Paleoecologic and paleoceanographic interpretation of δ¹⁸O variability in Lower Ordovician conodont species

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INTRODUCTION

The δ¹⁸O records of carbonate fluorapatite conodont elements are increasingly utilized to estimate Paleozoic–Triassic seawater temperatures, and have led to global-scale hypotheses concerning biodiversity 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 individual conodont δ¹⁸O in relation to conodont biology and oceanic thermal configurations.

Conodont morphologic diversity and their peritidal to deep-water facies distribution in the marine rock record implies occupancy of multiple energetic niches, which likely also represent a variety of seawater temperatures (Sweet, 1988). A number of models for conodont ecologic ecolögy 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 Fåhræus, 1975). For the Ordovician, these models have been combined to help explain conodont distributions (Zhen and Percival, 2003) but, to date, conodont δ¹⁸O 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 δ¹⁸O 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., Hermann et al., 2010).

The extent of inter-species δ¹⁸O 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 δ¹⁸O offsets within a single ‘conodont’ sample (~1–1.5‰; e.g., Hermann et al., 2010; Rosenau et al., 2012). Analyses by secondary ionization mass spectrometry (SIMS) identified δ¹⁸O 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 δ¹⁸O 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 δ¹⁸O species variability is that of differential δ¹⁸O 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 δ¹⁸O 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 δ¹⁸O variability. Some authors report no significant δ¹⁸O differences between conodont crown tissues via SIMS (Trotter et al., 2016), whereas others have (Wheeley et al., 2012; Zhang et al., 2017). The differing δ¹⁸O 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 δ¹⁸O 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 paleoceanography 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...
Group) (Floian, Lower Ordovician), western Newfoundland (Fig. 1; Fig DR1 in the GSA Data Repository). 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 δ18O 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 δ18O (Section DR5). Paleoecologic 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 δ18O signature (Trotter and Eggins, 2006).

**δ18O of Cow Head Conodonts**

In white matter, the maximum δ18O 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).](image1.png)

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 δ18O variability identified here is equivalent to an ~7–8 °C seawater temperature range utilizing the equation

![Figure 2. Conodont δ18O 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.](image2.png)

GSA Data Repository item 2018156, Sections DR1 (geologic setting), DR2 (methods), DR3 (conodont δ18O data), DR4 (Durango apatite standard data), DR5 (statistical model fitting), and DR6 (field data), is available online at www.geosociety.org/pubs/fl2018.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 δ18O variability can be excluded because of the deep marine, slope setting of the Cow Head Group. Similarly, δ18O variability due to spatial differentiation of surface water vaporization 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 δ18O variability between the species investigated here. Can the δ18O, 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 δ18O 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 theinterpretation 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 δ18O 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 δ18O 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 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., Bergstromognathus 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.
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 δ18O are considered. The results demonstrate the potential of SIMS analyses of conodont species δ18O for resolving the paleotemperature configuration of water masses in early Paleozoic oceans. The range of sample δ18O 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.

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