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The last glacial-interglacial cycle in Lake Ohrid (Macedonia/Albania): testing diatom response to climate

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Abstract

Lake Ohrid is a site of global importance for palaeoclimate research. This study presents results of diatom analysis of a ca. 136 ka sequence, Co1202, from the north-east of the lake basin. It offers the opportunity to test diatom response across two
5 glacial-interglacial transitions and within the Last Glacial, while setting up taxonomic protocols for future research. The results are outstanding in demonstrating the sensitivity of diatoms to climate change, providing proxy evidence for temperature change marked by glacial-interglacial shifts between the dominant planktonic taxa, *Cyclotella fottii* and *C. ocellata*, and exact correlation with geochemical proxies to mark the start of
10 the Last Interglacial at ca. 130 ka. Importantly, diatoms show much stronger evidence in this site for warming during MIS3 than recorded in other productivity-related proxies, peaking at ca. 39 ka, prior to the extreme conditions of the Last Glacial maximum. In the light of the observed patterns, and from the results of analysis of early Holocene sediments from a second core, Lz1120, the lack of a response to Late Glacial and
15 early Holocene warming from ca. 15–7.4 ka suggests the Co1202 sequence may be compromised during this phase. After ca. 7.4 ka, there is evidence for enhanced nutrient enrichment compared to the Last Interglacial, following by a post-Medieval cooling trend. Taxonomically, morphological variability in *C. fottii* shows no clear trends linked to climate, but an intriguing change in central area morphology occurs after ca. 48.7 ka,
20 coincident with a tephra layer. In contrast, *C. ocellata* shows morphological variation in the number of ocelli between interglacials, suggesting climatically-forced variation or evolutionary selection pressure. The application of a simple dissolution index does not track preservation quality very effectively, underlining the importance of diatom concentration data in future studies.

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1 Introduction

Ancient Lake Ohrid is a site of global importance for long-term palaeoclimate reconstruction, with its long sediment record and important geographic location between the Mediterranean and Western Europe (Wagner et al., 2008). Its value also extends to testing hypotheses concerning biodiversity and the evolution of endemism in ancient lakes (Albrecht and Wilke, 2008).

Elsewhere, Lake Baikal, Siberia, is the prime example of an ancient graben in which extensive limnological and palaeolimnological research has demonstrated that diatoms (single-celled siliceous protists, commonly referred to as “algae”) are the most important palaeoclimate proxy (Mackay, 2007). Mackay (2007) notes that although diatoms tend to be absent during glacial phases, they are the most consistently preserved biological proxy in the sediment record. In concert with modern limnological studies, palaeolimnological analysis of diatom data has been of fundamental importance in allowing a series of competing hypotheses to be tested concerning the limnological response to climate change in this complex system.

Previously, Quaternary research in the circum-Mediterranean has had a strong bias towards vegetation change and/or quantitative pollen-based modelling of temperature and precipitation (e.g., Allen, 1999; González-Sampériz et al., 2005), sometimes combined with physical evidence for shoreline displacement and lake-level change (Digerfeldt et al., 2000). Research on glacial-interglacial climate change in tectonic and volcanic lakes with relatively long sediment records has demonstrated that, while vegetation change appears to track glacial-interglacial climate change closely (e.g., Tzedakis et al., 2004; Allen and Huntley, 2009), the response is not linear, and uncertainty in regard to factors such as time lags in response hampers understanding of abrupt events in particular (Tzedakis, 2005; 2007).

The geographic influence of abrupt North Atlantic climatic events across terrestrial environments of Southern Europe and the Mediterranean during the last glacial-interglacial cycle is still uncertain (Wohlfarth et al., 2008; Wagner et al., 2010). It is only

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surprisingly recently that the potential of diatoms has been exploited to test hypotheses of climate change in this topographically and climatically diverse region. Diatom response to glacial-interglacial climate change has been demonstrated clearly for Italian crater lakes (Ryves et al., 1996). In Lake Ioannina, NW Greece (Wilson et al., 2008), diatom shifts across the last glacial-interglacial transition provided the first convincing evidence for the impact in NW Greece of a Younger Dryas type abrupt reversal to cold, arid conditions during late glacial warming, in a relatively humid location where vegetation response was subdued (Lawson et al., 2004). During the Last Glacial period, diatom-inferred fluctuations in lake level and productivity during marine isotope stage MIS3 – MIS2 in Les Echets, southeast France (Ampel et al., 2008; Wohlfarth et al., 2008) correlated closely with the climatic oscillations between Heinrich events and warmer Dansgaard-Oeschger interstadials which are strongly evident in the North Atlantic (e.g., Broecker, 2002) and Western Mediterranean (Cacho et al., 1999) marine record, and are arguably of hemispheric extent.

In comparison with most other ancient lakes, palaeolimnological research is in its infancy in Lake Ohrid. In advance of an International Continental Scientific Deep Drilling Project [ICDP], this study tests the response of diatoms to relatively well understood, major climate events during MIS6 (the penultimate glacial) to MIS1 (the Holocene). Core Co1202 is a well-dated sequence for which geochemical data are already published (Vogel et al., 2010a,b). Unlike the previous study of the last ca. 40 ka preserved in core Lz1120 from the south of the basin (Wagner et al., 2009), which had a hiatus from 14.6 to 9.4 cal. ka BP, and a pioneering low resolution study of a core to the north of the basin by Roelofs and Kilham (1983), this new record offers the potential to test response to major events across two glacial-interglacial transitions and during the Last Glacial, within the temporal limits of analytical resolution adopted here. In the spirit of setting up protocols for future international collaboration, we also focus on taxonomic harmonization, while exploring morphological response at a sub-species level in the dominant planktonic taxa.

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2 The study site

Lake Ohrid straddles the border of Macedonia and Albania in Southern Europe (41°01' N; 20°43' E; Fig. 1) and is located at 693 m a.s.l. (e.g., Stankovic, 1960) in the karstic mountainous region which extends in a continuous belt from the Dinaric Alps of Bosnia and Montenegro to the northeast, to the Pindus Mountains of Greece to the south. The lake has a surface area of 358 km² and maximum depth of 289 m. This is relatively small compared to other ancient graben lakes such as Baikal, Malawi or Tanganyika, so it has the potential advantage that it does not span several climate zones. Due to its topographic location, the climate is more continental than true Mediterranean climate zones, with hot, dry summers and cold winters (mean annual rainfall of 800–900 mm, maximum temperature <31.5 °C and minimum temperature >−5.7 °C; Vogel et al., 2010). Its open karst geology is an important influence both on the hydrology and nutrient budget of the lake; 55% of the inflow is from subterranean springs, and more than half of this volume is derived from a large aquifer which links Ohrid to Lake Prespa, located at a higher altitude 10 km to the east.

Lake Ohrid is highly oligotrophic (Stankovic, 1960; Ocevski and Allen, 1977), although there are concerns that a switch to a more eutrophic state is going on (Matter et al., 2010) or may occur in future due to global warming and local anthropogenic impact (Matzinger et al., 2006, 2007).

3 Methods

The core Co1202 was collected from 145 m water depth in a coring location to the northeast of the lake (Fig. 1) using UWITEC piston and gravity coring equipment (www.uwitec.at; Vogel et al., 2010a); core sections were stored in the Cologne laboratory at 4 °C. After correlation of individual core sections from which to construct a 14.89 m composite master sequence, firm chronological control was achieved through a combination of radiocarbon dating and tephrochronology. The chronology

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adopted here is that of Vogel et al. (2010a; see also Sulpizio et al., 2010), derived from linear interpolation between tie lines. The sequence investigated here (1489–17 cm depth) extends from ca. 135 ka to ca. 280 yrs BP. A ca. 16 ka hiatus has been identified within, between 97.6 and 81.7 ka, occurring between subsamples at 1098.4 cm and 1052.1 cm depth in this study.

For diatom analysis, ca. 1 cm³ subsamples were taken every ca. 24 cm (ca. 600 a to >3 ka resolution), placed in sealed rigid sterile plastic containers and shipped to Hull, UK. Half the sediment was subsampled again into small Sterilin tubes and shipped to Skopje, Macedonia for parallel analysis, being refrigerated again thereafter. In a preliminary study, the influence on diatom species assemblage composition of a range of different laboratory preparation techniques was investigated in Skopje, and proved to have little influence on diatom preservation. In the UK, slides were therefore prepared using standard techniques (Battarbee, 1986), using hot 30% H₂O₂ to oxidize organics, and a few drops of conc. HCl to remove carbonates; slides in Macedonia were prepared using cold H₂O₂, left overnight, and treatment with KMnO₄ prior to treatment with HCl and heating in a water bath for 30 min, with centrifuging between stages. Microscope slides were prepared using Naphrax™ as a mountant. To allow parallel counting of the full sequence by both laboratories, around 350 rather than 500 valves per slide were counted where preservation was relatively good; this should be sufficient to give good representativity in low-diversity assemblages such as in Lake Ohrid and to distinguish any major sub-species shifts in morphological variability. Diatoms were counted under oil immersion at ×1000 magnification on a Zeiss Axioscop 2 Plus in the UK. They were identified using standard texts (Krammer and Lange-Bertalot, 1991a, b, 1996, 1998, 2000), and the dedicated Ohrid works of Hustedt (1945) and Levkov et al. (2007). A standard transect-based approach to counting (Battarbee, 1986) was adopted.

Ohrid's diatom flora is dominated during the Late Quaternary by two planktonic centrics, the endemic *Cyclotella fottii* Hustedt (syn. *C. hustedtii*) and the cosmopolitan *Cyclotella ocellata* Pantocsek. Following recent modern taxonomic (Levkov et al., 2007) and palaeolimnological study (Wagner et al., 2009), it is clear that the two taxa

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described previously by Hustedt (1945) and Jurilj (1954) as *Cyclotella fottii* (valve diameter 40–90 μm) and *Cyclotella hustedtii* (valve diameter 20–30 μm), occur instead on a continuum, including in the range <20 μm and 30–40 μm , and have been merged as a consequence. Palaeolimnological variation in valve size could reflect important differences in limnological parameters such as mixing or light penetration, or the taxon may represent a species complex and should indeed be split at species level into various size classes (cf. Flower, 1993). Similarly, *C. ocellata* is highly variable morphologically, and probably represents a species complex (Håkansson, 2002). Since different morphotypes may exhibit different ecological preferences, numerous attempts have been made to explore variation according to parameters including valve diameter, number of ocelli and the morphology of the central area (e.g., Genkal and Popovskaya, 2008).

The criteria for taxonomic splitting in Macedonia and the UK are summarized in Table 1. With the primary aim of investigating the changing presence and absence of taxa over time to feed into evolutionary studies, the Macedonian team split *C. fottii* into 10 μm size classes. Since it is impossible to estimate valve diameter this accurately when the marginal area is dissolving, all partially-dissolved taxa were classed as “dissolved”. In the UK, *C. fottii* was split at a lesser resolution into “large” (>ca. 20 μm diameter) and “small” (<ca. 20 μm diameter), allowing stages of dissolution (pristine, striae missing, central area plus few striae preserved) to be identified for each size class, with a smaller proportion of valves designated as “dissolved”, where the valve diameter could not be discerned. In Macedonia, *C. ocellata* was split both by number of ocelli and by morphology of the central area, with a single dissolved category. To assign a larger proportion of valves to morphotypes, *C. ocellata* was split in the UK solely by number of ocelli, which can often be recognized in poorly-preserved specimens, using a 3-stage dissolution scale for each. Criteria were also set for taxonomic harmonization within the more diverse, and often endemic, facultative planktonic and benthic taxa, which have already been revised by Levkov et al. (2007). Since they are present at low abundance, the data for benthic taxa presented here are confined to the UK results; the Macedonian data will form the focus for future taxonomic studies. In

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the plankton-dominated lake, following Wilson et al. (2008), a plankton-only dissolution scale was applied, to prevent skewed results from complete valves of robust taxa such as small Fragilariales.

Counts were converted to percentage data and displayed using Tilia and TGView v. 2.0.2 (Grimm, 1991). Zone boundaries were defined with aid of Constrained Incremental Sum of Squares cluster analysis (Grimm, 1987).

Multivariate statistical techniques are often used to summarise variation in diatom data for palaeolimnological correlation and – importantly – for external correlation with global or regional palaeoclimate data. The influence of different splitting techniques on apparent variation in the diatom data was explored using indirect ordination techniques on three different diatom data-sets: UK unsplit (*C. fottii* and *C. ocellata* as single taxa), UK split and the full Macedonian split (Table 1), using the programs CANOCO (ter Braak and Šmilauer, 2002) and C2 v. 1.4.2 (S. Juggins). Initial detrended correspondence analysis gave gradient lengths of <2.5. At a gradient length of <2.5, the appropriate ordination technique was selected as correspondence analysis (CA) (Jongman et al., 1995), performed using downweighting of rare species.

4 Results

4.1 The influence of splitting techniques on diatom variability

Fifty-six diatom taxa were identified in the split UK data-set, compared to 92 taxa in the Macedonian data-set. The difference was due mainly to the additional criteria for splitting the two dominant planktonic taxa (Table 1) and in part to the more rigorous identification of rare valves (<1% occurrence) of endemic taxa such as *Diploneis* spp. which were merged in UK counts. A comparative plot of Axis 1 scores (Fig. 2) shows that there is little effect of lumping versus splitting of *C. fottii* and *C. ocellata* in the UK data-set (49.1% and 64.4% of the variance contained cumulatively in Axis 1 and Axis 2 for the lumped data, and 35.4% and 55.4% for the UK split). In contrast, the

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status, with an increase in dissolved centres of *C. fottii*, and rare *C. ocellata* at the upper zone boundary. COD6 (229.8–17 cm) is a major transition to a zone of good preservation, in which *C. fottii* morphotypes are co-dominant with *Stephanodiscus galileensis*, which occurs for the first time, consistently at >10% abundance, and *C. ocellata*, which is now dominated by “classic” valves with 3 ocelli. A return to interglacial conditions may be inferred. *Cyclotella ocellata* increases in abundance to a peak of 45% at 122.2 cm, after which *C. fottii* increases towards the top of the sequence at the expense of *C. ocellata* (5–10%) and *S. galileensis* (ca. 5%). A relatively wide range of facultative planktonic and benthic taxa are again present at low abundance, the notable exception being a 15% peak in *Gomphonema pumilum* at 74.2 cm depth. The maintenance of the more thermophilic planktonic taxa, and the peak in facultative planktonic and benthic taxa, indicate this is not a return to full glacial conditions.

5 Discussion

Summary diatom data are compared chronologically with selected data from Vogel et al. (2010b) in Fig. 4. Tephra layers occur at 1447–1440 cm, 825–822 cm, 696–689 cm, 620–617 cm and 277.5–269 cm, none of which correlate with diatom zone boundaries to suggest volcanic rather than climatic influence. Where appropriate, comparison is also made with the diatom zones of core Lz1120 (Wagner et al., 2009).

5.1 Palaeoclimate reconstruction

In general, there is strong correlation between diatom-inferred palaeoclimate change and geochemical inferences attributed mainly to shifts in within-lake productivity represented by carbonate, organic and biogenic silica content.

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5.1.1 The penultimate glacial, MIS6: COD1 (1489–1412.6 cm; ca. 135.4–127.4 ka)

Following previous glacial-interglacial comparisons (Roelofs and Kilham, 1983; Wagner et al., 2009), the dominance and poor preservation of *C. fottii* in diatom zone COD1 reflects cold, glacial conditions at the end of MIS6. As noted by Vogel et al. (2010b) this is in accord with pollen-based temperature estimates (Allen and Huntley, 2009). The Termination II transition occurs at 127.3 ka in the diatom record, matching exactly the transition in the lithofacies approach of Vogel et al. (2010b). From Fig. 4, the trend towards increasingly high negative CA Axis 1 scores correlates with the carbonate curve, starting below the upper COD1 zone boundary, and correlating with absence of ice-rafted debris from ca. 130 ka (Vogel et al., 2010b). The proxy data are in accord in showing strong evidence for global climate change, with the onset of MIS5e *sensu stricto* (130 ± 2 ka; Hearty et al., 2007).

5.1.2 MIS 5: COD2 (1412.6–1110.4 cm; 127.4–99.0 ka)

In MIS5, the increasing dominance of epilimnetic taxa suggests the delayed onset of stable, warm surface waters after 130 ka, in support of the previous geochemical interpretation of an unstable, stepwise transition (Vogel et al., 2010b). The prolonged diatom-inferred warm, stable phase at the start of COD2a (1412.6–1310.2 cm; 127.4–116.5 ka) correlates strongly with trends towards maxima in biogenic silica and carbonate content, suggesting sustained temperature increase during the spring and summer. The initial transition to high abundance of *C. ocellata* and low CA Axis 1 scores appears abrupt (unlike the stepwise transition in geochemical indicators), but at this resolution (ca. 2.5 ka between diatom subsamples) the data are not definitive. COD 2b (1310.2–1110.4 cm; 116.5–99.0 ka) is marked by the renewed dominance of *C. fottii*, strongly indicative of cooling, and is again matched by a decreasing trend in biogenic silica and carbonate content in the sediments. The inferred minimum temperature at ca. 108.4 ka in geochemical data correlates with a peak of >20% rather than a minimum in *C. ocellata*, suggesting correlation with the North Atlantic C24 event (Vogel et al.,

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2010) is unreliable. A short-lived trend in rising *C. ocellata* abundance and increasingly negative CA Axis 1 scores correlates well with geochemical data indicative of renewed warming thereafter, in interstadial MIS 5.3 (Vogel et al., 2010b). Overall, the diatom data match evidence for a return to glacial conditions after ca. 119 ka in Lake Baikal. This marks the end of MIS5d, the peak of the Last Interglacial (119 ± 2 ka; Hearty et al., 2007) again suggesting Ohrid is responding to global climate change linked to changes in orbital parameters (Mackay, 2007).

5.1.3 MIS 4-2: COD3-COD5a (1110.4–347.6; 99.0–13.8 ka)

The Last Glacial period is clearly recorded in the diatom record, with maximum cooling indicated during the Last Glacial Maximum, MIS2, by very poor preservation of *C. fottii* in COD5.

The diatom record is outstanding in providing the first clear evidence for warming during interstadial MIS3, during COD 4 (57.6–31.3 ka), culminating in a minor peak in *C. ocellata* at 39.3 ka (COD4b) indicative of warming. Previously, minor associated peaks in biogenic silica and organic content were considered inconclusive, but this study suggests their significance. The first geochemical results from the shallower feeder lake, Lake Prespa (Wagner et al., 2010) demonstrate a more marked signal for this phase, but the authors' initial conclusion that the event is not marked in Ohrid was premature; it supports the inference that diatoms respond rapidly and sensitively to warming of surface waters. The value of these proxies is all the more important because oxygen and carbon stable isotope data cannot be generated in glacial phases due to low carbonate content (Leng et al., 2010).

The phase also correlates approximately with the basal diatom zone (D1) of the Lz1120 sequence, which is co-dominated by well preserved assemblages of *C. ocellata* and *Discostella stelligera* (ca. 38.7–37.5 ka) prior to major inferred cooling (Wagner et al., 2009). Represented by only two samples, and without supporting geochemical variation, this had previously been interpreted with caution. *D. stelligera* is absent in Co1202, and Lz1120 is also distinguished by the greater dominance over *C. fottii* of

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epilimnetic plankton (>40%) and in number and abundance of benthic taxa. This might reflect spatial variability across the basin due to differences in interlinked parameters such as river and spring discharge, nutrient input, temperature, water depth, distance from the littoral zone or mixing. The Co1202 site (145 m water depth) is deeper than Lz1120 (105 m); TOC/TS indicates less oxic bottom waters in the former as they are close to or below the summer thermocline in the modern lake, with additional evidence from lipid biomarkers for differences in river discharge (Holtvoeth et al., 2010). Equally, the differences may be due to the effects of enhanced dissolution in Co1202; Lz1120 had a higher sediment accumulation rate (Holtvoeth et al., 2010), but slightly reduced mixing conditions in Co1202 would be more likely to favour preservation in the sediment record. If dissolution is a factor, this suggests it is likely to have occurred in the sediment column, prior to burial. A transect-based diatom study and, as noted, dissolution studies, would allow these hypotheses to be tested in more detail.

5.1.4 Last glacial-interglacial transition and the Holocene: COD5b – COD6 (347.6–17 cm; 13.8–0.3 ka)

It is surprising that the diatom record does not show a strong response to Late Glacial warming from ca. 15 ka, leading up to the start of the Holocene at ca. 11 ka. Instead, COD5b (13.8–6.9 ka) shows closer affinity with glacial phases, being dominated by *C. fottii*. This is clearly in part a function of extremely sparse assemblages with poor diatom preservation in the upper three samples of COD5 (prior to 6.9 ka). Again, diatom concentration data would demonstrate this more clearly. While the CA Axis 1 scores do appear to show the predicted trend towards higher negative scores, correlating with a trend in organic and carbonate content from ca. 15 ka, the lack of response in *C. ocellata* is mirrored by complacently low biogenic silica prior to ca. 7 ka. Taken at face value, the data indicate that rapid "Holocene" warming did not occur until the mid-Holocene. The sediment record does show evidence for the maintained deposition of ice-rafted debris during the Late Glacial, to support this. In the light of the diatom sensitivity to earlier climate fluctuations, and to the clear diatom-inferred evidence for warming by

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9.4 ka after a hiatus in core Lz1120 (Wagner et al., 2009), however, it is more likely that the sequence is compromised during this phase in core Co1202. It is not possible to test the impact of the well known climatic reversals of the Younger Dryas and 8.2 ka event (which here has not been sampled for diatoms). The resolution of the diatom record in this study is also too low to comment on abrupt change during the Holocene. It is notable for the first appearance of *Stephanodiscus galileensis* in the record, possibly indicating greater nutrient enrichment than in the previous interglacial; this declines in the post-Medieval period (last ca. 2000 a), which appears to show a cooling trend.

5.2 Diatom dissolution

The 3-point plankton diatom dissolution index adopted here proved not to be very sensitive, due in part to the unusual and temporally variable dissolution series of *C. fottii*, with its robust edge striae and margin, and to the preservation of small, relatively fragile dissolving centres of *C. ocellata* in zones of good preservation. The percentage of pristine, complete planktonic valves in Fig. 4 does track broad shifts from interglacial (high) to glacial (low preservation), and shows a clear minimum during the Last Glacial Maximum (COD5), supporting the interpretation of maximum cooling during this phase. Since the proportion of facultative planktonic and benthic taxa is so low, the profile is similar to that which would be produced using all valves, a simple index which has proved to be effective in Baikal studies, and is termed the F index (Mackay et al., 1998). As demonstrated in the study of Lz1120 (Wagner et al., 2009), it would be useful to combine this approach with the calculation of absolute diatom concentration (Battarbee and Kneen, 1982) in future studies on Ohrid.

The degree to which dissolution may have biased species assemblage composition is difficult to assess. *Asterionella formosa*, for example, is common in the modern lake (Levkov et al., 2007) but almost absent in the sediment record. While the results support the integrity of diatoms as a sensitive tracer of climate change, further studies are necessary (cf. Ryves et al., 2003) to test how far assemblages may be affected by taphonomic processes operating in the water column and sediment record.

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5.3 Morphological variability

The intriguing shift in central area morphology of *C. fottii*, which was observed clearly at 821.5 cm by both laboratories, occurred at ca. 48.7 ka, immediately after deposition of a tephra layer. It is unlikely that a single eruption would cause a permanent morphological shift, so this is difficult to explain. Other than this, *C. fottii* does not appear to show any significant trends in size classes other than those related to dissolution effects, such that the Last Glacial Maximum is dominated by larger, more robust valves. There is insufficient space here to report the full Macedonian results, but the lack of variability between 10 μm size intervals is reflected in the complacency of CA Axis 1 scores during glacial phases (Fig. 2). The co-dominance of large and small valves through glacial-interglacial cycles in Fig. 3 suggests little evolutionary change in this endemic taxon.

In contrast, *C. ocellata* exhibits a major shift from dominance by valves with 5 ocelli during the Last Interglacial, to valves with 3 ocelli in the Holocene. The presence of pristine valves with unusual central area morphology (unpubl. Macedonian data) is also more common in the Last Interglacial. A future, higher resolution study dedicated to *C. ocellata* alone is necessary to explore these trends in more detail; the shift suggests climatically-forced variation or evolutionary selection pressure.

6 Conclusions

In advance of an ICDP deep drilling project, this study demonstrates clearly the response of Lake Ohrid to global climate change. As in Lake Baikal, the results are outstanding in demonstrating the sensitivity of diatoms to climate change, providing proxy evidence for the character of temperature change during the Last Interglacial, and much stronger evidence in this site for warming during MIS3 than recorded in other productivity related proxies. Higher resolution studies will be necessary to test the impact of more abrupt climate events, and to establish in more detail the character

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of glacial-interglacial transitions, which appear abrupt at this relatively low resolution. It has also shown that the Late Glacial-mid-Holocene record may be compromised in Co1202. There is clear potential for more detailed studies of evolution and endemism, to test whether diatoms are tracking climate change or are responding to different evolutionary selection pressures, and the study has been successful in setting up taxonomic protocols for future research.

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References

- 10 Albrecht, C. and Wilke, T.: Ancient Lake Ohrid: biodiversity and evolution, *Hydrobiology*, 615, 103–140, 2008.
- Allen, J. R. M. and Huntley, B.: Last interglacial palaeovegetation, palaeoenvironments and chronology: a new record from Lago Grande di Monticchio, Southern Italy, *Quaternary Sci. Rev.*, 28, 1521–1538, 2009.
- 15 Allen, J. R. M., Brandt, U., Brauer, A., Hubberten, H.-W., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J. F. W., Nowaczyk, N. R., Oberhansli, H., Watts, W. A., Wulf, S., and Zolitschka, B.: Rapid environmental changes in Southern Europe during the last glacial period, *Nature*, 400, 740–743, 1999.
- Ampel, L., Wohlfarth, B., Risberg, J., and Veres, D.: Paleolimnological response to millennial and centennial scale climate variability during MIS 3 and 2 as suggested by the diatom record in Les Echets, France, *Quaternary Sci. Rev.*, 27, 1493–1504, 2008.
- 20 Battarbee, R. W.: Diatom analysis, in: *Handbook of Holocene Palaeoecology and Palaeohydrology*, edited by: Berglund, B. E., Wiley, Chichester, 527–570, 1986.
- Battarbee, R. W. and Kneen, M. J.: The use of electronically counted microspheres in absolute diatom analysis, *Limnol. Oceanogr.*, 27, 184–188, 1982.
- 25 Broecker, W. S.: Massive iceberg discharges as triggers for global climate change, *Nature*, 372, 421–424, 2002.
- Cacho, I., Grimalt, J. O., Pelejero, C., Canals, M., Sierro, F. J., Flores, J. A., and Shackleton, N.:

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- Dansgaard-Oeschger and Heinrich event imprints in Alboran Sea paleotemperatures, *Paleoceanography*, 14, 698–705, 1999.
- Digerfeldt, G., Olsson, S., and Per Sandgren, P.: Reconstruction of lake-level changes in Lake Xinias, Central Greece, during the last 40 000 yr, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 158, 65–82, 2000.
- 5 Flower, R. J.: A taxonomic re-evaluation of endemic *Cyclotella* taxa in Lake Baikal, *Nova Hedwigia*, 106, 203–220, 1993.
- Genkal, S. I. and Popovskaya, G. I.: Morphological variability of *Cyclotella ocellata* from Lake Khubsugul (Mongolia), *Diatom Res.*, 23, 75–91, 2008.
- 10 González-Sampériz, P., Valero-Garcés, B. L., Carrión, J. S., Peña-Monné, J. L., García-Ruiz, J. M., and Martí-Bono, C.: Glacial and lateglacial vegetation in Northeastern Spain: new data and a review, *Quatern. Int.*, 140–141, 4–20, 2005.
- Grimm, E. C.: CONISS: A FORTRAN 77 program for the stratigraphically constrained cluster analysis by the method of incremental sum of squares, *Comput. Geosci.*, 13, 13–35, 1987.
- 15 Grimm E. C.: *TILIA and TILIA-GRAPH*, Illinois State Museum, Springfield, USA, 1991.
- Håkansson, H.: A compilation and evaluation of species in the genera *Stephanodiscus*, *Cyclostephanos* and *Cyclotella* with a new genus in the family *Stephanodiscaceae*, *Diatom Res.*, 17, 1–139, 2002.
- 20 Hearty, P. J., Hollin, J. T., Neumann, A. C., O’Leary, M. J., and McCulloch, M.: Global sea-level fluctuations during the last interglaciation (MIS 5e), *Quaternary Sci. Rev.*, 26, 2090–2112, 2007.
- Holtvoeth, J., Vogel, H., Wagner, B., and Wolff, G. A.: Lipid biomarkers in holocene and glacial sediments from ancient Lake Ohrid (Macedonia, Albania), *Biogeosci. Discuss.*, submitted, 2010.
- 25 Hustedt, F.: *Diatomeen aus Seen und Quellgebieten der Balkan-Halbinsel*, *Arch. Hydrobiol.*, 40, 867–973, 1945.
- Jongman, R. H. G., ter Braak, C. J. F., and van Tongeren, O. F. R.: *Data analysis in community and landscape ecology*, Cambridge University Press, Cambridge, 1995.
- Jurilj, A.: *Flora i vegetacija dijatomeja Ohridskog jezera*, (Flora and vegetation of diatoms from Ohrid Lake in Yugoslavia), *JAZU (Yugoslavian Academy of Science)*, Zagreb, 26, 99–190, 1954.
- 30 Krammer, K. and Lange-Bertalot, H.: *Süßwasserflora von Mitteleuropa. Bacillariophyceae. 1. Teil: Naviculaceae (Vol. 2/1)*, Gustav Fischer Verlag, Stuttgart, 1986.

4706

- Krammer, K. and Lange-Bertalot, H.: Süßwasserflora von Mitteleuropa. Bacillariophyceae. 2. Teil: Epithemiaceae, Bacillariaceae, Surirellaceae (Vol. 2/2), Gustav Fischer Verlag, Stuttgart, 1988.
- Krammer, K. and Lange-Bertalot, H.: Süßwasserflora von Mitteleuropa. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae (Vol. 2/3), Gustav Fischer Verlag, Stuttgart, 1991a.
- Krammer, K. and Lange-Bertalot, H.: Süßwasserflora von Mitteleuropa. Bacillariophyceae. 4. Teil: Achnanthaceae (Vol. 2/4), Gustav Fischer Verlag, Stuttgart, 1991b.
- Krammer, K. and Lange-Bertalot, H.: Süßwasserflora von Mitteleuropa. Bacillariophyceae. 5. Teil: English and French translation of the keys. (Vol. 2/5), Gustav Fischer Verlag, Stuttgart, 2000.
- Lawson, I., Frogley, M., Bryant, C., Preece, R., and Tzedakis, P.: The Lateglacial and Holocene environmental history of the Ioannina basin, North-West Greece, *Quaternary Sci. Rev.*, 23, 1599–1625, 2004.
- Leng, M. J., Baneschi, I., Zanchetta, G., Jex, C. N., Wagner, B., and Vogel, H.: Late Quaternary palaeoenvironmental reconstruction from Lakes Ohrid and Prespa (Macedonia/Albania border) using stable isotopes, *Biogeosciences Discuss.*, 7, 3815–3853, doi:10.5194/bgd-7-3815-2010, 2010.
- Levkov, Z., Krstic, S., Metzeltin, D., and Nakov, T.: Diatoms of Lakes Prespa and Ohrid. About 500 taxa from ancient lake system, *Iconographia Diatomologica*, 16. ARG Gantner Verlag, Germany, 2007.
- Mackay, A.: The paleoclimatology of Lake Baikal: a diatom synthesis and prospectus, *Earth Sci. Rev.*, 82, 181–215, 2007.
- Mackay, A. W., Flower, R. J., Kuzmina, A. E., Granina, L. Z., Rose, N. L., Appleby, P. G., Boyle, J. F., and Battarbee, R. W.: Diatom succession and pollution trends in recent sediments from Lake Baikal and their relation to atmospheric pollution and to climate change, *Philos. T. R. Soc. Lon. B*, 353, 1011–1055, 1998.
- Matter, M., Anselmetti, F. S., Jordanoska, B., Wagner, B., Wessels, M., and Wüest, A.: Carbonate sedimentation and effects of eutrophication observed at the Kalista subaquatic springs in Lake Ohrid (Mazedonia), *Biogeosciences Discuss.*, submitted, 2010.
- Matzinger, A., Spirkovski, Z., Patceva, S., and Wüest, A.: Sensitivity of ancient Lake Ohrid to local anthropogenic impacts and global warming, *J. Great Lakes Res.*, 32, 158–179, 2006.
- Matzinger, A., Schmid, M., Veljanoska-Sarafiloska, E., Patceva, S., Guseka, D., Wagner, B.,

4707

- Sturm, M., Müller, B., and Wüest, A.: Assessment of early eutrophication in ancient lakes – A case study of Lake Ohrid, *Limnol. Oceanogr.*, 52, 338–353, 2007.
- Oceviski, B. T. and Allen, H. L.: Limnological studies in a large, deep, oligotrophic lake (Lake Ohrid, Yugoslavia), *Arch. Hydrobiol.*, 79, 429–440, 1977.
- Roelofs, A. K. and Kilham, P.: The diatom stratigraphy and paleoecology of Lake Ohrid, Yugoslavia, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 42, 225–245, 1983.
- Ryves, D. B., Jones, V. J., Guillizzoni, P., Lami, A., Marchetto, A., Battarbee, R. W., Bettinetti, R. and Devoy, E. C.: Late Pleistocene and Holocene environmental changes at Lake Albano and Lake Nemi (central Italy) as indicated by algal remains, in: *Paleoenvironmental Analysis of Italian Crater Lakes (PALICLAS)*, edited by: Guillizzoni, P. and Oldfield, F., *Memorie dell'Istituto Italiano di Idrobiologia*, 55, 1996.
- Ryves, D. B., Jewson, D. H., Sturm, M., Battarbee, R. W., Flower, R. J., Mackay, A. W., Granin, N. G.: Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia, *Limnol. Oceanogr.*, 48, 1643–1661, 2003.
- Stankovic, S.: The Balkan Lake Ohrid and its living world, *Monographiae Biologicae*, IX, Dr. W. Junk, Den Haag, 1960.
- Sulpizio, R., Zanchetta, G., D'Orazio, M., Vogel, H., and Wagner, B.: Tephrostratigraphy and tephrochronology of the lakes Ohrid and Prespa, *Balkans, Biogeoscience Discuss.*, submitted, 2010.
- ter Braak, C. J. F. and Šmilauer, P.: *CANOCO reference manual and CanoDraw for Windows user's guide*, Biometris, Wageningen, 2002.
- Tzedakis, P. C.: Towards an understanding of the response of southern European vegetation to orbital and suborbital climate variability, *Quaternary Sci. Rev.*, 24, 1585–1599, 2005.
- Tzedakis, P. C.: Seven ambiguities in the Mediterranean palaeoenvironmental narrative, *Quaternary Sci. Rev.*, 26, 2042–2066, 2007.
- Tzedakis, P. C., Frogley, M. R., Lawson, I. T., Preece, R. C., Cacho, I., and de Abreu, L.: Ecological thresholds and patterns of millennial-scale climate variability: the response of vegetation in Greece during the last Glacial period, *Geology*, 32, 109–112, 2004.
- Vogel, H., Zanchetta, G., Sulpizio, R., Wagner, B., and Nowaczyk, N.: A tephrostratigraphic record for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia, *J. Quaternary Sci.*, 25, 320–338, 2010a.
- Vogel, H., Wagner, B., Zanchetta, G., Sulpizio, R., and Rosén, P.: A paleoclimate record with

4708

- tephrochronological age control for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia, *J. Paleolimnol.*, *J. Paleolimnology*, 44, 295–310, doi:10.1007/s10933-009-9404-x, 2010b.
- 5 Wagner, B., Reicherter, K., Daut, G., Wessels, M., Matzinger, A., Schwalb, A., Spirkovski, Z., and Sanxhaku, M.: The potential of Lake Ohrid for long-term palaeoenvironmental reconstructions, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 259, 341–356, 2008.
- Wagner, B., Lotter, A. F., Nowaczyk, N., Reed, J. M., Schwalb, A., Sulpizio, R., Valsecchi, V., Wessels, M., and Zanchetta, G.: A 40 000-yr record of environmental change from ancient Lake Ohrid (Albania and Macedonia), *J. Paleolimnol.*, 41, 407–430, 2009.
- 10 Wagner, B., Vogel, H. Zanchetta, G., and Sulpizio, R.: Environmental changes on the Balkans recorded in the sediments from lakes Prespa and Ohrid, *Biogeosciences Discuss.*, submitted, 2010.
- Wilson, G. P., Reed, J. M., Lawson, I. T., Frogley, M. R., Preece, R. C., and Tzedakis, P. C.: Diatom response to the last glacial-interglacial transition in the Ioannina basin, Northwest Greece: implications for Mediterranean palaeoclimate reconstruction, *Quaternary Sci. Rev.*, 27, 428–440, 2008.
- 15 Wohlfarth, B., Veres, D., Ampel, L., Lacourse, T., Blaauw, M., Preusser, F., Andrieu-Ponel, V., Kéravis, D., Lallier-Vergès, E., Björck, S., Davies, S. M., de Beaulieu, J-L., Risberg, J., Mormes, A., Kasper, H. U., Possnert, G., Reille, M., Thouveny, N., and Zander, A.: Rapid ecosystem response to abrupt climate changes during the last glacial period in Western Europe, 60–16 ka, *Geology*, 36, 407–410, 2008.
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Table 1. Summary of criteria used for taxonomic splitting and dissolution stages of *Cyclotella fottii* and *C. ocellata* by laboratories in Macedonia and the UK.

<i>Cyclotella fottii</i>			
Valve diameter classes (µm), Macedonia	Dissolution stages	Valve diameter classes (µm), UK	Dissolution stages
>50, fine striae	1. Identifiable to size class	≥20	For each class: Pristine (rim intact) Striae missing Central area plus few striae to ID size Central area, unassignable to size
>50, coarse striae	2. Dissolved, any size		
40–50		<20	
30–40			
20–30			
10–20			
5–10			
< 5			
<i>Cyclotella ocellata</i>			
Valve morphology, Macedonia	Dissolution stages	Valve morphology, UK	Dissolution stages
<5 µm	1. Assignable to group	<5 µm (no. ocelli cannot be identified)	For each class: Pristine (rim intact) Striae missing Central area only Dissolved, unassignable
6, 5, 4, 3 classic		Number of ocelli:	
5, 4, 3 undulating	2. Dissolved, unassignable to group	3	
5, 4, 3 small round		4	
6, 5, 4, 3 large round		5	
5 irregular pentagon		6	
5 regular pentagon			
6, 5, 3 irregular star			
5, 4 regular star			
4 rhombic			

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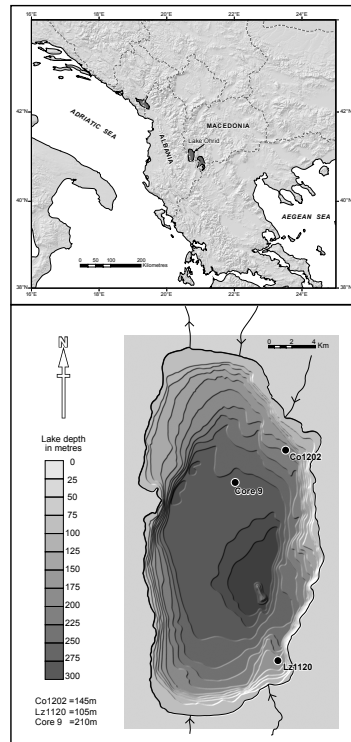


Fig. 1. Map showing the location of Ohrid on the border of Macedonia/Albania (inset) and the location of coring sites Co1202 (this study), Lz1120 (Wagner et al., 2009) and Co9 (Roelofs and Kilham, 1983), showing the direction of river flow. Modified from Albrecht and Wilke (2008) and Vogel et al. (2010b).

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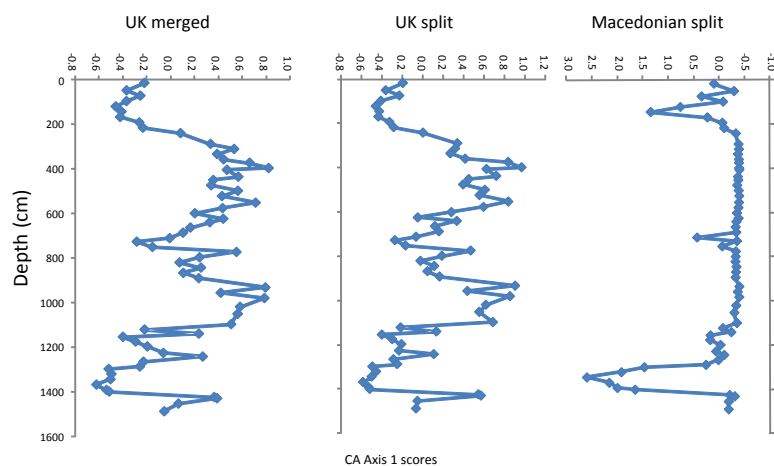


Fig. 2. Comparison of Axis 1 scores for correspondence analysis (CA) of the merged UK data-set (*Cyclotella fottii* and *C. ocellata* as single species), the UK split data-set and the Macedonian split data-set.

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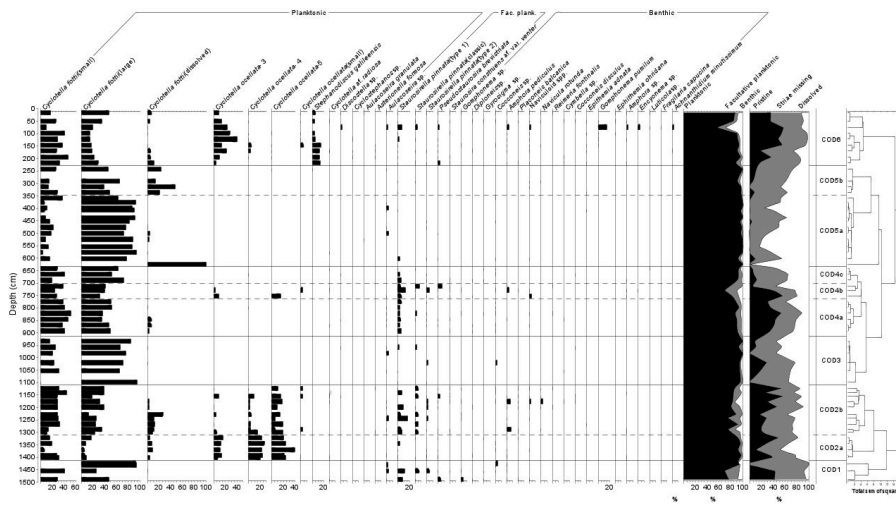


Fig. 3. Summary diatom diagram showing taxa present at >1% abundance in core Co1202, the proportion of planktonic, facultative and benthic taxa and proportions of taxa in different dissolution stages. Zones were defined by CONISS.

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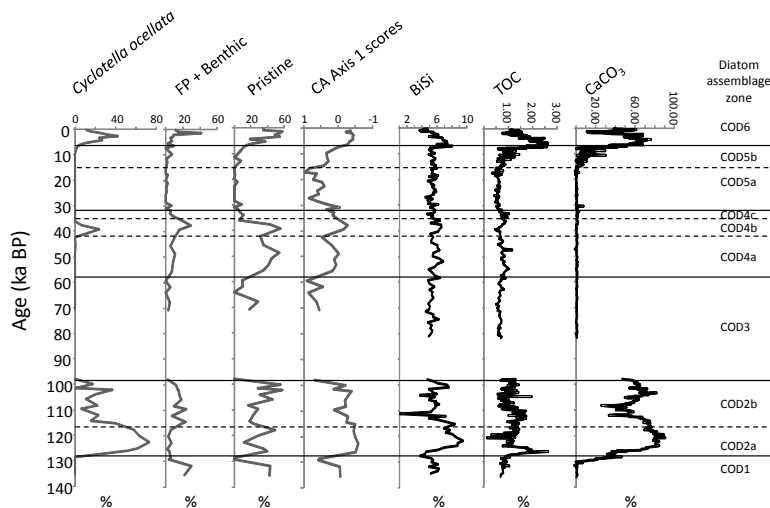


Fig. 4. Comparison of summary diatom data with selected geochemical data from Vogel et al. (2010b), on a chronological timescale. (FP=facultative planktonic; CA=correspondence analysis; BiSi=biogenic silica; TOC=total organic carbon; CaCO₃=calcium carbonate, measured by loss on ignition).

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