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Stable carbon and oxygen isotopic compositions of Recent charophyte oosporangia and water from Malham Tarn, U.K.: palaeontological implications

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Abstract. Charophyte oosporangia and water samples from a highly calcareous lake were measured for stable carbon and oxygen isotopic composition. The time period over which the oosporangia calcify is short, thus any biochemical relationship between the water and oosporangia's calcite represents only one 'time window' (late Summer in Malham Tarn). This important temporal restraint must also apply to interpretations of all fossil material measured. The $\delta^{18}O_c$ of the charophyte oosporangia is deduced to be in equilibrium with the $\delta^{18}O_w$ of the water for a given temperature. The $\delta^{13}C_c$ of the charophyte oosporangia was approximately 2.5 per mil lower than the $\delta^{13}C_{DIC}$ in the water we measured. With the release of CO_2 with phosphoric acid from the charophyte oosporangia, there was no significant difference in the $\delta^{18}O_c$ values obtained, regardless of whether or not the carbonate was separated from the organic center, however $\delta^{13}C_c$ values were marginally lower for carbonate plus organic center measurements. Our results indicate that fossil charophyte gyrogonites can be used to elucidate the geochemistry of the ancient water body in which they lived.

Introduction

Modern *Chara* (charophytes or stoneworts) are macrophytic green algae found mostly in freshwater environments, although a few species are found in brackish water. The *Chara* have a reproductive cell surrounded by vegetative cells forming an oosporangium which has a calcified layer surrounding the oospore. This calcite structure is known as a gyrogonite, and taphonomically can be considered as 'hard part' preservation. The potential therefore exist to use these gyrogonites to extract biogeochemical information, in a similar manner to other fossil 'hard parts' (shells, teeth, etc.). A prerequisite of any

such use of fossils is that the biochemical relationship between the charophytes and their environment is understood. To address that requirement this work focuses on some Recent charophytes.

Malham Tarn

Malham Tarn is a hardwater lake located 10 miles northwest of Skipton in the county of Yorkshire, UK. It formed where Carboniferous limestone lies unconformably on impervious Silurian slate (O'Connor 1964). The Carboniferous Limestone consists of reasonably pure calcite, and the lake water chemistry is dominated by Ca^{++} and HCO_3^- ions. The lake has the following general characteristics: a pH in the range 8.1–8.7; an annual water temperature range of 0 °C to 20 °C, with a mean of approximately 10 °C; a maximum depth of 4.3m and mean depth of 2.6m; and a total volume of 1.4×10^6 m^3 (Holmes 1965). The lake is fed by a number of small springs and has one outflow at Tarn Foot. Between 80%-90% of the tarn floor is covered by dense stands of the charophyte *Chara globularis* var. *virgata* (Lund 1961), and this alga is a major marl-former (Plate 1, 1–4). There is a significant negative correlation between lake water inorganic carbon content and *C. globularis* biomass, despite the through-flow of water, during peak *C. globularis* growing months (May–August) the dissolved inorganic carbon (DIC) content of the water decreases by approximately 33% (Pentecost 1984). We measured; the oxygen isotopic composition of the lake water ($\delta^{18}O_w$), the carbon isotopic composition of dissolved inorganic carbon (DIC) in the lake water ($\delta^{13}C_{DIC}$), and the oxygen and carbon isotopic compositions ($\delta^{18}O_c$ and $\delta^{13}C_c$) of the mature oosporangia of *C. globularis*, in order to further clarify the relationship between the isotopic composition of the lake water and the biomineralised oosporangia, and establish the biogeochemical potential of fossil gyrogonites (Plate 1, 5–8).

Charophytes

The *Characeae* are macrophytic green algae found mostly in oligotrophic calcareous freshwaters (Wood & Imahori 1965). The majority of *Characeae* species are found at depths of less than 10m and most grow in waters with high pH and high calcium content. The family, unique among algae, has a reproductive cell surrounded by vegetative cells, forming an oosporangium (Plate 1, 1–4). The oosporangium has a calcified layer deposited onto a compound oosporangial wall which surrounds the oospore (Leitch 1991). Calcification occurs within the cell wall of the ensheathing cells, but outside the plasmalemma. The nucleation process is similar to that seen in molluscs; and is therefore an 'extracytoplasmic calcification' (Leitch 1991). The calcite

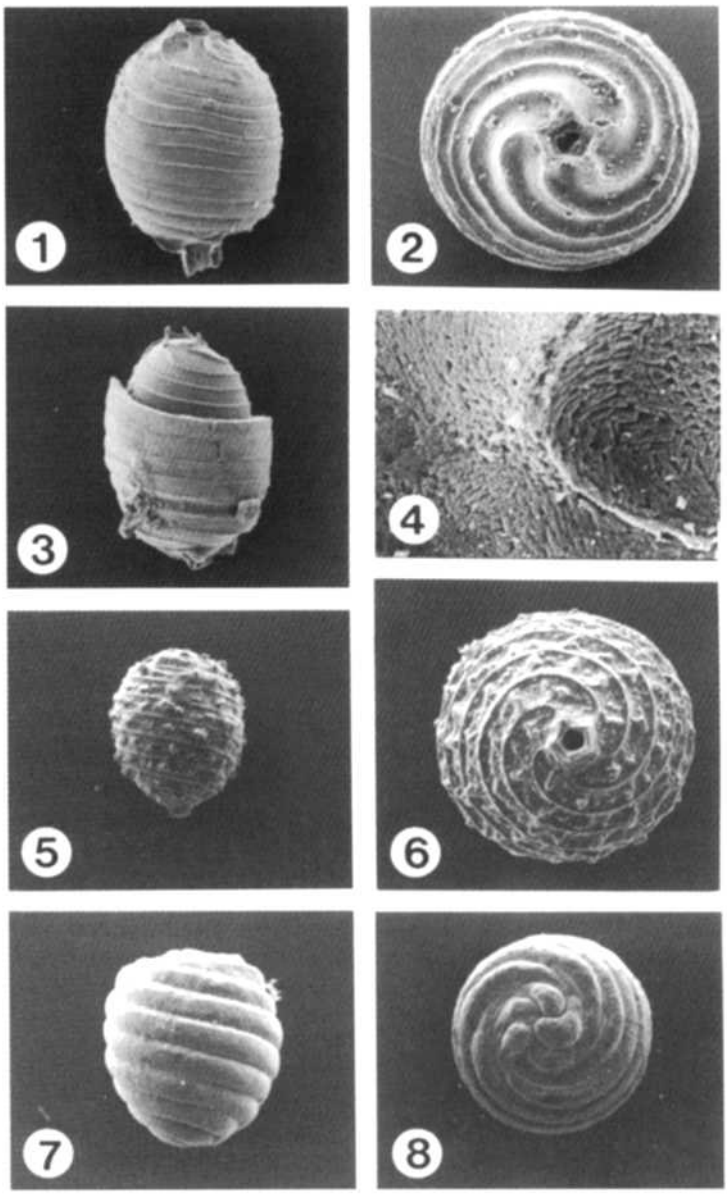

Plate 1. (1) A *Chara globularis* var. *virgata* oosporangium, lateral view. Scale 1 cm = 200 microns. (2) A *Chara globularis* var. *virgata* oosporangium, basal view. Scale 1 cm = 120 microns. (3) A *Chara globularis* var. *virgata* oosporangium with the top part of the calcite sheath broken away to reveal the vegetative cell, lateral view. Scale 1 cm = 200 microns. (4) A high magnification of the surface of the vegetative cell shows impressions of the calcite crystals of the ensheathing cells. Scale 1 cm = 20 microns. (5–8) Fossil gyrogonites from the Eocene of the Isle of Wight, U.K.; (5) *Harrischara vasiformis* (Reid & Groves), lateral view; Scale 1 cm = 400 microns. (6) *Harrischara vasiformis* (Reid & Groves), basal view; Scale 1 cm = 200 microns. (7) *Grovesichara distorta* (Reid & Groves), lateral view; Scale 1 cm = 500 microns. (8) *Grovesichara distorta* (Reid & Groves), apical view; Scale 1 cm = 500 microns.

crystals are tabular and stacked to form spiraling columns (Plate 1, 4). This mode of calcification suggests that the stable oxygen isotopic composition of the ensheathing cell calcite should be in equilibrium with the stable oxygen isotopic composition of the water in which the charophytes calcified (Urey 1947; Epstein et al. 1953; Craig 1965).

Experimental methods

The material was collected from Malham Tarn in the late Summer by grab samples taken in 2m to 3m of water, the water temperature that day was 14 °C. Sampling three weeks previous to this date showed that the oosporangia were then still green and soft, and not sufficiently calcified to yield $CaCO_3$ measurements (no reaction with acid). The oosporangia were fully calcified by the collection day, so there would have been no value in further collecting at a later date (i.e. the isotopic composition was already 'fixed'). The oosporangia were extracted from the bulk mass of collected material by vigorous washing in hot water and sieving. The oosporangia were air-dried immediately and picked from the sieved residue. Approximately 60 oosporangia were used (total weight between 10 and 11 mg) for the isotopic measurements where both the predominantly organic carbon central oospore and the surrounding calcite ensheathing cells were directly placed in phosphoric acid. Samples were measured for $\delta^{18}O_c$ and $\delta^{13}C_c$ following different periods of acid treatment. The measured production of CO_2 indicated that the oosporangium consisted of approximately 60% calcite by weight. For the measurements using only calcite ensheathing cells, the central cortex of the oosporangia was removed by manual crushing and extraction under a binocular microscope, 4 replicates were run. Further pre-treatment to remove any traces of organic matter consisted of soaking overnight in 5% sodium hypochlorite (Grossman & Ku 1986). A sample of Malham water was analysed in duplicate for $\delta^{18}O_w$ using a Salvis CO_2-H_2O equilibrium device on-line with the mass spectrometer. The analytical procedure is based on the method of Epstein & Mayeda (1953). Routine oxygen isotope analysis of a laboratory water standard yields a value of $\delta^{18}O_w = -11.61 \pm 0.06$ per mil (VSMOW) and analysis of the VSMOW international standard yields a value of -0.1 ± 0.1 per mil in our laboratory (Tuebingen). An aliquot of the same water sample was analysed (2 replicates) for the carbon isotope composition of the dissolved inorganic carbon (DIC = CO_2, HCO_3^-, CO_3^{--}) in solution via direct acidification of the sample in an evacuated reaction vessel. The technique used is essentially the same as that described in Sackett & Moore (1966), modified to meet the requirements of our extraction system. Carbonate carbon and oxygen isotopes were analysed on CO_2 released by phosphoric

Table 1. The stable carbon and oxygen isotopic compositions of water collected from Malham Tarn, U.K.

Sample number	$\delta^{18}O_w$ **per mil (SMOW)**
93-13-W-O-7/3	−5.48
93-14-W-O-8/3	−5.45
Mean	−5.46
Sample number	$\delta^{13}C_w$ **per mil (PDB)**
93-888-C	−4.34
93-889-C	−4.77
93-890-C	−5.00
Mean	−4.70 (+/−0.34)

acid treatment using a modified version of the method of McCrea (1950). Analysis of international carbonate standard yields the following values and uncertainties: NBS-19 carbonate; $\delta^{13}C_c = 1.96 \pm 0.02$ per mil (PDB); $\delta^{18}O_c = 28.69 \pm 0.08$ per mil (VSMOW). All isotopic data presented in this paper were measured on a Finnigan MAT gas source mass spectrometer.

Results and discussion

Water results and discussion

The stable carbon and oxygen isotopic compositions of the water sample are shown in Table 1.

The $\delta^{18}O_w$ of −5.46 per mil (VSMOW) for lake water collected in late Summer, is approximately 2 per mil higher than the average composition of the region's precipitation (−7.5 per mil VSMOW). The oxygen isotopic composition of small lakes, such as Malham Tarn, is primarily controlled by the composition of inflow and local precipitation. However shallow lakes are also significantly influenced by evaporation and isotopic exchange with the atmosphere. Most small lakes show significant seasonal variation in their isotopic composition with the highest values typically recorded in late summer (Stuiver 1970; Fritz & Poplawski 1974). It is therefore likely that our value of −5.46 per mil lies towards the uppermost part of the lake's seasonal variation and lies near the mean water oxygen isotopic composition over the short period when the charophyte's oosporangia were calcifying.

A value of $\delta^{13}C_{DIC} = -4.7 \pm 0.3$ per mil (PDB) was obtained for the dissolved inorganic carbon. As with the oxygen isotopic composition, the carbon isotopic composition is subject to seasonal variation and is influenced

Table 2. The stable carbon and oxygen isotopic compositions of the calcite ensheathing cells of oosporangia of *Chara globularis* var. *virgata*. Samples 93-36-C to 93-40-C intact oosporangia, samples 93-77-C to 93-112-C calcite ensheathing cells only.

Sample number	Number of oosporangia	$\delta^{13}C_c$ per mil (PDB)	$\delta^{18}O_c$ per mil (PDB)	Time in acid (hrs/mins)
93-36-C	Approx. 60	−7.56	−5.65	2/0
93-37-C	Approx. 60	−7.99	−5.65	3/18
93-38-C	Approx. 60	−7.78	−5.71	4/36
93-39-C	Approx. 60	−7.52	−5.46	5/55
93-40-C	Approx. 60	−6.92	−5.61	19/39
	Mean	−7.71 +/−0.22*	−5.61 +/−0.09	
93-77-C	Approx. 60	−7.12	−5.64	
93-110-C	Approx. 20	−6.57	−5.76	
93-111-C	Approx. 20	−7.23	−5.75	
93-112-C	Approx. 20	−6.63	−5.93	
	Mean	−6.89 +/−0.34	−5.77 +/−0.12	

* sample 93–40-C omitted.

by a number of factors. Oana & Deevey (1960) identified the main controlling factors to be isotopic exchange with atmospheric CO_2, the isotopic composition of inflowing water, and the decomposition of organic matter. They noted that deep lakes have a pronounced carbon isotopic stratification, with surface waters typically in the range −5 to −9 per mil, and the deeper water typically below −20 per mil. The value of $\delta^{13}C_w = -4.7$ per mil for the Malham Tarn (shallow) water thus falls just outside the typical range of Oana & Deevey (1960). Given the large amount of charophytes that grow in Malham Tarn (covering 80%–90% of the lake floor, the stands up to 30 cm deep; Pentecost 1984), the preferential removal of ^{12}C from the DIC during the charophytes's main growing period (May-August) must significantly affect the carbon isotopic composition of the lake water.

Charophyte results and discussion

The stable carbon and oxygen isotopic compositions of the charophytes are shown in Table 2. The amount of CO_2 evolved from the oosporangia vs. the duration of the acid treatment and its isotopic composition is shown in Figure 1.

Intact versus dissected oosporangia

For the intact oosporangia, samples 93-36-C to 93-40-C, it is assumed that the carbonate in the calcite ensheathing cells was completely dissolved after

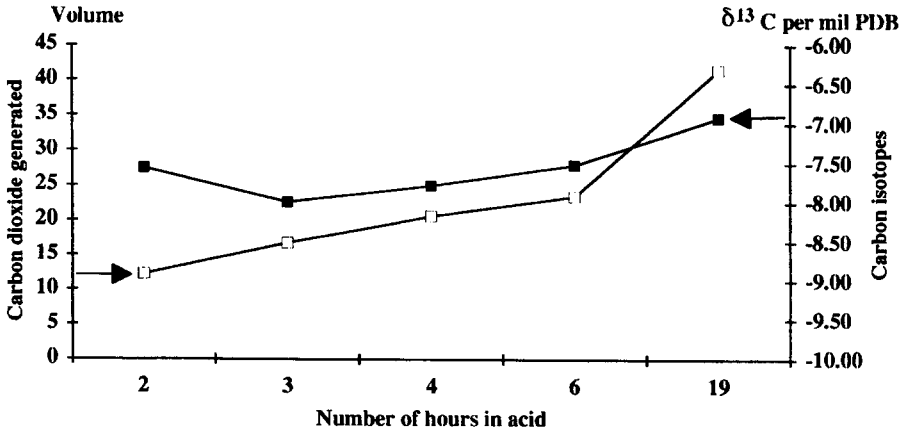

Figure 1. The volume and carbon isotopic composition of CO_2 released when intact oosporangia of *Chara globularis* var. *virgata* were placed in phosphoric acid. The horizontal axis = number of hours in the acid, the white boxes = CO_2 generated, the black boxes = stable carbon isotopic composition.

24 hours reaction time since this is normally an adequate reaction time for calcite (although this is dependent on the calcite fragment size), and no traces of carbonate was observed on the remaining organic cores (under SEM). It thus appears that approximately half the CO_2 is released within the first 5 hours with the rest coming off more slowly (Figure 1). If the carbonate sheath is completely dissolved away in the 19 hr sample, it is possible that contamination of the carbon isotopes may have occurred from acid attack on the organic matter. This however appears unlikely as the 19 hr sample (93-40-C) is isotopically the heaviest and any contamination from the organic core should make the sample lighter. This result is probably due to the scatter in the $\delta^{13}C_c$ data in samples 93-36-C to 93-40-C, and as such, is not significant. The $\delta^{18}O_c$ data show no significant difference for the differing run durations. The isotopic composition of carbonate from calcite ensheathing cells only is shown in samples 93-77-C to 93-112-C, Table 2. The $\delta^{13}C_c$ values are again scattered, and overlap within statistical uncertainty those obtained by the varying duration acid treatment described above; the mean $\delta^{13}C_c$ value is 0.8 per mil heavier for the dissected calcite sheath carbonate. The $\delta^{18}O_c$ values are the same as those above, with a similar degree of scatter. It is concluded that acid digestion of whole oosporangia, regardless of the time in acid, yields reproducible results for the $\delta^{18}O_c$ and $\delta^{13}C_c$ of the carbonate sheath.

These results indicate that there is no need to pre-treat the oosporangia by chemical oxidation or *in vacuo* heating to remove the organic carbon; isotopic composition measurements of the carbonate can be made on intact

oosporangia without affecting the results. With fossil material, this question does not arise, as the organic core is invariably lacking. However, care must be exercised to ensure that the resulting hollow center is not contaminated with other carbonate, such as cement or sediment.

$\delta^{18}O$ carbonate

The $\delta^{18}O_c$ values obtained for charophyte samples 93-36-C to 93-40-C (intact sporangia) have a mean of $\delta^{18}O_c$ (PDB) = -5.61 ± 0.09 per mil. The mean $\delta^{18}O_c$ value obtained for charophyte samples 93-77-C to 93-112-C (calcite ensheathing cells only) is -5.77 ± 0.12 per mil. Putting the measured water $\delta^{18}O_w$ (-5.46 per mil, mean of duplicates) and $\delta^{18}O_c$ (-5.65 per mil, mean of all values obtained) into Hays & Grossman's (1991) equation for meteoric calcite:

$$t°C = 15.7–4.36(\delta_c–\delta_w) + 0.12(\delta_c–\delta_w)^2$$

a temperature of 16.5 °C is calculated, as opposed to the 14 °C measured on the day of collection; however, as stated earlier, the biomineralization was already complete at the time of sampling. Putting the maximum and minimum charophyte calcite $\delta^{18}O_c$ values obtained (-5.46 and -5.93 per mil) into the same equation, suggests a variation of +/−1 °C. Pentecost (1984) records typical Malham Tarn summer water temperatures of 16 °C and notes a significant positive correlation with charophyte biomass and significant negative correlation with the tarn's water calcium concentration; clearly, this is the time when the biomineralisation occurs. Therefore we suggest that biomineralisation occurred at a water temperature of around 16 °C as calculated from Hays & Grossman's (1991) equation. The calcite $\delta^{18}O_c$ component of the charophyte oosporangia is therefore shown to be in probable oxygen isotopic equilibrium with their surrounding waters.

$\delta^{13}C_c$ carbonate

The $\delta^{13}C_c$ values obtained for charophyte samples 93-36-C to 93-39-C (intact sporangia) were mean $\delta^{13}C_c$ (PDB) = -7.71 ± 0.22 per mil. The $\delta^{13}C_c$ values obtained for charophyte samples 93-77-C to 93-112-C (calcite ensheathing cells only) were mean $\delta^{13}C_c$ (PDB) = -6.89 ± 0.34 per mil. Overall the values obtained for the carbonate plus organic centers were lower by approximately 0.8 per mil, possibly as a result of contamination by the organic (predominantly carbon) centre. If the charophytes were in isotopic equilibrium with their environment when the oosporangia biomineralised, then the water should have had a dissolved inorganic carbon composition around 1 per mil lower than the charophytes (Romanek et al. 1992), i.e. −8 per mil; as opposed to the $\delta^{13}C_{DIC}$ −4.7 per mil measured. The large range of the

values $\delta^{13}C_c$ obtained from the oosporangia is significant, reflecting either changes in the water's $\delta^{13}C_{DIC}$ over the very short time during which the oosporangia biomineralised, or $\delta^{13}C_{DIC}$ variations within the lake environs (e.g. isotopic stratification in the water column as described for example by Oana & Deevey [1960]).

Andrews et al. (1993) measured the isotopic composition of cyanobacterial crusts from lakes, including 4 containing stands of charophytes. From the wide range of $\delta^{13}C_c$ values they obtained for the cyanobacterial crusts ($\delta^{13}C_c$ = −6.4 to +1.4 per mil), they speculate that the photosynthetic removal of light carbon by charophytes is not a major mechanism in determining the carbon isotopic composition of aqueous HCO_3^-. Interestingly, Andrews et al.'s (1993) values for cyanobacterial crusts from Malham Tarn of $\delta^{13}C_c$ = −4.53 and −2.93 per mil, would make them approximately in isotopic equilibrium with the lake water for the late summer, assuming our measurements to be valid for their samples.

From the available empirical data, the precise chemical relationship between the charophyte oosporangia's $\delta^{13}C_c$ and the lake water's $\delta^{13}C_{DIC}$ is unclear. This is probably a reflection of the dynamic and complex nature of the lake water's $\delta^{13}C_{DIC}$. A further insight into this relationship is provided by looking at the carbon isotopic composition of other biomineralising biota from Malham Tarn. Three species of freshwater molluscs collected at the same time gave $\delta^{13}C_c$ values of *Pisidium corneum* −6.18 +/−0.27 per mil, *Valvata pulchella* −8.18 +/−0.32 per mil, *Bathyomphalus contortus* −11.22 +/−0.35 per mil (data from Jones et al., in preparation). Discounting the $\delta^{13}C_c$ value for *B. contortus* which probably acquired their light composition as a result of ingesting isotopically light plant matter, it is important to note both the similarity and the variations of the mollusc values to the charophyte values, and the implications this has for the use of fossil gyrogonites for biogeochemistry.

Palaeobiological implications

Background

We have established that charophyte oosporangia are biomineralised in oxygen (and possibly carbon) isotopic equilibrium with their surrounding waters. The combination of this improved understanding of the biochemistry of modern charophytes, along with the 'hard part' preservation of fossil gyrogonites (Plate 1, 5–8), allows us to adopt an actuopalaeontological (Ferguson 1993) approach to the biogeochemistry of these algae. This approach however, not only needs to take into account accepted reservations about 'nearest

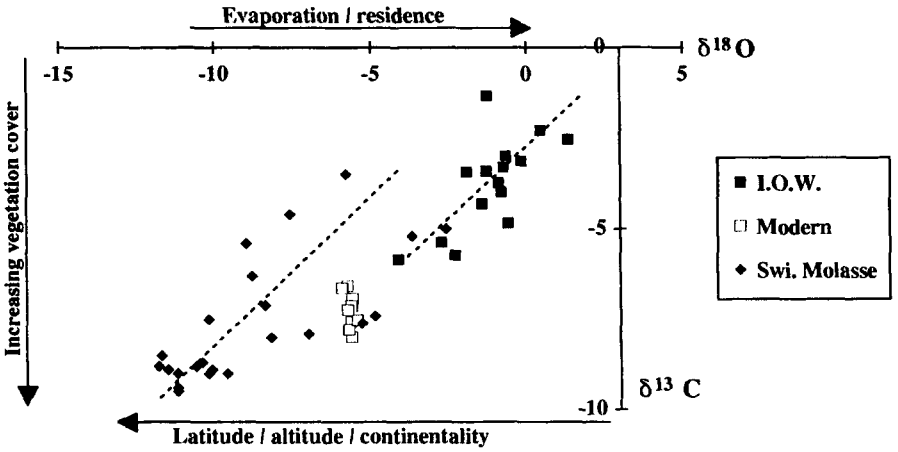

Figure 2. The carbon and oxygen isotopic compositions of Recent *Chara globularis* var. *virgata* from Malham Tarn, and suites of fossil gyrogonites from the Isle of Wight and the Swiss Molasse. The principle controlling factors are from Talbot (1990). The dashed lines are simple regression fits for the two separate fossil data sets.

living relatives' analyses, but also to allow for the rapid and complex variations which exist in the carbon and oxygen isotopic compositions of freshwater ecosystems. Biogeochemical information obtained will relate only to the short 'time window' when the ancient charophyte oosporangia biomineralised. However comparisons between different suites of fossil gyrogonites, potentially do themselves provide important palaeoenvironmental information.

Fossil gyrogonites

An example of the potential palaeontological implication of stable isotopes studies of gyrogonites (Figure 2) is provided by a suite of latest Eocene material from the Isle of Wight, U.K. (Feist-Castel 1977; Collinson et al. 1993; Hooker et al. 1995), (data from Jones et al. in preparation), sample numbers = 15, correlation ceofficient = 0.63; and a selection of gyrogonites from the Oligo-Miocene Molasse of western Switzerland (data from Berger 1990), sample numbers = 25, correlation coefficient = 0.75. The arrows and labels on Figure 2 are adapted from Talbot's (1990, Figure 7, page 270) schematic summary of principle environmental controls on isotopic compositions. Both fossil data sets include several different species of gyrogonites.

The charophytes from the Isle of Wight deposits (Bembridge Limestone Formation, Daley & Edwards (1990), Bed 6C – Collinson et al. 1993) accumulated in shallow, freshwater lakes or ponds (Collinson et al. 1993). The

Swiss material was deposited in a freshwater lake, during periods of hot and humid climate (Oligocene), followed by a temperature and humidity crisis (end Oligocene), and finally warm and low humidity conditions (Lower Miocene) (Berger 1990).

The mean carbon and oxygen isotopic compositions of the Swiss samples are isotopically lighter than those from the Isle of Wight. The slopes of simple regression lines fitted to the two fossil data sets are similar. The most obvious features of the data shown in Figure 2 are the linear correlations between the oxygen and carbon isotopes and the separate groupings for the two sets of fossil data. Talbot (1990) notes that:

> Within individual Basins, covariant trends may have remarkable long-term persistence despite major environmental changes.

Discussion

The covariance of carbon and oxygen isotopes in ancient lacustrine deposits is well established (e.g. in primary [abiogenic] carbonates, Talbot 1990; in freshwater molluscs, Fritz 1975; Fritz & Poplawski 1974), and have been used for palaeolimnological interpretations (Covich & Stuiver 1974; Keith et al. 1964). Any covariance of carbon and oxygen isotopes in carbonates is a result of covariance of the carbon and oxygen isotopic compositions of the lake water in which they formed (Mook & Vogel 1967; Pitty 1971), assuming they mineralized in equilibrium. A linear correlation between $\delta^{13}C_{aq}$ (DIC) and $\delta^{18}O_{aq}$ has been demonstrated for modern lake water by Fritz & Poplawski (1974).

Five variables are considered to be the principal controls on the oxygen isotopic composition (Talbot 1990), evaporation, residence time, latitude, altitude and continentality. Of these the palaeolatitude, palaeocontinentality and palaeoaltitude for these deposits are reasonably well-understood from palaeogeographical studies and lithostratigraphical correlations with marine deposits. Further indications on whether the lake was an 'open' or 'closed' hydrological system can potentially be obtained from the degree of correlation of the carbon and oxygen isotopes, higher correlation coefficients (R^2) values (for primary carbonates $R^2 \geq 0.7$) indicate a 'closed' regime (Talbot 1990); however, the fossil data sets shown here are probably too small and/or cover too long a period to be statistically significant. It is concluded that the most likely principal causes of the difference between the oxygen isotopic compositions of the two data sets is the more 'continental' nature and higher palaeoaltitude of the Swiss deposit.

Talbot (1990) lists increasing or decreasing vegetation cover as the principle controlling factor for the $\delta^{13}C$. With the two fossil data sets, the Swiss material is significantly isotopically lighter, thus indicating increased vegetation at this site (Berger 1990); it is therefore interesting to note that Collinson et al. (1993), inferred patchy wetlands with areas of open water, and little evidence for marginal woodland and forest for the Isle of Wight deposit. Another potential item of information which could be derived from the covariance of the carbon and oxygen isotopes in gyrogonites is the surface area:depth ratio of the lake; typically the steeper the regression line, the lower the surface area:depth ratio (for primary carbonates; Talbot 1990). For the two fossil data sets shown the slopes of the regression lines are very similar, suggesting similar ratios. The use of this last relationship is probably limited with gyrogonites, since modern charophytes tend to found in shallow waters (typically 10 metres or less); however they can be found in shallow areas within lakes, for example Lake Tanganyika.

Conclusion

An isotopic study has been undertaken on the water and charophytes in Malham Tarn to investigate the suitability of these organisms for palaeobiological applications. This was based on the obvious premise that an adequate understanding of isotopic systems (obtained using modern examples where many more of the parameters can be directly measured), is essential before a meaningful interpretation of fossil systems (containing similar biota) can be undertaken. The measurement of the carbon and oxygen isotopic composition of the calcium carbonate component of the charophyte's oosporangia, indicates that the calcite's $\delta^{18}O_w$ value is apparently in equilibrium with the water's $\delta^{18}O_w$. The similarity of the $\delta^{13}C_C$ value of the charophyte calcite to most of the mollusc species $\delta^{13}C_C$ values, supports the view that Malham Tarn water's mean $\delta^{13}C_{DIC}$ composition was in the region of = -9 per mil, during the period when these organisms biomineralised; and the charophyte $\delta^{13}C_C$ is probably in equilibrium with its environment. This has important palaeontological applications, given the presence of charophyte gyrogonites in the fossil record. Biogeochemical studies of these plant fossils can provide valuable insights into the chemistry of the ancient water bodies in which they grew.

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