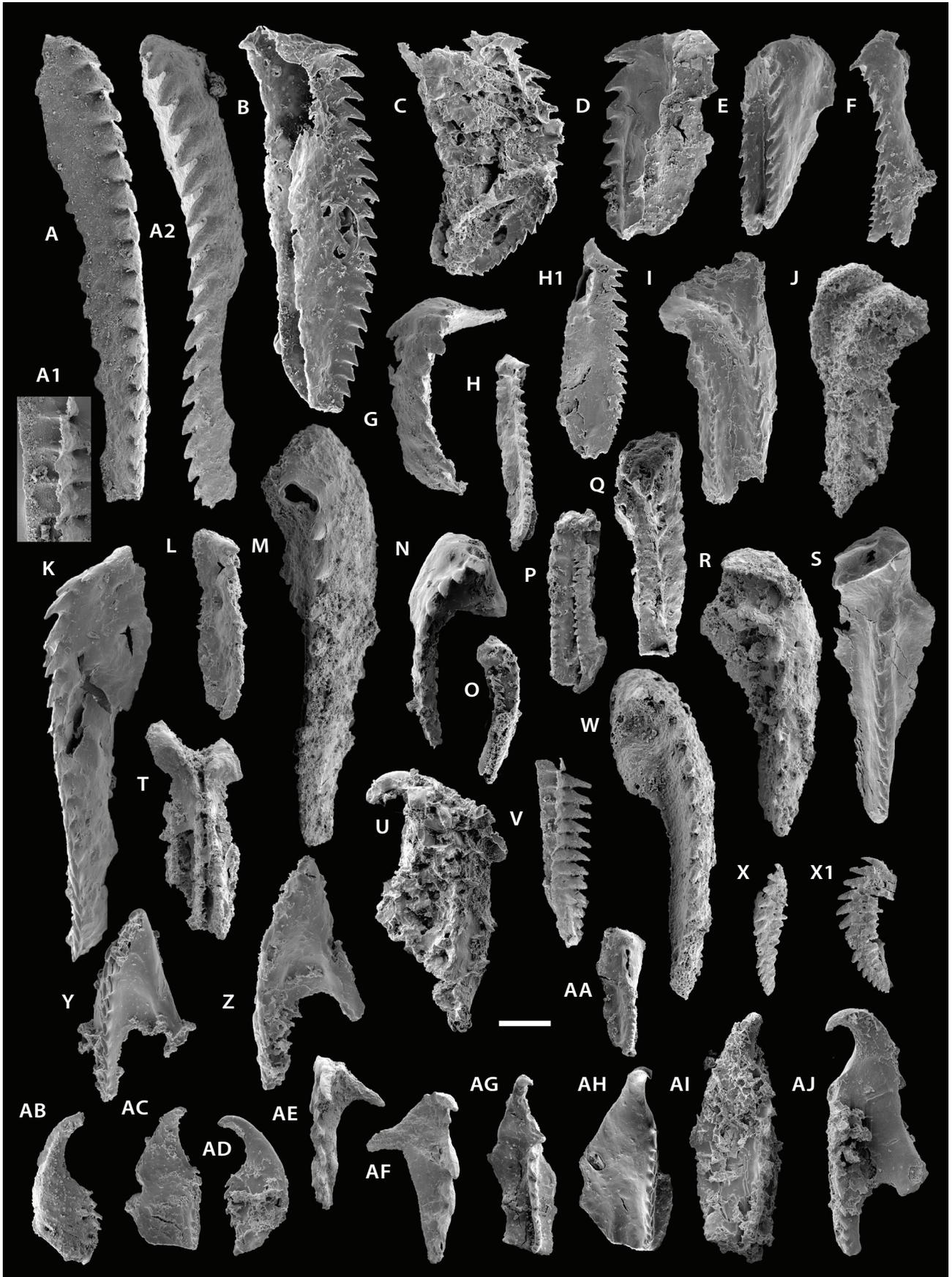
Assemblage II (samples K49–K94, Fig. 6)

The preservation of scolecodonts is relatively poor in Assemblage II (Fig. 6), which can complicate proper determination. The original organic matter looks more altered, inducing fragmentary preservation and lower abundances in the samples. The composition of the assemblage also differs from other parts of the section. In general, the long-ranging and more eurytopic taxa prevail; the mochttyellids are more common, and the polychaetaspids are less common than in other intervals (Fig. 4).

Polychaetaspids are represented by at least seven species, which is a comparable diversity to the rest of the section. *Oeononites* aff. *gadomskae* (Fig. 6N, Q) predominates, followed by *O. ex gr. wyszogrodensis*. *Oeononites* sp. 1 (Fig. 6L) first appears in this interval and ranges up to the youngest part of the succession studied. Paulinitids are also relatively common; for example, in sample K49, they dominate the assemblage. However, their diversity is low. *Kettnerites kosoviensis* (6V) is the most common species in the assemblage.

Xanioprionids (6AI) comprise 10% of the assemblage, which is higher than in other parts of the section. In this interval, mochttyellids and atraktoprionids (Figs 4, 6AB) reach their highest relative abundance, 50%, and 16% respectively in sample K94 (the values may be skewed due to the low number of specimens in this sample). *Protarabellites staufferi* (Fig. 6A, D) is the only ramphoprionid species in assemblage II suggesting its eurytopic nature. The species is also known from the lower Silurian of the Prague Basin (Tonarová *et al.* 2019). *Symmetropion* sp. is present in three out of six samples from this interval.

Figure 8. Scanning electron micrographs of selected scolecodonts from Assemblage III. The scale bar corresponds to 100 µm (except for figures A, V, AE, AF where it corresponds to 200 µm). All specimens are in dorsal view, if not stated otherwise. • A, A1, A2 – *Xanioprion* sp.; A–A2 – sample K7, PT149.11, lateral view (A), detail of ventral side (A1) and dorsal view (A2); G – right MII, sample K2, PT144.5. • B – *Rakvereprion balticus*, lateral view, sample K7, PT149.10. • C–E – *Mochtyella* sp. 1; C – part of the apparatus, sample K3, PT145.10; D – right MI, lateral view, sample K3, PT145.14; E – left MI, sample K6, PT148.4. • F, H, H1 – *Mochtyella* sp. 2; F – left MI, sample K2, PT144.4; H, H1 – sample K7, PT149.14, dorsal view (G), lateral view (G1). • I, J – *Mochtyella pragensis*; I – left MI, sample K4, PT146.1; J – right MI, sample K4, PT146.3. • K – *Tetraprion* sp. 2, sample K6, PT148.6. • L, M, O, P, AA – *Vistulella kozlowskii*; L – right MI, dorsolateral view, sample K7, PT149.13; M – left MI, sample K5, PT147.3; O – left MI, sample K7, PT149.15; P – right MI, sample K6, PT148.9; AA – right MII, sample K10, PT152.5. • N, W – *Pistoprion* sp. 2; N – right MII, sample K3, PT145.13; W – left MI, sample K10, PT152.1. • Q – *Mochtyella ex gr. fragilis*, left MI, sample K10, PT152.9. • R, S – *Rhytiprion magnus*; R – left MI, sample K7, PT149.6; S – right MI, sample K12, PT154.1. • T – *Mochtyella* sp. ??, fused MIs, sample K7, PT149.16. • U – *Symmetropion?* sp., left MI, sample K3, PT145.11. • V, X, X1 – *Lunoprionella* sp.; V – lateral view, sample K7, PT149.12; X, X1 – sample K10, PT152.10. • Y, Z – *Kallopion* sp.; Y – right MI, sample K4, PT146.2; Z – right MI, sample K3, PT145.12. • AB, AC – *Skalenoprion* sp.; AB – left MI, sample K10, PT152.3; AC – left MI, sample K3, PT145.15; AD – right MI, sample K3, PT145.16. • AE, AF – atraktoprionid MII; AE – sample K9, PT151.1; AF – sample K11, PT153.2. • AC–AI – *Leptoprion* sp.; AG – left MI, sample K10, PT152.4; AH – left MI, sample K7, PT149.8; AI – left MI, sample K3, PT145.17. • AJ – *Atraktoprion* aff. *major*, right MI, sample K6, PT148.3.



Assemblage III (samples K48–K13; Figs 6, 7, 8)

The reappearance of several taxa is characteristic of this assemblage. For instance, *Protarabellites* cf. *rectangularis* (Fig. 7A–K), *Tretoprion astae* (7AM, AN), *Mochtyella pragensis* (Fig. 8I, J), *Lunoprionella symmetrica* (8V, X), were recorded before and after the MLCIE. Polychaetaspids prevail, varying from 40 to 70% of the assemblage (Fig. 4), with at least six species distinguished. Typical are *Oeononites* sp. 1 (Fig. 6S), *Oeononites* sp. 2 (Fig. 7L, M, U, V), accompanied by the long-ranging *O.* aff. *gadomskae* (Fig. 7N, O) and *O.* ex gr. *wyszogrodensis* (Fig. 7P, Q, W). Among ramphoprionids, *Protarabellites* cf. *rectangularis* reappears in Assemblage III, but *P. staufferi* (Fig. 6B, C, E–H) is more abundant. Ramphoprionids comprise 18% of the assemblage (sample K3), which is the highest in the Kosov section.

Mochtyellids represent approx. 18% of the assemblage. *Vistulella kozlowskii* (Fig. 8L, M, O, P) is the most abundant, and *Mochtyella pragensis* reappears. In the Kosov section, the latter species occurs below and above the peak of the $\delta^{13}\text{C}$ excursion (Fig. 4). *Mochtyella* ex gr. *fragilis* (Fig. 8Q) first appears in this interval; however, it has previously been reported also from the *siluricus* conodont Biozone in Liščí Quarry (Tonarová *et al.* 2012), and very similar forms occur in early Silurian strata. The genus *Pistoprion* is very rare in assemblage III, represented by *Pistoprion* sp. 2 (Fig. 8N, W). *Rhytiprion* (Fig. 8R, S) appears, marking the first record of this genus in the Prague Basin.

In Assemblage III, the diversity of paulinitids is the highest within the section, with three species present: *Kettnerites kosoviensis* (Figs 6U, W–Y; 7AK, AL), *K.* aff. *huberti* (Fig. 7AF, AG, AH, AI) and *K.* aff. *sisyphi* (Fig. 7AB, AD, AE, AJ). *Rakvereprion balticus* (Fig. 8B) reaches its abundance maximum and *Tetraprion?* sp. 1 (Fig. 6AD–AH) has also its abundance peak (23%) in the lowermost samples.

Discussion

Polychaetes across ice ages and carbon isotope events

Several papers have been published on the impacts of environmental events on jawed polychaetes (Hints *et al.* 2004, 2006, 2010; Eriksson 2006a, b; Eriksson & Frisk 2011; Tonarová *et al.* 2012, 2014, 2017). In comparison with many other fossil groups, they seem to have endured various global environmental crises with no major extinctions. Polychaete faunas were temporarily disturbed, but the abundance often remained stable, and pre-extinction diversity was retained rather quickly.

They are also commonly pioneers in the post-event strata not only in the fossil record (Eriksson & Frisk 2011) but also in the recent oceans (Díaz-Castañeda & Reish 2009). For example, the end-Ordovician extinction event, which resulted in the disappearance of more than 80% of species and 60% of genera (Sheehan 2001), led to a reorganisation of polychaete fauna, but genus-level diversity did not decrease substantially (Eriksson *et al.* 2004, 2013; Hints & Tonarová 2023). Hints *et al.* (2003) showed that a massive Late Ordovician volcanic ash-fall resulting in the Kinnekulle K-bentonite Bed, did not affect the polychaete faunas to a large extent, but the assemblage got reorganised, and *Pistoprion transitans* temporally disappeared following the event.

The impact of the early Wenlock Ireviken event (IE) was studied in the Viki drill core, western Estonia (Tonarová *et al.* 2014). Results showed that coinciding with the onset of the IE, a stepwise four-fold drop in the abundance of scolecodonts is observed, with the minimum value reached between datum points 4 and 6. Eriksson (2006a) observed a similar decline in abundance from the Lower Visby to Upper Visby Formation on Gotland. The assemblage structure also changed markedly during the IE interval. Especially noteworthy is the “polychaetaspid crisis”, which was recorded from a single sample between datum points 4 and 6 in the Viki core. A sharp decline in the relative frequency of polychaetaspids from 50–70% in pre-event strata to 15–30% in post-event strata was also recorded in the Paatsalu section (Hints *et al.* 2006). At the species level, the disappearance or strong decline of *Oeononites latus* (Kielan-Jaworowska, 1966) just below datum point 4 and the appearance of *Dubichaetaspis bergmani* Eriksson, 1998 at that same level is similar for the Viki and Gotland sections.

With regard to other families, xanioprionids, and possibly mochttyellids, show similar trends during and after the IE interval in the Gotland and Viki successions. Xanioprionids that represented less than 5% of the fauna below the IE become a more prominent component in the event interval, reaching *ca.* 10% approximately at datum point 3 in the Viki drill core, and 17% above datum point 6.2 on Gotland (Eriksson 2006a). The taxonomic composition of mochttyellids went through notable changes. In particular, “*Mochtyella*” *pragensis* (= *Mochtyella* sp. D of Hints *et al.* 2006), a characteristic species of the Velise and lower Jaani formations, disappears immediately below datum point 4 in the Viki and Paatsalu drill core successions. *Mochtyella pragensis* is unknown from younger strata in Baltoscandia, but it has been recorded from the Ludlow of the Prague Basin (Tonarová *et al.* 2012; present study). In the Viki succession, the disappearance of *Tetraprion* sp. A and *Pistoprion* sp. were recorded within the IE interval. The latter taxon, however, does occur in younger strata on Gotland and elsewhere

(Tonarová et al. 2012). Moreover, the combined occurrence of *Kallopriion kilmisteri* Eriksson, 2006a on Gotland and in the post-event strata of the Viki drill core suggests that the species had a range gap during the IE interval, from approximately datum point 2 onwards (cf. Eriksson 2006a, b).

This pattern coincides with the major turnover interval of most other fossil groups (Lehnert et al. 2010). The disappearance and appearance of several taxonomic lineages within or close to the IE interval are recorded in the Viki, Paatsalu, and Viirelaid drill cores from Estonia, and on Gotland. However, as some of the range ends documented appear to be of local significance, more data from post-event strata are needed to fully assess the IE as a major extinction event for polychaetes. Moreover, careful taxonomic studies, particularly regarding taxa that are left in open nomenclature, are needed to evaluate the full impact and magnitude of the event.

Response of jawed polychaetes to mid-Ludfordian environmental changes

Only a few papers deal with the impact of the Lau Event on jawed polychaetes. Jeppsson & Aldridge (2000, p. 1144), referring to Bergman (1989), were the first to interpret changes in polychaete faunas as a response to the Lau Event. Bergman (1989) recorded gradual faunal changes in the Hemse-Eke interval on Gotland. Later, Eriksson et al. (2004) concluded that approximately 30% of the polychaete taxa on Gotland went extinct during the event and also reported that 20% of lineages have Lazarus gaps. During the event, paulinitids were very common whereas polychaetaspids and placognath taxa were quite rare. The post-event fauna differs considerably from the older one – new taxa appeared and several species, which were extremely rare or absent during the event, became abundant on Gotland. There is also a higher relative frequency of polychaetaspids (dwarfed *Oeononites* species are particularly common) and placognath forms, and a lower relative frequency of paulinitids. Eriksson et al. (2004) concluded that a possible “Lilliput effect”, disaster and recovery faunas, and Lazarus taxa can be identified on Gotland across the event. The most recent study on Baltic jawed polychaetes’ response to the Lau event is by Männik et al. (2024) based on data from the Bebirva-111 drill core (Lithuania). They did not observe any major extinction due to the event.

In the Prague Basin, Tonarová et al. (2012) studied the jawed polychaetes mainly from the *P. siluricus* conodont Biozone. Only a few samples covered the post-event interval, therefore a detailed evaluation of the event impact was impossible. With the beginning of the carbon isotope excursion (Lehnert et al. 2007b, Frýda et al. 2021a), the number of polychaete genera decreased from 15 to 4,

and only *Kettnerites* spp., *Oeononites* spp. and *Vistulella kozłowskii* and scolecodont fragments were recorded in the beds above the LAD of *P. siluricus*. However, the samples came from gravity flow deposits (turbidites or tempestites according to Lehnert et al. 2007b), and therefore, the results could have been skewed due to taphonomy. Altogether, it seemed that the extinction had only a mild effect.

In the present study, we have confirmed that the jawed polychaete assemblage was temporarily disturbed during the CIE, but several species such as *Protarabellites* cf. *rectangularis*, *Tretoprion astae*, *Mochtyella pragensis* and *Lunoprionella symmetrica* reappeared when the conditions returned to the previous state. Also, *Pistoprion* disappeared for the critical interval and later re-appeared in a slightly different morphology (*P.* sp. 2). A similar pattern was observed on Baltica as mentioned above. In general, simple maxillae of mochtlyellids and xanioprionids, together with tetraprionids, are viewed as rather primitive forms with stratigraphical ranges commencing in the Lower Ordovician (Paxton 2009). They have a comb-like appearance, the apparatus is complex with numerous single teeth, and they are often long-ranging. Courtinat (1998, p. 438) even assumed that mochtlyellids adapted to extreme environments of weak dissolved oxygen content and great depths. He supposed that, similarly to modern polychaetes, they consumed energy through tubes or burrows. When suboxic and then anoxic conditions are reached, oxic metabolism shift to anoxic metabolism in a gradual transition (Scott 1976). However, placognaths are known only from extinct species; therefore, a comparison with living worms remains speculative. Tonarová et al. (2023) also reported a raised number of placognath taxa in the interval of assumed lower oxygen levels (above the first diamictite bed). However, it should be noted that placognath- and ctenognath-type jaw apparatuses are very common in Baltica throughout the Middle and Upper Ordovician (Hints 1998b, 2000; Eriksson & Hints 2009; Hints & Eriksson 2010).

With the beginning of the cooling episode (sample K49), the role of paulinitids increased. Similarly, on Gotland paulinitids were abundant during the CIE interval which corresponds to glaciation (Eriksson et al. 2004, fig. 6; Frýda et al. 2021b, fig. 5). Previously, a dominance of this group was reported in the Middle Devonian Malvinokhosan (Malvinokaffric) cool/cold water realm (Eriksson et al. 2011) that could suggest endurance of the group to reductions in temperature. Bergman (1989) studied paulinitids in detail and showed that they flourished in relatively shallow, sheltered, lagoonal environments where a high diversity was exhibited. In contrast, deeper water faunas were less diverse and abundant, and most specimens in such environments were small.

Polychaetaspids commonly represent the most prominent component of the assemblage, which is true also for

the Prague Basin. In the Silurian succession of Gotland, ten species belonging to three genera (*Kozlowskiprion* Kielan-Jaworowska, 1966, *Oeononites* and *Dubichaetaspis* Eriksson, 1998) have been described (Eriksson *et al.* 2004). In the Kosov section, only one genus, *Oeononites*, with eight species was recorded. It should be noted that other polychaetaspid genera, *Incisiprion* Hints, 1998b and *Dubichaetaspis* were found in the Aeronian volcanic-carbonate succession of the Prague Basin (Tonarová *et al.* 2019). Some of the Kosov specimens of *Oeononites* also resemble *Dubichaetaspis* (see Fig. 6P), but the diagnostic left first maxilla has not been found. The genus *Kozlowskiprion* has not been reported from the Prague Basin.

Changes in the distribution of ramphoprionids can be observed in the Kosov section. Two species, *Protarabellites staufferi* and *Protarabellites cf. rectangularis*, were found. The longest stratigraphical record was observed for *Protarabellites cf. rectangularis*; on the other hand, *P. staufferi* is the only ramphoprionid in the MLCIE interval suggesting its endurance. *P. staufferi* has a relatively long stratigraphical record also on Gotland – from the lower Sheinwoodian to upper Ludfordian (Eriksson 2001). *P. rectangularis* was identified from the lowermost Wenlock to Ludfordian of Gotland (Eriksson 2001). However, the ramphoprionids were more diverse on Gotland, with two more genera *Megaramphoprion* and *Ramphoprion*, as well as more species of *Protarabellites*. On Gotland, the ramphoprionids represented 2–30% of the polychaete fauna; but rarely exceeding 10%. The exception is the Ludfordian Burgsvik Formation, in which ramphoprionids comprised 20% of the fauna (Eriksson 2001). In the Prague Basin, *Megaramphoprion* has not been found and *Ramphoprion* was confirmed only in the Upper Ordovician (Tonarová *et al.* 2023).

In the present study, the family Rhytiprionidae was documented in the Prague Basin from the upper Ludlow. The family is known since the Middle Ordovician from Baltica and the youngest occurrence hitherto known was from lower Ludlow of Gotland. However, its intercontinental distribution to the Mid-Continent Laurentia (Indiana) was described, and proliferation in inter-reef basin with a muddy, terrigenous bottom sediment was confirmed (Bergman *et al.* 2003). The migration of *Rhytiprion* between Laurentia and Baltica confirms closer biogeographic links towards the end of Silurian and Devonian, as was observed for other groups of organisms (McKerrow *et al.* 2000).

In the Kosov JF195 section, lingulate brachiopods were analysed in detail by Mergl *et al.* (2018). A monospecific *Kosoidea fissurella* Community occurs in the interval of high $\delta^{13}\text{C}$ values. It was, therefore, interpreted as an opportunistic species. Nevertheless, the bimodal stratigraphical distribution of some lingulate brachiopods (*Acrotretella siluriana* Ireland, 1961, *Chynithele vexata*

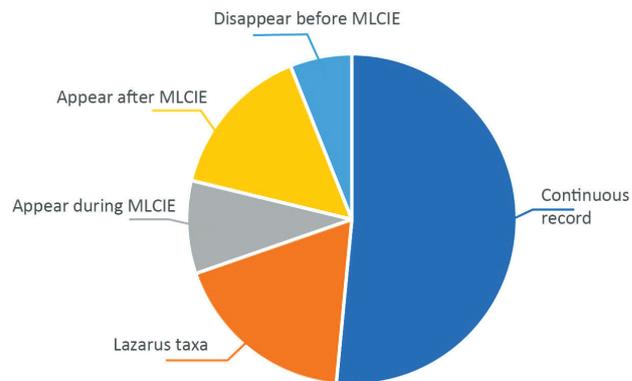


Figure 9. Pie chart of distribution of the scolecodont taxa in the Kosov JF195 section. Each section represents a proportional portion of taxa that have a continuous record, Lazarus taxa, taxa appearing during the MLCIE, appearing after the MLCIE and disappearing before the MLCIE.

(Barrande, 1879), *Schizotreta* sp., and *Schizobolus* sp.), which occur before as well as after the MLCIE, suggested that these species were not affected by the Lau and Kozlowskii extinction events, but only decreased their ecospace and lived in other areas during the post-extinction (recovery) period, and then returned when environmental conditions ameliorated (Mergl *et al.* 2018). In the present study, we have observed that the jawed polychaete assemblage is also disturbed during the period of high $\delta^{13}\text{C}$ values, the diversity decreased, and the composition of fauna changed. However, the recovery of jawed polychaetes took place earlier than that of brachiopods (approx. 3 m in the Kosov succession).

Summary

The most distinct change in the jawed polychaete fauna was documented at the end of the *Polygnathoides siluricus* conodont Biozone, marking the beginning of the glaciation. During the MLCIE and the Mid-Ludfordian Glaciation interval, the jawed polychaete fauna was disturbed and the composition was temporarily changed. However, the recovery was relatively quick. We did not observe such prominent changes among jawed polychaetes due to the Ludfordian environmental changes as described *e.g.* from Gotland, Baltica (Eriksson *et al.* 2004). Only two species (6%) disappear during the event and 20% of species can be viewed as Lazarus taxa (*Protarabellites cf. rectangularis*, *Tretoprion astae*, *Mochtyella pragensis*, *Lunoprionella symmetrica*). Approximately half of the taxa have a continuous record. The rest of the species documented from the Kosov section appear either during or after the event (Fig. 9). *Mochtyella pragensis* was previously described as an environmentally sensitive species (Tonarová *et al.* 2014) which was confirmed by

our study. Another confirmed trend observed in other event-influenced strata is the more prominent role of placognath and ctenognath taxa, together with paulinitids, during the disturbed interval, similarly to the Ireviken event (Tonarová et al. 2014).

Acknowledgements

We are grateful to reviewers Anthony Butcher and David Loydell (University of Portsmouth) for their thorough reviews that significantly improved the manuscript. This is a contribution to the Strategic Research Plan of the Czech Geological Survey (DKRVO/ČGS 2023–2027; Nos 311410, 311650). Multidisciplinary study of the mid-Ludfordian environmental changes and high-resolution stratigraphical sampling was financially supported by the Grant Agency of the Czech Republic (GA23-06198S). Taxonomical evaluation of the jawed polychaetes was financially supported by the Grant Agency of the Czech Republic (23-05944K) and the Estonian Research Council (grant PRG1701). This paper is a contribution to IGCP project 735 “Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification” and represents our research activity in the Subcommittee on Silurian Stratigraphy (the International Commission on Stratigraphy; the International Union of Geological Sciences).

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