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Trophic position of some Late Devonian-Carboniferous (Mississippian) conodonts revealed on carbon organic matter isotope signatures: a case study of the East European basin

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ABSTRACT

An isotopic investigation of organic matter of the Late Devonian-Carboniferous (Mississippian) conodont elements of various morphology was carried out. $\delta^{13}C_{org}$ values of conodont elements measured in this study range from -32.6‰ to -22.4‰, with an average value of –26.1 ± 4.8‰. The study taxa represent four types of conodont apparatus, which differ one from another by morphology of P1 elements. In spite of apparently different morphology all the studied conodonts possess close $\delta^{13}C_{org}$ values. Taxonomic control on the carbon isotope composition is insufficient as well. High consistency of the carbon isotope composition of conodont organic matter suggests that the Late Devonian and Carboniferous (Mississippian) conodonts occupied similar trophic levels. Quite low $\delta^{13}C_{org}$ values in conodont organic matter allow supposing that conodonts were low level consumers, probably seston and plankton feeders.

KEY WORDS
Conodonts,
Late Devonian,
Mississippian,
$\delta^{13}C_{org}$,
palaeoecology,
trophic position.

RÉSUMÉ

Position trophique de certains conodontes du Dévonien supérieur et du Carbonifère (Mississippian) révélée par des signatures d'isotopes de matière organique carbone : étude de cas du bassin de l'Europe de l'Est.
Une étude isotopique de la matière organique d'éléments de conodontes du Dévonien supérieur-Carbonifère (Mississippien) de morphologie différente a été réalisée. Les valeurs de $\delta^{13}C_{org}$ des éléments de conodontes mesurées dans cette étude vont de –32,6‰ à –22,4‰ avec une valeur moyenne de –26,1 ± 4,8‰. Les taxons étudiés représentent quatre types d'appareils de conodontes, qui diffèrent les uns des autres par la morphologie des éléments P1. Malgré une morphologie apparemment différente, tous les conodontes étudiés possèdent des valeurs proches de $\delta^{13}C_{org}$. Le contrôle taxonomique de la composition en isotopes de carbone est également insuffisant. La forte cohérence de la composition en isotopes du carbone de la matière organique des conodontes suggère que les conodontes du Dévonien supérieur et du Carbonifère (Mississippian) occupaient des niveaux trophiques similaires. Des valeurs assez faibles de $\delta^{13}C_{org}$ dans la matière organique des conodontes permettent de supposer que les conodontes sont de faibles consommateurs, probablement de seston et de plancton.

MOTS CLÉS
Conodontes,
Dévonien supérieur,
Mississippien,
$\delta^{13}C_{org}$,
paléoécologie,
position trophique.

INTRODUCTION

Conodonts were the Cambrian-Triassic extinct group of the small free-swimming, probably nektonic, marine animals having debated affinities (e.g. Donoghue *et al.* 2000; Blieck *et al.* 2010; Turner *et al.* 2010). The only mineralized parts of conodonts are fifteen or nineteen tooth-like elements arranged in a bilaterally subsymmetrical apparatus. Conodont elements are composed of protein-apatite nanocomposites, which form highly mineralized tissues (Trotter & Eggins 2006; Rosseeva *et al.* 2011). Previous investigations demonstrated that mineral component of conodont elements is represented by apatite-(CaF) and organic matter, consisting of less than 3 wt.% of a conodont element, composed of collagen-like protein (e.g. Kemp 2002; Rosseeva *et al.* 2011; Zhuravlev 2017; Medici *et al.* 2019). The protein network is surrounded by aligned crystallites of apatite and strongly incorporated into the mineral matrix. This incorporation provides unique conservation of the organic matter demonstrating preserved supramolecular protein structure (Zhuravlev 2017). Recrystallization of the bioapatite starts at 300° C (Li *et al.* 2015). Thus changes in mineral component of conodont elements are expected at Conodont Alteration Index (CAI) > 5. Collagen thermal denaturation starts at 60-65° C in hydrated condition and at 150° C in dry environment (Bozec & Odlyha 2011), that promises good preservation of conodont organic components at CAI<3.

Low content of carbonate ions in conodont apatite of lamellar, paralamellar, and albid tissues (less than 1.5% according to Trotter & Eggins 2006; Frank-Kamenetskaya *et al.* 2014) makes it possible to study of carbon isotope values of organic matter in conodont elements without their demineralization (Zhuravlev & Smoleva 2018).

The isotope composition of conodont organic matter is hardly known. Over & Grossman (1992) reported $\delta^{13}C_{org}$ in conodont elements of the Late Devonian *Palmatolepis* Ulrich & Bassler, 1926 (value ranges from –24.5‰ to –24.0‰), Mississippian *Siphonodella* Branson & Mehl, 1944 (–26.3‰ and –27.3‰), and Pennsylvanian *Streptognathodus elegantulus* Stauffer & Plummer, 1932 (value ranges from –23.0‰ to –24.0‰). These authors 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). Trophical aspect of the Late Viséan (Mississippian) conodont $\delta^{13}C_{org}$ values was considered by Nicholas *et al.* (2004). Study of $\delta^{13}C_{org}$ values of the latest Devonian and Mississippian (Tournaisian) conodont species *Polygnathus parapetus* Druce, 1969 revealed significant intraspecific variations probably attributed to changes in global carbon cycle and local fluctuations in source of organic matter (Zhuravlev & Smoleva 2018). Analysis of composition of organic matter, apatite matrix, and organic carbon isotope values of the Late Devonian and Mississippian conodonts based on the limited material (13 samples) demonstrates that studied conodont elements are characterized by quite high Sr/Ca values in the albid tissue (from 0.002 up to 0.016) and low $\delta^{13}C_{org}$ values in the collagen-like protein (from –30.4 up to –22.5‰) (Zhuravlev *et al.* 2020). These data suggest low trophic level of studied conodonts. Also this conclusion was supported by study of Ca isotopes in the apatite of Late Devonian conodonts (Balter *et al.* 2019).

Generally, isotopic biogeochemistry of organic matter of fossil is a promising approach in reconstruction of terrestrial and aquatic paleoecosystems (Schoeninger & DeNiro 1982, 1984; Grey 2006; Heiri *et al.* 2009).

The key objectives of this study are to evaluate variations in $\delta^{13}C_{org}$ in conodont elements in respect to taxa, element and apparatus morphology on the basis of the extended database; to test the hypothesis about sufficient role of conodont apparatuses morphological variations in trophic differentiation of conodonts; and to reconstruct probable position of conodonts in the shallow-water trophic web.

MATERIAL

Conodont elements were studied from the Kamenka River section (65°04’27.4”N, 56°42’50.9”E). Study outcrops are located in the Kozhva River basin, on the banks of the Kamenka River, locating on the Pechora-Kozhva Uplift (Fig. 1). The uplift situates in the eastern part of the Pechora Plate, passive margin of the Laurussia paleocontinent. The Upper Devonian and Carboniferous are represented here by shallow-water, mainly marine siliciclastic and carbonate deposits. The terminal Famennian and lower-middle Tournaisian are represented by the Edzhid Formation comprising clayey-carbonate shallow-water deposits (Vevel’ *et al.* 2012) (Fig. 2). About 170 limestone and clay samples collected from these deposits contain more than 2700 conodont elements, including 1440 P1 elements that provide reliable conodont biostratigraphy. The stratigraphic interval under consideration contains abundant conodont associations composed of representatives of genera *Polygnathus* Hinde, 1879, shallow-water *Siphonodella* of the European lineage, and *Hindeodus* Rexroad & Furnish, 1964. Species of *Patrognathus* Rhodes, Austin & Druce, 1969, *Pseudopolygnathus* Branson & Mehl, 1934, and *Ligonodina* Ulrich & Bassler, 1926 occur as well. The Devonian/Carboniferous boundary is marked by the first appearance of *Siphonodella sulcata* (Huddle, 1934) in association with *Siphonodella semichatovae* Kononova & Lipnjagov, 1976 and *Patrognathus crassus* Kononova & Migdisova, 1984, that provides reliable recognition of this level (Zhuravlev 2017). The Tournaisian part of the section is correlated with standard conodont zones: from sulcata Zone through Lower crenulata Zone. The conodont associations of the study interval are dominated by the shallow-water taxa *Polygnathus communis communis* Branson & Mehl, 1943, *Polygnathus parapetus* Druce, 1969, and *Ligonodina* sp.

The preservation of conodont elements is fine and they have a Conodont Alteration Index (CAI) value of 1 (i.e. T < 50°C). Most of the conodont elements demonstrate good preservation of histological composition proved with SEM studies and absence of traces of re-crystallysation, weathering, and

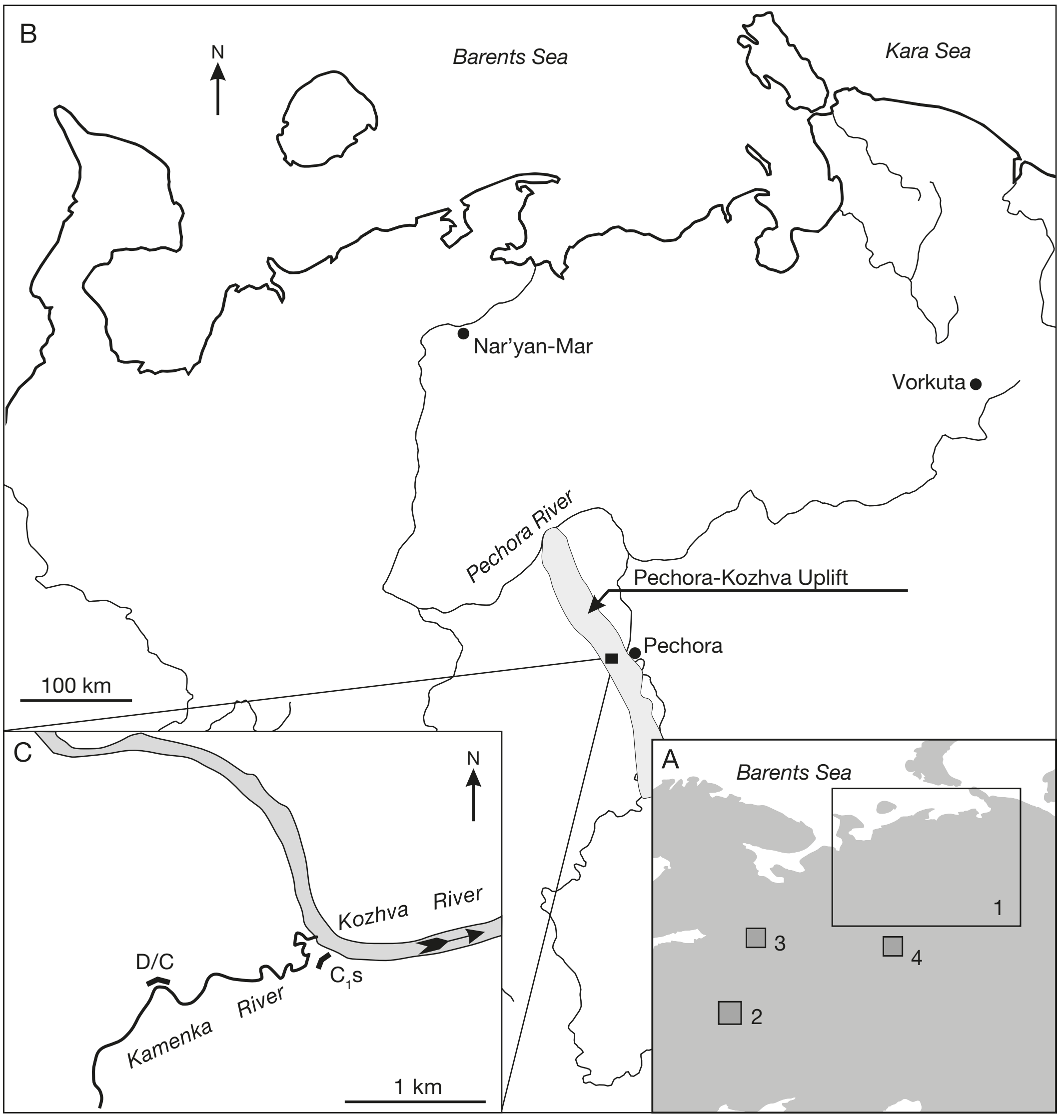

FIG. 1. — Localization of the sites under consideration: **A**, Generalized map of Eastern Europe; rectangles mark the localities: **1**, Pechora Craton; **2**, Voronezh Anteclise (Kamenka Quarry and Russkiy Brod Quarry sections); **3**, Ilmen Lake region (Chudovo section, Syas River section, Ilmen Lake borehole 8, Ilmen Lake section); **4**, Chimbulat Quarry. **B**, Map of Pechora Craton; **C**, Scheme of outcrops' position in the Kozhva River basin.

biodegradation (Zhuravlev & Smoleva 2018; Zhuravlev *et al.* 2020). The low grade of thermal maturity suggests the preservation of the original (near-primary) carbon isotope composition of organic matter (Zhuravlev & Smoleva 2018).

On the whole 50 conodont elements of good preservation and representing dominant taxa from the Kamenka River section were studied for $\delta^{13}C_{org}$ value. Additionally, $\delta^{13}C_{org}$ values were obtained for the Late Devonian (Early and Middle Frasnian *Ligonodina, Polygnathus, Youngquistognathus* Myshkina & Zhuravlev, 2005, and *Mehlina* Youngquist, 1945 from the site 3 on Fig. 1A, and Early Famennian *Icriodus* Branson & Mehl, 1938, *Jablonnodus* Dzik, 2006, and *Mitrellataxis* Chauff & Price, 1980 from the site 2 on Fig. 1A), Serpukhovian (*Mestognathus* Bischoff, 1957 and *Idioprioniodus* Gunnell, 1933 from the Kamenka River section, Fig. 1C), and Middle Permian (Roadian *Stepanovites* from the site 4 on Fig. 1A) conodonts of the East European Platform (Fig. 1A). All the measured samples have a Conodont Alteration Index (CAI) value of 1.

The early Famennian sections of the Voronezh Anteclise (Kamenka Quarry and Russkiy Brod Quarry sections, site 2, Fig. 1A) cropping out wavy alternation of the bluish-gray laminated clay, and gray coarse detrital wavy laminated limestone with brachiopods and bored/encrusted carbonate cobbles. The environment can be identified as a partly restricted shoreface (Zatoń *et al.* 2014). The Frasnian of the Ilmen Lake region (Chudovo section, Syas River section, Ilmen Lake borehole 8, Ilmen Lake section, site 3, Fig. 1A) is mainly composed of alternation of the light-gray detrital limestones and greenish-gray limy clays. These deposits correspond to the shallow-water open marine and shoal environments (Zhuravlev *et al.* 2006). The Roadian

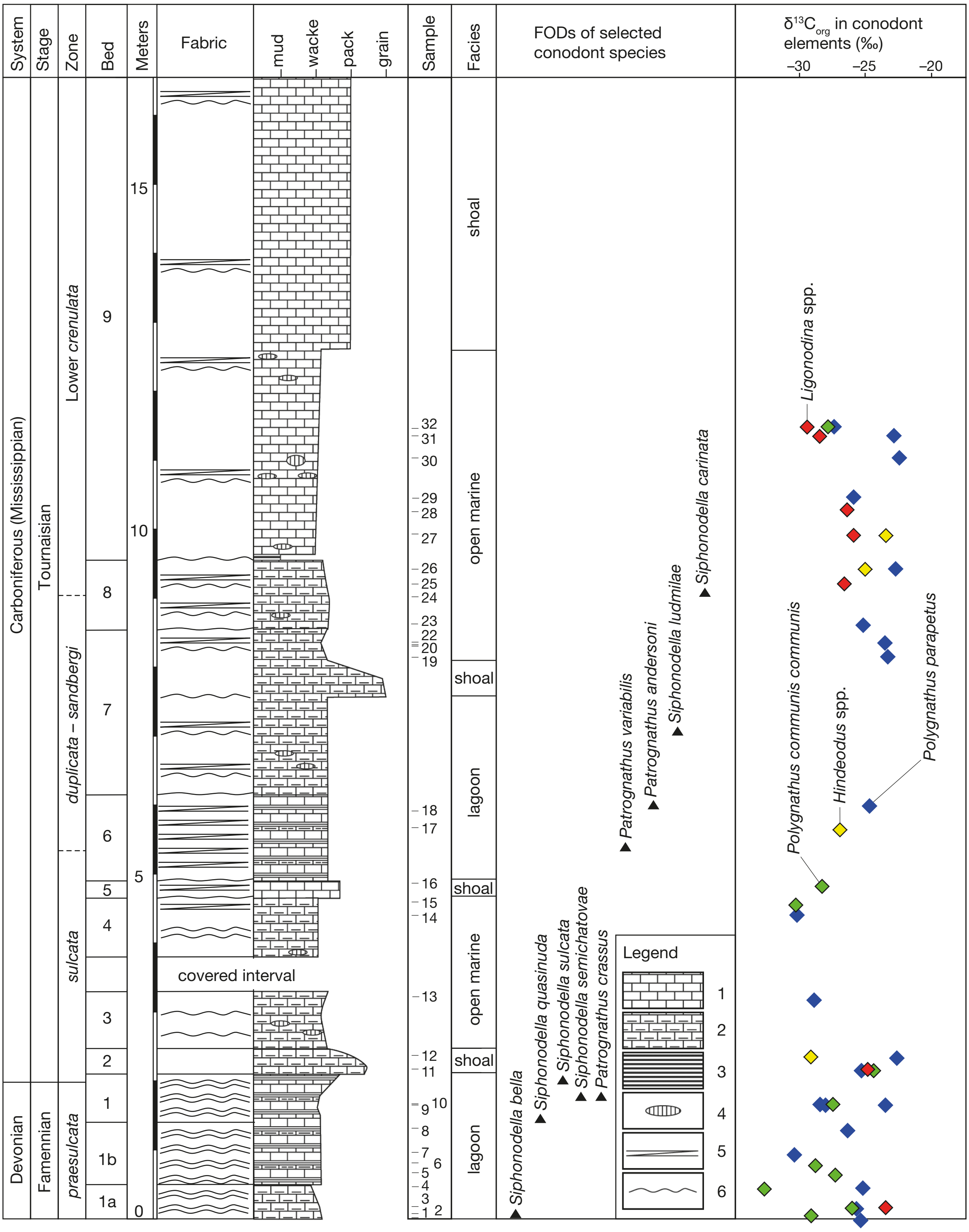

Fig. 2. — Lithology, biostratigraphy, and facies distribution of the Kamenka River section (Pechora Craton). Legend: **1**, limestone; **2**, clayey limestone; **3**, clay; **4**, cherty nodules; **5**, flat lamination; **6**, wavy lamination.

(lower Kazanian in the regional nomenclature) exposed in the Chimbulat Quarry (site 4, Fig. 1A) is represented by light-gray limestones with algal-bryozoan bioherms of the shallow-water carbonate platform environment (Zhuravlev 2005). Thus all the studied localities represent shallow-water marine environments of various ages.

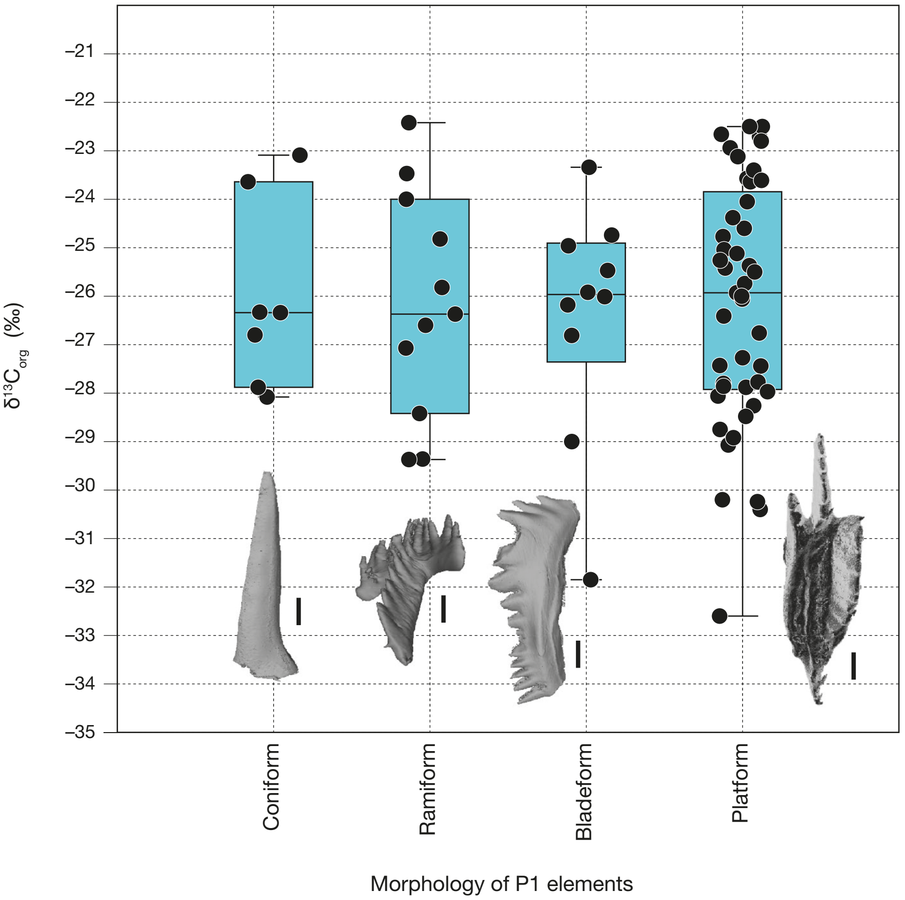

Fig. 3. — Distribution of $\delta^{13}C_{org}$ values among conodonts having different morphological types of P1 elements. Scale bar: 0.1 mm.

Totally $\delta^{13}C_{org}$ values were measured of 75 specimens, which are distributed as follows: *Ligonodina*, n=9; *Polygnathus*, n=38; *Youngquistognathus*, n=2; *Mehlina*, n=3; *Icriodus*, n=3; *Jablonnodus*, n=4; *Mitrellataxis*, n=3; *Patrognathus,* n=2; *Hindeodus*, n=5; shallow-water representatives of *Siphonodella*, n=3; *Mestognathus,* n=1; *Idioprioniodus,* n=1; *Stepanovites*, n=1 (see Appendix 1).

Most of the taxa belong to so-named shallow-water biofacies and dwelt the near-shore shallow-water environment (Sandberg & Gutschick 1984; Savoy *et al.* 1999). *Ligonodina*, *Polygnathus communis*, *Hindeodus*, *Mehlina*, and *Idioprioniodus* probably occupied upper part of the water column and their remains distributed over the wide facies range (Sandberg & Gutschick 1984; Zhuravlev & Tolmacheva 1995; Savoy *et al.* 1999; Zhuravlev *et al.* 2006). Palaeoecology of *Jablonnodus*, *Mitrellataxis*, and *Stepanovites* is unclear.

METHODS

The processing of conodont 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. Some elements polluted with crystals of carbonates were treated with 1N solution of HCl. Then the conodont elements were washed in ethanol and distilled water. Control of conodont element preservation was performed with optic microscopy and SEM (see Zhuravlev & Smoleva 2018 for details).

Selected conodont elements of good preservation were 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 $\delta^{13}C_{org}$ values are reported relative to the PDB standard. The international standard USGS-40 (L-Glutamic acid) was used. The analytical reproducibility (1σ) for $\delta^{13}C_{org}$ value is ±0.15‰.

$\delta^{13}C_{carb}$ values in the same carbonate samples were studied as well. Carbonate powder was drilled from the samples with steel micro-drill. The isotope studies of the powder were performed with DELTA V Advantage mass spectrometer equipped with Element Analyzer (Flash EA 1112). $\delta^{13}C_{carb}$ values were reported relative to the PDB standard. The precision of the $\delta^{13}C_{carb}$ value is ±0.04‰.

Isotope analyzes were performed at the CKP 'Geonauka' of the Institute of Geology Komi SC UrB RAS (Syktyvkar, Russia).

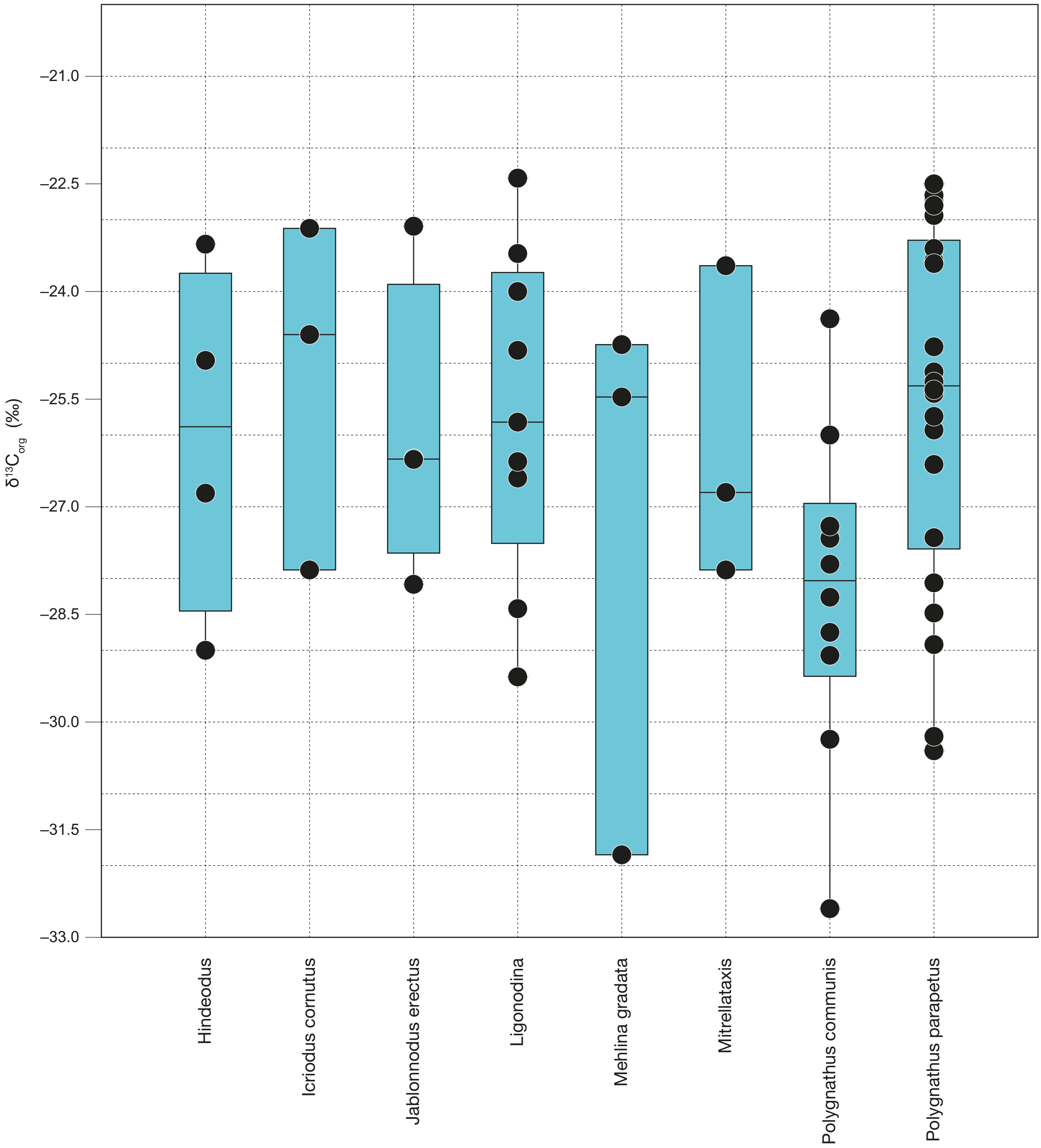

FIG. 4. — Organic carbon isotope compositions of conodonts measured in the study.

RESULTS

Carbon isotope composition was studied in 75 samples (Figs 3, 4). The results of the isotopic investigation of organic matter of the conodont elements are summarized in the Appendix 1. $\delta^{13}C_{org}$ values of conodont elements measured in this study range from –32.6‰ to –22.1‰, with an average value of –26.0 ± 4.8‰ (±2 s.d., n = 75). The average $\delta^{13}C_{org}$ value is –26.2 ± 4.9‰ (±2 s.d., n = 49) at the terminal Famennian – Tournaisian of the Kamenka River section, –25.4‰ ± 5.4‰ (±2 s.d., n = 12) at the Frasnian of the Ilmen Lake region (East European Platform), –25.8 ‰ ± 4.0‰ (±2 s.d., n = 10) at the lower Famennian of the Kamenka Quarry and Russkiy Brod Quarry (Voronezh Anteclise, East European Platform).

The study taxa represent four types of conodont apparatus, which differ one from another by morphology of P1 elements (Zhuravlev 2007). The types are the following: 1) apparatus composed of coniform elements only (genera *Mitrellataxis* and *Jablonnodus*); 2) apparatus characterized

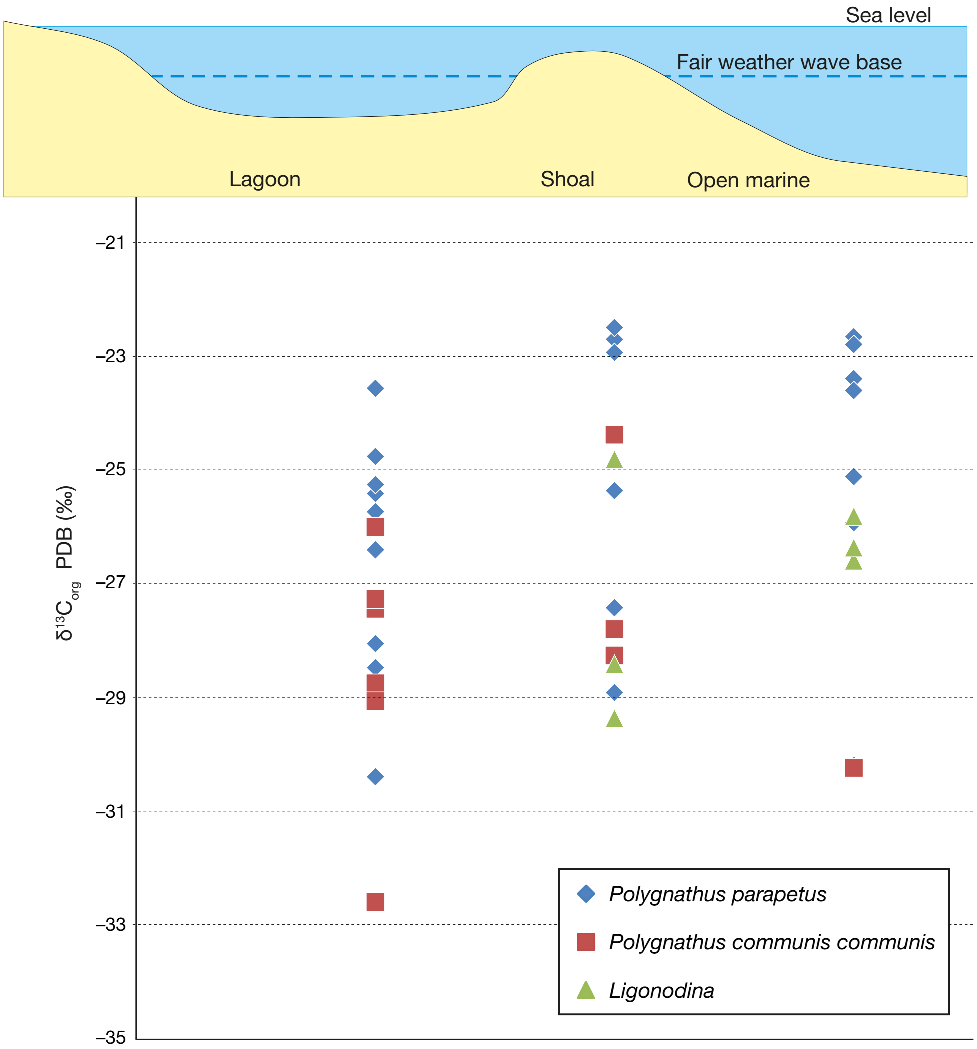

FIG. 5. — $\delta^{13}C_{org}$ distribution along the facies profile plotted for dominating taxa (latest Famennian-middle Tournaisian; Kamenka River section).

by ramiform elements in P position (genera *Ligonodina, Idioprioniodus, Stepanovites*); 3) apparatus having bladeform elements in P1 position (genera *Mehlina* and *Hindeodus*); and 4) apparatus demonstrating platform elements in P1 position (genera *Icriodus, Polygnathus, Youngquistognathus, Siphonodella, Mestognathus*). Specimens grouped on the basis of morphological types of apparatus demonstrate close $\delta^{13}C_{org}$ values without statistically significant differences (Fig. 3). The average $\delta^{13}C_{org}$ values are distributed as following: –26.0 ± 3.9‰ (±2 s.d., n = 7) for the first type; –26.2 ± 4.7‰ (±2 s.d., n = 11) for the second type; –26.4 ± 4.8‰ (±2 s.d., n = 10) for the third type; and –26.1 ± 5.0‰ (±2 s.d., n = 45) for the fourth type. Thus in spite of apparently different morphology all the studied conodonts possess close $\delta^{13}C_{org}$ values.

Comparisons between conodonts grouped by species reveal no taxonomic difference in $\delta^{13}C_{org}$ value, excluding the Famennian-Tournaisian ubiquitic species *Polygnathus communis communis* Branson & Mehl (Fig. 4). This species, having platform P1 elements of simple morphology, demonstrates low $\delta^{13}C_{org}$ values (mean value is –28.2‰). The other species under consideration reveal similar $\delta^{13}C_{org}$ values. For example, the average $\delta^{13}C_{org}$ value of *Polygnathus parapetus* Druce is –25.5± 1.1‰ (±2 s.d., n = 22), and the average $\delta^{13}C_{org}$ value of *Ligonodina* sp. is –25.7± 1.5‰ (±2 s.d., n = 9). At the order level the average $\delta^{13}C_{org}$ values are indistinguishable as well. Representatives of the order Ozarkodinida Dzik, 1976 comprising genera *Polygnathus*, *Youngquistognathus*, *Siphonodella*, *Hindeodus*, and *Mehlina* show the average $\delta^{13}C_{org}$ value of –26.2± 4.9‰ (±2 s.d., n = 52). Representatives of another order Prioniodinida Sweet, 1988 (genera *Ligonodina*, *Stepanovites*, and *Idiorioniodus*) demonstrates the same average value of –26.2± 4.7‰ (±2 s.d., n = 11). Thus there is no evident taxonomic control on the $\delta^{13}C_{org}$ values in conodont organic matter in the studied material.

The material obtained allows evaluating facies control on the $\delta^{13}C_{org}$ values in conodont elements of the three Famennian-Tournaisian taxa: *Polygnathus parapetus, Polygnathus communis communis,* and *Ligonodina* sp. $\delta^{13}C_{org}$ values in conodont elements of all the species show high consistency through facies gradient (Fig. 5).

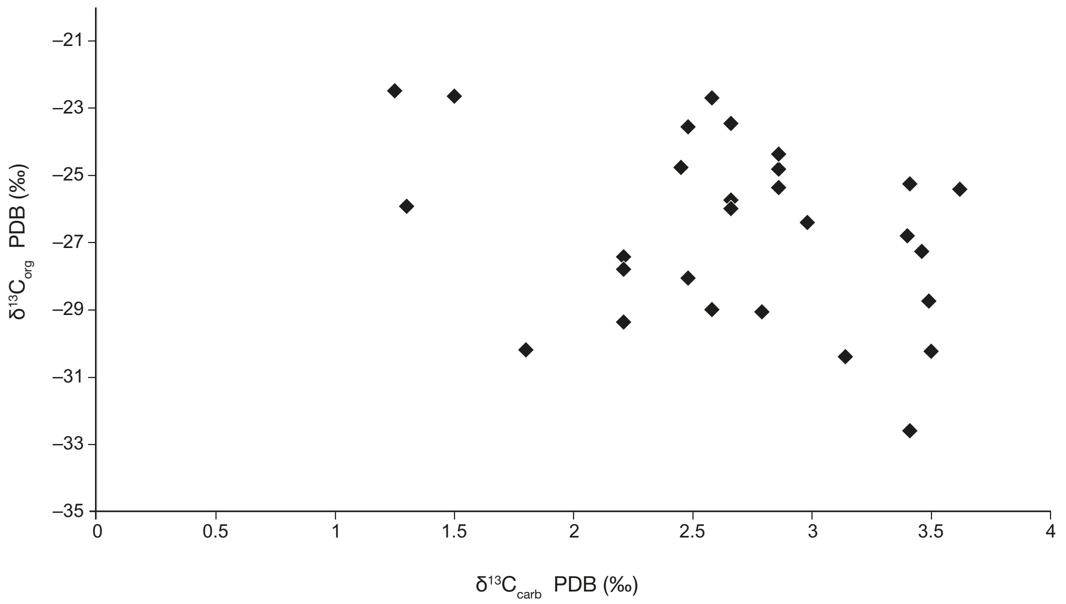

FIG. 6. — Bivariate plot for bulk carbonate $\delta^{13}C_{carb}$ and conodont $\delta^{13}C_{org}$ values.

DISCUSSION

Low grade of thermal maturity of the studied specimens (CAI<2) promises weak degree of degradation of conodont organic matter and good preservation of conodont $\delta^{13}C_{org}$ signatures (Zhuravlev & Smoleva 2018). For studied specimens no traces of microbial activity were detected that promises low level of isotope exchange between the conodont elements and water or sediment (Zazzo *et al.* 2004). Also no signs of conodont element re-crystallisation were observed. Another line of evidence of primary nature of conodont δ^{13}Corg is based on discordant variations of $\delta^{13}C$ values in conodont elements and host carbonates (Zhuravlev & Smoleva 2018) (Fig. 6). Just weak negative trend is observed, which can be caused by influence of the primary productivity recorded in $\delta^{13}C_{carb}$ on trophic peculiarities of conodonts reflected by $\delta^{13}C_{org}$. Taking into account high resistance of the conodont mineralized tissues against degradational factors (Zhuravlev 2017; Zhuravlev & Shevchuk 2017; Zhuravlev & Smoleva 2018) it can be supposed that material under consideration reveals near-primary isotope composition of the organic matter.

$\delta^{13}C$ value in consumer tissues is being used as tools in assigning trophic status, because of the carbon isotope ratio of an organism closely reflects the carbon isotope ratio of its food (Schoeninger & DeNiro 1984). The mean value of $\delta^{13}C_{org}$ of conodont organic matter is quite low and corresponds to that of recent zooplankton and other low-level consumers (Bohata & Koppelmann 2013), but far from $\delta^{13}C_{org}$ values of high-level consumers, e.g. marine vertebrates (from –14‰ up to –10‰) (Schoeninger & DeNiro, 1984). Thus it is possible to suppose that studied conodonts were low-level consumers. This conclusion is compatible with data on Ca isotopes interpreted as sign of low trophic level of the Late Devonian conodonts (Balter *et al.* 2019), and with information on rather high Sr/Ca ratio in conodont bioapatite (Zhuravlev *et al.* 2020).

Surprising high consistency of $\delta^{13}C_{org}$ values of conodonts belonging to different taxa and morphological groups supports weak trophic differentiation among conodonts (Figs. 3, 4). At least, the Late Devonian-Mississipian shallow-water conodonts probably occupied similar trophic levels corresponding to seston and phytoplankton feeders (see also Zhuravlev & Smoleva 2018). The morphological differences in conodont apparatuses and elements were perhaps responsible to the fine trophic specialization only. Thus the hypothesis about sufficient role of conodont apparatuses morphological variations in trophic differentiation of conodonts (e.g. Purnell 1995; Purnell & Donoghue 1997; Zhuravlev 2007; Purnell & Jones 2012) is not confirmed by the isotopic data.

Moreover the temporal variations in average $\delta^{13}C_{org}$ values observed in the Late Devonian-Mississippian interval are of low amplitude. The range of these variations is about 1‰ that suggests rather statistically insignificant stratigraphic trend. It seems that trophical position of the shallow-water conodonts remained unchanged over the long time.

Rather low trophic level of the middle Palaeozoic conodonts is also supported by signs of predation of fishes (cladoselachian sharks, coelacanth, palaeoniscoid and actinopterygian fishes) on conodonts (Nicoll 1977; Choo *et al.* 2009; Zatoń & Rakociński 2014; Zatoń *et al.* 2017). These data suggest that conodonts occupied trophic levels below of those of fishes.

CONCLUSIONS

An isotopic investigation of organic matter of the Late Devonian-Mississippian conodont elements of various morphology and taxonomic position demonstrate weak variations in $\delta^{13}C_{org}$ values. High consistency of the carbon isotope composition of conodont organic matter suggests that the Late Devonian and Mississippian conodonts occupied similar trophic levels despite of different morphology and apparatus composition. Quite low $\delta^{13}C_{org}$ values in conodont organic matter (–26.0 ± 4.8 ‰) allow supposing that conodonts were low level consumers, probably seston and phytoplankton feeders. Results obtained promise approach to reconstructing of the trophic structure of the Palaeozoic pelagic ecosystems, where conodonts were one of the most abundant and diverse group of animals.

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Appendix 1. — Table of the carbon isotope measurements.

Section and age	**Sample**	**Taxon**	**$\delta^{13}C_{org}$ PDB ‰**	**$\delta^{13}C_{carb}$ PDB ‰ (host rock)**
Chimbulat Quarry, P_2 rd	Chm-3/04	*Stepanovites*	–29.36	n/a
Chudovo section, D_3 f	CH1-6/97	*Mehlina gradata*	–25.47	n/a
Chudovo section, D_3 f	CH1-6/97	*Polygnathus reimersi*	–25.04	n/a
Ilmen Lake, borehole 8, D_3 f	8/50P	*Polygnathus reimersi*	–22.5	n/a
Ilmen Lake, borehole 8, D_3 f	8/50P	*Mehlina gradata*	–24.74	n/a
Ilmen Lake, D_3 f	1314/3	*Ligonodina* sp.	–22.42	n/a
Ilmen Lake, D_3 f	5102/4	*Polygnathus webbi*	–23.64	n/a
Ilmen Lake, D_3 f	5102a-2	*Youngquistognathus* sp.	–24.05	–3.86
Ilmen Lake, D_3 f	5103/10	*Polygnathus efimovae*	–22.08	n/a
Ilmen Lake, D_3 f	5130/3-2	*Ligonodina* sp.	–24	n/a
Ilmen Lake, D_3 f	5132/0	*Mehlina gradata*	–31.85	n/a
Ilmen Lake, D_3 f	F-2-0	*Polygnathus ilmenensis*	–27.77	n/a
Ilmen Lake, D_3 f	F-2-0	*Polygnathus efimovae*	–27.86	n/a
Kamenka Quarry, D_3 fm_1	D04-5/12	*Icriodus cornutus*	–24.6	n/a
Kamenka Quarry, D_3 fm_1	D04-6/12	*Icriodus cornutus*	–27.88	n/a
Kamenka River section, C_1 s	125-1-8/90	*Mestognathus bipluti*	–25.5	n/a
Kamenka River section, C_1 s	125-5b/16	*Idioprioniodus* sp.	–27.07	n/a
Kamenka River section, D_3 fm	1	*Polygnathus parapetus*	–25.42	3.62
Kamenka River section, D_3 fm	2	*Polygnathus communis communis*	–29.07	2.79
Kamenka River section, D_3 fm	3	*Ligonodina* sp.	–23.47	2.66
Kamenka River section, D_3 fm	3	*Polygnathus parapetus*	–25.74	2.66
Kamenka River section, D_3 fm	3	*Polygnathus communis communis*	–26	2.66
Kamenka River section, D_3 fm	4	*Polygnathus communis communis*	–32.6	3.41
Kamenka River section, D_3 fm	4	*Polygnathus parapetus*	–25.26	3.41
Kamenka River section, D_3 fm	5	*Polygnathus communis communis*	–27.27	3.46
Kamenka River section, D_3 fm	6	*Polygnathus communis communis*	–28.75	3.49
Kamenka River section, D_3 fm	7	*Polygnathus parapetus*	–30.4	3.14
Kamenka River section, D_3 fm	8	*Polygnathus parapetus*	–26.41	2.98

APPENDIX 1. — Continuation.

Section and age	**Sample**	**Taxon**	**$\delta^{13}C_{org}$ PDB ‰**	**$\delta^{13}C_{carb}$ PDB ‰ (host rock)**
Kamenka River section, C_1 tn	9	*Polygnathus parapetus*	–23.57	2.48
Kamenka River section, C_1 tn	9	*Polygnathus parapetus*	–28.06	2.48
Kamenka River section, C_1 tn	10	*Polygnathus communis communis*	–27.44	n/a
Kamenka River section, C_1 tn	10	*Polygnathus parapetus*	–28.48	n/a
Kamenka River section, C_1 tn	11	*Polygnathus parapetus*	–25.37	2.86
Kamenka River section, C_1 tn	11	*Ligonodina* sp.	–24.82	2.86
Kamenka River section, C_1 tn	11	*Polygnathus communis communis*	–24.38	2.86
Kamenka River section, C_1 tn	11	*Siphonodella bella*	–22.52	2.86
Kamenka River section, C_1 tn	11	*Hindeodus crassidentatus*	–24.65	2.86
Kamenka River section, C_1 tn	12	*Polygnathus parapetus*	–22.71	2.58
Kamenka River section, C_1 tn	12	*Hindeodus crassidentatus*	–29	2.58
Kamenka River section, C_1 tn	13	*Polygnathus parapetus*	–28.92	n/a
Kamenka River section, C_1 tn	14	*Polygnathus parapetus*	–30.2	1.8
Kamenka River section, C_1 tn	15	*Polygnathus communis communis*	–30.24	3.5
Kamenka River section, C_1 tn	16	*Polygnathus communis communis*	–28.26	n/a
Kamenka River section, C_1 tn	17	*Hindeodus penescitulus*	–26.81	3.4
Kamenka River section, C_1 tn	18	*Polygnathus parapetus*	–24.77	2.45
Kamenka River section, C_1 tn	19	*Polygnathus parapetus*	–23.4	n/a
Kamenka River section, C_1 tn	20	*Patrognathus andersoni*	–26.01	n/a
Kamenka River section, C_1 tn	21	*Patrognathus andersoni*	–26.18	n/a
Kamenka River section, C_1 tn	22	*Polygnathus parapetus*	–23.61	n/a
Kamenka River section, C_1 tn	23	*Polygnathus parapetus*	–25.12	n/a
Kamenka River section, C_1 tn	24	*Polygnathus parapetus*	–22.66	1.5
Kamenka River section, C_1 tn	25	*Ligonodina* sp.	–26.6	n/a
Kamenka River section, C_1 tn	26	*Polygnathus parapetus*	–22.8	n/a
Kamenka River section, C_1 tn	26	*Siphonodella carinata*	–26.76	n/a
Kamenka River section, C_1 tn	26	*Hindeodus crassidentatus*	–24.96	n/a
Kamenka River section, C_1 tn	27	*Ligonodina* sp.	–25.82	n/a
Kamenka River section, C_1 tn	27	*Hindeodus crassidentatus*	–23.34	n/a
Kamenka River section, C_1 tn	28	*Ligonodina* sp.	–26.37	n/a
Kamenka River section, C_1 tn	29	*Polygnathus parapetus*	–25.93	1.3
Kamenka River section, C_1 tn	30	*Polygnathus parapetus*	–22.5	1.25
Kamenka River section, C_1 tn	31	*Polygnathus parapetus*	–22.94	n/a
Kamenka River section, C_1 tn	31	*Siphonodella carinata*	–26.06	n/a
Kamenka River section, C_1 tn	31	*Ligonodina* sp.	–28.42	n/a
Kamenka River section, C1 tn	32	*Ligonodina discreta*	–29.37	2.21
Kamenka River section, C_1 tn	32	*Polygnathus parapetus*	–27.43	2.21
Kamenka River section, C_1 tn	32	*Polygnathus communis communis*	–27.8	2.21
Russkiy Brod Quarry, D_3 fm_1	D02-2/12	*Jablonnodus erectus*	–23.09	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-2/12	*Mitrellataxis*	–23.64	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-2/12	*Jablonnodus erectus*	–26.33	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-2/12	*Mitrellataxis*	–26.8	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-2/12	*Jablonnodus erectus*	–28.08	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-3/12	*Jablonnodus erectus*	–26.34	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-3/12	*Icriodus cornutus*	–23.12	n/a
Russkiy Brod Quarry, D_3 fm_1	D02-3/12	*Mitrellataxis*	–27.88	n/a
Syas River section, D_3 f_1	5174a/1	*Youngquistognathus praeangustidiscus*	–25.92	n/a