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Article

Sr/Ca and Ba/Ca ratios support trophic partitioning within a Silurian conodont community from Gotland, Sweden

David F. Terrill, Emilia Jarochowska* , Charles M. Henderson, Bryan Shirley, and Oskar Bremer

Abstract.—Conodonts were a highly diverse and abundant vertebrate group whose fossils are found in marine Paleozoic and Triassic strata around the world. They inhabited environments ranging from lagoons to open oceans and are represented by a wide variety of dental morphologies. Conodonts may have filled many different ecological niches and represent a significant proportion of nekton before the Devonian. Despite this, very little is known about trophic ecology of conodonts. While morphological diversity suggests a complex trophic structure within conodont communities, there is little evidence to support dietary niche partitioning among conodonts.

We tested the hypothesis that individual conodont taxa occupied different trophic niches, using Sr/Ca and Ba/Ca ratios preserved in the dental elements of assemblages from Silurian strata of Gotland, Sweden. Sr/Ca and Ba/Ca have been shown to vary in vertebrate skeletal tissues depending on trophic positioning, although biological and environmental conditions can affect these ratios. Environmental influences were minimized by examining entire conodont communities from a tropical epeiric sea and by measuring strontium isotope ratios using thermal ionization mass spectrometry in the most metropolitan taxon (*Ozarkodina confluens*). Composition of white matter, a tissue unique to conodonts, was also analyzed using microprobe analysis, revealing significantly lower Sr concentrations than in surrounding lamellar tissue, suggesting taxon-specific histology should be considered when analyzing conodonts for geochemical data. Excluding taxa with highly variable quantities of white matter, the results show that each taxon preserves different Sr/Ca and Ba/Ca ratios with limited overlap, indicating variation in trophic positioning.

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Introduction

Conodonts are an extinct group of jawless, boneless fishes that first appeared in the Cambrian and went extinct at the end of the Triassic. Their fossil record primarily consists of mineralized oral and oropharyngeal denticle-bearing elements (referred to as “conodont elements”) analogous to teeth (Murdock et al. 2013), and these elements are frequently

preserved. As a result, conodont fossils are found in marine rocks on all continents and can be very common in some localities. While some workers dispute the vertebrate affinities of conodonts (Blieck et al. 2010; Turner et al. 2010), most work in the last 30 years has suggested a vertebrate affinity based on studies of preserved soft tissues, composition of tooth-like elements, and phylogenetic analyses (Aldridge 1993;

Donoghue et al. 2000; Donoghue 2001; Terrill et al. 2018). Although the exact relationships between conodonts and other vertebrates are still uncertain, recent work has suggested conodonts are closely affiliated with cyclostomes, a group that consists of hagfish and lampreys (Donoghue and Rücklin 2016; Terrill et al. 2018; Miyashita et al. 2019).

The conodont fossil record is unusual among vertebrates. The lack of bones has led to a dearth of body fossils, similar to other boneless vertebrates such as lampreys and hagfish (Miyashita et al. 2019). The record of their mineralized elements is, however, among the best of any group of organisms (Foote and Sepkoski 1999) from the upper Cambrian through the Upper Triassic. Their relative abundance and high evolutionary rates have made conodonts ideal index fossils for biostratigraphy, where they are used to define many important geologic boundaries such as the Permian/Triassic (Yin et al. 2001) and the Frasnian/Famennian boundaries (House et al. 2000). Conodonts have been well documented and analyzed since they were first described by Pander (1856) and have been the subject of numerous paleoecological studies over the last half century (Clark 1974, 1984; Barnes 1976; Ji and Barnes 1994; Donoghue and Purnell 1999; Armstrong and Smith 2001; Jarochowska et al. 2017), yet their role in ecosystems, such as their dietary niches, remains elusive.

The lack of knowledge surrounding conodont trophic paleoecology is problematic for the understanding of marine ecology in the Paleozoic and Triassic, as highlighted by a recent study reexamining the Devonian nekton revolution (Whalen and Briggs 2018). The Devonian nekton revolution refers to the apparent rapid occupation of the water column during the Devonian Period, with nektic biodiversity rising from 15% of non-benthic taxa at the end of the Silurian to approximately 85% by the end of the Devonian (Klug et al. 2010). By simply including conodonts as probable nektic swimmers, Whalen and Briggs (2018) showed that nektonism had not risen suddenly in the Devonian, but rather gradually since the first appearance of conodonts in the Cambrian. Given the importance of conodonts in the shift toward nektic environmental occupation,

understanding the dietary niches of conodonts is vital to our understanding of how and why animals began to increasingly occupy the water column.

While the question of what conodonts ate remains uncertain, there have been a number of studies directed at understanding how conodont elements may have been used to capture and process food. Microwear analyses have shown that conodont elements frequently possess wear facets and damage consistent with use in food processing (Purnell 1995; Purnell and Jones 2012), with wear patterns indicating occlusion similar in complexity to mammals in platform elements (Donoghue and Purnell 1999). Dental function is further supported by microstructural analysis of conodont crown tissues (tissues thought to be partially or completely exposed in the oral cavity; Donoghue 2001), while occlusion between platform elements is further supported by structural modeling of stress distribution during function (Martínez-Pérez et al. 2014). Mechanical models created based on clusters of conodont elements preserved in positions close to their relative orientation in the apparatus *in vivo* have been used to formulate hypotheses for how the oral apparatus may have functioned to capture food (Goudemand et al. 2011). Due to these efforts, the current hypothesis is that the preserved conodont elements did indeed function as teeth, without any direct evidence of dietary preferences being known. It has been suggested that size of conodont elements could be used as a proxy for trophic position (Balter et al. 2019; Ginot and Goudemand 2019), with larger elements possibly being indicative of a more carnivorous diet (Ginot and Goudemand 2019). Using size as a proxy for trophic position has been observed to be somewhat inconsistent in modern cyclostomes, however, with a positive correlation among lampreys and no statistical relationship among hagfish (Romanuk et al. 2011). Conodont body size also may not be directly related to conodont element size, so inferring conodont trophic positioning based on element size is heavily reliant on assumptions that may not be well founded.

One possible path to explore conodont dietary niches is to examine the chemistry

preserved in conodont elements. The crown of a conodont element is comparable in composition to vertebrate tooth enamel; it is hypermineralized and composed of hydroxyapatite. As such, conodont elements are highly resistant to diagenetic processes and often record chemical signatures that reflect original biological composition (Barham et al. 2012). Thus far there have only been a few studies that applied chemical analysis to the question of conodont trophic structure using calcium isotopes and organic carbon isotopes (Shirley et al. 2018; Balter et al. 2019; Zhuravlev 2020), which concluded that several Devonian conodont taxa were low-level consumers that most likely fed on plankton. While compelling, data reported in these studies still show a significant variation in isotopic values within each taxon and do not address the very large diversity of morphologies that exist throughout the conodont fossil record.

In this study, we analyzed the Sr/Ca and Ba/Ca content of several co-occurring Silurian conodont species from the Gotland succession in Sweden. Sr and Ba are common trace elements in vertebrate hard tissues, substituting for Ca in bones and teeth in vivo (Reynard and Balter 2014; Shirley et al. 2018). The relative abundances of these trace elements can be affected by several ecological factors. In terrestrial vertebrates, the ratio is dominated by diet, with carnivores typically having lower Sr/Ca and Ba/Ca ratios than herbivores (Gilbert et al. 1994; Burton et al. 1999; Blum et al. 2000; Peek and Clementz 2012; Kohn et al. 2013). The proposed mechanism for this trophic proxy is the biopurification of Ca, a biological process in which Ca preferentially accumulates in the skeleton over trace elements such as Sr and Ba, which results in an organism having lower Sr/Ca and Ba/Ca ratios relative to their dietary source (Burton et al. 1999; Peek and Clementz 2012). The relationship between trophic positioning and Sr/Ca and Ba/Ca ratios has also been observed in marine vertebrates (Peek and Clementz 2012); however, additional factors may impact these ratios. It has been observed that Sr and Ba can bioaccumulate near the base of marine food webs (Peek and Clementz 2012), while water temperature has been shown to also impact

Sr/Ca and Ba/Ca ratios in the bones of captive seabreams (Balter and Lécuyer 2010; Balter et al. 2011). To date, there have been very few examinations of Sr/Ca and Ba/Ca ratios in modern fish apatite beyond the studies mentioned, while examinations of Sr/Ca and Ba/Ca ratios preserved in modern fish otoliths (which are composed of biogenic aragonite) are much more numerous. Studies on otoliths have shown Sr/Ca and Ba/Ca ratios are significantly impacted by water temperature (Martin and Thorrold 2005; Nelson et al. 2018) and salinity (Diouf et al. 2006; Martin and Thorrold 2005; Zimmerman 2005; MacDonald and Crook 2010; Nelson et al. 2018). While otoliths do not consist of apatite, these results still reinforce the observations of Balter and Lécuyer (2010) that temperature is an important variable to consider when making interpretations, while indicating that salinity should be considered as well. Finally, it is worth noting that, apart from the study by Peek and Clementz (2012), there have been no comprehensive studies of marine trophic relationships between vertebrates using Sr/Ca and Ba/Ca ratios preserved in apatite, so the application of these methods to a fossil conodont community is not only novel from a paleontological perspective but represents one of the very few attempts to characterize the trophic structure of any marine community using these methods.

As conodont elements are not completely homogenous in terms of tissue composition, we investigate here whether histological differences between taxa might confound our interpretations of the Sr/Ca proxy. Conodont elements are composed of lamellar (or hyaline) tissue, finely laminated apatite that is considered structurally and chemically analogous to vertebrate enamel (Donoghue 1998; Terrill et al. 2022: SI fig. 2). A second tissue is known as white (or albid) matter due to its white appearance in reflected light microscopy. White matter is often found in the denticles of conodont elements, but the distribution and volume vary greatly between taxa. It has different crystallographic properties (Trotter et al. 2007; Atakul-Özdemir et al. 2021) and elemental composition than the lamellar tissue (Trotter and Eggins 2006). The compositional variation is therefore very important to determine; if

white matter contains varying amounts of Sr, Ba, or Ca in comparison to the lamellar tissue, it could have a significant impact on the measured Sr/Ca and Ba/Ca ratios measured in taxa with systematically different proportions of these tissues.

In addition to Sr/Ca and Ba/Ca ratios, we also analyzed Sr isotopes preserved in different ontogenetic stages of *Ozarkodina confluens*. This was done to test the hypothesis that some conodonts may have displayed anadromous behavior, possibly migrating to freshwater environments to spawn. Sr isotope ratios in conodont elements are believed to directly reflect the water in which they lived (Bertram et al. 1992; Armstrong et al. 2001). Sr isotope ratios are consistent throughout the world's oceans at a given moment in geologic time (Veizer 1989), as a result of mixing from fluvial sources of highly variable composition. Sr isotopic ratios should therefore be relatively consistent between individuals that lived exclusively in the marine realm. In contrast, ontogenetically younger individuals that partially inhabited fresh or brackish waters would have been exposed to a wider range of environmental Sr isotope values, resulting in higher variability in the preserved Sr isotope ratios. To determine whether conodonts may have spent time in fresh or brackish water environments (possibly related to spawning activities), comparisons were made between young and adult specimens.

We evaluate here the potential for using Sr/Ca and Ba/Ca ratios to study the trophic structure of conodont communities. This was done by analyzing the Sr/Ca and Ba/Ca ratios preserved in nine different conodont taxa from Gotland, Sweden (see Fig. 1 for examples of each taxon). By combining these data with Sr isotope ratios, in situ analysis of elemental composition through use of a microprobe, and paleoenvironmental information provided by facies analysis, we were able to account for several environmental and biological factors that may have influenced the preserved Sr/Ca and Ba/Ca ratios. This enabled us to test the hypothesis that morphological differences between conodont taxa reflect trophic diversification (Ginot and Goudemand 2019; Petryshen et al. 2020; Kelz et al. 2021), while also examining whether proxies for the trophic position



FIGURE 1. Typical morphologies of P1 elements of taxa discussed in the study. A, *Zieglerodina remscheidensis*, NRM-PZ Co99 from Ängvards 7, Sundre Fm. (sample G00-26 LJ). B, C, *Ozarkodina bohémica* from Gothemsхамmar 9, Halla Fm. (sample EJ-14-407); B, EJ-14-407-0001; C, EJ-14-407-0002. D, *Ozarkodina confluens* from Storms 2, Sundre Fm., NRM-PZ Co155 (sample G94-42 LJ). E, *Ctenognathodus munchisoni* from Gothemsхамmar 9, Klinteberg Fm., EJ-14-410-0001 (sample EJ-14-410). F, *Oulodus ?excavatus* from Rivviken 2, Hamra or Sundre Fm. NRM-PZ Co153 (sample G04-739 LJ). G, *Pseudooneotodus beckmanni* from Närshamn 1, Burgsvik Fm., NRM-PZ Co79 (sample G83-11LJ). H, *Wurmiella excavata* from Barshageudd 2, Sundre Fm., G14-18-OB-0001 (sample G14-18OB). I, *Panderodus equicostatus* from Närshamn 2, Burgsvik Fm., NRM-PZ Co72 (sample G83-12LJ). Scale bar, 100 μ m. Collection identifications starting with NRM-PZ refer to Swedish Museum of Natural History, Stockholm; all other specimens are hosted at Friedrich-Alexander-Universität, Erlangen.

proposed here are influenced by the histological composition of conodont elements.

Methods

Conodonts

Conodont assemblages were extracted from 10 rock samples collected in the Swedish island of Gotland. The strata exposed in Gotland represent carbonate deposits formed on a tropical carbonate platform, which during the Silurian Period formed in an epeiric sea on the shelf of Baltica (Baarli et al. 2003). The cratonic position and lack of tectonic deformation led to excellent conodont preservation (Conodont Alteration Index [CAI] = 1) in the absence of substantial burial. They also allowed the development of a detailed stratigraphic interpretation across coeval paleoenvironments

TABLE 1. Summary of biostratigraphic ages (according to Jeppsson et al. 2006) and environments represented by each sample in this study, as well as taxa found in those samples. Taxa abbreviations are as follows: Ou., *Oulodus*; Oz., *Ozarkodina*; Pa., *Panderodus*; Ps., *Pseudooneotodus*; W., *Wurmiella*; Z., *Zieglerodina*.

Conodont biozone	Age	Taxa represented	Environment	Sample no.
<i>Oz. crista</i>	Ludfordian	<i>Ou. excavatus</i> , <i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>Pa. unicostatus</i> , <i>Ps. beckmanni</i> , <i>W. excavata</i> , <i>Z. remscheidensis</i>	Lagoon	G14-18-OBA G14-19-OB
<i>K. variabilis</i> to <i>K. cf. sardoa</i>	Gorstian	<i>Ou. excavatus</i> , <i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>W. excavata</i>	Reef talus	EJ-16-33
Unzoned		<i>Ctenognathodus</i> spp., <i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>W. excavata</i>	Lagoon	EJ-16-6
<i>C. murchisoni</i>	Homerian	<i>Oz. bohemia</i> , <i>Oz. confluens</i>	Hypersaline lagoon	EJ-14-410
<i>K. ortus</i> <i>absidata</i>	Homerian	<i>Ctenognathodus</i> spp., <i>Oz. confluens</i> , <i>W. excavata</i>	Hypersaline lagoon	EJ-14-407 EJ-14-411
<i>Oz. bohemia</i> <i>longa</i>	Homerian	<i>Oz. bohemia</i> , <i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>W. excavata</i>	Outer platform/shelf	EJ-15-415
<i>Oz. sagitta</i> <i>sagitta</i>	Homerian	<i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>W. excavata</i>	Outer platform/shelf	EJ-15-407
<i>Oz. sagitta</i> <i>rhenana</i>	Sheinwoodian	<i>Oz. confluens</i> , <i>Pa. equicostatus</i> , <i>W. excavata</i>	Backreef/lagoon	EJ-15-394

represented in the outcrops in Gotland (Calner et al. 2004; Jeppsson et al. 2006). Reviews of depositional environments in the Silurian of Gotland have been compiled by Samtleben et al. (2000) and Calner et al. (2004). Rock samples used in this study are summarized in Table 1. Except for the two youngest samples (G14-18OB and G14-19OB), they have been processed at GeoZentrum Nordbayern following the technique of Jeppsson et al. (1999), that is, digested in buffered 7% acetic acid and wet sieved. The fraction between 63 μm and 1 mm was retained, separated from lighter residue in sodium polytungstate with the density of $2.83 \text{ g} \times \text{cm}^{-3}$, and hand-picked. Samples G14-18OB and G14-19OB were processed at Department of Geology at Lund University as described in Bremer et al. (2020).

Elemental Abundances

Identifiable elements were hand-picked from digested rock samples and separated into 256 monospecific analytical samples. Thus, conodonts extracted from one rock sample yielded multiple analytical samples. Analytical samples were first cleaned through immersion in a 7% unbuffered acetic acid solution for a minimum of 1 hr. This was done to remove any remaining carbonate material and other contaminating particles attached to the fossil's surface. After removal from acid, each fossil was

transferred to a deionized water bath for another hour to rinse off and dilute remaining acid before being placed in clean microfossil slides for transport. Conodont fossils were then weighed using a scale to create analytical samples for measurement. While some individual conodont fossils were massive enough to constitute a complete analytical sample, other analytical samples were amalgamations of multiple specimens belonging to the same taxon. Minimum sample mass was 20 μg , with most analytical samples having a mass exceeding 50 μg (see Terrill et al. 2022: SI table 1).

Analytical samples were then digested in 30 μl of 3 M nitric acid. Digestion was typically complete after just 1 hr; however, all samples were allowed to digest for at least 2 hr. One milliliter of deionized water was then added to dilute the analytical sample, which was mixed using a vortex machine. Samples were further diluted by a factor of 5 to 50, depending on the initial mass of the sample, using deionized water. An internal calibration standard was then added before each analytical sample was again mixed using the vortex machine. Samples were then loaded into a tray and sampled using a Thermo Scientific iCAP Qc quadrupole inductively coupled plasma mass spectrometry (ICP-MS) mass spectrometer in the Department of Geology at Friedrich-Alexander-Universität Erlangen-Nürnberg and

measured in triplicate. Results were compared with the Bone Ash NIST SRM 1400 standard. Full results are presented in Terrill et al. (2022: SI table 1).

Electron Microprobe Analysis

In addition to analyzing the bulk Sr/Ca and Ba/Ca content of conodont elements, we employed an electron microprobe to examine the potential variation in composition between tissue types. Conodont elements can generally be divided into two major tissue types, the crown tissue and the basal tissue, based on differences visible under the light microscope, crystallographic properties, and composition. The basal tissue is less mineralized and more organic than the crown tissue (Müller and Nogami 1971; Donoghue 1998). As a result, basal tissue is more likely to experience diagenetic alteration and is not ideal for chemical analyses (Holmden et al. 1996; Wenzel et al. 2000). In this study, we only analyzed conodont crowns to eliminate the possible impacts of basal tissues on our results.

Using an electron microprobe, we measured the variation in Sr concentrations between white matter and lamellar tissue in three cross-sectioned conodont crowns. The measurement was set up with the following elements to be detected: Na, F, Ba, and P (as P_2O_5). The sections were prepared following the methods described by Shirley et al. (2020). The measurements were made at University of Calgary electron microprobe facility using a JEOL JXA-8200 equipped with five wavelength-dispersive spectrometers using a spot size of 5 μm to minimize sample damage.

All conodont specimens for microprobe analysis were P_1 elements of *Ozarkodina confluens* (for anatomical notation, see Purnell et al. 2000). Specimens EJ-14-111-3 and EJ-14-407-016 were collected from rock samples using the same methods as described in “Conodonts.” They derive from samples EJ-14-111 and EJ-14-407, collected in the uppermost part of the “Gothemshammar member” (informal unit) of the Halla Formation (Homerian, Wenlock) at Gothemshammar 9 (57°36′33.46″N, 18°47′46.32″E; Jarochowska et al. 2016). EJ-14-111-3 was a subadult specimen, visibly smaller and with fewer denticles than the

others. EJ-14-407-016 was characterized in terms of histology and chemical composition by Shirley et al. (2018). Specimen Co0000203 comes from rock sample G89-797 in the collection of Lennart Jeppsson housed at Swedish Museum of Natural History. It was collected at Linde 3 (Gorstian, Ludlow; 57°16′30.22590″N, 18°22′52.29829″E) and processed at the Department of Geology at Lund University. The elements were embedded individually in an epoxy resin (Körapox 398, Kömmerling) and allowed to harden for at least 24 hr. They were then ground using a progression of 800 and 1200 grit silicon carbide until the optimal section plane was reached. The sections were polished mechanically using a 1 μm diamond spray for 20 min and chemically in OP-S Nondry colloidal silica suspension for 2 min using a Logitech WG2 polishing head. Polished specimens were coated with 3.8 nm of carbon to prevent charging.

Statistical Evaluation of Electron Microprobe Results

The differences in chemical composition between the lamellar tissue and the white matter were evaluated by fitting a mixed-effects general linearized model using the lme4 package (Bates et al. 2015) for R Software v. 3.5.1 (R Core Team 2018). A model with tissue as a fixed effect and specimen as a random effect was compared against the null model accounting only for the variability between specimens. This comparison was carried out individually for all elements that could be detected using the microprobe, that is, values above the detection limit (Table 2). Instead of using p -values, likelihood ratios were used to evaluate the strength of the fixed effect; to that end, the estimates of the effects were chosen to optimize the log-likelihood criterion.

Previous research by Trotter and Eggins (2006) and Shirley et al. (2018) indicated that changes in Sr composition can also be detected within the lamellar tissue. To evaluate this, measurements from the lamellar tissue have been divided into two classes: (1) center, close to the growth axis; and (2) side, close to the specimen edge. The role of the position within the lamellar tissue was evaluated using a mixed-effects model with position as a fixed

TABLE 2. Comparison of the chemical composition of the lamellar tissue ($N = 30$; 18 for BaO) and the white matter ($N = 10$; 6 for BaO) obtained with electron microprobe using mixed-effects generalized linear models. The values have been rounded to reflect the precision of the microprobe; for Ba, the difference between estimated effects of the tissues lies below the detection limit. AIC, Akaike information criterion.

Variable	AIC null model	AIC model with tissue effects	Likelihood ratio for tissue effect	Estimated effect of the lamellar tissue [ppm]	Estimated effect of the white matter [ppm]
SrO	0.5353	-23.7447	26.28	0.536	0.160
BaO	-196.18	-194.18	0	0.015	0.015
Sr/Ca	-315.38	-340.27	26.88	0.010	0.003
Na ₂ O	14.348	-18.631	34.97	0.934	0.456
F	-45.939	-51.127	7.19	3.359	3.241
P ₂ O ₅	92.848	64.810	30.04	39.479	40.669

effect and specimen as a random effect, analogous to the model comparing the tissues.

The total number of measurements depended on the detection limits of the microprobe. For CaO, SrO, Na₂O, F, and P₂O₅, all 40 measured points yielded values above the detection limit (10 in the white matter, 30 in the lamellar tissue). Ba measurements yielded results above the detection limit at 24 points only, the remainder was coded for the needs of the analysis as zero. The complete dataset of measurements is provided in Terrill et al. (2022: SI table 2).

Sr Isotope Ratios

For this study, we analyzed the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio preserved in 13 elements belonging to *Oz. confluentis*. Three ontogenetic stages were distinguished qualitatively under the light microscope based on the size of the element and the number of denticles. Conodonts with a low CAI (as determined through visual inspection and comparison with defined standards) and no visual evidence of recrystallization have been demonstrated to be good sources of original Sr isotope data and have been used as a proxy for determining global marine values through geologic time (Kurschner et al. 1992; Diener et al. 1996; McArthur et al. 2020). Marine Sr isotope ratios are considered to be globally consistent due to the Sr residence time being much longer than the global ocean mixing rate (Veizer 1989). Marine values are only expected to vary under specific circumstances, such as in a restricted basin, where connection between an inland sea and the larger ocean is minimal or absent. Freshwater or brackish water ecosystems can, however, show significant variation, as the Sr

content will be mostly controlled by local inputs such as bedrock weathering (Veizer 1989). As conodont elements grew through external apposition (Dzik 2008), they potentially retain a record of the elemental composition of waters they inhabited through their ontogeny. If a conodont species were to spend time in a coastal river or estuary (to spawn, for example), the Sr isotope ratios preserved in the oral/oropharyngeal elements would be expected to show variations depending on ontogeny and would also vary with respect to species that lived entirely in marine settings.

All Sr isotope ratios were measured using thermal ionization mass spectrometry (TIMS) at the University of Calgary. Measurement error ranged between 0.000004 and 0.000042 and averaged 0.000008 across all analyses. Before analysis, elements were first exposed to diluted acetic acid to remove any diagenetic material that might be present on the outer surface of the fossils. They were then digested in 0.5 ml of 3.0 M nitric acid and 30 μl of peroxide. An ion-exchange procedure was then performed to concentrate the Sr ions before analysis. The results are reported in Terrill et al. (2022: SI table 3).

Results

Elemental and Isotopic Composition of Conodont Crowns

Sr/Ca and Ba/Ca ratios are summarized in Figure 2 and Terrill et al. (2022: SI table 1). Of the nine taxa analyzed in this study, five (*Oulodus excavatus*, *Ozarkodina bohémica*, *Panderodus equicostatus*, *Wurmiella excavata*, and *Zieglrodina remscheidensis*) produced measurements with distinct and well-constrained ranges of

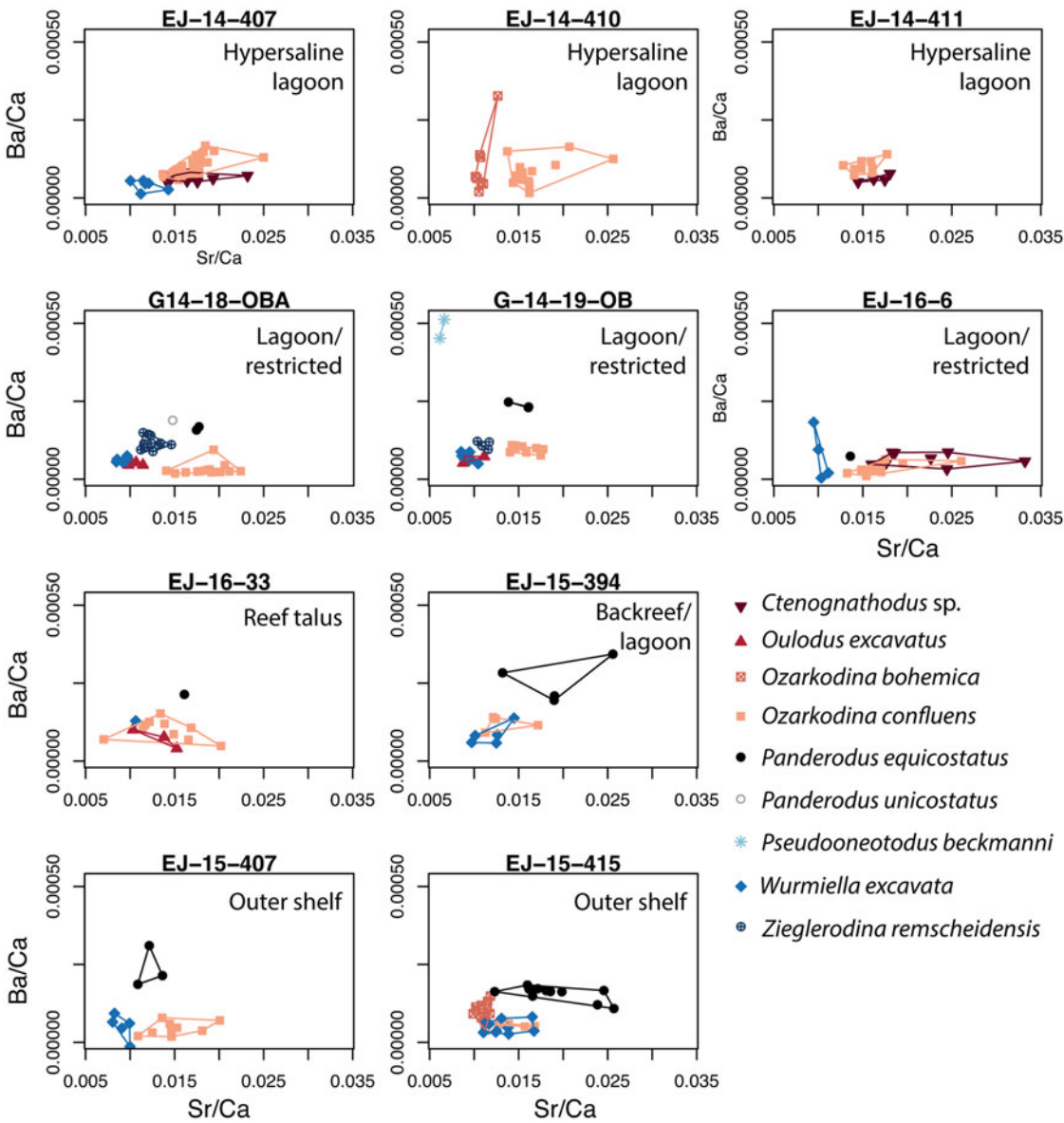


FIGURE 2. Ba/Ca vs. Sr/Ca values in crown tissues of nine conodont taxa from 10 rock samples in this study. Polygons encompass the complete range of values in each taxon. Samples are arranged according to the interpreted paleoenvironment represented in each rock sample.

Sr/Ca and Ba/Ca values. *Panderodus equicostatus* contained generally high Ba/Ca and Sr/Ca ratios, while *W. excavata* and *Ou. excavatus* both contained low Ba/Ca and Sr/Ca ratios. *Oz. bohémica* also recorded low Sr/Ca and Ba/Ca ratios; however, there was more variability in Ba/Ca ratios than seen in other taxa. *Zieglerodina remscheidensis* recorded moderate ratios, with lower Sr/Ca and Ba/Ca ratios than *Pa.*

equicostatus, but higher values than *Ou. excavatus* and *W. excavata*. Two taxa (*Ctenognathodus* spp. and *Ozarkodina confluens*) recorded much more variable Sr/Ca ratios, with some specimens recording the highest Sr/Ca ratios in this study, while Ba/Ca ratios of these taxa were consistently low in most measurements. The two remaining species (*Panderodus unicostatus* and *Pseudooneotodus beckmanni*) were

only found in a single assemblage. *Panderodus unicostatus* recorded Sr/Ca and Ba/Ca ratios in line with *Pa. equicostatus*, while *Ps. beckmanni* recorded low Sr/Ca ratios and very high Ba/Ca ratios.

In addition to Sr/Ca and Ba/Ca ratios, Sr isotope data were also collected from *Oz. confluens*. Dental elements representing different ontogenetic stages and different horizons were selected and analyzed for $^{87}\text{Sr}/^{86}\text{Sr}$, with the results summarized in Figure 3. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios clearly show very little variation within a rock sample regardless of ontogeny, with almost all elements within a horizon reporting values within the margin of error (see Terrill et al. 2022: SI table 2).

Chemical Differences between the Lamellar Tissue and the White Matter

Sr, Ba, P, and Na content differed substantially between the three specimens of *Oz. confluens* (Fig. 4 A–C,F). After correcting for this interspecimen variation using a mixed-effects model, the effect of tissue type on the concentration of Sr and P, as well as on the Sr/Ca ratio, had more support (Table 2) than the null model. Sr and the Sr/Ca ratio were higher in the lamellar tissue (effect estimate for the Sr/Ca ratio = 0.010; Table 2) than in the white matter (effect estimate for the Sr/Ca ratio = 0.003).

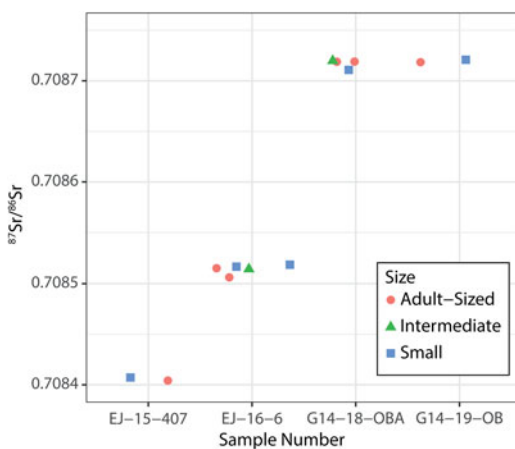


FIGURE 3. Strontium isotope ratios preserved in *Ozarkodina confluens* from different rock samples and stratigraphic ages (see Terrill et al. 2022: SI table 3). Data points have been spread horizontally to increase readability, as the overlap is substantial.

White matter, in turn, was enriched in P (effect estimate = 40.669 ppm) compared with the lamellar tissue (effect estimate = 39.479 ppm).

Ba content in all three specimens was slightly higher in the white matter compared with the lamellar tissue (Fig. 4D), but this difference disappeared after accounting for intraspecimen variability (effect estimate 0.015 ppm for both tissues). The null model explaining the overall variation in Ba content by interspecimen differences had more support (AIC = −196.18) than the full model explaining it also by differences between the tissues (AIC = −194.18). Therefore, no systematic differences in Ba content between both tissues could be demonstrated.

Variations in F and Na content could be compared between tissues only in two specimens: Co0000203 and EJ-14-407-016, as no measurements of these elements were obtained in the white matter of EJ-14-111-3 (Fig. 4E,F). In the two specimens, F content was minimally higher in the white matter (effect estimate 3.241 ppm) than in the lamellar tissue (effect estimate 3.359 ppm). The absolute content was very consistent between measurements in either tissue and varied little between the specimens. Na content was similar across the lamellar tissue of all three specimens (effect estimate 0.934 ppm) and twice as high as in the white matter in the two specimens where it was measured (effect estimate 0.456 ppm). For both elements, F and Na, the model accounting for differences between the tissues had more support (Table 2).

Variation of the Sr/Ca Ratio in the Lamellar Tissue during Ontogeny

It has been previously shown that the Sr content can also vary within the lamellar tissue in relation to its position within the element, that is, between inner (older) and outer (younger) growth layers (Shirley et al. 2018). Therefore, we tested whether this variation is manifested in the Sr/Ca ratio between growth stages. We assigned each of the 34 microprobe measurements taken within the lamellar tissue to either growth center (older, $N = 9$) or the side of the element (younger, $N = 25$) and compared it against a model accounting only for the differences between specimens (Fig. 5). In one of the

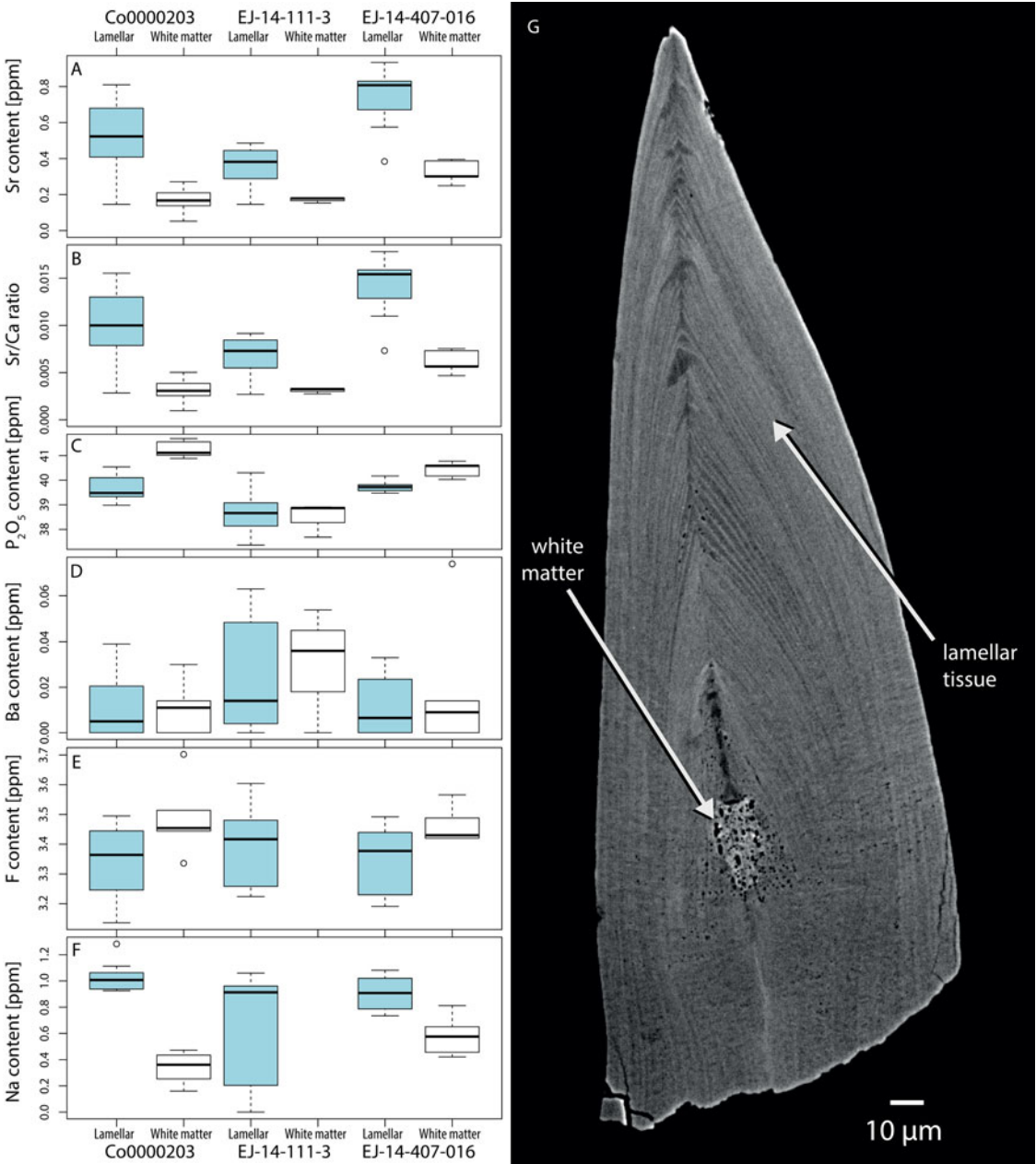


FIGURE 4. Microprobe analysis of white matter and lamellar tissue from three specimens of *Ozarkodina confluens* (A–F) and an elemental contrast image of the specimen EJ-14-407-016 (G).

specimens, EJ-14-111-3, measurements could only be made in the outer part, but not in the center. In spite of strong variation between the specimens, the model accounting for the position within the element as the main driver of Sr/Ca had more support (AIC = −288.07) than the null model accounting for this

variation only (AIC = −284.59, log ratio = 5.5). The effects of the position as estimated in the full model were 0.0079 for the central (ontogenetically older) position and 0.0116 for the marginal (ontogenetically younger) position, indicating a significantly higher Sr/Ca ratio at younger ontogenetic stages.

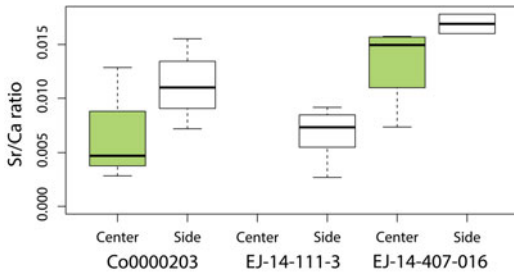


FIGURE 5. Comparison of the Sr/Ca ratios between ontogenetic stages in three specimens: green, young (central part of the element); white, adult (outer part of the element). Specimen no. EJ-14-111-3 was ontogenetically younger than the remaining two; measurements in its center were not successful.

Discussion

When interpreting the ecological significance of Sr/Ca and Ba/Ca ratios preserved in vertebrate tissues of marine organisms, several variables need to be considered. These include the trophic position of the organism (diet), water chemistry (concentrations of dissolved ions), water temperature, salinity, and taxonomic effects. As this study was primarily interested in the trophic structure of the Gotland Silurian conodont community presented here, the other variables identified were considered first, with the relative importance of these variables being detailed in Figure 6. We focused on the variability of Sr/Ca and Ba/Ca between individuals and taxa within individual assemblages, as opposed to cross-site or cross-time differences, which could be driven by changes in seawater temperature or composition. We hypothesized that if individual taxa occupied trophic levels that were different but stable between communities, they would show a consistent order along the Sr/Ca and Ba/Ca axes. Even if absolute values within communities were shifted owing to different background values of temperature or Sr concentration in the seawater, the trophic order shown by the proxy is expected to be preserved. Based on this hypothesis, we first discuss whether observed Sr/Ca and Ba/Ca variability is consistent with trophic diversity, and we then address histological and environmental factors.

Effect of Diet

The final variable considered here is that of trophic positioning. Ba and Sr can both

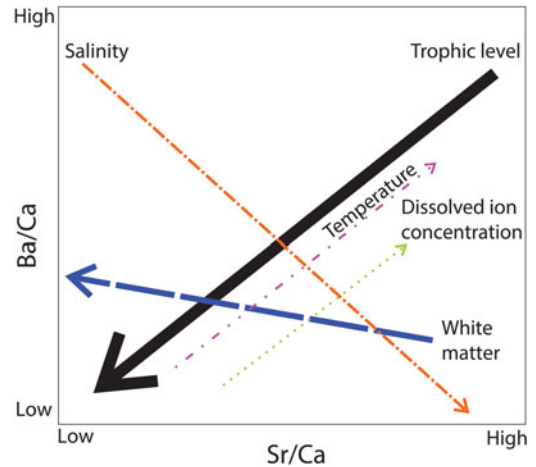


FIGURE 6. Summary of factors affecting Sr/Ca and Ba/Ca ratios compiled from the literature discussed in this study. The arrow direction indicates an increase in the corresponding variable, while the weight represents the relative importance of that variable in our interpretations. The most important variables are trophic level followed by white matter composition, with salinity followed by dissolved ion concentration (Bath et al. 2000; Kraus and Secor 2003) and temperature providing a limited influence on our results.

substitute for Ca in vertebrate tissue due to similarities in their charge and ionic radius (Balter 2004). Both trace elements are, however, selected against during metabolic processes, as described in Balter (2004). As diet is a primary source for Ba and Sr, this results in a decrease in the concentration of both elements at higher trophic levels (Gilbert et al. 1994; Blum et al. 2000; Balter 2004; Peek and Clementz 2012). This produces a noticeable trend in Ba/Ca and Sr/Ca ratios, with vertebrates inhabiting higher trophic positions preserving lower Ba/Ca and Sr/Ca ratios than those in lower trophic positions (Blum 2000; Balter 2004; Peek and Clementz 2012). We see such a trend in our data; the two *Panderodus* species analyzed here have relatively high Ba/Ca and Sr/Ca, suggesting a lower trophic position, while *Wurmiella excavata* and *Oulodus excavatus* have relatively low ratios, suggesting a higher trophic position. *Zieglerodina remscheidensis* and *Ozarkodina bohémica* preserve more intermediate Ba/Ca and Sr/Ca ratios, suggesting a trophic position between *Panderodus* and both *W. excavata* and *Ou. excavatus*. The three remaining taxa in this study fall outside the expected

Ba/Ca to Sr/Ca relationship based on trophic positioning. *Pseudooneotodus beckmanni* preserved very high Ba/Ca and low Sr/Ca ratios, a unique result in this study, suggesting a specialized dietary niche. The final two taxa, *Ozarkodina confluens* and *Ctenognathodus* spp., both have low to moderate Ba/Ca ratios and moderate to high Sr/Ca ratios, with significant variability in Sr/Ca ratios. The variability in these two taxa makes interpreting their trophic position challenging.

To evaluate whether environmental variables, taxon effects (abundance of white matter), or trophic positioning are responsible for the taxonomic signals in Ba/Ca and Sr/Ca ratios obtained here, it is important to consider what is already known about these taxa, including composition, morphology, environmental distribution (Fig. 7), and occlusion patterns. This will allow a general evaluation of the estimated trophic structure, as detailed earlier.

Conodont Distribution.—Basin-scale models of lateral and vertical distribution of conodont taxa can be broadly divided into two groups. The depth-stratification model group assumes that conodonts had a pelagic mode of life and different taxa occupied different levels in the water column (Seddon and Sweet 1971). The lateral segregation models assume a nekto-benthic mode of life, in which different taxa occupied environmental niches tied to the conditions on the seafloor (Barnes and Fåhræus 1975). Lateral biofacies supporting the latter model have been identified in multiple time slices (e.g., Clark 1984), but consistent findings of certain taxa in black shales indicate they were constrained to the upper part of the water column (e.g., Heckel 1991; Dzik 1999). Comparisons with extant biological models (Klapper and Barrick 1978), quantitative analyses of distribution across facies (Zhang and Barnes 2004; Jarochovska et al. 2017), and geochemical comparisons between conodont taxa and between conodont elements and the surrounding strata all highlight that individual taxa followed one type of distribution or the other, resulting in death assemblages that are a mixture of pelagic and nekto-benthic species (Herrmann et al. 2015; Wheelley et al. 2018).

Ozarkodinins.—The majority of the taxa in this study belong to ozarkodinids, the most

diverse group among “complex” (i.e., non-coniform) conodonts (Donoghue et al. 2008). The dental function of their elements has been widely reconstructed from patterns of micro-wear on their surfaces (Purnell 1995; Purnell and Jones 2012) and in histological sections (Donoghue and Purnell 1999; Shirley et al. 2018), from mechanical properties (Jones et al. 2012b), and from clusters preserving occlusion (Martínez-Pérez et al. 2014). For ozarkodinins (represented here by *Ozarkodina*, *Wurmiella*, and *Zieglerodina*), articulated clusters of relatively primitive forms are known (Pollock 1969; Nicoll and Rexroad 1987). These clusters indicate rotational occlusion of the P₁ elements, which has been reconstructed for *W. excavata* (Jones et al. 2012a). This species is distinguished by outstandingly sharp, bladed denticles that bear evidence of in vivo wear. Combined with results of structural modeling of stress distribution during function, these characteristics are interpreted as evidence for processing tough, viscoelastic food (Jones et al. 2012a,b).

Ozarkodina confluens (Fig. 1D) differs from *W. excavata* (Fig. 1H) by having a straight, higher, blunter blade and comparably shorter troughs between denticles. Based on Baltic sections, Viira (1999) suggested a shoal and open-shelf environment for *Oz. confluens* and a more basinward distribution of *W. excavata*, but a quantitative analysis by Barrick (1983) indicated uniform frequencies of *W. excavata* across lithofacies, consistent with a pelagic type of distribution. Both taxa are found up to hypersaline, periodically emerged environments (Viira and Einasto 2003; Jarochovska et al. 2017).

The relatively high amounts of white matter in *Oz. confluens* and *W. excavata* should be expected to result in low Sr/Ca ratios in both taxa. We see this in *W. excavata*, which also has low Ba/Ca ratios. In the case of *Oz. confluens*, we see substantially more intraspecific variability in Sr/Ca ratios and much higher values despite the high concentrations of white matter. This may be the result of more variation in white matter concentrations between individuals. These two species likely lived in the same environments, but differed in their trophic niches, with functional

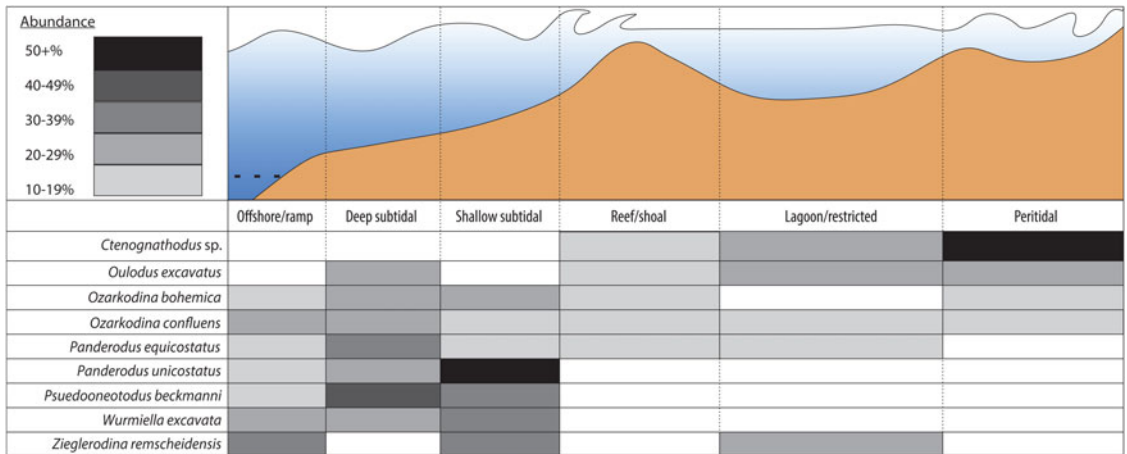


FIGURE 7. Environmental distribution of conodont taxa in this study. Distributions are based on data obtained from the Paleobiology Database (methods are described in Terrill et al. 2022). Due to a lack of entries, *Ctenognathodus* was examined as a genus for the purposes of this figure. The distribution of *Zieglerodina remscheidensis* is incomplete due to a lack of sufficient data. This is the result of taxonomic classification issues that are still ongoing.

morphology and chemical composition reported here suggesting *W. excavata* feeding on a higher trophic level.

Other ozarkodinins examined here, *Oz. bohemia* (Fig. 1B,C) and *Z. remscheidensis* (Fig. 1A), are zonal taxa with much shorter stratigraphic ranges and could not be investigated in as many assemblages as the previous two. The synonymy of *Z. remscheidensis* has been revised multiple times (Jarochovska et al. 2021), making it very difficult to analyze reports on its distribution. A quantitative analysis by Jarochovska et al. (2017) indicated a pelagic type of distribution for *Oz. bohemia*. *Zieglerodina remscheidensis* has shorter, more compact denticles than *W. excavata* and less white matter than *Oz. bohemia* or *Oz. confluens*. These two taxa hold similar positions relative to other taxa in Ba/Ca and Sr/Ca ratios, but do not co-occur in any assemblages in this study. It is possible they may have filled similar ecological niches and intermediate trophic positions.

Prioniodinins.—Functional morphology and ecology of prioniodinin species studied here, *Ctenognathodus* sp. (Fig. 1E) and *Ou. excavatus* (Fig. 1F), is less understood. *Ctenognathodus* is considered a shallow-water specialist (Strömberg 1997; Viira and Einasto 2003; Jarochovska et al. 2017). This preference for shallow-water habitats may also include hypersaline environments. This may be partly responsible for the

high variability in the Sr/Ca ratios, corresponding with relatively low Ba/Ca ratios. Not enough reports of this large and relatively rare genus are available to afford a quantitative analysis, but it shares many traits with *Oz. confluens*: thick P₁ elements with long, compact denticles, a very high proportion of white matter, and a miniature basal cavity (for anatomical notation, see Supplementary Fig. 2 and Purnell et al. [2000]). As with *Oz. confluens*, variability in the high concentrations of white matter may also serve to increase the variability seen in the Sr/Ca ratios, further obscuring the trophic signal. Typical S elements and, in certain species, P elements have peg-like denticles, rounded in cross-section (for anatomical notation, see Purnell et al. 2000). Such morphology indicates a very distinct type of occlusion from that performed by the sharp blades of *W. excavata*, which may be consistent with a lower (less predatory) trophic position.

Peg-like, thick, long, and clearly separated denticles formed entirely by white matter are characteristic of all elements in the large species *Ou. excavatus*, for which no clusters and no reconstructions of occlusion currently exist. In Upper Ordovician and lower Silurian strata, various species of *Oulodus* are characteristic of shallow-water biofacies (Nowlan and Barnes 1981; Watkins and Kuglitsch 1997; Jing et al. 2017). *Oulodus excavatus* retains very low Ba/

Ca and Sr/Ca ratios, overlapping with *W. excavata*, suggesting a similar combination of trophic position and white matter concentrations are responsible for the observed chemical data. Given the relatively small environmental overlap between *W. excavata* and *Ou. excavatus*, it is possible the two taxa filled similar trophic positions without directly competing with each other.

Panderodus.—Among taxa examined here, the coniform genus *Panderodus* (Fig. 1I) consistently had the highest Sr/Ca ratios, which would correspond to the lowest position in the trophic chain. This genus has been regarded as pelagic, even in the nekto-benthic model (Barnes and Fåhræus 1975). Although its apparatus is nearly homodont compared with “complex” conodonts, mechanical properties compatible with dental tools that were used to restrain prey and then cut it have been identified by Murdock et al. (2013) and elaborated upon in the occlusal model by Murdock and Smith (2021). The model included grasping, piercing, and cutting elements. *Panderodus* is also proposed to have been venomous based on the presence of a lateral groove on its elements (Szaniawski 2009). In contrast to these interpretations based on morphology, histological sections have not revealed wear or damage (Leonhard et al. 2021), characteristic for “complex” conodonts and indicative of processing hard food (Donoghue and Purnell 1999; Martínez-Pérez et al. 2014; Shirley et al. 2018). These characteristics suggest that *Panderodus* had a distinct trophic niche and did not consume food requiring shearing, crushing, or grinding, so it might have been limited to soft-bodied or very small prey.

Pseudooneotodus.—*Pseudooneotodus* (Fig. 1G) is possibly the least understood conodont genus, with squat conical elements and trimembrate apparatuses proposed for two of its species (Barrick 1977; Armstrong 1990). It has been assigned to conodonts based on histology (Sansom 1996). *Pseudooneotodus beckmanni* is a long-ranging species (Sheinwoodian to Emsian; Corradini 2007). Armstrong and Owen (2002) placed the genus in Upper Ordovician shelf (as opposed to oceanic) facies, whereas Barrick et al. (2010) reported dominance of this genus in offshore, argillaceous strata; therefore, the

environmental niche remains unknown. As only a small number of *Ps. beckmanni* elements were analyzed, it is difficult to interpret the trophic position of this taxon. However, given the very high Ba concentrations observed, we suggest it may have preyed upon Ba-rich food sources, as Ba transfer from the diet to enamel is well documented (e.g., Healy and Ludwig 1968; Austin et al. 2013). There is some evidence that diet affects Ba/Ca ratios in modern fish bone, although few studies have examined this question (Balter and Lécuyer 2010). It has previously been shown that Sr and Ba can bioaccumulate near the base of marine food webs, which could then be reflected at higher trophic levels (Peek and Clementz 2012). Some modern planktic foraminifera such as *Globorotalia* have been observed to significantly concentrate Ba in their tests, with Ba/Ca ratios nearly 10 times those of other foraminiferal taxa (Lea and Boyle 1991) while maintaining Sr/Ca ratios that are largely comparable to those of other taxa (Anand and Elderfield 2005). It should be noted, however, that planktic foraminifera did not exist in the Paleozoic, so another Ba-rich food source would need to be identified.

Histology

We compare our observations with vertebrate enamel, structurally similar to conodont lamellar tissue. Vertebrate bone and dentine, although mineralized with apatite, are structurally and developmentally very distinct from conodont crown tissues and, thus, not discussed here. Variability in Sr and Ba concentrations, as well as in the Sr/Ca ratio, along crown enamel is known from terrestrial vertebrates. It has been attributed to two factors: dust intake driven by seasonality or other climatic variability (e.g., Kohn et al. 2013; De Winter et al. 2016; Tacail et al. 2017) or changes in elemental composition along the tooth related to enamel maturation (e.g., Montgomery et al. 2010) and weaning in mammals (Tacail et al. 2017). The former factor is difficult to account for without knowing the life span of a conodont individual (see Dzik [2008] and Leonhard et al. [2021] for speculations on this topic), but marine organisms in tropical environments are less likely to record strong seasonal variations than those from terrestrial, temperate settings. Nothing is

known of a process akin to enamel maturation in conodonts, but multiple studies point to them maintaining their teeth throughout the entire life span (e.g., Müller and Nogami 1971; Donoghue and Purnell 1999; Shirley et al. 2018).

The most important aspect distinguishing the growth and histology of examined conodont taxa is the abundance of white matter. Compositional differences between white matter and lamellar tissue could therefore have a very significant impact on the preserved Sr/Ca and Ba/Ca ratios. From our microprobe analysis of *Oz. confluens*, we observed substantially lower Sr concentrations and slightly higher Ba concentrations in white matter than in lamellar tissue. As previously discussed, *Ctenognathodus* and *Oz. confluens* both contain a very high amount of white matter in the denticles of their oral elements; however, the proportion of white matter is somewhat variable. It is likely that this is responsible for the high variability seen in these two taxa, particularly in the preserved Sr/Ca ratios.

Effects of Seawater Composition

Within a single assemblage, it is possible that individual conodonts may have traversed different environments during life. However, geographic variations in the availability of dissolved ions are unlikely to be a significant factor in this study, given the proximity of all studied environments within a single carbonate platform. Past studies have shown Sr/Ca ratios to vary by up to 3% in modern oceanic waters (De Villiers 1999), while a more recent work suggests this variability could be greater than 30% (Lebrato et al. 2020). However, this variability is global and is minimized in this study through the analysis of local communities. Dissolved Ba does not significantly change in concentration in near-surface waters (water depths less than 100 m) that lack a significant freshwater input (Cao et al. 2016; Bates et al. 2017), which suggests a minimal impact on our data, considering the relatively shallow-water environments in this study. One possible exception to this would be if a conodont species were to exhibit anadromous behavior, splitting the life cycle between freshwater and marine environments. Recent work has suggested that modern cyclostomes (lampreys and

hagfish) are the closest living relatives to conodonts (Terrill et al. 2018; Miyashita et al. 2019, 2021). As modern lampreys are largely anadromous (Kelly and King 2001), we explored this possibility using Sr isotope ratios in *Oz. confluens*, one of the taxa with the greatest observed variability in Sr/Ca ratios in this study. If *Oz. confluens* was spawning in freshwater, this would be reflected in the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio, with smaller (ontogenetically younger) individuals having higher (freshwater) values than large adult individuals. The observed variability in the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio is very small with no discernible pattern with regard to individual size (Fig. 3). This observation coupled with a close adherence to expected marine values from the Silurian of Gotland (Terrill et al. 2022: SI fig. 1) strongly supports a purely marine habitat for *Oz. confluens*, effectively ruling out the possibility of anadromous behavior and the associated geographic variation in dissolved ions being responsible for the observed variations in Sr/Ca and Ba/Ca in this taxon. As other taxa in this study do not show the same variability in Sr/Ca as *Oz. confluens*, it is unlikely any of them had an anadromous life cycle.

Effects of Ambient Temperature

Water temperature was also a variable to consider, as experimental studies have shown significant impacts on Sr/Ca and Ba/Ca ratios in fish otoliths (Eldson and Gillanders 2002; Martin et al. 2004; Nelson et al. 2018), as well as bone and enamel apatite (Balter and Lécuyer 2010; Balter et al. 2011), with a positive correlation between temperature and both ratios in water warmer than 15°C. During the Silurian, Gotland was located in the tropics, with oxygen isotopes suggesting surface-water temperatures comparable to (or slightly warmer than) modern tropical seas (24°C–40°C; Wenzel et al. 2000; Cummins et al. 2014). Water temperature also does not typically vary more than 2°C–4°C with depths less than about 100 m in modern tropical environments (Rebert et al. 1985; Venancio et al. 2018), and it is probable this relationship would have been similar in the Silurian. As none of the assemblages in this study come from deep-water facies, water temperature is unlikely to have varied

significantly between different taxa preserved in a single rock sample. Furthermore, the epeiric nature of the Silurian Gotland sea (Baarli et al. 2003) would limit ocean depths and minimize the likelihood of a significant thermocline. As we do not directly compare absolute values between geologic samples, temperature changes over geologic time are not a factor in our analysis.

Effect of Salinity

The final environmental variable to consider is salinity. Salinity has been shown to correlate positively with Sr/Ca ratios while correlating negatively with Ba/Ca ratios in fish otoliths (Eldson and Gillanders 2002; Martin et al. 2004; Macdonald and Crook 2010; Nelson et al. 2018). This effect is particularly pronounced at lower salinities under 10 psu (practical salinity unit) (Macdonald and Crook 2010; Nelson et al. 2018), which is considerably lower than typical modern marine environments, which average approximately 35 psu. Salinity therefore has a significant impact on Sr/Ca and Ba/Ca ratios in vertebrates inhabiting estuaries and coastal marshes (Martin and Thorrold 2005; Macdonald and Crook 2010; Nelson et al. 2018) but is significantly less impactful at the higher salinities found in open-marine environments. Unfortunately no studies on the effect of salinity on Sr/Ca and Ba/Ca ratios in vertebrate skeletal tissues are available to date.

Based on the environmental distribution of taxa in this study and Sr isotope ratios in *Oz. confuens*, all conodonts examined here lived exclusively in marine environments. It is unlikely that changes in salinity would explain differences in Sr/Ca and Ba/Ca ratios between taxa. The only possible exception is *Ctenognathodus*, a taxon that is often associated with hypersaline environments (Strömberg 1997; Jarochowska et al. 2017). While it is possible that the preference of *Ctenognathodus* for hypersaline environments may contribute somewhat to its high Sr/Ca and low Ba/Ca ratios, it is unlikely to be a dominant factor, due to the decreasing impact of salinity above 10 psu (Macdonald and Crook 2010; Nelson et al. 2018).

Diagenesis

Conodonts are famously resistant to diagenesis in conditions presented by marine

sediment and shallow burial, represented by conodonts studied here (Trotter and Eggins 2006). This stability applies particularly to trace elements incorporated in the hydroxyapatite crystal lattice, whereas rare earth elements, Th and U—not of interest here—are subject to postmortem uptake. Among known bioapatites in which elemental systematics have been investigated in marine diagenetic environments, conodont crown tissues are the least prone to exchange of Sr and Ca (Holmden et al. 1996). Sr isotope values can be used to screen for diagenetic Sr uptake, and in this study, the values (Fig. 3, Supplementary Fig. 1) indicated no detectable deviation from ambient seawater. Furthermore, we employed cleaning, which has been shown to remove almost all diagenetically incorporated Sr (Hoppe et al. 2003). We did observe an increase of Sr/Ca between internal layers of the lamellar tissue and the outermost ones; this was noted previously by Trotter and Eggins (2006) and Shirley et al. (2018), as well as by Holmden et al. (1996), who attributed it to diagenesis. In contrast, higher-resolution studies in coniform conodonts by Leonhard et al. (2021) showed no detectable change throughout the crown tissue, interpreted to reflect homogeneous diet and environmental conditions. It is not known whether Sr/Ca variability within conodont crowns is primarily due to diagenesis or to in vivo factors such as diet or migration. The Ca/P proxy used to assess the preservation state of bioapatite marks conodonts as the least altered (Holmden et al. 1996; Hoppe et al. 2003). Even if some diagenetically enriched Sr contributed to our results, the burial conditions were the same for all elements within any given assemblage, making the relative Sr/Ca ratios comparable between elements, even if absolute values were shifted. This interpretation could be questioned in the future if major differences in the diagenetic susceptibility between taxa can be detected, for example, owing to their different surface-to-volume ratios.

Comparison with Other Studies

In recent years, there have been a few attempts to study the trophic position of conodonts using geochemical methods such as carbon isotopes (Zhuravlev and Smoleva 2018;

Zhuravlev 2020; Zhuravlev et al. 2020) and Ca isotopes (Balter et al. 2019), all of which focused on Devonian or Mississippian conodont genera such as *Polygnathus*, *Hindeodus*, *Icriodus*, and *Palmatolepis*. These studies have concluded that conodonts were likely low-level or first-order consumers, feeding largely on zooplankton, but were unable to meaningfully distinguish trophic differences between different conodont taxa. The results of this study strongly suggest different trophic positions for different taxa, which accounts for the wide variety of morphologies within a sampled conodont community. These results are particularly compelling, considering the epeiric nature of the Silurian Gotland sea greatly limits environmental variations that otherwise may have impacted observed Sr/Ca and Ba/Ca ratios, as different conodont taxa have clearly been shown to occupy the water column at depths above and below the thermocline in other regions based on variations in oxygen isotope ratios in conodont elements (Herrmann et al. 2015; Wheeley et al. 2018).

There remain many unanswered questions regarding conodont trophic positions and ecological function, but this study provides a model that can be expanded upon to further study these questions. More conodont communities in different geologic settings could be analyzed to assess the validity of studying conodont trophic structure beyond coastal environments in an epeiric sea using Sr/Ca and Ba/Ca ratios. Conodont elements also become more complex later in the Paleozoic, with many developing platforms that have been compared to mammalian molars in their morphological complexity (Donoghue and Purnell 1999). Determining the impact these more complex elements had on conodont trophic structure may help to elucidate how conodonts managed to remain a significant taxonomic group in marine environments throughout most of the Paleozoic and Triassic. More study should also be given to the compositional variations between different tissue types within conodont elements, given the wide use of conodonts in geochemical studies.

This study represents one of only a few to study the trophic structure of a marine community of vertebrates using Sr/Ca and Ba/Ca

ratios preserved in vertebrate tissues in either a paleontological or modern context. Further examination of the impact of trophic positioning on the Sr/Ca and Ba/Ca ratios preserved in the bioapatite of modern marine vertebrates is needed to further confirm the results of this study.

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Data Availability Statement

Results of ICP-MS and microprobe measurements as well as the R code used for analyses are available as an electronic archive under <https://doi.org/10.17605/OSF.IO/NCZB6>.

Literature Cited

- Aldridge, R. J., D. E. G. Briggs, M. P. Smith, E. N. K. Clarkson, and N. D. L. Clark. 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London B* 340:405–421.
- Anand, P., and H. Elderfield. 2005. Variability of Mg/Ca and Sr/Ca between and within planktonic foraminifers *Globigerina bulloides* and *Globorotalia truncatulinoides*. *Geochemistry, Geophysics, Geosystems* 6:1–15.
- Armstrong, H. A. 1990. Conodonts from the Upper Ordovician–lower Silurian carbonate platform of North Greenland. *Grønlands Geologiske Undersøgelse* 159:1–151.
- Armstrong, H. A., and A. W. Owen. 2002. Euconodont diversity changes in a cooling and closing Iapetus Ocean. In J. A. Crame and A. W. Owen, eds. *Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic–Cenozoic radiations*. Geological Society of London Special Publication 194:85–98.
- Armstrong, H. A., and C. J. Smith. 2001. Growth patterns in euconodont crown enamel: implications for life history and mode-of-life reconstruction in the earliest vertebrates. *Proceedings of the Royal Society of London B* 268:815–820.
- Armstrong, H. A., D. G. Pearson, and M. Griselin. 2001. Thermal effects on rare earth element and strontium isotope geochemistry in single conodont elements. *Geochimica et Cosmochimica Acta* 65:435–441.
- Atakul-Özdemir, A., X. Warren, P. G. Martin, M. Guizar-Sicairos, M. Holler, F. Marone, C. Martínez-Pérez, and P. C. J. Donoghue. 2021. X-ray nanotomography and electron backscatter diffraction demonstrate the crystalline, heterogeneous and impermeable nature of conodont white matter. *Royal Society Open Science* 8:202013.

- Austin, C., T. M. Smith, A. Bradman, K. Hinde, R. Joannes-Boyau, D. Bishop, D. J. Hare, P. Doble, B. Eskenazi, and M. Arora. 2013. Barium distributions in teeth reveal early-life dietary transitions in primates. *Nature* 498:216–219.
- Baarli, B. G., M. E. Johnson, and A. I. Antoshkina. 2003. Silurian stratigraphy and palaeogeography of Baltica. Geological Society of Australia Abstracts 61:146–146.
- Balter, V. 2004. Allometric constraints on Sr/Ca and Ba/Ca partitioning in terrestrial mammalian trophic chains. *Ecosystem Ecology* 139:83–88.
- Balter, V., and C. Lécuyer. 2010. Determination of Sr and Ba partition coefficients between apatite from fish (*Sparus aurata*) and seawater: the influence of temperature. *Geochemica et Cosmochemica Acta* 74:3449–3458.
- Balter, V., C. Lécuyer, and J.-A. Barrat. 2011. Reconstructing seawater Sr/Ca during the last 70 My using fossil fish tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310:133–138.
- Balter, V., J. E. Martin, T. Tacail, G. Suan, S. Renaud, and C. Girard. 2019. Calcium stable isotopes place Devonian conodonts as first level consumers. *Geochemical Perspectives Letters* 10:36–39.
- Barham, M., M. M. Joachimski, J. Murray, and D. M. Williams. 2012. Diagenetic alteration of the structure and $\delta^{18}\text{O}$ signature of Palaeozoic fish and conodont apatite: potential use for corrected isotope signatures in palaeoenvironmental interpretation. *Chemical Geology* 298–299:11–19.
- Barnes, C. R., ed. 1976. Conodont paleoecology. Geological Association of Canada Special Paper 15.
- Barnes, C. R., and L. E. Fähræus. 1975. Provinces, communities, and the proposed nektonic habit of Ordovician conodontophorids. *Lethaia* 8:133–149.
- Barrick, J. E. 1977. Multielement simple cone conodonts from the Clarita Formation (Silurian), Arbuckle Mountains, Oklahoma. *Geologica et Palaeontologica* 11:47–68.
- Barrick, J. E. 1983. Wenlockian (Silurian) conodont biostratigraphy, biofacies, and carbonate lithofacies, Wayne Formation, central Tennessee. *Journal of Paleontology* 57:208–239.
- Barrick, J. E., M. A. Kleffner, M. A. Gibson, F. N. Peavey, and H. R. Karlsson. 2010. The mid-Ludfordian Lau event and carbon isotope excursion (Ludlow, Silurian) in the southern Laurentia—preliminary results. *Bollettino della Società Paleontologica Italiana* 49:13–33.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bates, S. L., K. R. Hendry, H. V. Pryer, C. W. Kinsley, K. M. Pyle, E. M. S. Woodward, and T. J. Horner. 2017. Barium isotopes reveal role of ocean circulation on barium cycling in the Atlantic. *Geochemica et Cosmochemica Acta* 204:286–299.
- Bath, E. B., S. R. Thorrold, C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. *Geochemica et Cosmochemica Acta* 64:1705–1714.
- Bertam, C. J., H. Elderfield, R. J. Aldridge, and S. Conway-Morris. 1992. $^{87}\text{Sr}/^{86}\text{Sr}$, $^{143}\text{Nd}/^{144}\text{Nd}$ and REEs in Silurian phosphatic fossils. *Earth and Planetary Science Letters* 113:239–249.
- Blick, A., S. Turner, C. J. Burrow, H. Schultz, C. B. Rexroad, P. Bultynck, and G. S. Nowlan. 2010. Fossils, histology, and phylogeny: why conodonts are not vertebrates. *Episodes* 33:234–241.
- Blum, J. D., E. H. Taliaferro, M. T. Weisse, and R. T. Holmes. 2000. Changes in Sr/Ca, Ba/Ca and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between trophic levels in two forest ecosystems in the Northeastern USA. *Biogeochemistry* 49:87–101.
- Bremer, O., E. Jarochowska, and T. Märss. 2020. Vertebrate remains and conodonts in the upper Silurian Hamra and Sundre formations of Gotland, Sweden. *GFF* 142:1–29.
- Burton, J. H., D. Price, and W. D. Middleton. 1999. Correlation of Bone Ba/Ca and Sr/Ca due to Biological Purification of Calcium. *Journal of Archaeological Science* 26:609–616.
- Calner, M., L. Jeppsson, and A. Munnecke. 2004. The Silurian of Gotland—Part I: Review of the stratigraphic framework, event stratigraphy, and stable carbon and oxygen isotope development. *Erlanger geologische Abhandlungen, Sonderband* 5:113–131.
- Cao, Z., C. Siebert, E. C. Hathorne, M. Dai, and M. Frank. 2016. Constraining the oceanic barium cycle with stable barium isotopes. *Earth and Planetary Science Letters* 434:1–9.
- Clark, D. L. 1974. Factors of Early Permian conodont paleoecology in Nevada. *Journal of Paleontology* 48:710–720.
- Clark, D. L., ed. 1984. Conodont biofacies and provincialism. Geological Society of America Special Paper 196.
- Corradini, C. 2007. The conodont genus *Pseudoonoteodus* Drygant from the Silurian and Lower Devonian of Sardinia and the Carnic Alps (Italy). *Bollettino della Società Paleontologica Italiana* 46:139–148.
- Cummins, R. C., S. Finnegan, D. A. Fike, J. M. Eiler, and W. W. Fischer. 2014. Carbonate clumped isotope constraints on Silurian ocean temperature and sea water $\delta^{18}\text{O}$. *Geochemica et Cosmochemica Acta* 140:241–258.
- De Villiers, S. 1999. Seawater strontium and Sr/Ca variability in the Atlantic and Pacific oceans. *Earth and Planetary Science Letters* 171:623–634.
- de Winter, N. J., C. Snoeck, and P. Claeys. 2016. Seasonal cyclicity in trace elements and stable isotopes of modern horse enamel. *PLoS ONE* 11:e0166678.
- Diener, A., S. Ebneth, J. Veizer, and D. Buhl. 1996. Strontium isotope stratigraphy of the Middle Devonian: brachiopods and conodonts. *Geochemica et Cosmochemica Acta* 60:639–652.
- Diouf, K., J. Panfili, M. Labonne, C. Aliaume, J. Tomás, and T. D. Chi. 2006. Effect of salinity on strontium:calcium ratios in the otoliths of the West African black-chinned tilapia *Sarotherodon melanotheron* in a hypersaline estuary. *Environmental Biology of Fish* 77:9–20.
- Donoghue, P. C. J. 1998. Growth and patterning in the conodont skeleton. *Philosophical Transactions of the Royal Society of London B* 353:633–666.
- Donoghue, P. C. J. 2001. Microstructural variation in conodont enamel is a functional adaptation. *Proceedings of the Royal Society of London B* 268:1691–1698.
- Donoghue, P. C. J., and M. A. Purnell. 1999. Growth, function, and the conodont fossil record. *Geology* 27:251–254.
- Donoghue, P. C. J., and M. Rücklin. 2016. The ins and outs of the evolutionary origin of teeth. *Evolution and Development* 18:19–30.
- Donoghue, P. C. J., P. L. Forey, and R. J. Aldridge. 2000. Conodont affinity and chordate phylogeny. *Biological Reviews of the Cambridge Philosophical Society* 75:191–251.
- Donoghue, P. C. J., M. A. Purnell, R. J. Aldridge, and S. Zhang. 2008. The interrelationships of “complex” conodonts (Vertebrata). *Journal of Systematic Palaeontology* 6:119–153.
- Dzik, J. 1999. Relationship between rates of speciation and phyletic evolution: stratophenetic data on pelagic conodont chordates and benthic ostracods. *Geobios* 32:205–221.
- Dzik, J. 2008. Evolution of morphogenesis in 360-million-year-old conodonts calibrated in days. *Evolution and Development* 10:769–777.
- Eldson, T. S., and B. M. Gillanders. 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. *Canadian Journal of Fish and Aquatic Sciences* 59:1796–1808.
- Foote, M., and J. J. Sepkoski. 1999. Absolute measures of the completeness of the fossil record. *Nature* 398:415–417.
- Gilbert, C., J. Sealy, and A. Sillen. 1994. An investigation of barium, calcium and strontium as palaeodietary indicators in the

- Southwestern Cape, South Africa. *Journal of Archaeological Science* 21:173–184.
- Genot, S., and N. Goudemand. 2019. Conodont size, trophic level, and the evolution of the platform elements. *Paleobiology* 45:458–468.
- Goudemand N., M. J. Orchard, S. Urdy, H. Bucher, and P. Tafforeau. 2011. Synchrotron-aided reconstruction of the conodont feeding apparatus and implications for the mouth of the first vertebrates. *Proceedings of the National Academy of Sciences USA* 108:8720–8724.
- Healy, W. B., and T. G. Ludwig. 1968. Barium content of teeth, bone and kidney of twin sheep raised on pastures of differing barium content. *Archives of oral Biology* 13:559–563.
- Heckel, P. H. 1991. Thin widespread Pennsylvanian black shales of Midcontinent North America: a record of a cyclic succession of widespread pycnoclines in a fluctuating epeiric sea. *Geological Society of London Special Publication* 58:259–273.
- Herrmann, A. D., J. E. Barrick, and T. J. Algeo. 2015. The relationship of conodont biofacies to spatially variable water mass properties in the Late Pennsylvanian Midcontinent Sea. *Paleoceanography* 30:269–283.
- Holmden, C., R. A. Creaser, K. Muehlenbachs, S. M. Bergstrom, and S. A. Leslie. 1996. Isotopic and elemental systematics of Sr and Nd in 454 Ma biogenic apatites: implications for paleoseawater studies. *Earth and Planetary Science Letters* 142:425–437.
- Hoppe, K. A., P. L. Koch, and T. T. Furutani. 2003. Assessing the preservation of biogenic strontium in fossil bones and tooth enamel. *International Journal of Osteoarchaeology* 13:20–28.
- House, M. R., V. V. Menner, R. T. Becker, G. Klapper, N. S. Ovnatanova, and V. Kuz'min. 2000. Reef episodes, anoxia and sea-level changes in the Frasnian of the southern Timan (NE Russian platform). *Geological Society of London Special Publication* 178:147–176.
- Jarochowska, E., O. Bremer, D. Heidlas, S. Pröpper, T. R. Vandenbroucke, and A. Munnecke. 2016. End-Wenlock terminal Mulde carbon isotope excursion in Gotland, Sweden: integration of stratigraphy and taphonomy for correlations across restricted facies and specialized faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 457:304–322.
- Jarochowska, E., V. Viira, R. Einasto, R. Nawrot, O. Bremer, P. Männik, and A. Munnecke. 2017. Conodonts in Silurian hypersaline environments: specialized and unexpectedly diverse. *Geology* 45:3–6.
- Jarochowska E., O. Bremer, A. Yiu, T. Märss, H. Blom, T. Mörs, and V. Vajda. 2021. Revision of vertebrates, conodonts, and the depositional environments in the Burgen outlier (Ludlow, Silurian) of Gotland, Sweden. *GFF* 143:168–189.
- Jeppsson, L., R. Anehus, and D. Fredholm. 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. *Journal of Paleontology* 73:964–972.
- Jeppsson, L., M. E. Eriksson, and M. Calner. 2006. A latest Llandovery to latest Ludlow high-resolution biostratigraphy based on the Silurian of Gotland—a summary. *GFF* 128:109–114.
- Ji, Z., and C. Barnes. 1994. Conodont paleoecology of the Lower Ordovician St George Group, Port au Port Peninsula, western Newfoundland. *Journal of Paleontology* 68:1368–1383.
- Jing, X., S. Stouge, L. Ding, X. Wang, and H. Zhou. 2017. Upper Ordovician conodont biostratigraphy and biofacies from the Sigang section, Neixiang, Henan, central China. *Palaeogeography, Paleoclimatology, Palaeoecology* 480:18–32.
- Jones, D., A. R. Evans, E. J. Rayfield, K. K. W. Siu, and P. C. J. Donoghue. 2012a. Testing microstructural adaptation in the earliest dental tools. *Biology Letters* 8:952–955.
- Jones, D., A. R. Evans, K. K. W. Siu, E. J. Rayfield, and P. C. J. Donoghue. 2012b. The sharpest tool in the box? Quantitative analysis of conodont elemental functional morphology. *Proceedings of the Royal Society of London B* 279:2849–2854.
- Kelly, F. L., and J. J. King. 2001. A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (L.), *Lampetra planeri* (Bloch) and *Petromyzon marinus* (L.): a context for conservation and biodiversity considerations in Ireland. *Biology and Environment Proceedings of the Royal Irish Academy* 101B:165–185.
- Kelz, V. S., P. Guenser, M. Mazza, M. Rigo, and E. Jarochowska. 2021. Growth allometry and dental topography in Upper Triassic conodonts supports trophic differentiation and molar-like element function. *bioRxiv*. doi: 10.1101/2021.06.10.447946.
- Klapper, G., and J. E. Barrick. 1978. Conodont ecology: pelagic versus benthic. *Lethaia* 11:15–23.
- Klug, C., B. Kröger, W. Kiessling, G. L. Mullins, T. Servais, J. Frýda, D. Korn, and S. Turner. 2010. The Devonian nekton revolution. *Lethaia* 43:465–477.
- Kohn, M. J., J. Morris, and P. Olin. 2013. Trace element concentrations in teeth—a modern Idaho baseline with implications for archeometry, forensics, and palaeontology. *Journal of Archaeological Science* 40:1689–1699.
- Kraus, R. T., and D. H. Secor. 2003. Incorporation of strontium into otoliths of an estuarine fish. *Journal of Experimental Marine Biology and Ecology* 302:85–106.
- Kurschner, W., R. T. Becker, D. Buhl, and J. Veizer. 1992. Strontium isotopes in conodonts: Devonian–Carboniferous Transition, the Northern Rhenish Slate Mountains, Germany. *Annales de la Société géologique de Belgique* 115:595–621.
- Lea, D. W., and E. A. Boyle. 1991. Barium in planktonic foraminifera. *Geochemica et Cosmochemica Acta* 55:3321–3331.
- Lebrato, M., D. Garbe-Schönberg, M. N. Müller, S. Blanco-Ameijeiras, R. A. Feely, L. Lorenzoni, J. Molinero, K. Bremer, D. O. B. Jones, D. Iglesias-Rodríguez, D. Greeley, M. D. Lamare, A. Paulmier, M. Graco, J. Cartes, J. Barcelos e Ramos, A. de Lara, R. Sanchez-Leal, P. Jimenez, F. E. Paparazzo, S. E. Hartman, U. Westernströmer, M. Küter, R. Benavides, A. F. da Silva, S. Bell, C. Payne, S. Olafsdottir, K. Robinson, L. M. Jantunen, A. Korablev, R. J. Webster, E. M. Jones, O. Gilg, P. B. du Bois, J. Beldowski, C. Ashjian, N. D. Yahia, B. Twining, X. Chen, L. Tseng, J. Hwang, H. Dahms, and A. Oschiles. 2020. Global variability in seawater Mg:Ca and Sr:Ca ratios in the modern ocean. *Proceedings of the National Academy of Sciences USA* 117:22281–22292.
- Leonhard, I., B. Shirley, D. J. Murdock, J. Repetski, and E. Jarochowska. 2021. Growth and feeding ecology of coniform conodonts. *PeerJ* 9:e12505.
- Macdonald, J. I., and D. A. Crook. 2010. Variability in Sr:Ca and Ba:Ca ratios in water and fish otoliths across an estuarine salinity gradient. *Marine Ecology Progress Series* 413:147–161.
- Martin, G. B., and S. R. Thorrold. 2005. Temperature and salinity effects on magnesium, manganese, and barium incorporation in otoliths of larval and early juvenile spot *Leiostomus xanthurus*. *Marine Ecology Progress Series* 293:223–232.
- Martin, G. B., S. R. Thorrold, and C. M. Jones. 2004. Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). *Canadian Journal of Fish Aquatic Science* 61:34–42.
- Martínez-Pérez, C., E. J. Rayfield, M. A. Purnell, and P. C. J. Donoghue. 2014. Finite element, occlusal, microwear and microstructural analyses indicate that conodont microstructure is adapted to dental function. *Palaeontology* 57:1059–1066.
- McArthur, J. M., R. J. Howarth, G. A. Shields, and Y. Zhou. 2020. Strontium isotope stratigraphy. Pp. 211–232 in F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg, eds. *Geologic time scale 2020*, 1st ed., Vol. 1. Elsevier, Amsterdam.
- Miyashita, T., M. I. Coates, R. Farrar, P. Larson, P. L. Manning, R. A. Wogelius, N. P. Edwards, J. Anné, U. Bergmann, A. R. Palmer, and P. J. Currie. 2019. Hagfish from the Cretaceous Tethys Sea and a reconciliation of the morphological-molecular

- conflict in early vertebrate phylogeny. *Proceedings of the National Academy of Sciences USA* 166:2146–2151.
- Miyashita, T., R. W. Gess, K. Tietjen, and M. I. Coates. 2021. Non-ammonocoete larvae of Palaeozoic stem lampreys. *Nature* 591:408–412.
- Montgomery, J., J. A. Evans, and M. S. A. Horstwood. 2010. Evidence for long-term averaging of strontium in bovine enamel using TIMS and LA-MC-ICP-MS strontium isotope intra-molar profiles. *Environmental Archaeology* 15:32–42.
- Müller, K. J., and Y. Nogami. 1971. Über den Feinbau der Conodonten. *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy* 38:1–87.
- Murdock, D. J. E., and M. P. Smith. 2021. *Panderodus* from Waukesha Lagerstätte of Wisconsin, USA: a primitive macrophagous vertebrate predator. *Papers in Palaeontology* 7:1977–1993.
- Murdock, D. J. E., X. Dong, J. E. Repetski, F. Marone, M. Starnpanoni, and P. C. J. Donoghue. 2013. The origin of conodonts and of vertebrate mineralized skeletons. *Nature* 502:546–549.
- Nelson, T. R., D. R. DeVries, and R. A. Wright. 2018. Salinity and temperature effects on element incorporation of Gulf Killifish *Fundulus grandis* otoliths. *Estuaries and Coasts* 41:1164–1177.
- Nicoll, R. S., and C. B. Rexroad. 1987. Re-examination of Silurian conodont clusters from northern Indiana. Pp. 49–62 in R. J. Aldridge, ed. *Paleobiology of conodonts*. Ellis Harwood, Chichester, U.K.
- Nowlan, G. S., and C. R. Barnes. 1981. Late Ordovician conodonts from the Vauréal Formation, Anticosti Island, Quebec. *Geological Survey of Canada Bulletin* 329, part 1:1–49.
- Pander, C. H. 1856. *Monographie der fossilen Fische des Silurischen Systems der russisch-baltischen Gouvernements*. Akademie der Wissenschaften, St. Petersburg, pp. 1–91.
- Peek, S., and M. T. Clementz. 2012. Sr/Ca and Ba/Ca variations in environmental and biological sources: a survey of marine and terrestrial systems. *Geochimica et Cosmochimica Acta* 95:36–52.
- Petryshen, W., C. M. Henderson, K. De Baets, and E. Jarochowska. 2020. Evidence of parallel evolution in the dental elements of *Sweetogathus* conodonts. *Proceedings of the Royal Society of London B* 287:20201922.
- Pollock, C. A. 1969. Fused Silurian conodont clusters from Indiana. *Journal of Paleontology* 43:929–935.
- Purnell, M. A. 1995. Microwear on conodont elements and macrophagy in the first vertebrates. *Nature* 374:798–800.
- Purnell, M. A., and D. Jones. 2012. Quantitative analysis of conodont tooth wear and damage as a test of ecological and functional hypotheses. *Paleobiology* 38:605–626.
- Purnell, M. A., P. C. J. Donoghue, and R. J. Aldridge. 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology* 74:113–122.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>.
- Rebert, J. P., J. R. Donguy, and G. Eldin. 1985. Relationships between sea level, thermocline depth, heat content, and dynamic height in the tropical Pacific Ocean. *Journal of Geophysical Research* 90:11719–11725.
- Reynard, B., and V. Balter. 2014. Trace elements and their isotopes in bones and teeth: diet, environments, diagenesis, and dating of archaeological and paleontological samples. *Palaeogeography, Palaeoclimatology, Palaeoecology* 416:4–16.
- Romanuk, T. N., A. Hayward, and J. A. Hutchings. 2011. Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography* 20:231–240.
- Samtleben, C., A. Munnecke, and T. Bickert. 2000. Development of facies and C/O-isotopes in transects through the Ludlow of Gotland: evidence for global and local influences on a shallow-marine environment. *Facies* 43:1–38.
- Sansom, I. J. 1996. *Pseudooneotodus*: a histological study of an Ordovician to Devonian vertebrate lineage. *Zoological Journal of the Linnean Society* 118:47–57.
- Seddon, G., and W. C. Sweet. 1971. An ecologic model for conodonts. *Journal of Paleontology* 45:869–880.
- Shirley, B., M. Grohgan, M. Bestmann, and E. Jarochowska. 2018. Wear, tear and systematic repair: testing models of growth dynamics in conodonts with high-resolution imaging. *Proceedings of the Royal Society of London B* 285:20181614.
- Shirley, B., M. Bestmann, and E. Jarochowska. 2020. The conodonts and conodont's of phosphatic microfossil preparation and microanalysis. *Micron* 138:102924.
- Strömberg, C. 1997. The conodont genus *Ctenognathodus* in the Silurian of Gotland, Sweden. M.S. thesis. *Dissertations in Geology at Lund University*. Lund University, Lund, Sweden.
- Szaniawski, H. 2009. The earliest known venomous animals recognized among conodonts. *Acta Palaeontologica Polonica* 54:669–676.
- Tacail, T., L. Kovačiková, J. Brůžek, and V. Balter. 2017. Spatial distribution of trace element Ca-normalized ratios in primary and permanent human tooth enamel. *Science of the Total Environment* 603:308–318.
- Terrill, D. F., C. M. Henderson, and J. A. Anderson. 2018. New applications of spectroscopy techniques reveal phylogenetically significant soft tissue residue in Paleozoic conodonts. *Journal of Analytical Atomic Spectrometry* 33:992–1002.
- Terrill, D. F., E. Jarochowska, C. M. Henderson, B. Shirley, and O. Bremer. 2022. Sr/Ca and Ba/Ca ratios support trophic partitioning within a Silurian conodont community from Gotland, Sweden (Dataset). doi: 10.17605/OSF.IO/NCZB6
- Trotter, J. A., and S. M. Eggins. 2006. Chemical systematics of conodont apatite determined by laser ablation ICPMS. *Chemical Geology* 233:196–216.
- Trotter, J. A., J. D. Fitz Gerald, H. Kokkonen, and C. R. Barnes. 2007. New insights into the ultrastructure, permeability, and integrity of conodont apatite determined by transmission electron microscopy. *Lethaia* 40:97–110.
- Turner, S., C. J. Burrow, H. Schultze, A. Blicke, W. Reif, C. B. Rexroad, P. Bultynck, and G. S. Nowlan. 2010. False teeth: conodont–vertebrate phylogenetic relationships revisited. *Geodiversitas* 32:545–594.
- Veizer, J. 1989. Strontium isotopes in seawater through time. *Annual Review of Earth and Planetary Sciences* 17:141–167.
- Venancio, I. M., S. Mulitza, A. Govin, T. P. Santos, D. O. Lessa, A. L. S. Albuquerque, C. M. Chiessi, R. Tiedemann, M. Vahlenkamp, T. Bickert, and M. Schulz. 2018. Millennial- to orbital-scale responses of western equatorial Atlantic thermocline depth to changes in the trade wind system since the last interglacial. *Paleoceanography and Paleoclimatology* 33:1490–1507.
- Viira, V. 1999. Late Silurian conodont biostratigraphy in the northern East Baltic. *Bollettino della Società Paleontologica Italiana* 37:299–310.
- Viira, V., and R. Einasto. 2003. Wenlock-Ludlow boundary beds and conodonts of Saaremaa Island, Estonia. *Estonian Academy of Sciences Proceedings* 52:213–238.
- Watkins, R., and J. J. Kuglitsch. 1997. Lower Silurian (Aeronian) megafaunal and conodont biofacies of the northwestern Michigan Basin. *Canadian Journal of Earth Science* 34:753–764.
- Wenzel, B., C. Lécuyer, and M. M. Joachimski. 2000. Comparing oxygen isotope records of Silurian calcite and phosphate- $\delta^{18}\text{O}$ compositions of brachiopods and conodonts. *Geochimica et Cosmochimica Acta* 64:1859–1872.
- Whalen, C. D., and D. E. G. Briggs. 2018. The Palaeozoic colonization of the water column and the rise of global nekton. *Proceedings of the Royal Society of London B* 285:20180883.
- Whealey, J. R., P. E. Jardine, R. J. Raine, I. Boomer, and M. P. Smith. 2018. Paleoeccologic and paleoceanographic interpretation of

- $\delta^{18}\text{O}$ variability in Lower Ordovician conodont species. *Geology* 46:467–470.
- Yin, H. F., K. X. Zhang, Z. Y. Tong, Z. Y. Yang, and S. B. Wu. 2001. The global stratotype section and point (GSSP) of the Permian–Triassic boundary. *Episodes* 24:102–114.
- Zhang, S., and C. R. Barnes. 2004. Late Cambrian and Early Ordovician conodont communities from platform and slope facies, western Newfoundland: a statistical approach. *Geological Society of London Special Publication* 230:47–72.
- Zhuravlev, A. V. 2020. Trophic position of some Late Devonian–Carboniferous (Mississippian) conodonts revealed on carbon organic matter isotope signatures: a case study of the East European Basin. *Geodiversitas* 42:443–453.
- Zhuravlev, A. V., and I. V. Smoleva. 2018. Carbon isotope values in conodont elements from the latest Devonian–Early Carboniferous carbonate platform facies (Timan-Pechora Basin). *Estonian Journal of Earth Sciences* 67:238–246.
- Zhuravlev, A. V., A. N. Plotitsyn, and D. A. Gruzdev. 2020. Carbon isotope ratios in the apatite-protein composites of conodont elements—paleobiological proxy. Pp. 749–764 in O. Frank-Kamenetskaya, D. Vlasov, E. Panova, and S. Lessovaia, eds. *Processes and phenomena on the boundary between biogenic and abiogenic nature. Lecture notes in Earth system sciences.* Springer, Cham, Switzerland.
- Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. *Canadian Journal of Fish Aquatic Science* 62:88–97.