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Carbon isotope variations during ontogeny of Frasnian (Late Devonian) conodont *Mehlina gradata*

A. V. Zhuravlev

Institute of Geology FRC Komi SC UB RAS, Syktyvkar, Russia

This study investigates the ontogenetic (growth-related) dietary shifts of the Frasnian conodont *Mehlina gradata* from the East European Platform localities. While the morphological shape of P1 elements of this species remained remarkably stable throughout its life, isotopic analysis revealed a significant correlation between the size of the element and its carbon isotope composition. As the P1 elements grew larger, they showed an increase in ^{13}C enrichment. This suggests that while the feeding apparatus did not change shape, the trophic position did. Our results indicate that *Mehlina gradata* likely transitioned to higher trophic levels such as more active predation or scavenging as it matured, demonstrating that morphological stability does not necessarily imply ecological stasis.

Keywords: *conodonts, ontogeny, C-isotopes, ecology*

Вариации изотопного состава углерода в онтогенезе франских (позднедевонских) конодонтов *Mehlina gradata*

А. В. Журавлев

Институт геологии ФИЦ Коми НЦ УрО РАН , Сыктывкар, Россия
micropalaeontology@gmail.com

Данное исследование посвящено изучению онтогенетических (связанных с процессами роста) трофических сдвигов франских конодонтов *Mehlina gradata* из разрезов Восточно-Европейской платформы. Несмотря на то что морфология P1-элементов этого вида оставалась практически неизменной на протяжении всего жизненного цикла, изотопный анализ выявил значимую корреляцию между размером элемента и его изотопным составом углерода. С увеличением размеров элементов наблюдается обогащение изотопом ^{13}C. Это позволяет предположить, что при сохранении стабильной морфологии ротового аппарата трофическая позиция организма претерпевала изменения. Результаты указывают на то, что по мере роста *Mehlina gradata*, вероятно, переходила на более высокие трофические уровни (например, к активному хищничеству или потреблению падали), демонстрируя тем самым, что морфологическая стабильность не обязательно влечет за собой экологический стазис.

Ключевые слова: *конодонты, онтогенез, изотопы углерода, экология*

Introduction

Conodonts are a group of small free-swimming, probably nektic or nekto-planktic marine animals (Briggs et al., 1983) that flourished during the Palaeozoic and became extinct during the earliest Jurassic (Du et al., 2023). The only mineralized parts of conodonts are tooth-like phosphate elements (conodont elements) organized into a bilaterally subsymmetrical feeding apparatus. The apparatus organization is a trait of genus level, but the morphology of P1 elements is a trait of species level in most of the middle and late Palaeozoic conodonts.

The conodont genus *Mehlina* Youngquist, 1945 is characterized by simple blade-like morphology of P elements (Figure 1), and robust S and M elements (Youngquist, 1945). P1 elements of this genus are composed of laterally compressed fused denticles, and are slightly curved in both the dorso-ventral and rostro-caudal direction. The basal pit is small and has narrow flanks transforming into a slightly inverted keel in the anterior and posterior processes. The cusp is commonly reduced in mature specimens (Figure 1). The morphology of P1 elements resembles Class II symmetry of Lane (1968). The symmetrical sinistral and dextral elements compose a pair with supposed scissor-like biomechanics characteristic of the blade-shaped P1 elements (e. g. Nicoll, 1987; Purnell and von Bitter, 1992).

Due to accretional growth of elements, their size is proportional to the individual age (e. g. Muller and Nogami, 1972). Consequently, ontogenetic changes are frequently investigated based on element length (e. g. Zhuravlev, 1995; Plotitsyn and Zhuravlev, 2016).

Blade-form elements generally show minimal size-shape dependence. Small elements possess a similar general morphology as large elements of the same species. Given this observed morphological stability, this study aims to test a hypothesis: Does the trophic position of

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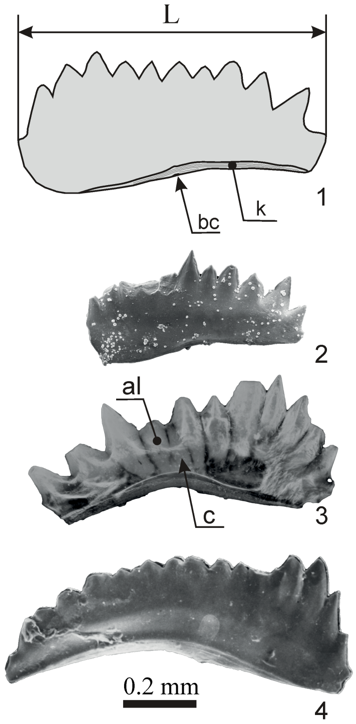

Fig. 1. Morphology of P1 elements of *Mehlina gradata* Youngquist, 1945:

1 — schematic drawing of the P1 element (L — element length, bc — basal cavity, k — keel); 2 — immature element, SEM image, sample 1314/3, Buregi Beds; 3 — mature element, optic image, sample 5132/1, Ilmen Beds (al — albid tissue, c — cusp); 4 — mature element, SEM image, sample 5102/7, Buregi Beds

Рис. 1. Морфология P1-элементов *Mehlina gradata* Youngquist, 1945:

1 — схематический рисунок P1-элемента (L — длина элемента, bc — базальная полость, k — киль); 2 — элемент на ранней стадии онтогенеза, СЭМ-изображение, обр. 1314/3, бургеские слои; 3 — элемент на поздней стадии онтогенеза, оптическое изображение, обр. 5132/1, ильменские слои (al — альбидная ткань, c — главный зубец); 4 — элемент на поздней стадии онтогенеза, СЭМ-изображение, обр. 5102/7, бургеские слои

Mehlina gradata undergo significant changes during its ontogeny despite the lack of clear P1 element morphology shifts?

Material and methods

The studied specimens originated from shallow-water nearshore Frasnian sequences deposited on the Northwest East European Platform, specifically within the Main Devonian Field (Figure 2). The analyzed stratigraphic interval encompasses conodont zones MN4 and MN6 across three geographically distinct localities: Shelon River, Tchudovo, and Ilmen Lake (Figure 3). The stratigraphical framework follows Zhuravlev (2022). The upper portion of the Lower Frasnian, comprising the Tchudovo and Dubnik beds, is biostratigraphically equivalent to the upper part of the MN4 conodont Zone (*Polygnathus reimersi* local Zone). The Tchudovo Beds are characterized by thin, rhythmic alternations of clayey limestone and limy clay, while the overlying Dubnik Beds consist of limy clays containing marl lenses and layers. The Middle Frasnian encompasses the Porkhov and Svinord beds, which correlate with the MN5 conodont Zone (*Polygnathus pollocki* local Zone), as well as the Ilmen and Buregi beds, corresponding to the MN6 conodont Zone (*Polygnathus ilmenensis* local Zone and *Polygnathus efimovae* local Zone, respectively). The Porkhov and Svinord beds consist of alternating clayey limestone and limy clays. In contrast, the Ilmen Beds are composed of silty clays with intercalated thin limestone and silt layers, whereas the Buregi Beds consist of shelly limestones. The study specimens of *Mehlina gradata* came from the Tchudovo, Dubnik, Ilmen, and Buregi beds (Figure 3).

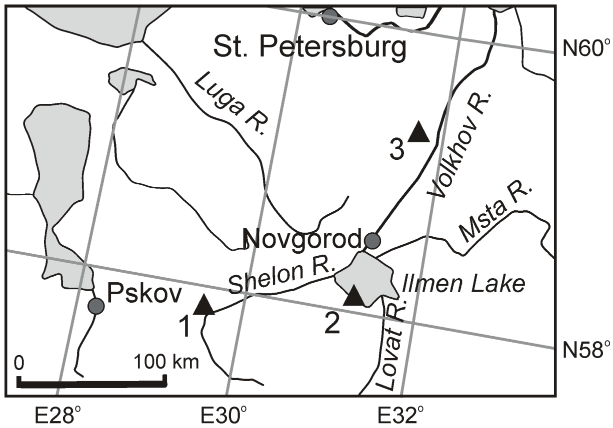

Fig. 2. Locality map of sections:
1 — Shelon; 2 — Ilmen; 3 — Tchudovo

Рис. 2. Схема расположения разрезов:
1 — Шелонь; 2 — Ильмень; 3 — Чудово

The P1 elements of *Mehlina gradata* were studied with a number of analytical techniques, including morphological investigations with scanning electron microscopy (SEM) and optic microscopy, simple biometry (7 conodont elements), trace element analysis (8 conodont elements), and C-isotope geochemistry (20 conodont elements). Because most of the isotopically analysed conodont elements are fragmented, it is impossible to accurately determine their original length. SEM imaging in secondary electron mode was employed for morphological assessment (Figure 1). Standardized measurement of P1element includes element length and number of denticles (Figure 1).

The trace element analysis was performed on albid tissue that demonstrates most homogenous composition among conodont hard tissues. Strontium-to-Calcium ratios (Sr/Ca) as well as content of P and F in the albid tissue were determined using energy-dispersive X-ray spectroscopy (EDX) coupled with a VEGA3 TESCAN microprobe. Four chemical elements (Ca, Sr, P, and F) were analyzed per counting cycle at an accelerating voltage of 20 kV, emission current of 78—88 mA, and a probe diameter of 190—290 nm. Sample standards include wollastonite for Ca, GaP for P, fluorite for F, and SrF_2 for Sr.

Analysis of carbon isotope composition (δ^{13}Ccon) was performed on P1 elements (CAI = 1) following method described earlier (Zhuravlev, 2023). The δ^{13}Ccon values were determined by a DELTA V Advantage mass spectrometer equipped with a Thermo Electron continuous flow interface (ConFlo III) and an elemental analyser (Flash EA 1112) (CKP Geonauka, Syktyvkar). Carbon dioxide produced by

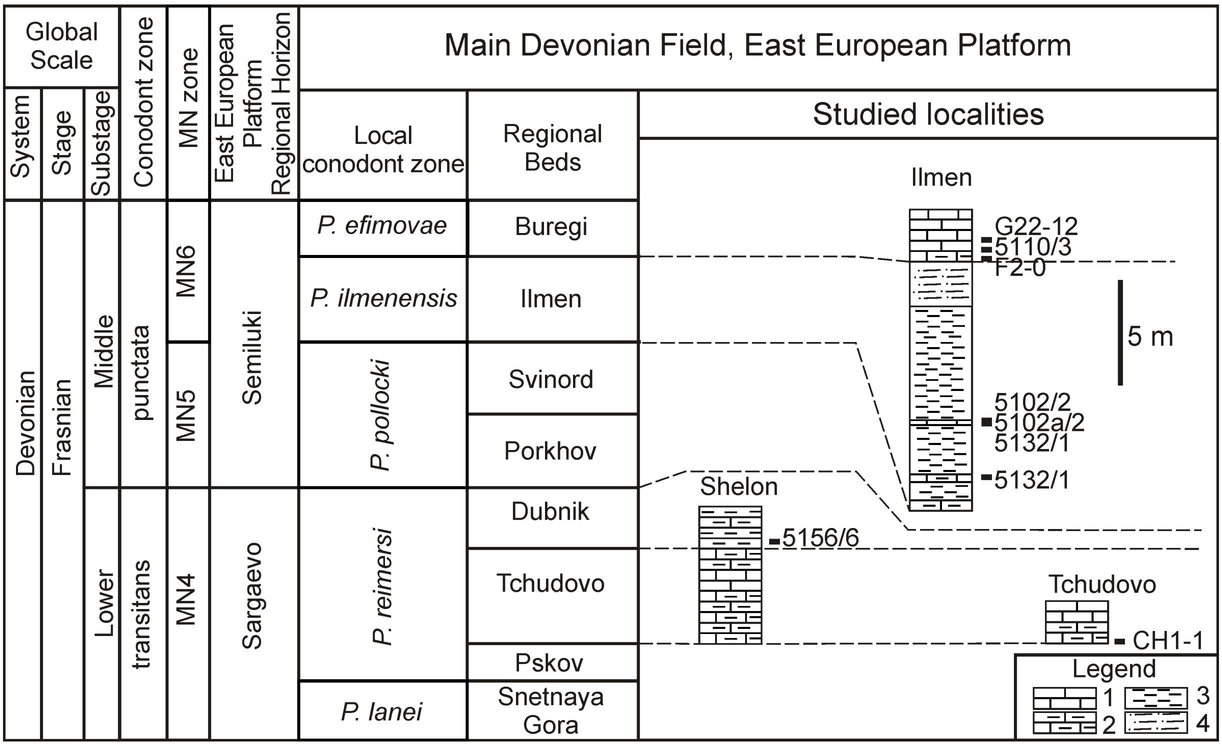

Fig. 3. Stratigraphic correlation of study sections.

Legend: 1 — limestones; 2 — clayey limestones; 3 — clays; 4 — silts and silty sands. The numbers indicate samples

Рис. 3. Стратиграфическая корреляция изученных разрезов.

Условные обозначения: 1 — известняки; 2 — глинистые известняки; 3 — глины; 4 — алевриты и алевритистые пески

high-temperature (900 °C) combustion of conodont elements in oxygen was analysed. At this temperature, both carbon from organic matter and carbon from hydroxyapatite are converted to carbon dioxide (Zhuravlev, 2023). The $\delta^{13}C$ values are given in ppm relative to the VPDB standard. The international standard USGS-40 (L-glutamic acid) is used for calibration. The error of the $\delta^{13}C$ determination is ±0.15‰.

Results

P1 element length of the study specimens of *Mehlina gradata* range from 0.4 mm to 1.0 mm. The number of denticles varies from 11 to 18 that correspond to original description of the species (Youngquist, 1945). Morphological analysis indicates that the general blade-form morphology and small basal pit are maintained throughout ontogeny, while the P1 element shows minimal variation in shape — only an increase in size and number of denticles occur between early and late developmental stages (Figure 1). The number of denticles is proportional to the element length (Figure 4) (n=7, R^2=0.805).

Mean Sr/Ca (mol/mol) in albid tissue is about 0.007 (n=8, Standard deviation 0.005) (Table 1). It is slightly higher than mean Sr/Ca of other Frasnian conodonts from the same localities (about 0.004, n=17, Standard deviation 0.002) (Figure 5).

C-isotope composition of P1 elements of *Mehlina gradata* varies from −31.9 ‰ to −24.7 ‰. Mean δ^{13}Ccon value is of −27.4 ‰ (n=20, Standard deviation 1.993). The biometrically studied seven specimens show δ^{13}Ccon values ranging from -30.1‰ to −24.7 ‰ with the mean value is of −27.3 ‰ (n=7, Standard deviation 1.881) (Table 2). Element length and C-isotope composition show significant positive correlation (n=7, R^2 = 0.8689, p=0.0022) that is independent on stratigraphic position of the study specimens (Figure 6). Mean values for MN4, MN5, and MN6 zones vary insignificantly (Figure 7).

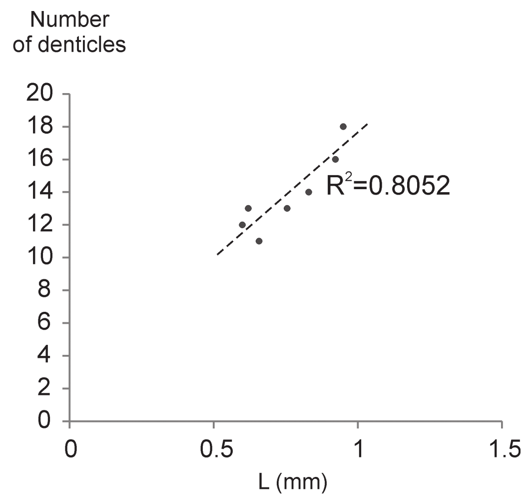

Fig. 4. Correlation of P1 element length (L) and number of denticles in study specimens of *Mehlina gradata*

Рис. 4. Корреляция длины P1-элемента (L) и количества зубцов у изученных экземпляров *Mehlina gradata*

The combination of a relatively high Sr/Ca ratio paired with lower mean δ^{13}Ccon suggests that *Mehlina gradata* may have occupied a comparatively low trophic level (Shirley et al., 2018; Zhuravlev, 2023).

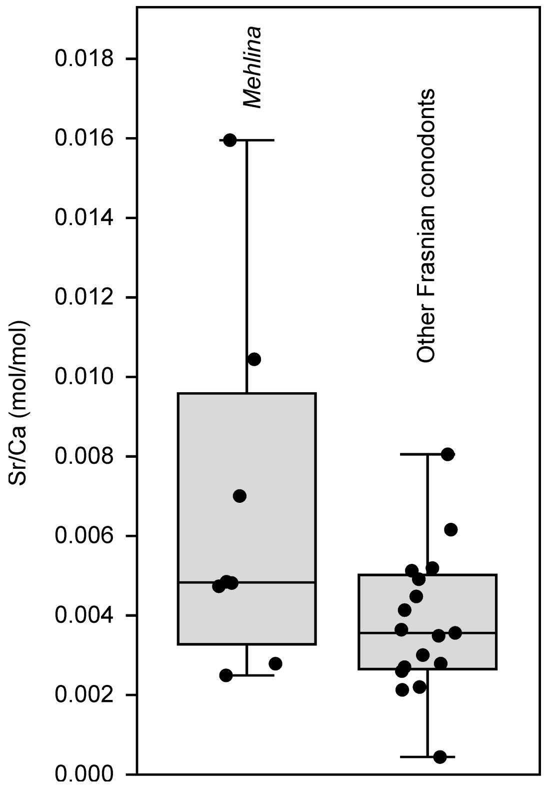

Fig. 5. Distribution of Sr/Ca ratios in *Mehlina gradata* and other Frasnian conodonts from the same localities. Boxes represent the 25—75 % interquartile range, with the horizontal line indicating the median. Whiskers represent minimum and maximum values; individual points correspond to specific Sr/Ca values of specimens

Рис. 5. Распределение соотношения Sr/Ca у *Mehlina gradata* и других франских конодонтов в изученных разрезах. Прямоугольники ограничивают интерквартильный интервал 25—75 %; горизонтальная линия отмечает медианное значение. Засечки соответствуют минимальным и максимальным значениям, а точки отвечают значениям Sr/Ca для отдельных экземпляров

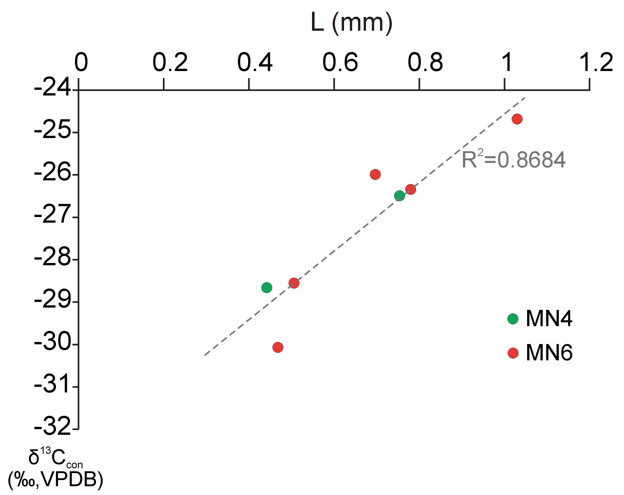

Fig. 6. Bivariate plot of element length (L) versus carbon isotope composition of conodont elements of *Mehlina gradata* from the MN4 and MN6 conodont zones

Рис. 6. График соотношения длины элемента (L) и изотопного состава углерода конодонтовых элементов для *Mehlina gradata* из конодонтовых зон MN4 и MN6

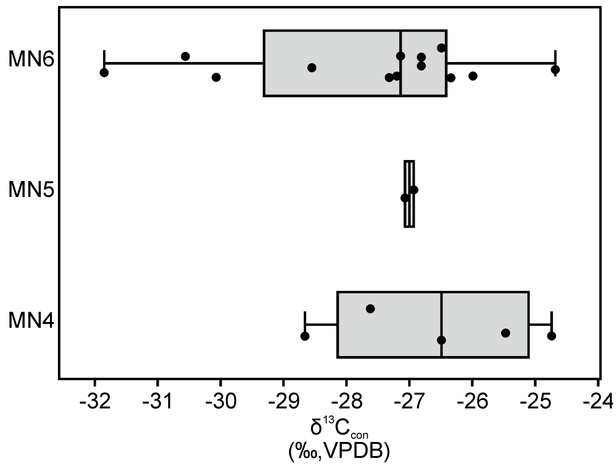

Fig. 7. Stratigraphic distribution of carbon isotope composition of conodont elements of *Mehlina gradata* across the MN4, MN5, and MN6 conodont zones of the study region. Boxes represent the 25—75 % interquartile range, with the horizontal line indicating the median. Whiskers represent minimum and maximum values; points correspond to individual sample values

Рис. 7. Стратиграфическое распределение изотопного состава углерода конодонтовых элементов *Mehlina gradata* в конодонтовых зонах MN4, MN5 и MN6 изученного региона. Прямоугольники ограничивают интерквартильный интервал 25—75 %; горизонтальная линия отмечает медианное значение. Засечки соответствуют минимальным и максимальным значениям, а точки отвечают значениям для отдельных экземпляров

Discussion

The range of δ^{13}Ccon variations in the studied specimens of *Mehlina gradata* is about 7 ‰, but Sr/Ca ratio ranges from 0.002 to 0.016 mol/mol (Tables 1, 2). Notably, these variations occur in rather small parts of the paleobasin and in the short time intervals. For example, variations of δ^{13}Ccon values within a single sample (sample 5110/3) reach approximately 4 ‰ (Table 2). The positive correlation between δ^{13}Ccon values and P1 element length suggests a clear ontogenetic trend: larger elements are associated with higher δ^{13}C values. Due to a small number of studied specimens (seven P1 elements) this is a preliminary finding that warrants further investigation with larger sample sets.

By analogy with modern low vertebrates, it can be supposed that the ontogenetic ^{13}C enrichment of mineralized tissue in *Mehlina gradata* was caused by ontogenetic dietary shifts (e. g., moving to higher trophic levels), habitat transitions (e. g., migrating from inshore nurseries to offshore adult habitats), and metabolic changes that alter the balance of respired and environmental carbon incorporated into the tissue (e. g. Carlisle et al., 2015; Sakamoto et al., 2023; Díaz-Delgado et al., 2026).

The lack of locality and facies control on the ontogenetic variations of δ^{13}Ccon in *Mehlina gradata* in study material suggests that habitat and migration patterns probably played an insufficient role in these variations. Metabolic effects remain a theoretical possibility. High metabolic rates in younger, faster-growing individuals could lead to a greater proportion of metabolic (respired)

Table 1. Composition of P1 and P2 elements of *Mehlina gradata*

Таблица 1. Состав P1- и P2-элементов *Mehlina gradata*

Sample Образец	Taxon / Таксон	Tissue Ткань	F (mol %)	P (mol %)	Ca (mol %)	Sr (mol %)	Sr/Ca (mol/mol)
F2-0	*Mehlina gradata*	albid	5.19	13.68	22.84	0.16	0.007005
F2-0	*Mehlina gradata*	albid	3.97	14.06	23.23	0.11	0.004735
G22-12	*Mehlina gradata*	albid	4.72	18.06	38.3	0.40	0.010444
G22-12	*Mehlina gradata*	albid	5.88	18.24	38.86	0.62	0.015955
5132/1	*Mehlina gradata*	albid	4.99	14.95	24.75	0.12	0.004848
5102/2	*Mehlina gradata*	albid	6.44	14.63	24.91	0.12	0.004817
5102A-2	*Mehlina gradata*	albid	4.93	14.92	25.11	0.07	0.002788
5102A-2	*Mehlina gradata*	albid	4.90	14.72	24.06	0.06	0.002494

Table 2. C-isotope composition of the P1 elements of *Mehlina gradata*

Таблица 2. Изотопный состав углерода P1-элементов *Mehlina gradata*

Sample / Образец	Zone / Зона	L (mm)	δ^{13}Ccon (‰, VPDB)	Taxon / Таксон
5156/6	MN4	0.44	−28.7	*Mehlina gradata*
8/50P	**MN4**	n/a	−24.7	*Mehlina gradata*
5174a/2	**MN4**	n/a	−27.6	*Mehlina gradata*
CH-1-1	**MN4**	0.75	−26.5	*Mehlina gradata*
CH-1-6	MN4	n/a	−25.5	*Mehlina gradata*
F-5-1	**MN5**	n/a	−27.1	*Mehlina gradata*
F-5-5	**MN5**	n/a	−26.9	*Mehlina gradata*
1314/3	**MN6**	n/a	−26.5	*Mehlina gradata*
5102/4	MN6	n/a	−30.6	*Mehlina gradata*
5102A-2	**MN6**	n/a	−26.8	*Mehlina gradata*
5103/10	**MN6**	n/a	−27.2	*Mehlina gradata*
5103/10	**MN6**	n/a	−27.1	*Mehlina gradata*
5103/10	MN6	n/a	−26.8	*Mehlina gradata*
5110/3	**MN6**	n/a	−26.0	*Mehlina gradata*
5110/3	**MN6**	0.70	−26.0	*Mehlina gradata*
5110/3	**MN6**	0.47	−30.1	*Mehlina gradata*
5110/3	MN6	0.51	−28.6	*Mehlina gradata*
5132/0	**MN6**	n/a	−31.9	*Mehlina gradata*
F2-0	**MN6**	n/a	−27.3	*Mehlina gradata*
G22-12	**MN6**	1.03	−24.7	*Mehlina gradata*
G22-12	**MN6**	0.78	−26.3	Mehlina gradata

carbon being incorporated into the mineralized tissue compared to environmental carbon. Because respired carbon is typically ^{13}C-depleted, this could result in lower δ^{13}C values in early life stages. However, as the metabolic peculiarities of conodont biomineralization remain unknown, we cannot definitively evaluate "vital effects" on δ^{13}Ccon values. The most probable cause of the observed variations is dietary diversity, a hypothesis further supported by the wide range in Sr/Ca ratios.

The positive correlation found between element length (as individual age proxy) and δ^{13}Ccon values indicates ontogenetic dietary shifts that transcend simple morphological stability. Early life stages were probably associated with feeding at a lower trophic level than those observed in mature individuals, suggesting an adaptive shift toward a predatory or scavenging lifestyle as the conodont grew. These findings support the hypothesis that despite maintaining a consistent shape of P1 elements, *Mehlina gradata* exhibited dynamic trophic plasticity throughout its life cycle. In general, *Mehlina gradata* shows wide range of δ^{13}C variations among individuals and ontogenetic trends similar to modern small fishes occupying low trophic level (Sakamoto et al., 2023).

Similar changes in trophic position during ontogeny have been reconstructed for blade-form *Ozarkodina confluens* (Branson et Mehl, 1933) on the basis of Sr/Ca ratio (Shirley et al., 2018). In contrast, conodonts bearing coniform elements in the apparatus, such as *Panderodus equicostatus* (Rhodes, 1953) and *Proconodontus muelleri* Miller, 1969, show lack of substantial variations in trophic level during ontogeny (Leonhard et al., 2021). Probably, an ontogenetic trend in trophic position may be a common feature of conodonts possessing blade-form elements in P1 position.

These findings suggest that P element morphology cannot be used as a main trait for reconstructing the position of conodonts in a trophic web. The study of the Late Devonian *Palmatolepis* provided further evidence of the weak relationship between the morphology of P elements and trophic position (Goudemez et al., 2026). Notably, the calcium stable isotope ratio in conodont elements (as a trophic level proxy) remained unchanged in *Palmatolepis*, despite significant modifications in element morphology during the Famennian (Goudemez et al., 2026).

Conclusions

The substantial range of δ^{13}Ccon values strongly suggests that *Mehlina gradata* utilized a diverse and varied food source throughout its life despite of morphological stability of P1 elements. This trophic variability challenges the interpretations of feeding ecology based only on morphology of P1 elements. Element size may play a principal role in trophic specialization of conodonts.

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References

Briggs D. E. G., Clarkson E. N. K., Aldridge R. The conodont animal. Lethaia. 1983;16:1—14.

Carlisle A. B., Goldman K. J., Litvin S. Y., Madigan D. J., Bigman J. S., Swithenbank A. M., Kline Jr T. C., Block B. A. Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proceedings of the Royal Society: Biological Sciences. 2015; 282:20141446. http://dx.doi.org/10.1098/rspb.2014.1446

Díaz-Delgado E., Chung M.-T., Magozzi S., Willis T. J., Trueman C. N. Potential metabolic records in isotope signals of chondrichthyan hard tissues. Journal of Fish Biology. 2025;107(3):1001—1017. https://doi.org/10.1111/jfb.70109

Du Y., Onoue T., Tomimatsu Y., Wu Q., Rigo M. Lower Jurassic conodonts from the Inuyama area of Japan: implications for conodont extinction. Frontiers in Ecology and Evolution. 2023;11:1135789. https://doi.org/10.3389/fevo.2023.1135789

Goudemez C., Assemat A., Thiery G., Girard C. 3D topography as an indicator of change in food processing ability in elements of the conodont genus *Palmatolepis*. Lethaia. 2026;59(3):1—16. https://doi.org/10.18261/let.59.3.2

Lane H. R. Symmetry in conodont element-pairs. Journal of Paleontology. 1968;42:1258—1263.

Leonhard I., Shirley B., Murdock D. J. E., Repetski J., Jarochowska E. Growth and feeding ecology of coniform conodonts. PeerJ. 2021;9:e12505 https://doi.org/10.7717/peerj.12505

Müller K. J., Nogami Y. Growth and function of conodonts. Int. Geol. Congr. Rep. 24th Sess. Montreal. Sect.7;1972. p. 20—27.

Nicoll R. S. Form and function of the Pa element in the conodont animal. In: Aldridge R.L. ed., Palaeobiology of conodonts. Chichester: Ellis Horwood; 1987. p. 77—90.

Plotitsyn A. N., Zhuravlev A. V. Morphology of the early ontogenetic stages of advanced siphonodellids (conodonts, Early Carboniferous). Vestnik of Institute of Geology Komi SC UB RAS. 2016;8:3—8.

Purnell M. A., Von Bitter P. H. Blade-shaped conodont elements functioned as cutting teeth. Nature. 1992;359:629—631.

Sakamoto T., Kodama T., Horii S., Takahashi K., Tawa A., Tanaka Y., Ohshmio S. Geographic, seasonal and ontogenetic variations of δ^{15}N and δ^{13}C of Japanese sardine explained by baseline variations and diverse fish movements. Progress in Oceanography. 2023;219:103163. https://doi.org/10.1016/j.pocean.2023.103163

Shirley B., Grohganz M., Bestmann M., Jarochowska E. Wear, tear and systematic repair: testing models of growth dynamics in conodonts with high-resolution imaging. Proceedings of the Royal Society: Biological Sciences. 2018;285(1886):20181614. https://doi.org/10.1098/rspb.2018.1614.

Youngquist W. L. Upper Devonian conodonts from the Independence Shale (?) of Iowa. Journal of Paleontology. 1945;19(4):355—367.

Zhuravlev A. V. Lower–middle Frasnian organic carbon isotope record of conodonts in East European Platform. Palaeoworld. 2022;31(2):249—257. https://doi.org/10.1016/ j.palwor.2021.07.003

Zhuravlev A. V. Ontogeny and trophic types of some Tournaisian Polygnathacea (Conodonta). Courier Forschungsinstitut Senckenberg. 1995;182:307—312.

Zhuravlev A. V. Carbon isotope study of conodont elements: Applications and limitations. Marine Micropaleontology. 2023;178:102200. https://doi.org/10.1016/j.marmicro.2022.102200

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