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DOI:
[10.1130/G40145.1](https://doi.org/10.1130/G40145.1)

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Document Version
Publisher's PDF, also known as Version of record

Citation for published version (Harvard):
Wheeley, J, Jardine, PE, Raine, RJ, Boomer, I & Smith, MP 2018, 'Paleoecologic and paleoceanographic interpretation of $\delta^{18}\text{O}$ variability in Lower Ordovician conodont species', *Geology*, vol. 46, no. 5, pp. 467-470.
<https://doi.org/10.1130/G40145.1>

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Publisher Rights Statement:

Checked for eligibility: 11/04/2018
<https://pubs.geoscienceworld.org/gsa/geology/article/529805/Paleoecologic-and-paleoceanographic-interpretation>
<https://doi.org/10.1130/G40145.1>

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Paleoecologic and paleoceanographic interpretation of $\delta^{18}\text{O}$ variability in Lower Ordovician conodont species

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ABSTRACT

Conodont $\delta^{18}\text{O}$ is increasingly used to reconstruct Paleozoic–Triassic seawater temperature changes. Less attention has been paid to $\delta^{18}\text{O}$ variation in time slices across paleoenvironments, within sample assemblages, or for reconstructing the thermal structure of Paleozoic oceans. Furthermore, there have been few independent tests of conodont ecologic models based on biofacies and lithofacies distributions. Here we present the first test of ecologic models for conodonts based on $\delta^{18}\text{O}$ values of a Laurentian Lower Ordovician (Floian) shelf edge–upper slope assemblage in debrites of the proximal lower slope Shallow Bay Formation, Cow Head Group, western Newfoundland. Nine species yield a 1.6–1.8‰ intra-sample $\delta^{18}\text{O}$ variability based on mixed tissue and white matter-only analyses, equivalent to an ~7–8 °C range. Linear mixed models demonstrate statistically significant differences between the $\delta^{18}\text{O}$ of some species, supporting the interpretation that an isotopic and temperature gradient is preserved. By considering conodont $\delta^{18}\text{O}$ in a geologic context, we propose an integrated paleoecologic and paleoceanographic model with species tiered pelagically through the water column, and confirm the utility of conodonts for water-mass characterization within Paleozoic oceans.

INTRODUCTION

The $\delta^{18}\text{O}$ records of carbonate fluorapatite conodont elements are increasingly utilized to estimate Paleozoic–Triassic seawater temperatures, and have led to global-scale hypotheses concerning biodiversification and mass extinction, reef evolution, climate change, and glacioeustasy (e.g., Trotter et al., 2008, 2016; Joachimski et al., 2009; Elrick et al., 2013; Rosenau et al., 2012). Despite these advances, little research has addressed variation of conodont $\delta^{18}\text{O}$ in relation to conodont ecology and oceanic thermal configurations.

Conodont morphological diversity and their peritidal to deep-water facies distribution in the marine rock record implies occupancy of multiple ecologic niches, which likely also represent a variety of seawater temperatures (Sweet, 1988). A number of models for conodont ecology have been proposed that suggest they either lived tiered pelagically in the water column (Seddon and Sweet, 1971), or that the majority were segregated by depth as nektobenthos (Barnes and Fähræus, 1975). For the Ordovician, these models have been combined to help explain conodont distributions (Zhen and Percival, 2003) but, to date, conodont $\delta^{18}\text{O}$ has not been used to test the models directly.

Conodont paleothermometry assumes precipitation of fluorapatite in oxygen-isotopic equilibrium with seawater, no species-vital effects, and retention of primary oxygen-isotopic signatures in the fossil record (see the review in MacLeod, 2012). Thus, conodont $\delta^{18}\text{O}$ variability is interpreted as representing an environmental signal, most commonly seawater temperature. Although some researchers report no significant isotopic distinction between Ordovician taxa from temperature-differentiated oceanic realms (Buggisch et al., 2010), others have considered the importance of isotopic variability between taxa to reflect varying occupation of temperature-stratified water masses (e.g., Herrmann et al., 2010).

The extent of inter-species $\delta^{18}\text{O}$ variability is known from two approaches. Analyses by thermal conversion–elemental analyzer–isotope ratio mass spectrometry (TC-EA-IRMS) of silver phosphate from conodont fluorapatite have demonstrated significant species $\delta^{18}\text{O}$ offsets within a single ‘conodont’ sample (~1–1.5‰; e.g., Herrmann et al., 2010; Rosenau et al., 2012). Analyses by secondary ionization mass spectrometry (SIMS) identified $\delta^{18}\text{O}$ offsets of up to 2‰ across shelf taxa from an Ordovician sample (Wheeley et al., 2012), and 0.9‰ variability between genera in a Devonian basin (Narkiewicz et al., 2017). These ~1–2‰ taxonomic offsets equate to significant temperature ranges (~4–8 °C) when converted using phosphate-temperature

equations (e.g., Lécuyer et al., 2013). Therefore, it is important to consider how isotopic variability in samples relates to autecology or other controls (Wheeley et al., 2012), especially because conodont $\delta^{18}\text{O}$ is being used more widely in studies of seawater temperature evolution (e.g., Trotter et al., 2016).

A potential complicating factor to an ecologic explanation of $\delta^{18}\text{O}$ species variability is that of differential $\delta^{18}\text{O}$ from the constituent hard tissues of conodont elements: the white matter (albid crown), hyaline crown, and basal body (e.g., Zhang et al., 2017). TC-EA-IRMS analyses have established that $\delta^{18}\text{O}$ variability increases when the basal body is included (Wenzel et al., 2000), but this tissue is rarely preserved and therefore unlikely to be a source of $\delta^{18}\text{O}$ variability. Some authors report no significant $\delta^{18}\text{O}$ differences between conodont crown tissues via SIMS (Trotter et al., 2016), whereas others have (Wheeley et al., 2012; Zhang et al., 2017). The differing $\delta^{18}\text{O}$ values between conodont tissues may relate to carbonate content, although this effect is probably minimal as the majority of oxygen is contained within diagenetically stable phosphate (Wheeley et al., 2012). Basal body tissue has the most carbonate, with lesser amounts in hyaline crown, and it is not detected in albid crown (Trotter and Eggins, 2006). The high spatial resolution of SIMS analyses enables targeting of tissues and evaluation of where analyses have occurred and, along with multiple analyses of individual conodont elements, enables potential histological bias to be overcome.

This paper has two aims: (1) to appraise the SIMS conodont $\delta^{18}\text{O}$ variability of a species-rich sample from a setting with potential for seawater-column temperature differences, and (2) to contextualize these data in an integrated paleoecologic and paleoceanographic model, thus testing the potential for determining the paleothermometry of ancient oceans, and conodont ecologic models.

METHODS

The analyzed conodonts come from an 8.5 kg sample of Bed 11 (unit 2) of the Factory Cove Member (Shallow Bay Formation, Cow Head

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Group) (Floian, Lower Ordovician), western Newfoundland (Fig. 1; Fig. DR1 in the GSA Data Repository¹). Limestone samples were digested with buffered acetic acid following the protocols of Wheeley et al. (2012) and conodonts were picked direct from residues (Section DR2 in the Data Repository). Conodont elements of nine species were analyzed for $\delta^{18}\text{O}$ on a CAMECA 1270 ion microprobe (Sections DR3 and DR4). A linear mixed model (LMM) was fitted to the data to determine the statistical significance of taxonomic differences in $\delta^{18}\text{O}$ (Section DR5). Paleoeologic and paleoceanographic interpretations are based on white matter analyses, as this tissue is present for all species analyzed and is considered to be the most robust histology for retaining a primary $\delta^{18}\text{O}$ signature (Trotter and Eggins, 2006).

$\delta^{18}\text{O}$ OF COW HEAD CONODONTS

In white matter, the maximum $\delta^{18}\text{O}$ offset between the mean values of different species is 1.8‰, between *Tropodus sweeti* and *Drepanodus planus*; when all tissues are sampled, the equivalent offset is 1.6‰ (Fig. 2; Section DR3). The mean values for the individual species are robust, with raw data (i.e., not derived from the LMM) 95% confidence intervals typically <0.3‰. The LMM indicates a statistically significant difference between species means ($F = 3.49$, $p = 0.014$), with the four isotopically lightest taxa (*D. planus*, *Paroistodus proteus*, *Oepikodus evae*, and *Cornuodus longibasis*) being different from *T. sweeti* (the isotopically heaviest taxon; Section DR5) at levels of statistical significance, indicating that a true isotopic gradient is present. The results when measurements from all histologies are included show high similarity to those based on white matter alone (Section DR5).

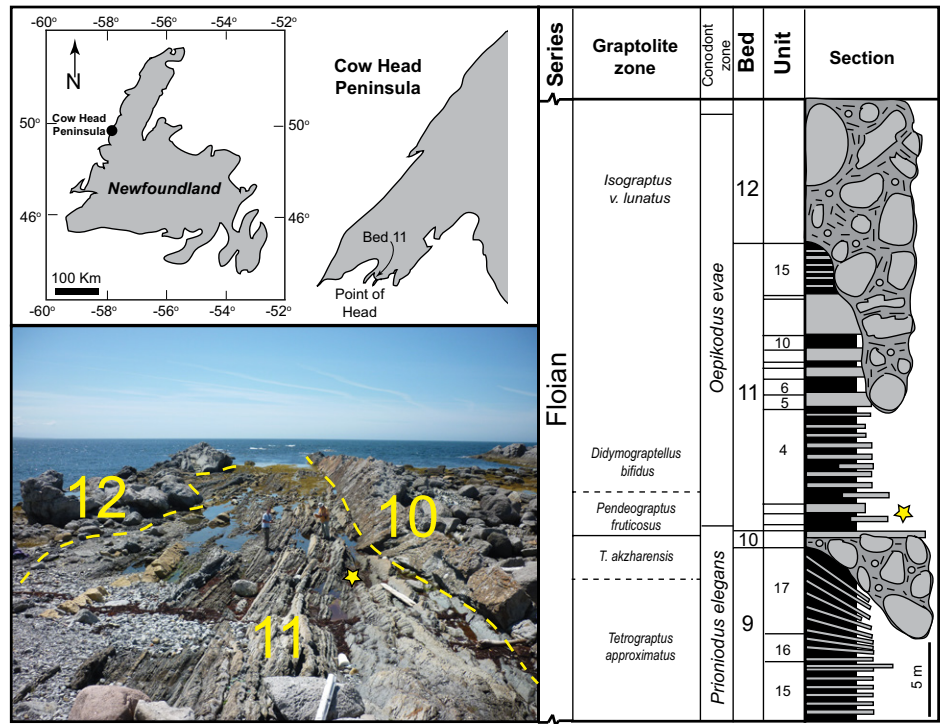


Figure 1. Location and stratigraphic context of sample horizon (star), Factory Cove Member (Shallow Bay Formation, Cow Head Group), Cow Head Peninsula, western Newfoundland, Canada. Log re-drawn from James and Stevens (1986).

The maximum intra-specific variation recorded between mean values for individual elements of the same species was 1.5‰ (*O. evae*, $n = 5$) based on white matter analyses. *C. longibasis* and *Bergstroemognathus extensus* have the greatest intra-species variability (1.3‰) when element means are compared between species representatives with analyses in either single or mixed tissues; for the remaining taxa, this range is 0.1–1.2‰ (Section DR3). Intra-species variability may be interpreted as a result of a range

of paleobiologic and sedimentologic variables (Quinton and MacLeod, 2014), and highlights the importance of dealing with multiple representatives of species for meaningful interpretation.

DISCUSSION

Paleotemperature of Cow Head Conodonts

The 1.6–1.8‰ interspecies $\delta^{18}\text{O}$ variability identified here is equivalent to an ~7–8 °C sea-water temperature range utilizing the equation

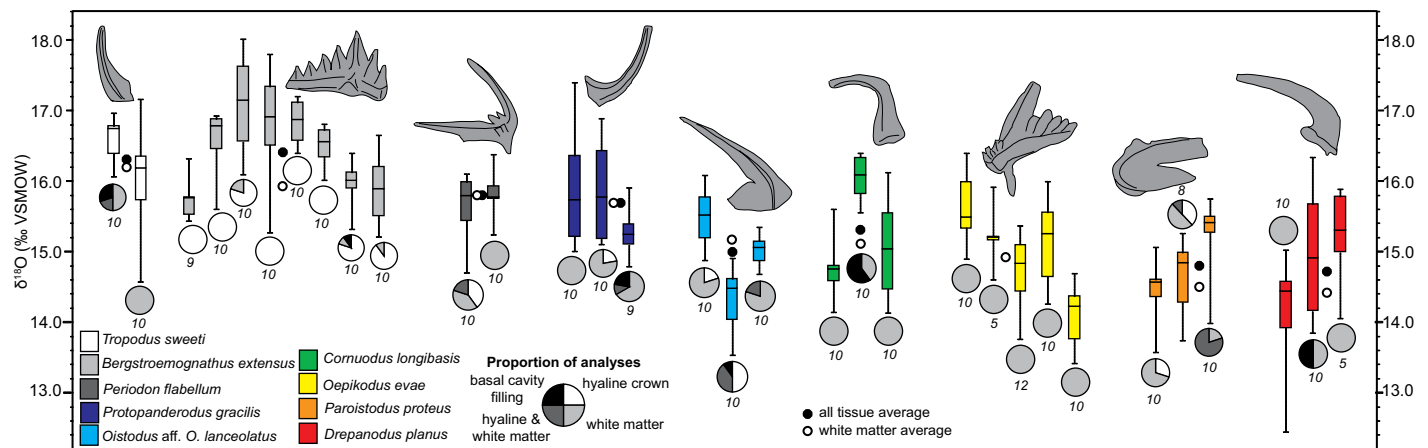


Figure 2. Conodont $\delta^{18}\text{O}$ values, ordered left to right by white matter means. Each box and whisker plot shows the mean, 25th, and 75th percentiles, and range. Pie charts indicate the relative proportions of analyses in different histologies for each conodont element. Numbers of analyses per conodont element are indicated in each pie chart.

¹GSA Data Repository item 2018156, Sections DR1 (geologic setting), DR2 (methods), DR3 (conodont $\delta^{18}\text{O}$ data), DR4 (Durango apatite standard data), DR5 (statistical model fitting), and DR6 (field data), is available online at www.geosociety.org/pubs/ft2018.htm, or on request from editing@geosociety.org.

of Lécuyer et al. (2013). Absolute values (14.4–16.4‰) are supportive of warm Early Ordovician seawater (e.g., Bassett et al., 2007) and equate to comparable temperature estimates for Floian seawater obtained through SIMS conodont analyses by others (Trotter et al., 2008) when differences in Durango apatite standard values are accounted for. The possibility of freshwater effects explaining the inter-species $\delta^{18}\text{O}$ variability can be excluded because of the deep marine, slope setting of the Cow Head Group. Similarly, $\delta^{18}\text{O}$ variability due to spatial differentiation of surface water evaporation and salinity can be excluded because the variation observed is larger than that seen in modern oceans over inter-ocean scales (e.g., Tiwari et al., 2013). Thus, seawater temperature differences are the most likely driver of the $\delta^{18}\text{O}$ variability between the species investigated here. Can the $\delta^{18}\text{O}$, and thus temperature variation, observed in conodonts of the Cow Head Group be accommodated within its tropical Laurentian margin setting, and does this inform models for conodont ecology?

Paleothermometry of the Laurentian Margin and Conodont Ecology

To date, conceptual models for conodont paleoecology have been defined on spatial distribution and relationships with host lithology, but since the 1990s there has been a call for conodont ecologic models to be elucidated through geochemistry (Pohler and Barnes, 1990). Oxygen isotopes offer the possibility of independently testing nektobenthic versus tiered pelagic hypotheses for conodont ecology.

The depositional location of the Cow Head sediments was under hundreds of meters of water, based on a range of geologic evidence (James and Stevens, 1986; Pohler, 1994; Johnston and Barnes, 1999), with sediment derived from

shelf-edge to upper slope settings. Applying a temperature–depth gradient typical for modern tropical oceans (e.g., Levitus and Boyer, 1994) to the statistically significant conodont $\delta^{18}\text{O}$ offset suggests ~250–300 m vertical separation between the ‘warmest’ and ‘coolest’ species in the slope water column (Fig. 3). This temperature gradient will also have been present at the intersection of the slope water column with the slope seafloor, implying that either the nektobenthic or tiered pelagic ecological scenarios, or a combination, could account for the isotopic signature between species. However, independent sedimentologic evidence within the Cow Head Group helps distinguish which model is more parsimonious.

James and Stevens (1986) recorded the presence of phosphate and chert nodules within black shales and limestones at the level of the studied sample (see also Section DR6). This has led to the interpretation of this interval as being deposited under anoxic conditions within an upwelling setting (James and Stevens, 1986; Johnston and Barnes, 1999). Where upwelling occurs against continental margins, the thermocline can shoal (e.g., Ford et al., 2015) and juxtapose cool oxygen-depleted water against the continental slope. If conodonts were nektobenthic, they must have been restricted to a condensed thermal gradient on the slope above the upper limit of anoxia. However, gravity flows deposited on the slope contain reworked black shales and phosphatic conglomerates (Pohler, 1994), which indicate that anoxic upwelling extended up the slope from the depositional site (Fig. 3). These observations have important implications for nektobenthic models of conodont paleoecology because the extent of habitable slope below the mixed surface layer was insufficient to generate the observed temperature range (~7–8 °C) (Fig. 3).

The range of $\delta^{18}\text{O}$ values and inferred temperatures indicate that the majority of conodonts in this study lived in waters encompassing the mixed surface layer (MSL; epipelagic) and the cooler, deeper water column below the MSL and outboard of the shelf break (mesopelagic) (Fig. 3). The conodont $\delta^{18}\text{O}$ values record temperatures at the point of biomineralization, and because vital effects are unknown, only relative temperature estimates are possible. Despite this, the conodonts at Cow Head do record the thermocline in terms of relative temperature decrease with depth. Although there was some local transport of elements to their final depositional site, as indicated by the scour in which they were recovered (Fig. DR1), the quality of conodont element preservation at Cow Head is exceptional, with very minimal fracturing and no evidence of abrasion, suggesting that transport was limited. Well-preserved pelagically sourced radiolarians in our sample and associated beds (Won and Iams, 2011), along with the abundance of delicate fused clusters of conodont elements, also indicates that sediment transport distances were low.

Some of the taxa that occur in the deeper, cooler water deposits at Cow Head do occur in shallower subtidal environments within platform settings elsewhere in Laurentia (e.g., *Bergstroemognathus* and *Tropodus* in Greenland) (Stouge, 1982; Smith, 1991). This occurrence in demonstrably warmer, shallower waters indicates that some conodonts did have a wide range of temperature tolerance, but that shallow-water representatives of these taxa were not the main source of elements being transported down the slope at Cow Head. In contrast, *Periodon flabellum* is restricted to deeper, cooler, outer-shelf and slope settings (Pohler, 1994; Johnston and Barnes 1999), and appears to be an obligate cool-water taxon.

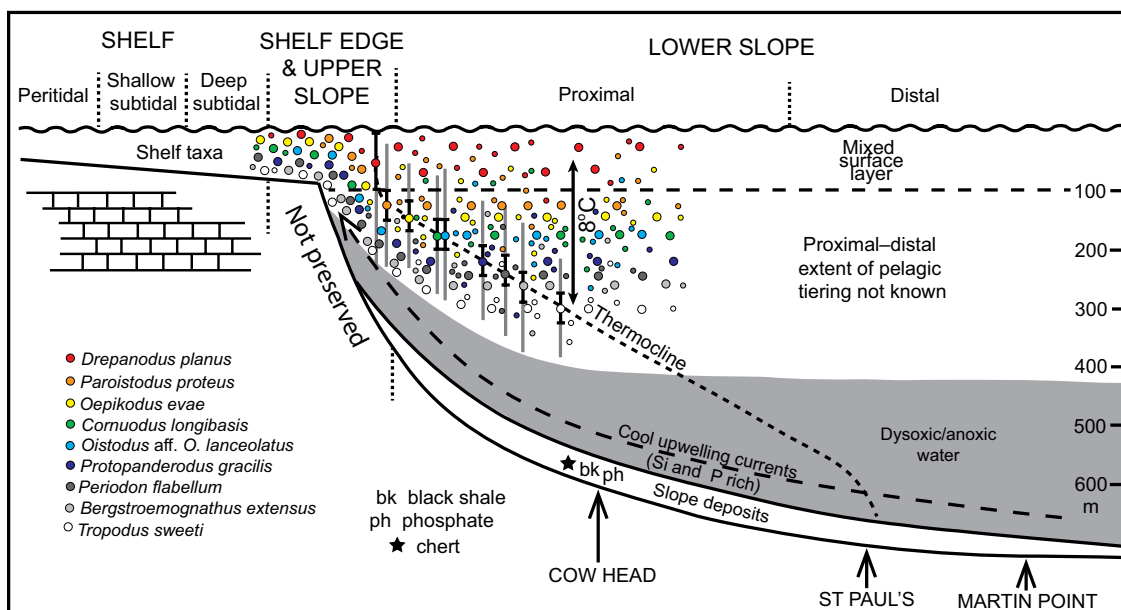


Figure 3. Paleoecologic and paleoceanographic model for the Cow Head (Newfoundland, Canada) margin based on $\delta^{18}\text{O}$ analyses of conodont white matter, with nine species distributed vertically through the water column arrayed along the thermocline. Error bars: inner black terminations are analytical uncertainty, outer gray bars are 95% confidence levels on species white-matter fitted means from a linear mixed model (Table DR5.3 [see footnote 1]).

These results for an Ordovician continental margin contrast with the Devonian, where oxygen isotopic studies have suggested that conodonts lived only in mixed surface waters (Joachimski et al. 2009). A thermally tiered pelagic model for conodont ecology may not have applied throughout their history, and warrants further investigation in different time periods.

CONCLUSIONS

The first oxygen isotopic test of conodont paleoecologic models establishes that, for the Floian of the Laurentian margin at Cow Head, Newfoundland, conodonts occupied a vertical profile of several hundred meters within a thermally stratified water column, across epipelagic and mesopelagic niches. This model favors interpretations of a pelagic life mode for Ordovician conodonts over a nektobenthic one when the geologic context of the conodonts and their $\delta^{18}\text{O}$ are considered. The results demonstrate the potential of SIMS analyses of conodont species $\delta^{18}\text{O}$ for resolving the paleotemperature configuration of water masses in early Paleozoic oceans. The range of sample $\delta^{18}\text{O}$ evident in this study highlights the need to fully interrogate species variability before making decisions on sample or time-slice representative values in studies of temporal seawater temperature evolution. Finally, these results confirm that conodonts have the potential to be used in Paleozoic oceanography in the same way that planktonic foraminifera are used in younger oceans.

ACKNOWLEDGMENTS

Analyses were funded by Natural Environment Research Council facility grant IMF414/1010, and we are grateful to John Craven and Mike Hall (Edinburgh Ion Micro-Probe Facility) for assistance with analyses. Fieldwork was supported by the Royal Society and the Palaeontological Association. The Newfoundland National Parks Authority gave kind permission to sample for conodonts. Two anonymous reviewers and Stephen A. Leslie are thanked for their constructive reviews. Wheeley dedicates this work to Euphemia B. Wheeley (1926–2014).

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Manuscript received 20 November 2017

Revised manuscript received 8 March 2018

Manuscript accepted 9 March 2018

Printed in USA