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Growth Rate and Ecology of the Giant Heteromorph Ammonite Diplomoceras maximum Using Stable Isotopes of Accretionary Shell Carbonate

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May 2016

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Abstract

*Diplomoceras maximum* is a large, hamitocone heteromorph ammonite with a shell that resembles a giant paperclip. A 1.5 meter long specimen representing more than 3 meters of linear shell growth from the late Cretaceous Lopez de Bertodano Formation of Seymour Island, Antarctica, now resides at the Paleontological Research Institution (PRI) in Ithaca, NY. Its growth rate and ecology have been the subject of much discussion but are completely unknown. Stable carbon and oxygen isotope analysis of serially sampled shell material can provide insight into the growth and habitat of these peculiar cephalopods. A roughly half-meter section of shell containing a hook and both adjoining portions of shafts, with aperture diameter ~15 cm, was sampled at a resolution of 5 samples per sculptural rib on the shell (total of 145 analyses). $\delta^{18}$O values vary between +1.9 to -1.7‰, roughly the same range expressed by co-occurring benthic mollusks. A 15-point moving average defines a broad sinusoid that likely reflects ~1.5 years of shell growth. If so, and if accretion were constant, the PRI animal would have been about 9 years old at death. Superimposed on this sinusoid is regular variation of up to 2‰ that corresponds to sculptural ribs and covaries with $\delta^{13}$C, suggesting the potential for disequilibrium effects during precipitation of ribs or, potentially, repeated vertical migrations through the water column. Carbon isotope values overlap those of typical benthic mollusks and other ammonites, but also include extremely negative values (+1.7 to -30‰). Values are low between ribs and higher on them; regular swings to low values become significantly more extreme in the hook than they are in the shafts. If
related to disequilibrium and/or incorporation of metabolic CO2, this suggests more rapid growth in the hook section. Exceedingly negative δ¹³C values may also reflect precipitation in the presence of methane, as suggested in the literature by unusual carbonate precipitates, chemosymbiotic cold-seep bivalve taxa, and very low δ¹³C values of cemented burrow fills. Taken together, our data suggest a pelagic habit near the bottom, with a vertically oriented shell, closely associated with cold methane seeps. Shell growth is fast, consistent with living coleoids, and large individuals are likely less than 10 years old at death.
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Acknowledgements

We thank Anton Oleinik and Christopher Junium for valuable feedback, PRI for access to their specimens, Lora Wingate at the University of Michigan Stable Isotope Lab for running the carbonate isotopes, and Zunli Lu at SU for elemental analysis. Funding was provided by grants from the Northeastern Section of the Geological Society of America, the Paleontological Society, the Rochester Academy of Science, and Sigma Xi.
Introduction

Heteromorph ammonites are characterized by diverse and peculiar shell coiling and represent a rapidly evolving component of the cephalopod fauna during the Late Cretaceous (Olivero & Zinsmeister, 1989). *Diplomoceras maximum* from the Lopez de Bertodano Formation on Seymour Island, Antarctica, is 1.5 meters long and shaped like a giant paperclip. Its ecology is completely unknown. We have evaluated growth rate, habitat, and diet using stable isotopes of oxygen, carbon, and nitrogen preserved in the shell material.

Growth rate of ammonoids is dependent on influences such as quality of habitat, water temperature, and injuries to individuals (Bucher et al., 1996 (408)). Much of our understanding of extinct ammonites is based on comparisons to the extant shelled cephalopod, *Nautilus*. Although they are not closely related groups, it can be assumed that ammonoids and *Nautilus* share fundamental similarities in their means of growth (Bucher et al., 1996 (408)). For *Nautilus*, the basic steps involved in growth are secretion of septum, formation of siphuncular segment, removal of cameral fluid, and forward movement of the body. Shell growth at the apertural margin is continuous. This mode of growth can probably be applied to ammonoids as well. As chambers formed, the shell margin and soft tissue most likely grew at a continuous rate (Bucher et al., 1996 (409)). Ribs on the surface of the shell form parallel to growth lines, which mark former positions of the apertural margin. The process may have involved activation and inhibition of the growth program at the mantle edge (Bucher et al., 1996 (422)). However,
this explanation of rib formation contradicts the hypothesis of continuous growth at the shell margin.

The life history of ammonoids consisted of multiple stages, which can be recognized by features such as shifts in growth rate, shell shape, and appearance of ornamentation. The postembryonic stages begin with the neanic stage. In most taxa, this stage is characterized by planktonic life habit. The second stage is juvenile, and the third stage is adulthood, which is marked by simultaneous changes in body chamber length and shape, changes in coiling pattern, increase in ornamentation, increase in whorl width, and thickness of aperture. It is believed that the adulthood stage represents the individual reaching sexual maturity (Bucher et al., 1996 (414)). Westermann (1992) suggested that small, shallow water ammonoids reached maturity in 1 to 2 years, while midshelf ammonoids reached maturity in 3 to 5 years and deep water ammonoids matured in up to a few decades. This is hypothesized due to similarities in Nautilus, which take about 10 years to mature, and have identical septal nacre and analogous incrementation in septal thickness. The modifications to the adult shell improve hydrostatic stability, increase speed by reducing drag, and improve protection against predators (Bucher et al., 1996 (623)). All of these changes accumulated from the embryonic stage to adulthood were instituted to achieve the desired adult shape (Callomon, 1963). For heteromorph ammonites like Diplomoceras, the formation of a hooked shell concluded in an adult body with an upturned aperture that is thought to be an adaptation that facilitated vertical movement and a planktic lifestyle (Ward, 1976). The orientation of
hamitocone ammonites was studied by Ward (1976) using cast models of the shell in liquid and observing the specific densities. The final stage indicates old age, deteriorating locomotor skills, and reduction of metabolic activity. This is known as the senescent stage Van Heukelem, 1978 (415).

As ammonoids reached maturity, growth rate was most likely decelerated (Callomon, 1963). This is inferred since mature *Nautilus* have a slower growth rate at the apertural margin (Bucher et al., 1996 (418)). This pattern of growth, fast (during neanic), constant (during juvenile), and slow (during maturity), is a generalized notion given the diversity of ammonoids. In addition, there are other factors that influence growth rate. Those factors include temperature, dissolved oxygen, day length, and food availability. Habitat depth is thought to affect growth rate due to the amount of hydrostatic pressure (Bucher et al., 1996 (437)). Ward (1982) has found a negative correlation between hydrostatic pressure and growth rate. Therefore it can be assumed that ammonoids that lived in deep water grew more slowly than those in shallow water (Bucher et al., 1996 (437)). Fast growth implies different physiological and ecological roles than slow growth, and hence growth rate in *Diplomoceras* is an important variable to investigate. Since the habitat is thought to be seasonal, we can presume that the growth rate of *Diplomoceras* was rapid enough to record these seasonal changes, which can then be differentiated due to fluctuations in rate and translated into a pattern of growth (Bucher et al., 1996 (441)). Growth rates and lifespans of accretionary organisms can be evaluated using oxygen isotope analysis of serially sampled shell material to define seasonal cycles and therefore years (Jones & Quitmyer,
1996). Just as there were many factors affecting growth rate, there are a number of components that influence the isotopic composition of the biogenic calcium carbonate, such as temperature during accretion, state of shell preservation (Buchart & Weiner, 1981), isotopic composition of the surrounding water (Grossman & Ku, 1986), and species-specific effects related to growth (McConnaughey, 1989). As well, with such unusual shell morphology, accretion might have been faster in the 'hooks' than it was in the 'shafts' of the shell so as to maintain orientation in the water column (Okamoto & Shibata, 1997). This hypothesis can be tested with δ¹⁸O sclerochronology.

Habitat depth also remains a mystery. In addition to a slower growth rate, gigantism in ammonoids is also associated with cold, deep water (Stevens, 1988). Given the unusual large size of Diplomoceras, this could be a reasonable assumption of its habitat. However, the characteristics presented in the Lopez de Bertodano formation suggest it was once a shallow sea. According to Elmi and Benshili (1987), growth rates were higher and sizes were larger for ammonoids in shallow platforms than in basins. Though once thought be to slow, demersal animals, ammonoids in general are now thought to have been pelagic, swimming and drifting in epeiric seas (Bucher et al., 1996 (608)). Tanabe (1979), based on a well-documented neritic-oceanic gradient with ammonoid biofacies, suggest that all ammonoid morphogroups, including hamitocones, inhabited a depth of 100 m to 200 m. Hamitocones in general are depicted as planktic vertical migrants in deep midwater (80-120 m) with an upturned aperture (Ward, 1976 (661)), that fed on mesopelagic organisms such as zooplankton and juvenile
ammonoids which were caught in umbrella-like tentacles. These hypotheses are based on data on ammonoid prey and buccal organs (Bucher et al., 1996 (677)). Stable isotope values can provide insights when compared to organisms with known habitats. A comparison of the $\delta^{18}O$ values of belemnites from the same formation with co-occurring benthic and planktonic foraminiferans argue for a benthic lifestyle for those cephalopods (Dutton, 2007). We compared the isotope values of Diplomoceras with these and co-occurring benthic mollusks. $\delta^{18}O$ values similar to other mollusks would suggest a benthic life mode, while more negative values would suggest a pelagic life mode.

**Geological Setting**

The Lopez de Bertodano Formation of Seymour Island, Antarctica is characterized by mudstone-dominated beds with inclined heterolithic stratification. The filing of tide-influenced channels is apparent by the marked lenticular geometry (Olivero et al., 2007). Bioturbated bedding is common, and the absence of wave-generated structures indicates deposition below wave base (Zinsmeister et al., 1989). The depositional landscape has been interpreted as an open marine shelf with a relatively low energy deposition (Dutton et al., 2007).

Diverse and abundant vertebrates, invertebrates, and carbonized wood can be found in the upper 200 meters of the Lopez de Bertodano Formation (Zinsmeister et al., 1989). Well preserved mollusks are found in the upper four units of the formation, ammonites being the most common.
Hydrocarbon seeps can also be found on Seymour Island. Seeps are shallow to deep water sites around continental margins where hydrocarbon-rich fluids leak onto the sea floor. These areas support high-biomass communities that have a symbiotic relationship with chemotrophic bacteria. The seeps on Seymour Island occurred periodically and contained a large concentration of biogenic methane. Micrite-cemented burrow systems acted as preferential pathways for upward flow of fluid and provided a moderate environment for the formation of chemosymbiotic communities (Little et al., 2015).

**Methods**

A specimen of *Diplomoceras maximum* collected at PU 1613 and housed in the collection at the Paleontological Research Institute was sampled sequentially using a Brasseler hand-held dental drill on the surface of the shell. Samples were spaced regularly such that one centered on each rib and three others evenly spanned the trough between ribs. Sampling encompassed (52.5 cm) of shell growth spanning two portions of shaft and the connecting hook between them. To evaluate potential differences in composition associated with variation in shell thickness, an additional 10 samples were collected in a vertical section through the shell from outer surface to inner matrix. Stable oxygen and carbon isotope analysis of calcium carbonate was performed at the University of Michigan’s Stable Isotope Laboratory. Additional sets of sequential samples spanning 5 ribs each were collected from portions of a shaft and hook at higher spatial resolution (5 per node) and analyzed for their Sr/Ca ratios at Syracuse University.
The isotope data collected from Diplomoceras are compared with data from co-occurring taxa published by Tobin and Ward (2015) and Dutton (2007).

Results

The isotopes observed in the shell of Diplomoceras exhibit extremely negative $\delta^{13}C$ in the hook, and values closer to zero in the shafts. The data show a cyclic nature at both the individual sample level, and at the sample area as a whole. $\delta^{13}C$ ranges from 1.15 to -32.84. $\delta^{18}O$ has a much smaller range of values, from 2.5 to -3.3 (Figure 1). In addition to the cyclic patterns lining up, trend lines show a sine-like curve through both carbon and oxygen plots, indicating a high level of covariance between the two.

Discussion

Our data give surprising insights into the life history of Diplomoceras. The most striking feature of the database is the very low carbon values. As sampling came closer to the hook, both $\delta^{18}O$ and $\delta^{13}C$ become extremely negative. Where the hook starts, carbon is more negative than in the shaft. It may be that the organism was incorporating extra carbon from respired CO$_2$ into the shell carbonate. This might imply that when growing the hooks, the animal became stressed and pulled its own respired carbon from the water to make the turn. This supports the Ward (1976) description of hamitocone ammonites as having alternating stable and unstable growth stages, marked by the organism's need to flip over in orientation. Biomass as a whole is isotopically negative, because the phytoplankton in the organism's diet prefer $^{12}C$ over $^{13}C$ during
photosynthesis. Metabolism of food (biomass) releases CO\(_2\) with a negative signature, while the inorganic carbonate precipitating in the ocean will have standard marine carbon isotope values, around 0 or +2. Negative isotope values could also be the result of very fast (disequilibrium) precipitation, as the light isotopes diffuse to the site of precipitation faster than the heavy isotopes. As the hook ends and the next shaft begins, the carbon once again becomes less negative and remains in the range of approximately 0 to -5. This rapid shift of values back to equilibrium suggests that there is some sort of change in behavior and shell accretion as the hooks form.

Several factors could have contributed to the unusually low \(\delta^{13}C\) values found in the shell of Diplomoceras. Diagenetic alteration of original aragonite is always a possibility in ancient carbonates and can produce very low isotope values in replaced shell. However, diagenesis tends to have an earlier and more profound effect on \(\delta^{18}O\) than on \(\delta^{13}C\). While Diplomoceras \(\delta^{13}C\) values are strongly negative in the hook and fall quite low in each sculptural trough, \(\delta^{18}O\) values show much less fluctuation and do not fall below -2 \(\%\). It is therefore unlikely that this can explain the low \(\delta^{13}C\) values. Inadvertently contamination by matrix and/or cement in the thinner inter-rib portions of the shell is also possible. Analysis of sediment adjacent to the inner shell surface reveals quite low \(\delta^{13}C\) values (\(~-15 \%\)). However, after careful observation, the area sampled on the hook, where values are most negative, has thick shell clean of matrix, and sampling did not penetrate the shell in any instance.
Carbon isotope values are exceedingly negative in parts of the shell, and the change in $\delta^{13}C$ consistently correlates with that in $\delta^{18}O$ values. A possible explanation for the data is covariance in isotope values, particularly on the small scale associated with production of sculptural ribs and troughs, is disequilibrium precipitation. $\delta^{18}O$ values deviate from the long-term trend consistently and systematically by 1-2%o generally in association with inter-rib precipitation. $\delta^{13}C$ values show the same pattern, though the magnitude of variation is far greater. If production of sculptural ribs were associated with the changes in the rate of calcification such that troughs were produced fast enough to deplete the local water from which the shell precipitates of $^{13}C$ and $^{18}O$, then disequilibrium could explain at least in part of the high-frequency shifts to more negative values. Disequilibrium precipitation in mollusks is exceedingly rare, but the very large size of this shell combined with the potential for rapid precipitation makes this a possibility. However, the magnitude of the negative shifts is far greater for carbon than oxygen, suggesting that other factors are still required to explain the majority of the depletion in the $\delta^{13}C$ values.

Hydrocarbons are known to have very low $\delta^{13}C$ signatures. The Lopez de Bertodano formation on Seymour Island once had methane seeps that supported chemosymbiotic communities. Calcite cement found in articulated bivalves on Seymour Island had $\delta^{13}C$ isotope values between -58.0‰ and -24.6‰. These low values indicate biogenic methane contributed to their formation. If *Diplomoceras* inhabited these shallow seep areas, it is reasonable to believe that biogenic methane is responsible for the low $\delta^{13}C$ values found in the shell.
However, these low values are not found consistently across the whole length of sampled shell. Methane may contribute to the low carbon values, but it does not explain the sudden change in light to heavily negative carbon.

Variation in oxygen isotope values that corresponds with sculptural ribs may be seasonal in nature, or could be associated with metabolic/precipitation effects related to formation of the ribs. Oxygen isotope values are not unusually negative, suggesting a primary environmental (temperature) signal, so if an annual record can be discerned, they can be used to determine growth rate. Dutton (2007) reports δ¹⁸O values from belemnites of the same formation that are comparable to these. In addition, similarity to the values of co-occurring benthic foraminifera, but not planktonic foraminifera, suggested a benthic habitat for the belemnites and hence also of this heteromorph (Figure 2). Data from Tobin and Ward (2015) also support the hypothesis of a benthic lifestyle. Both bivalves and gastropods show fairly positive δ¹⁸O values and somewhat neutral δ¹³C values (Figure 3). Not only are bivalves and gastropods benthic organisms, the δ¹⁸O and δ¹³C values are representative of cold, deep waters. When plotted with the *Diplomoceras* data, there is overlap of data points in that region of the graph. When *Diplomoceras* is plotted with Tobin’s ammonite data and Dutton’s belemnite data, the ammonite and belemnite data points almost exclusively fall in the same “benthic” range as the bivalves and gastropods (Figure 3). This is all evidence that clearly shows that *Diplomoceras* most likely occupied a demersal habitat: pelagic, but near the sea floor. Its vertical orientation would have facilitated migration up and down the water column, where it could easily feed on
plankton, which are also vertical migrators. Its diet of plankton would affect its carbon isotopes due to photosynthetic carbon being slightly negative, and even more so if the plankton feed on chemosynthetic bacteria from the methane seeps. Daily vertical migrations would also influence the isotope signals in the shell due to temperature differences from the epipelagic zone to the benthic zone. This could be an explanation for the cyclic nature of carbon and oxygen seen in the sample areas.
References


Figure 1: Fluctuations in $\delta^{13}$C and $\delta^{18}$O along the sampled shell. The grey bars represent ribs. The arrows below the graph indicate sampling on the hook and shafts of the specimen. The trend lines have a moving average of 15.
Figure 2: Diplomoceras vs. benthic and pelagic foraminifera (Dutton 2007). Only the benthic foraminifera are similar isotopically to Diplomoceras. Diplomoceras vs. ammonites (Tobin and Ward 2015) and belemnites (Dutton 2007). The isotope values for ammonites and belemnites display a strong positive correlation with Diplomoceras. This suggests the isotopes we are collecting are typical for Late Cretaceous cephalopods.
Figure 3: Diplomoceras vs. bivalves & gastropods (Tobin and Ward 2015). Overall both bivalve and gastropod values are consistent with typical benthic isotope values and have some overlap with Diplomoceras.