

Carbon isotope values in conodont elements from the latest Devonian–Early Carboniferous carbonate platform facies (Timan-Pechora Basin)

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Abstract. The $\delta^{13}\text{C}_{\text{org}}$ values and their variations in conodont elements of the latest Famennian–Tournaisian species *Polygnathus parapetus* Druce are considered. The conodonts studied come from the latest Famennian–Tournaisian interval of the Kamenka River section (Timan-Pechora Basin). The carbon isotope composition of conodont elements had an average value of -25.2‰ , suggesting a low trophic level of this species. During the latest Famennian (*praesulcata* conodont Zone) $\delta^{13}\text{C}_{\text{org}}$ shifted to more negative values (up to -30.4‰), which may be attributed to changes in the global carbon cycle and local influx of organic matter of terrestrial origin during the terminal Famennian regression.

Key words: Famennian, Tournaisian, conodonts, $\delta^{13}\text{C}_{\text{org}}$, Timan-Pechora Basin.

INTRODUCTION

Conodonts were the Palaeozoic and Early Mesozoic extinct group of marine animals possessing debated affinities (e.g. Donoghue et al. 2000; Blicek et al. 2010; Turner et al. 2010). The only mineralized parts of conodonts are tooth-like elements disposed in a bilaterally symmetrical apparatus. Conodont elements are composed of complex aggregates of proteins and apatite-(CaF) (e.g. Trotter & Eggins 2006; Rosseeva et al. 2011). The mineral composition of conodont elements is known in detail; however, their organic matter is studied to a lesser degree. Previous investigations have demonstrated that organic matter, consisting of less than 4% of a conodont element, is composed of collagen-like protein (e.g. Fähræus & Fähræus-van Ree 1987; Kemp 2002; Rosseeva et al. 2011; Zhuravlev 2017a). The protein network is surrounded by aligned crystallites of apatite-(CaF) and strongly incorporated into the mineral matrix. This incorporation provides unique conservation of organic matter, demonstrating a preserved supra-molecular protein structure (Zhuravlev 2017a).

The low content of carbonate ions in conodont apatite of lamellar, paralamellar and albid tissues (Trotter & Eggins 2006; Frank-Kamenetskaya et al. 2014) makes it possible to study carbon isotope values of organic matter in conodont elements without their demineralization. The first information about isotope composition of conodont organic matter was published by Over &

Grossman (1992). These authors reported $\delta^{13}\text{C}_{\text{org}}$ in conodont elements of the Late Devonian genus *Palmatolepis* (from -24.5‰ to -24.0‰), Early Carboniferous (Mississippian) siphonodellids (-26.3‰ and -27.3‰) and Late Carboniferous (Pennsylvanian) *Streptognathodus elegantulus* (from -23.0‰ to -24.0‰), and noted that significant isotopic differences may be related to ‘local changes in source of organic carbon, global changes in the carbon budget, or to dietary differences among conodont animals’ (Over & Grossman 1992 p. A214). Some data on the trophic differentiation of the Late Viséan (Mississippian) conodonts based on $\delta^{13}\text{C}_{\text{org}}$ were published later (Nicholas et al. 2004).

This study considers $\delta^{13}\text{C}_{\text{org}}$ values and their variations in conodont elements of the latest Famennian–Tournaisian species *Polygnathus parapetus* Druce. The key objective is to evaluate potential implications of $\delta^{13}\text{C}_{\text{org}}$ of conodont elements for palaeoecological reconstructions, including the position of conodonts in the food web and probable causes of temporal fluctuation of $\delta^{13}\text{C}_{\text{org}}$ during the Devonian–Carboniferous transition.

MATERIAL AND METHODS

Conodont elements were studied from the Kamenka River section in the southern part of the Pechora Swell (northern Cis-Urals, N $65^{\circ}04'27.4''$, E $56^{\circ}42'50.9''$) (Fig. 1). The section was located on the northeastern

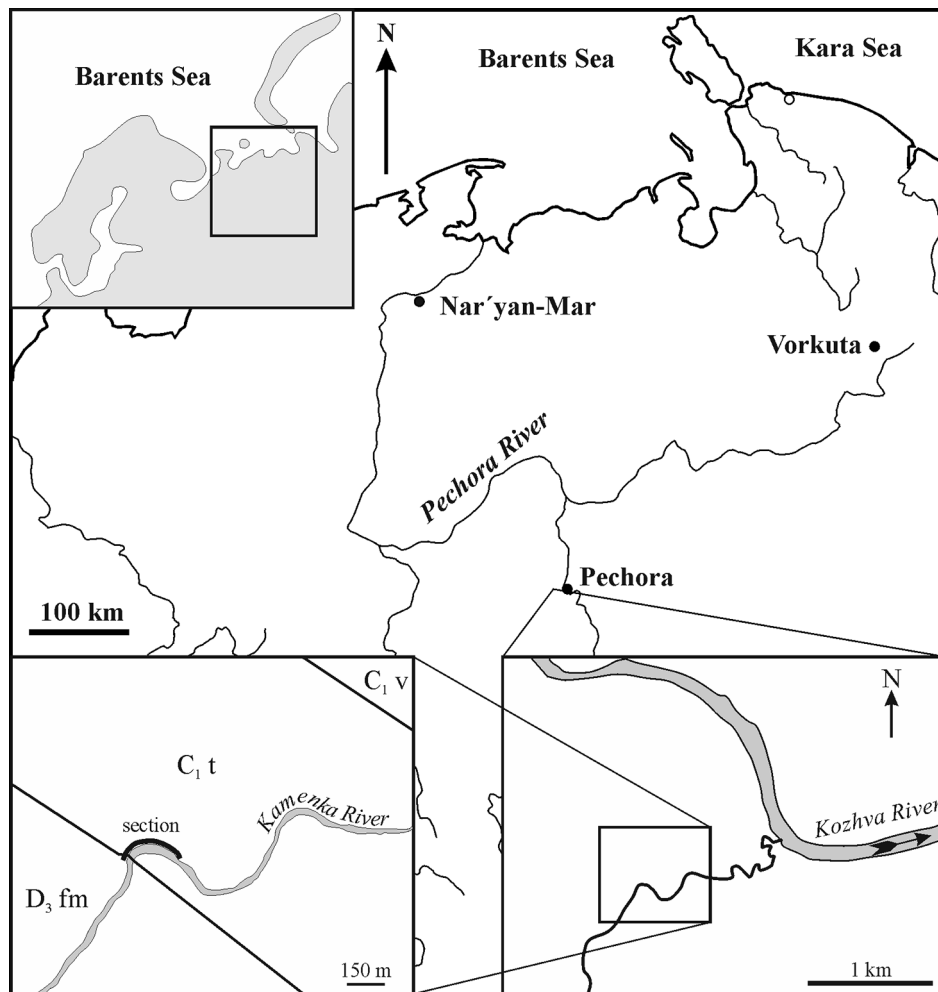


Fig. 1. The location of the Kamenka River section.

margin of Laurussia during the late Famennian–Tournaisian and comprises the stratigraphical interval from the latest Famennian *praesulcata* Zone through the late Tournaisian *crenulata* Zone, being 16.5 m thick (Zhuravlev et al. 1998; Vevel' et al. 2012; Zhuravlev 2017b). The sedimentological and palaeoenvironmental characteristics of the section reflect a palaeoenvironmental setting in shallow tropical waters (Zhuravlev et al. 1998; Vevel' et al. 2012). About 100 limestone samples were taken from the section. The processing of samples followed the standard procedure (dissolution of limestone in 10% buffered acetic acid). The residues were washed through a sieve of 70 μm , dried and conodont elements were picked out. Rather rich and diverse conodont faunas were obtained from the Kamenka River section, which provided the biostratigraphical framework (Zhuravlev et al. 1998; Vevel' et al. 2012; Zhuravlev 2017b) (Fig. 2). The preservation of conodont elements is fine and they have a Conodont Alteration

Index (CAI) value of 1 (i.e. $T < 50\text{ }^{\circ}\text{C}$). The low grade of thermal maturity suggests the preservation of the original carbon isotope composition of organic matter (McKirdy & Powell 1974). According to McKirdy & Powell (1974), unmetamorphosed organic matter is isotopically lighter than metamorphosed material, and postdepositional thermal alteration may lead to a positive shift in carbon isotope composition. In contrast, no significant correlation between thermal alteration and $\delta^{13}\text{C}_{\text{org}}$ was discernible from data by Strauss & Peters-Kottig (2003).

The P1 elements of the long-lived conodont species *Polygnathus parapetus* Druce (Fig. 3), which are abundant in the study samples, were selected for investigating organic carbon isotope values. The predominance of organic-rich lamellar and paralamellar tissues in these conodont elements makes them suitable for this study (Müller & Nogami 1971). The histological study of conodont elements demonstrates good

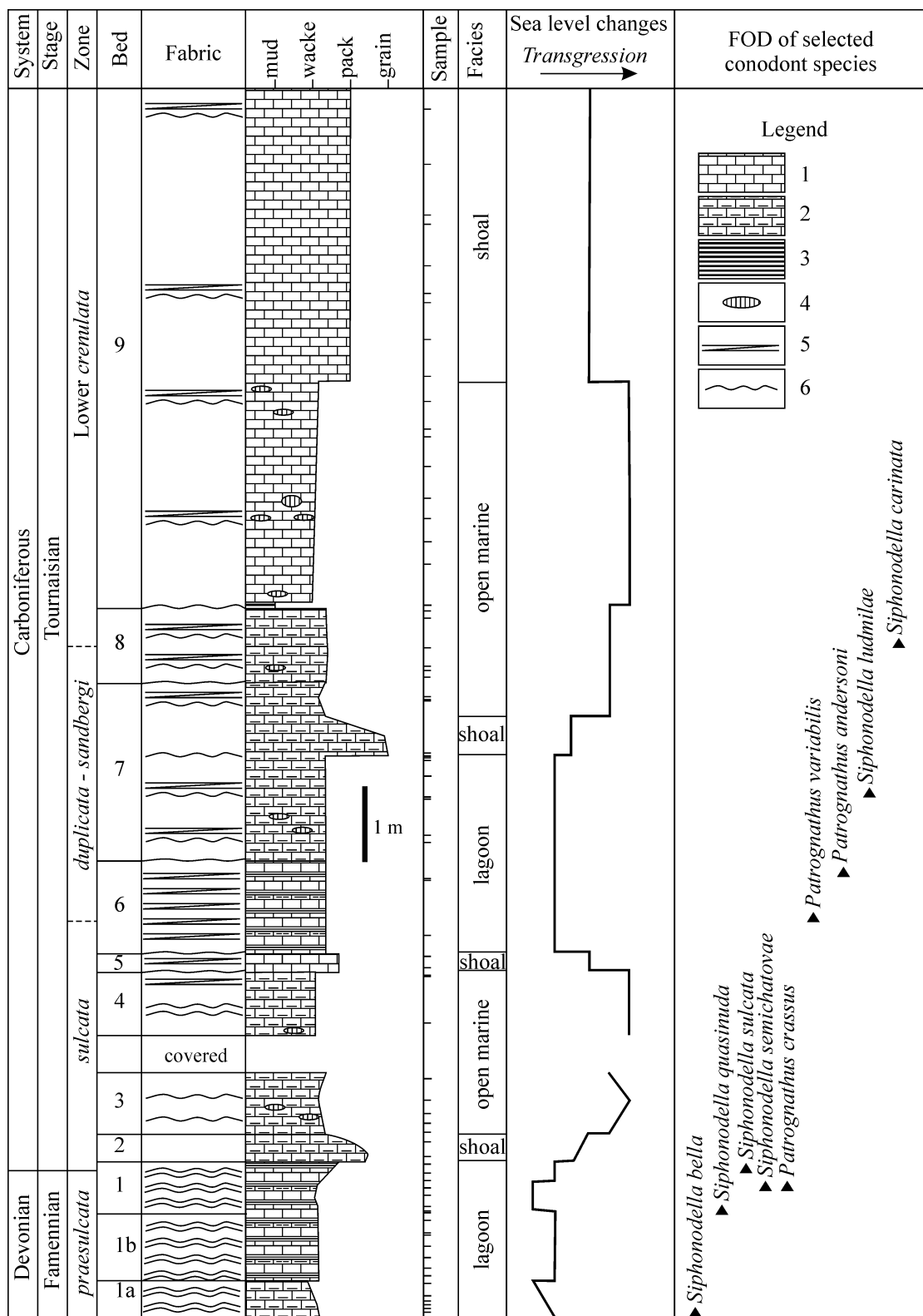


Fig. 2. Lithology, biostratigraphy and facies distribution of the Kamenka River section. Legend: 1, limestone; 2, clayey limestone; 3, clay; 4, cherty nodules; 5, flat lamination; 6, wavy lamination.

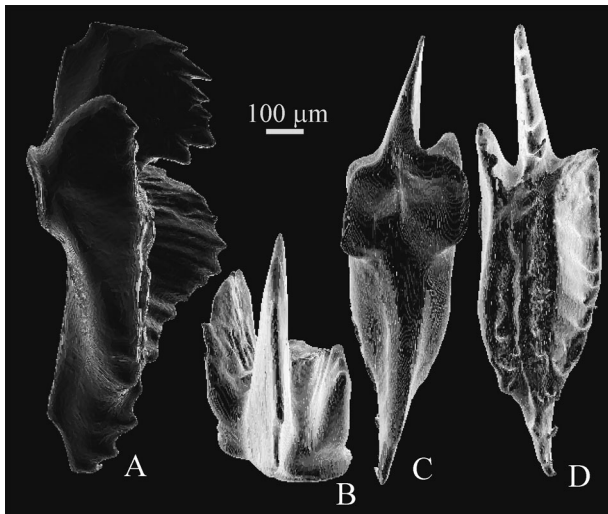


Fig. 3. P1 element of *Polygnathus parapetus* Druce. Images based on micro-CT scan of the specimen from the basal part of bed 8, Kamenka River section. A, lateral view; B, anterior view; C, aboral view; D, oral view.

preservation of the primary structure of hard tissues. A number of thin and polished sections of P1 elements of *P. parapetus* were studied with SEM, microprobe (EDS), and optic microscopy. The hard tissues of conodont elements prove the absence of re-crystallization and post-mortem uptake of minerals such as sulphides (Fig. 4A–C). Geochemical analysis of bioapatite of two polished sections of P1 elements, mounted in the low molecular weight epoxy resin and coated in carbon, was performed using a VEGA TESCAN microprobe with the precision of 0.1 wt.%. Microprobe (EDS) data demonstrate the absence of Fe, Mn, Al, Zn and Pb, which are supposed to be post-mortem contaminants (Trotter & Eggins 2006; Zhuravlev & Shevchuk 2017) in all hard tissue types. The Ca/P and Sr/Ca values of 2.18–2.20 and 0.005–0.011, respectively, are close to the Ca/P and Sr/Ca values of unaltered conodont elements reported earlier (Zhuravlev & Shevchuk 2017). The lamellar structure of the lamellar and paralamellar tissues is well preserved (Fig. 4A, C). These observations suggest a rather good preservation of the conodont

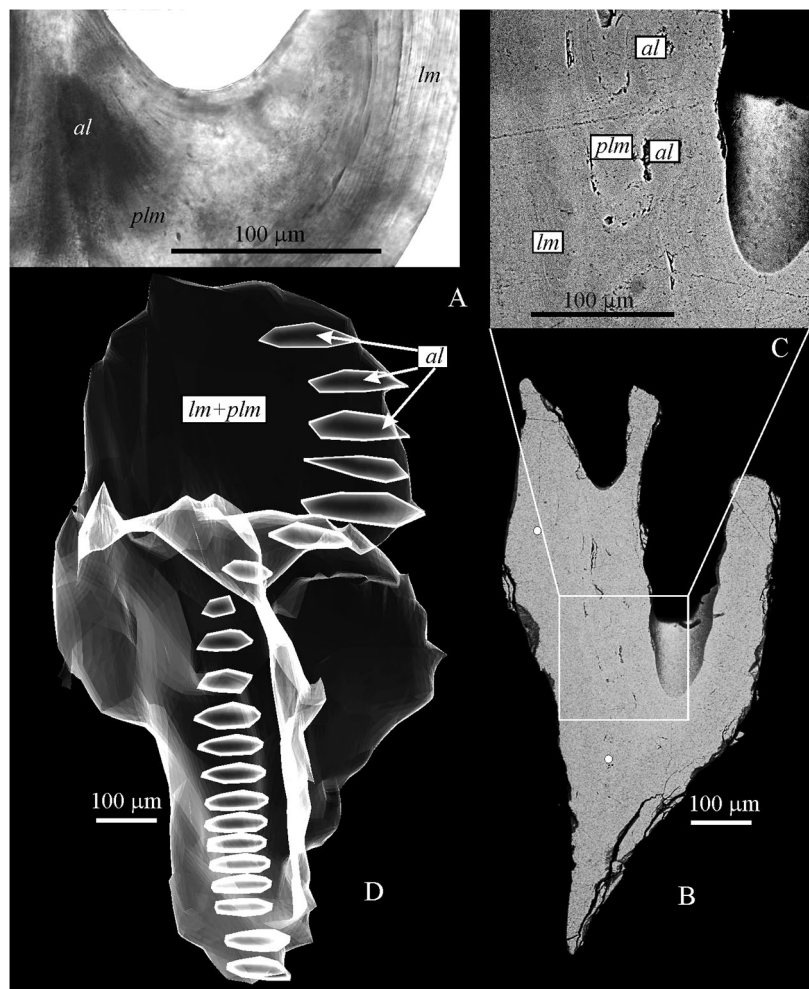


Fig. 4. Histological features of P1 elements of *Polygnathus parapetus* Druce. A, thin section of the platform, specimen from the lower part of bed 8; B, C, SEM images of the oblique polished section of the anterior part of the element, specimen from the middle part of bed 9; white dots mark microprobe sites; D, histological model of P1 element. Legend: *al*, albid tissue; *lm*, lamellar tissue; *plm*, paralamellar tissue.

element matter and indicates the conservation of carbon isotope composition of organic matter.

The study of thin and polished sections of conodont elements in association with micro-CT and optic microscopy data allow elaborating the histological model of the P1 element of *P. parapetus*, demonstrating the distribution of albid tissue (Fig. 4D). According to the model, lamellar and paralamellar tissues compose about 94% of the P1 element of *P. parapetus*. Albid tissue, comprising about 6% of the element, forms cores of denticles of the fixed blade and the uppermost parts of denticles of the anterior free blade only.

Separated P1 elements of *P. parapetus* were washed with ethanol and distilled water and then used for analysis of carbon isotope values with the DELTA V Advantage mass spectrometer equipped with the Thermo Electron Continuous Flow Interface (ConFlo III) and Element Analyzer (Flash EA 1112). The $\delta^{13}\text{C}_{\text{org}}$ values are reported relative to the PDB standard. Isotope analyses were performed at the CKP ‘Geonauka’ of the Institute of Geology Komi SC UrB RAS (Syktyvkar, Russia). The international standard USGS-40 (L-Glutamic acid) was used. The precision of the $\delta^{13}\text{C}_{\text{org}}$ value is $\pm 0.15\text{‰}$.

The diagenetic degradation of the organic matter of conodont elements was estimated by their demineralization in 1N solution of HCl. The demineralization of conodont elements yields a protein ‘pseudomorph’ possessing the same size and shape as the original element. The presence of a protein ‘pseudomorph’ is likely a guarantee of the structural integrity and good preservation of organic matter (Sealy et al. 2014). The ‘pseudomorphs’ exist due to collagen molecules which are still bonded together to form the organic framework of conodont element tissues. In poorly preserved diagenetically altered conodont elements, demineralization does not yield a ‘pseudomorph’. In this case the conodont element may yield amorphous fragments of gelatinous material composed of degraded collagen molecules, and isotopic measurements can produce unreliable results (Sealy et al. 2014).

In any case similar preservation of the studied conodont elements provides uniform degradation of organic matter and suggests good preservation of relative variations in the isotope composition.

RESULTS

Ten samples were analysed for $\delta^{13}\text{C}_{\text{org}}$ in P1 elements of *Polygnathus parapetus*. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the host carbonate rocks were studied as well (Table 1). The $\delta^{13}\text{C}_{\text{org}}$ values in P1 elements of *P. parapetus* vary

Table 1. Summary of carbon isotopic composition of conodont elements (*Polygnathus parapetus*) and bulk carbonates used in Figs 5 and 6. Isotopic values are reported in ‰ notation relative to the PDB standard

Sample	$\delta^{13}\text{C}_{\text{org}}$ in conodont element (‰)	$\delta^{13}\text{C}_{\text{carb}}$ in carbonate (‰)
1	-25.42	3.62
2	-30.4	3.14
3	-26.41	2.98
4	-23.57	2.48
4a	-28.06	2.48
5	-22.71	2.58
6	-24.77	2.45
7	-22.66	1.5
8	-25.93	1.3
9	-22.5	2.71

from -30.4‰ up to -22.5‰ ; the average value is -25.2‰ (Fig. 5).

During the latest Famennian (*praesulcata* conodont Zone) $\delta^{13}\text{C}_{\text{org}}$ shifted to more negative values (up to -30.4‰). The early Tournaisian $\delta^{13}\text{C}_{\text{org}}$ record shows weak variations around the average value (from -25.9‰ up to -22.5‰). The highest $\delta^{13}\text{C}_{\text{org}}$ value of -22.5‰ is observed in the Lower *crenulata* conodont Zone (Fig. 5, bed 9). Significant intraspecific isotopic differences (about 8‰) may be related to environmental changes as well as to the influence of the host rock composition and diagenetic degradation of conodont organic matter.

Very weak negative correlation (correlation coefficient $R^2 = 0.0965$) is observed between the carbon isotope composition of conodont elements and host carbonates (Fig. 6), which allows excluding the significant influence of the composition of surrounding media on $\delta^{13}\text{C}_{\text{org}}$ values. Similar preservation of all the studied conodont specimens supports the low probability of the taphonomic control on variations in the $\delta^{13}\text{C}_{\text{org}}$ value.

The composition of the main types of hard tissues of two P1 elements from the upper part of bed 7 and bed 9 was determined by microprobe (Fig. 4B; Table 2). All the tissue types possess a similar Sr/Ca ratio of 0.005–0.011. These values of Sr/Ca are close to those of the Frasnian polygnathid conodont elements of exceptional preservation (0.003–0.012) (Zhuravlev & Shevchuk 2017).

It was suggested that the distribution pattern and concentrations of Sr in conodont element tissues was most likely controlled by biomineralization and hardly affected by secondary processes (Trotter & Eggins 2006; Zhuravlev & Shevchuk 2017). Thus rather high Sr/Ca values in conodont bioapatite suggest a low level of bio-purification of Sr in conodonts (Peek & Clementz 2012).

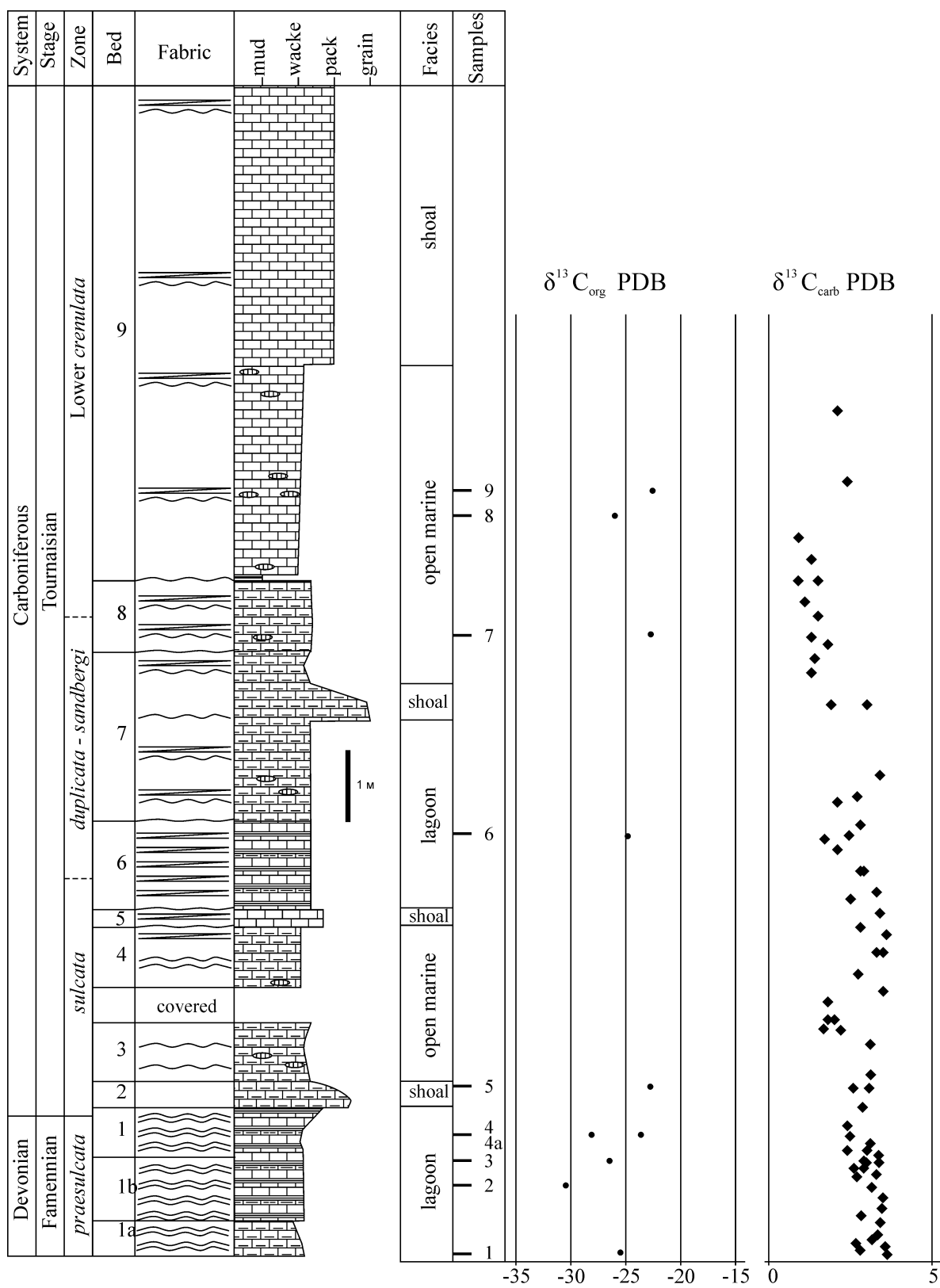


Fig. 5. Lithology, conodont $\delta^{13}C_{org}$ and bulk carbonate $\delta^{13}C_{carb}$ logs of the Kamenka River section. For legend see Fig. 2.

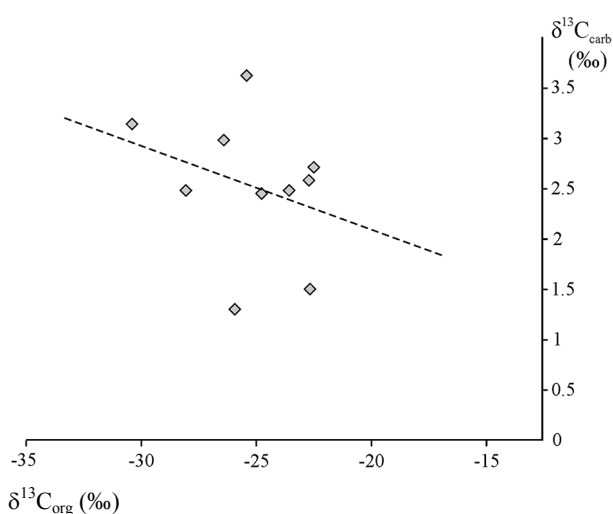


Fig. 6. Bivariate plot for conodont $\delta^{13}\text{C}_{\text{org}}$ and bulk carbonate $\delta^{13}\text{C}_{\text{carb}}$ values in the Kamenka River section.

Table 2. The composition (in wt.%) of hard tissues of the P1 element of *Polygnathus parapetus* (specimens from the upper part of bed 7) based on EDS data

Tissue type	P	Ca	Sr	Sr/Ca	Ca/P
Albid	17.3	37.7	0.2	0.005	2.18
Albid	17.4	37.1	0.2	0.005	2.13
Albid	17.4	37.5	0.4	0.010	2.16
Lamellar	17.6	37.0	0.2	0.006	2.10
Lamellar	17.5	37.3	0.25	0.007	2.13
Lamellar	17.6	37.2	0.3	0.008	2.11
Paralamellar	17.4	36.8	0.3	0.007	2.12

DISCUSSION

The average $\delta^{13}\text{C}_{\text{org}}$ values in P1 elements of *Polygnathus parapetus* of -25.2‰ are close to those of recent zooplankton (Bohata & Koppelman 2013), but far from the $\delta^{13}\text{C}_{\text{org}}$ values of collagen of bones of most marine vertebrates (from -14‰ up to -10‰) (Schoeninger & DeNiro 1984). The carbon isotope ratio in consumer tissues is used as a tool in assigning the trophic status, because the $\delta^{13}\text{C}$ of an organism closely reflects the $\delta^{13}\text{C}$ of its food. The low $\delta^{13}\text{C}_{\text{org}}$ values in P1 elements of *P. parapetus*, if supposed as unaltered, suggest a low position of the species in the food chain. This $\delta^{13}\text{C}_{\text{org}}$ value is close to that of primary producers which utilize the C_3 photosynthetic plant system ($\delta^{13}\text{C}_{\text{org}}$ values range from -35‰ to -20‰) (Hare et al. 1991; Peters et al. 2005). Primary producers, which use the C_3 pathway to fix carbon from CO_2 during photosynthesis, are eukaryotic algae, autotrophic bacteria, and some marine and terrestrial plants (Peters et al. 2005). So we

can suppose that marine algae may constitute a main food of *P. parapetus*, and conodonts of this species were low-level consumers. Besides the $\delta^{13}\text{C}_{\text{org}}$ value, the Sr/Ca ratio (0.005–0.008) in *P. parapetus* bioapatite is quite high in relation to high-level marine consumers (Peek & Clementz 2012). According to data on recent marine organisms, the higher Sr/Ca values, close to those of sea water, are characteristic of lower trophic levels (Peek & Clementz 2012). It is suggested that the Sr/Ca value in conodont bioapatite of *P. parapetus* is most likely caused by the low trophic level of this species.

There is no apparent contradiction between rather herbivorous or basal carnivorous feeding specialization and tooth-like morphology of conodont elements of this species. Tooth-like morphology, the presence of micro-wears and traces of *in-vivo* injuries, reported for elements of conodont apparatuses of Ozarkodinida, allow just reconstructing biomechanics of the apparatuses (Purnell 1993, 1995; Purnell & Donoghue 1997; Donoghue 2001; Zhuravlev 2007; Purnell & Jones 2012). These studies demonstrate that P1 elements of ozarkodinid conodonts, including the genus *Polygnathus*, are acting as occluding pairs (Nicoll 1987; Purnell & von Bitter 1992; Donoghue & Purnell 1999; Martínez-Pérez et al. 2016). A commonly supposed function of these elements is the cutting and grinding of food particles (e.g. Nicoll 1987; Purnell & von Bitter 1992; Zhuravlev 2007). Following interpretations related to the trophic specialization of conodonts are very circumstantial, and based on doubtful analogies with Vertebrata teeth (see discussion in Turner et al. 2010; Blicek et al. 2010). Thus the interpretation of the trophic position of *P. parapetus* based on $\delta^{13}\text{C}_{\text{org}}$ and Sr/Ca values allows us to suppose what kind of food particles were cut and ground by P1 elements. Establishing a correlation between conodont element morphology and the position of the corresponding conodont taxon in the food web may be subject to future research.

Variations in the carbon isotope ratio through time, reflected in the stratigraphical sequence (Fig. 5), may result from changes in environmentally induced conodont metabolism, the trophic level of feeding, or isotopic fractionation at the base of the food web (phytoplankton) that is transferred through the food web.

Intraspecific variations in the metabolism of *P. parapetus* are difficult to estimate because of lack of data on conodont physiology. Recent marine consumers demonstrate weak intraspecific fluctuations of the $\delta^{13}\text{C}_{\text{org}}$ value. DeNiro & Schoeninger (1983) reported variations of up to 1.0‰ in bone collagen resulting from inter-individual differences in metabolism. The observed fluctuations of about 8‰ are too great to be attributed to the inter-individual differences.

The variations in the isotope composition of the food source seem to be a more probable cause of the observed changes in the $\delta^{13}\text{C}_{\text{org}}$ value of *P. parapetus* through the stratigraphic sequence. The latest Devonian negative shift in the terrestrial organic carbon isotope ratio, followed by the early Carboniferous positive trend, was reported by Strauss & Peters-Kottig (2003). These authors attributed the variations to changes in the global carbon cycle (Strauss & Peters-Kottig 2003). The marine and terrestrial $\delta^{13}\text{C}_{\text{org}}$ fluctuations were linked via atmospheric carbon dioxide (Hayes et al. 1999; Strauss & Peters-Kottig 2003). A marine $\delta^{13}\text{C}_{\text{org}}$ shift from -25‰ to -23‰ was reported by Hayes et al. (1999) for the latest Devonian–earliest Carboniferous transition (360–355 Ma). Increase in the $\delta^{13}\text{C}_{\text{org}}$ value of *P. parapetus* at the late *praesulcata*–early *sulcata* conodont zones may be linked to this shift via the food web.

The very low values of $\delta^{13}\text{C}_{\text{org}}$ (from -30.4‰ to -25.4‰) in conodont elements from the latest Famennian lagoon facies (Fig. 5, beds 1a–1) may reflect the fresh-water inputs of river-transported organic matter of terrestrial origin ($\delta^{13}\text{C}_{\text{org}} = -29\text{‰}$ to -27‰). Another possible cause of these extremely low values of $\delta^{13}\text{C}_{\text{org}}$ is some temperature decrease in the shallow-water realm. However, that possibility is not proved by Ca/Mg thermometry, suggesting rather high temperatures, about 23–25 °C, in the earliest Tournaisian in this region (Vevel' et al. 2012).

The most probable causes of intraspecific variations in $\delta^{13}\text{C}_{\text{org}}$ observed in P1 elements of *P. parapetus* through the latest Famennian–Tournaisian are local changes in the source of organic carbon and/or dietary changes of conodont animals.

CONCLUDING REMARKS

A case study from the Kamenka River section indicates that the carbon isotope composition of conodont elements of *Polygnathus parapetus* during the latest Famennian–Tournaisian had an average value of -25.2‰ . Similar values of $\delta^{13}\text{C}_{\text{org}}$ are characteristic of recent zooplankton, and a low trophic level of this species is suggested. This supposition is supported by a quite high Sr/Ca value of about 0.005–0.008 in conodont bioapatite. During the latest Famennian (*praesulcata* conodont Zone) $\delta^{13}\text{C}_{\text{org}}$ shifted to more negative values (up to -30.4‰). This shift may be caused by an influx of organic matter of terrestrial origin during the terminal Famennian regression. The carbon isotope composition of organic matter of conodont elements provides information about the position of conodonts in the food web and peculiarities of trophic relations in the Palaeozoic pelagic ecosystems.

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Süsiniku isotoopide sisaldusest konodontides, mis leiduvad Hilis-Devoni kuni Vara-Karboni vanusega karbonaatse platvormi faatsiese kivimites Timaani-Petšora basseinis

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Uuriti $\delta^{13}\text{C}_{\text{org}}$ sisalduse muutusi Devoni ja Karboni piirikihtides (Hilis-Famenni–Tournai) Timaani-Petšora basseinis Kamenka jõe läbilõikes. Materjalina kasutati konodondi *Polygnathus parapetus* Druce elementides leiduvat süsinikku ja võrdluseks ka ümbriskivimi $\delta^{13}\text{C}_{\text{carb}}$ andmeid. Konodontelementides tuvastati keskmine $\delta^{13}\text{C}_{\text{org}}$ sisaldus $-25,2\text{‰}$, mis lubab oletada, et uuritud konodondi troofiline olelus toimus madalal tasandil. Väärrib märkimist, et uuritud läbilõike alguses (*praesulcata* konodondi tsoon) näitasid analüüsid enam negatiivseid $\delta^{13}\text{C}_{\text{org}}$ väärtusi ($-30,4\text{‰}$), mida võib seostada nii muutustega süsiniku globaalses ringes kui ka kohaliku mandrilise orgaanika sissevooluga basseini Devoni lõpu regressiooni käigus.