



Lateglacial and early Holocene climatic fluctuations recorded in the diatom flora of Xiaolongwan maar lake, NE China

QIANG GAO, PATRICK RIOUAL AND GUOQIANG CHU

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A palaeolimnological study of the annually laminated sediment sequence of Lake Xiaolongwan, a small maar lake in northeastern China, revealed distinct diatom responses to Lateglacial and early Holocene climate change between *c.* 19 700 and *c.* 10 700 a BP. In addition to analyses of diatom assemblage composition and of the bio-volume accumulation rate of planktonic diatoms, geochemical (total nitrogen, total organic carbon) and physical (varve type and thickness) indicators were used to assess past environmental change. The diatom assemblages reveal a complex interplay between direct climate effects on the seasonal lake conditions (timing of ice cover break-up, water column mixing and thermal stratification), catchment-mediated effects on the concentrations of nutrients and dissolved organic carbon and, possibly, biotic interactions between the different algal groups present in the phytoplankton of Lake Xiaolongwan (diatoms, Chrysophyceae and Dinophyceae). The most remarkable changes in the aquatic system were: (i) a sharp increase in *Asterionella formosa* and the collapse of *Handmannia balatonis* at *c.* 14 780 a BP, corresponding with the onset of the Bølling – Allerød interstadial; (ii) a sharp rise in *Stephanodiscus minutulus* at *c.* 12 840 a BP, marking the start of the Younger Dryas event and (iii) when the lake phytoplankton became dominated by Dinophyceae instead of diatoms at *c.* 11 170 a BP, after the Pre-Boreal oscillation. Two diatom assemblage zones characterize the Younger Dryas at Lake Xiaolongwan, suggesting a bipartite division of this stadial event as in several records from eastern Asia and Europe. The quasi-synchronicity of these events with the oscillations described in the North Atlantic realm demonstrates that during the Lateglacial, North Atlantic dynamics at centennial and millennial time scales had a strong control upon the climate in northeastern China.

Qiang Gao, University of the Chinese Academy of Sciences, Beijing 100049, China; Patrick Rioual (corresponding author: prioual@mail.iggcas.ac.cn) and Guoqiang Chu, Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics Chinese Academy of Sciences, Beijing 100029, China; received 8th April 2015, accepted 3rd June 2015.

In recent years, many high-resolution palaeoclimatic records spanning the interval of global warming from the end of the Last Glacial Maximum to the start of the Holocene have been developed and investigated. This period of deglaciation is of particular interest because the climate was then characterized by several rapid changes and high variability, especially in the North Atlantic realm where these events are well recorded in ice, marine and terrestrial records (Shakun & Carlson 2010; Clark *et al.* 2012; Rasmussen *et al.* 2014).

In East Asia, the most detailed records of this period are provided by speleothems from central China (Wang *et al.* 2001; Liu *et al.* 2008, 2013; Ma *et al.* 2012; Zhang *et al.* 2014). There are also several lake and peat records of the Lateglacial period in East Asia, especially in northeastern China. However, conflicting interpretations have arisen from these records especially regarding the variations in monsoonal precipitation that have been inferred from the pollen and geochemical data. In particular, the statement of Hong *et al.* (2010, 2011) that the Younger Dryas period was wetter than the previous Lateglacial was refuted by Schettler (2011) and Stebich *et al.* (2011). In that context, it is useful to study more sites and different proxy records to improve our understanding of this period.

Lake Xiaolongwan is located in the Longgang Volcanic Field (LGVF), Jilin province, northeast China (Fig. 1). It is one of the eight maar lakes of the LGVF. Maar lakes are especially sensitive to climate change owing to their characteristic morphology such as a small catchment area and limited inflow/outflow (Marchetto *et al.* 2015). Moreover, they often provide seasonally laminated sediments that can be used to establish precise chronologies. Lake Xiaolongwan sediments therefore represent an excellent archive to decipher natural climate variability, as already demonstrated by previous studies (Chu *et al.* 2008, 2009, 2014; Sun *et al.* 2013; Xu *et al.* 2014). In particular, Xu *et al.* (2014) using pollen and Chu *et al.* (2014) using compound-specific carbon isotope analyses found significant periodicities in the Xiaolongwan Holocene sediment record that suggest a strong link between solar activity and temperature and monsoonal precipitation, respectively.

Changes in diatom species composition have been extensively used in palaeolimnological inferences of climatic and environmental change. Diatoms are outstanding indicators because they form a very diverse group of microscopic algae that are found in abundance in both planktonic and benthic habitats of lakes. Owing to their siliceous walls, they are generally well preserved in the sediment record. Therefore, diatom

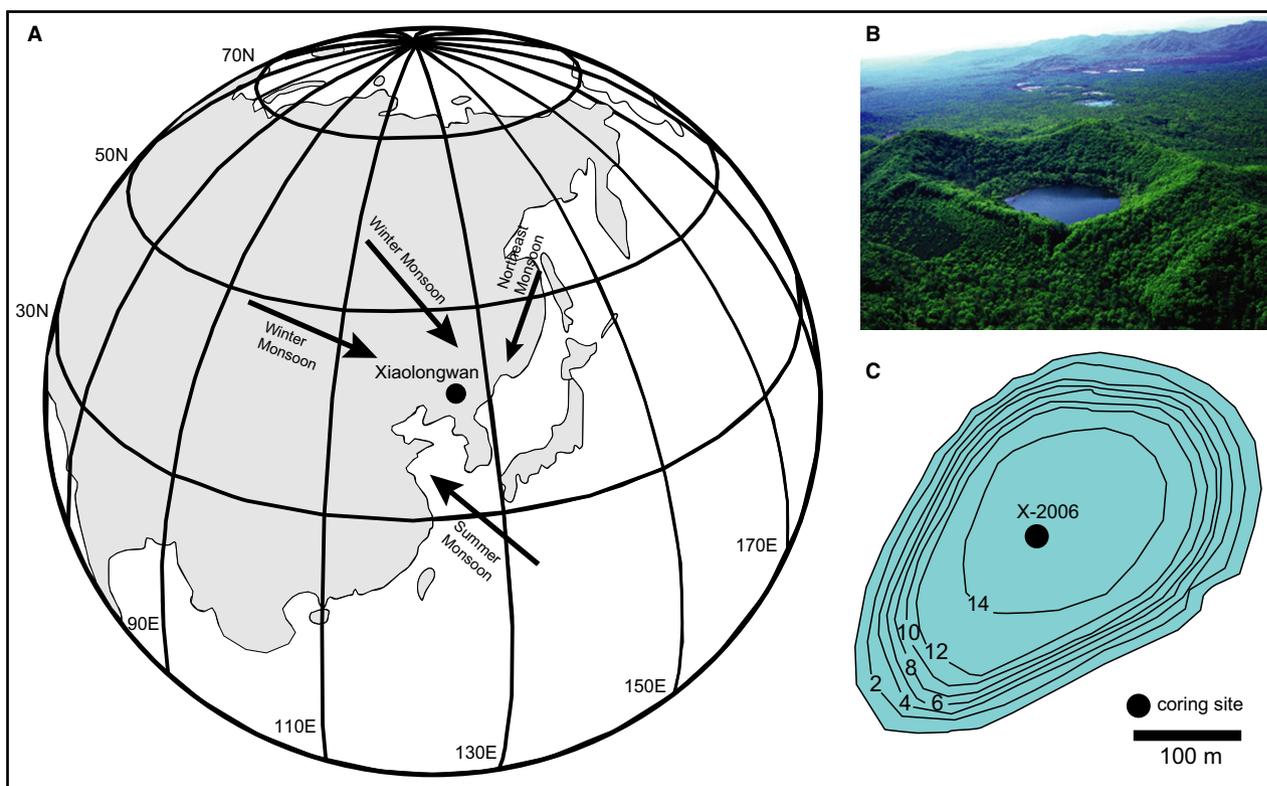


Fig. 1. A. Map showing the geographical location of Lake Xiaolongwan and selected elements of atmospheric circulation over East Asia. B. Aerial view of Xiaolongwan maar lake and its forested catchment. C. Bathymetric map showing the coring site (isobath intervals are in metres).

analysis of the sedimentary record can provide an insight into past environmental conditions within the lake itself. Moreover, because of their very short life cycle, diatom assemblages can be considered to respond almost instantaneously to changes in the environment. The diatom record of Lake Xiaolongwan is also sensitive to environmental change, as shown by Panizzo *et al.* (2013) for the last 130 years. These authors found that the recent increase in planktonic diatoms was driven by changes in the duration of ice cover, the length of the growing season and/or increased dissolved organic carbon.

The primary aims of this study were to present the Lateglacial diatom record from Lake Xiaolongwan and use this record, in association with geochemical and physical data of the sediment, to assess the palaeo-environmental evolution of this lake and provide new information on the regional climate development in northeastern China.

Study site and regional climate

Lake Xiaolongwan (latitude 42°18.0'N, longitude 126°21.5'E, altitude 655 m a.s.l.) is a small, closed maar lake with a maximum depth of 16 m and a

catchment area of 0.16 km². Currently Lake Xiaolongwan is slightly acidic (pH = 6.5–6.9), with low electrical conductivity. It is mesotrophic with ranges for total phosphorus, total nitrogen and dissolved silica of 4–26 µg L⁻¹, 780–1820 µg L⁻¹ and 0.1–1.3 mg L⁻¹, respectively. It has relatively high dissolved organic carbon concentration (DOC, 2.4–12.3 mg L⁻¹; Rioual *et al.* 2013) and relatively low Secchi depth (2.1 m, as measured on 27th August 2014).

Present climate conditions are determined by the East Asian monsoon and are characterized by pronounced seasonality in temperature and precipitation. In summer, rainfall is mainly associated with the Southeast Asian summer monsoon and the Northeast Asian summer monsoon (Fig. 1). These cause warm and humid conditions during summer. The rainy season lasts from June to October and accounts for at least 60% of the mean annual precipitation of ~760 mm. In winter and spring, the Siberian High controls the strong winter monsoon winds, causes cold and dry climate conditions and creates favourable conditions for snow and dust storms. The ice-covered season lasts from the end of November until early April. The mean annual temperature for the period AD 1955–2005 was 3.2 °C (Chu *et al.* 2011). The vegetation

around Lake Xiaolongwan is a dense, mixed broad-leaf/conifer forest dominated by *Betula costata* (Chu *et al.* 2014; Xu *et al.* 2014).

Material and methods

Sediment sampling and chronology development

In the late winter of 2006 when the lake was still ice covered, overlapping sediment cores were retrieved from a water depth of 14.5 m near the centre of the lake using a modified rod-operated piston corer. The core sections (diameter = 9 cm) were split in half longitudinally, with one half used for diatom and geochemical analyses sampled at 1-cm intervals, whereas the other half was used for making thin sections. For the preparation of thin sections, overlapping sediment slabs of 6.5 cm in length were cut off with a 1.5-cm overlap, then shock-frozen with nitrogen, vacuum-dried and impregnated with epoxy resin. Previous sediment trap experiments and independent radiometric dating have demonstrated the annual nature of the laminations observed in the sediment sequence of Lake Xiaolongwan (Chu *et al.* 2008). Varves were identified and counted from thin sections under a Leitz[®] polarizing microscope. The main types of varves that were

identified in the sequence analysed were: clastic varves, dinocyst varves and chrysophyte cyst varves. Intermediate types of varve were also identified such as clastic-chrysophyte cyst, clastic-dinocyst, chrysophyte cyst-dinocyst varves (Fig. 5). It is important to note that diatom valves, because they are transparent and generally very small, cannot be seen at the magnification used to analyse thin sections. The varved sequence is continuous for the intervals 0–387 cm and below 415 cm. Between 387 and 415 cm, a slump interrupts the laminated sequence. In this paper, we focus on the bottom part of the sequence, below the slump.

In addition to varve counting, 25 radiocarbon ages were obtained from leaf and bulk samples and dated using the AMS ¹⁴C method (Table 1). All ¹⁴C ages were calibrated using the atmospheric data set from CALIB 4.0 (Stuiver *et al.* 1998). A detailed description of the age model based on varve counting has already been published for the upper 387 cm of the core (Chu *et al.* 2014). The floating varve-chronology for part of the core below the slump was anchored by using an AMS ¹⁴C date (11 298 cal. a BP, from leaf material). Figure 2 shows that the varve chronology closely corresponds to the AMS ¹⁴C data from terrestrial plant macrofossils. The AMS ¹⁴C data from bulk samples seem to be older than from the macrofossils. This

Table 1. Radiocarbon ages from Lake Xiaolongwan.

Lab. code	Material	Depth (cm)	¹⁴ C a BP	Cal. a BP (median)	Cal. a BP (range)	Laboratory	Remarks
BA07706	Bulk	20	400±40	482	508–341	Peking University, China	1
BA07707	Leaf	56	1215±40	1156	1225–1063	Peking University	1
BA06527	Wood	107	1875±40	1822	1871–1736	Peking University	1
BA07708	Leaf	154	2615±40	2749	2760–2741	Peking University	1
BA07709	Leaf	165	2880±40	2979	3124–2948	Peking University	1
CG-4761	Bulk	186	3490±90	3757	3871–3639	Earthquake Institute, China	1
BA07710	Leaf	219	3850±40	4244	4350–4154	Peking University	1
CG-4762	Bulk	266	4780±80	5507	5597–5332	Earthquake Institute	1
BA07711	Leaf	280	4840±35	5592	5601–5493	Peking University	1
Poz-42550	Leaf	310	6230±35	7160	7232–7029	Poznan, Poland	1
Poz-47182	Leaf+charcoal	416	11 850±70	13 832	14 043–13 651	Poznan, Poland	2
Poz-47596	Leaf+charcoal	416	11 690±70	13 680	13 831–13 480	Poznan, Poland	2
Poz-42545	Leaf	424	11 680±100	13 687	13 832–13 468	Poznan, Poland	3
Poz-42553	Leaf	430	9960±50	11 298	11 548–11 241	Poznan, Poland	4
Poz-42554	Bulk	430	10 170±50	11 818	12 098–11 660	Poznan, Poland	4
Poz-47135	Leaf+charcoal	454	10 400±50	12 337	12 623–11 984	Poznan, Poland	4
BA07712	Leaf	506	11 120±55	13 137	13 166–13 005	Peking University	4
Poz-42549	Bulk	579	13 550±60	16 272	16 510–16 044	Poznan, Poland	4
BA07713	Bulk	606	14 485±80	17 348	17 618–17 092	Peking University	4
Poz-42546	Leaf	674	15 600±70	18 631	18 936–18 345	Poznan, Poland	4
Poz-42548	Bulk	674	16 320±80	19 459	19 783–19 148	Poznan, Poland	4
BA07714	Bulk	696	17 080±85	20 334	20 669–20 006	Peking University	4
Poz-42551	Bulk	754	17 260±80	20 541	20 876–20 213	Poznan, Poland	4
BA07715	Bulk	834	19 070±70	22 624	22 998–22 271	Peking University	4
Poz-42552	Bulk	845	17 760±80	21 116	21 459–20 784	Poznan, Poland	4

¹Dates for the Holocene already published in Chu *et al.* (2014), not shown in Fig. 2.

²Dates obtained from samples within the sediment slump, excluded from the age model.

³Date excluded from the age model because of the low C content of the sample (~0.3 mg).

⁴Dates plotted on Fig. 2.

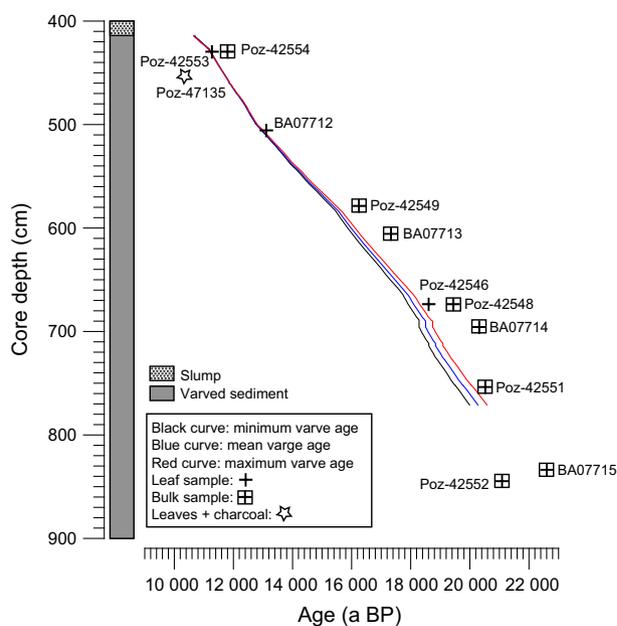


Fig. 2. Age-depth plot of the Xiaolongwan sequence showing varve ages and AMS ^{14}C dates.

might be because of the lower reservoir effect associated with the macrofossil samples, or the presence of erosional material from catchment soil in the bulk samples. This is why we chose to use Poz-42553 (11 298 cal. a BP) instead of Poz-42554 (11 818 cal. a BP), which was taken at the same depth but from a bulk sample. Note that the date obtained at 424 cm, Poz-42545, from a macrofossil sample taken immediately below the sediment slump was not reliable because of the small amount of carbon available for dating. The error of the varve chronology is <4% for the past 9.0 ka BP and 6% for the past 10–20 ka BP. Figure 2 shows varve age and AMS ^{14}C dating plotted against the sediment core depth.

Geochemical analysis

The water content and bulk density were calculated after freeze-drying and weighing each sample taken at 1-cm intervals. The concentrations of total organic carbon (TOC) and total nitrogen (TN) were analysed for freeze-dried subsamples. Details of the analytical method are given in Chu *et al.* (2009).

Diatom analysis

Diatom samples were prepared in test tubes from approximately 0.05 g freeze-dried sediment using hot H_2O_2 to remove organic matter (Renberg 1990). Diatom concentrations (valves per g dry matter) were calculated by the addition of divinylbenzene microspheres

Table 2. Valve dimensions and cell biovolumes for the dominant diatom taxa found in the Lake Xiaolongwan sediment sequence.

Taxon	Valve length/diameter (μm)		n	Cell biovolume (μm^3)
	Range	Median		
<i>Asterionella formosa</i>	30.6–68.0	45.8	46	313
<i>Cyclotella comensis</i>	5.0–9.5	5.5	35	64
mo. <i>comensis</i>				
<i>Cyclotella comensis</i>	3.5–4.9	4.4	35	34
mo. <i>minima</i>				
<i>Discostella tetrica</i>	4.3–8.8	5.4	31	62
<i>Fragilaria</i> sp.	72–135	93.1	32	326
<i>Handmannia balatonis</i>	6.4–15.5	11.1	31	530
<i>Stephanodiscus minutulus</i>	7.1–9.2	8.1	30	213
<i>Urosolenia</i> (resting spore)	2.9–11.8	6.2	35	94 ¹

¹The value given for *Urosolenia* corresponds to the biovolume of the resting spores only, not that of the vegetative cells as these were not preserved in the sediment.

(Battarbee & Kneen 1982). Subsamples of the homogenized suspension were diluted by adding distilled water and left to settle onto glass coverslips until dry. The coverslips were fixed onto glass slides with Naphrax[®]. For most samples at least 300 valves were counted under an Olympus[®] light microscope using oil immersion phase-contrast at $\times 1000$ magnification. In some samples from the Pleniglacial (before 15 ka BP) only 200 valves were counted owing to low diatom concentration and the high content of clastic material. Diatom identification and taxonomy were mainly based on Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b) but numerous taxonomic publications were also used to aid identification, principally for centric taxa such as Procházková *et al.* (2012) for *Discostella tetrica*; Solak & Kulikovskiy (2013) for *Handmannia balatonis*; Scheffler & Morabito (2003) and Scheffler *et al.* (2005) for *Cyclotella comensis* morphotypes *comensis* and *minima*; and Edlund & Stoermer (1993) for *Urosolenia* resting spores.

Biovolumes of the dominant planktonic diatoms were determined following the guidelines of Hillebrand *et al.* (1999) (Table 2). The biovolumes were then multiplied by the diatom concentration, the dry bulk density and the sedimentation rate to derive the biovolume accumulation rate (BVAR) for each of the dominant planktonic diatoms (Wang *et al.* 2012). BVAR are expressed in $\mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$.

Stratigraphical diagrams were constructed using C2 version 1.5.1 (Juggins 2007). Diatom assemblage zones (DAZ) were delimited by optimal partitioning (Birks & Gordon 1985) of the diatom percentage data using the unpublished program ZONE (version 1.2) (Lotter & Juggins, pers. comm.). Statistically significant zones were determined using BSTICK (Birks & Line, pers. comm.) based on the broken-stick approach (Bennett 1996).

Results

Diatom stratigraphy and varve analysis

Diatoms in the Lateglacial sediment of Lake Xiaolongwan are generally well preserved as the proportions of fragmented and/or dissolved valves were low. The diatom stratigraphy for the most common taxa identified in the 94 levels analysed is summarized in Fig. 3. The taxa are arranged in successional order and only the most abundant planktonic taxa are displayed along with the sum of benthic taxa. The diatom flux and BVAR are shown in Fig. 4 whereas the results of the varve analysis (varve types and thickness), the chryso-phyte cyst flux and some geochemical data are presented in Fig. 5. Over the sequence investigated (10.6–19.7 ka BP), the 1-cm-thick samples represent between 14.5 and 53.5 years. On average a 1-cm sample represents 28.3 years of sedimentation. The time intervals between each sample analysed for diatoms range from 25 to 380 years, with an average of 97 years. After 15 ka BP, the maximum interval is 84 years with an average interval of 55 years between samples. Before 15 ka

BP, the time resolution is much lower, with an average of 269 years between the analysed samples (range of 70–380 years).

Taxonomic remarks on the main diatom species

Handmannia balatonis. – *Cyclotella balatonis* Pantocsek was considered a synonym of *Cyclotella radiosa* Grunow and/or *Cyclotella comta* (Ehrenberg) Kützing following the broad species concept that has been in use until recently for this group of centric diatoms (e.g. Krammer & Lange-Bertalot 1991a) (Supporting Information Fig. S1: 39–47). Using a more narrow species concept, Houk *et al.* (2010) re-instated *C. balatonis* as a valid species after investigating the type specimens. The group of species to which *C. balatonis* belongs was separated from *Cyclotella* by Håkansson (2002) who created for that purpose the genus *Puncticulata*. In a recent review paper, however, Khursevich & Kociolek (2012) re-instated the genus *Handmannia* that has been overlooked by Håkansson (2002). The transfer of the species *Cyclotella balatonis* to the genus *Handmannia* was carried out by Solak & Kulikovskiy (2013). Owing

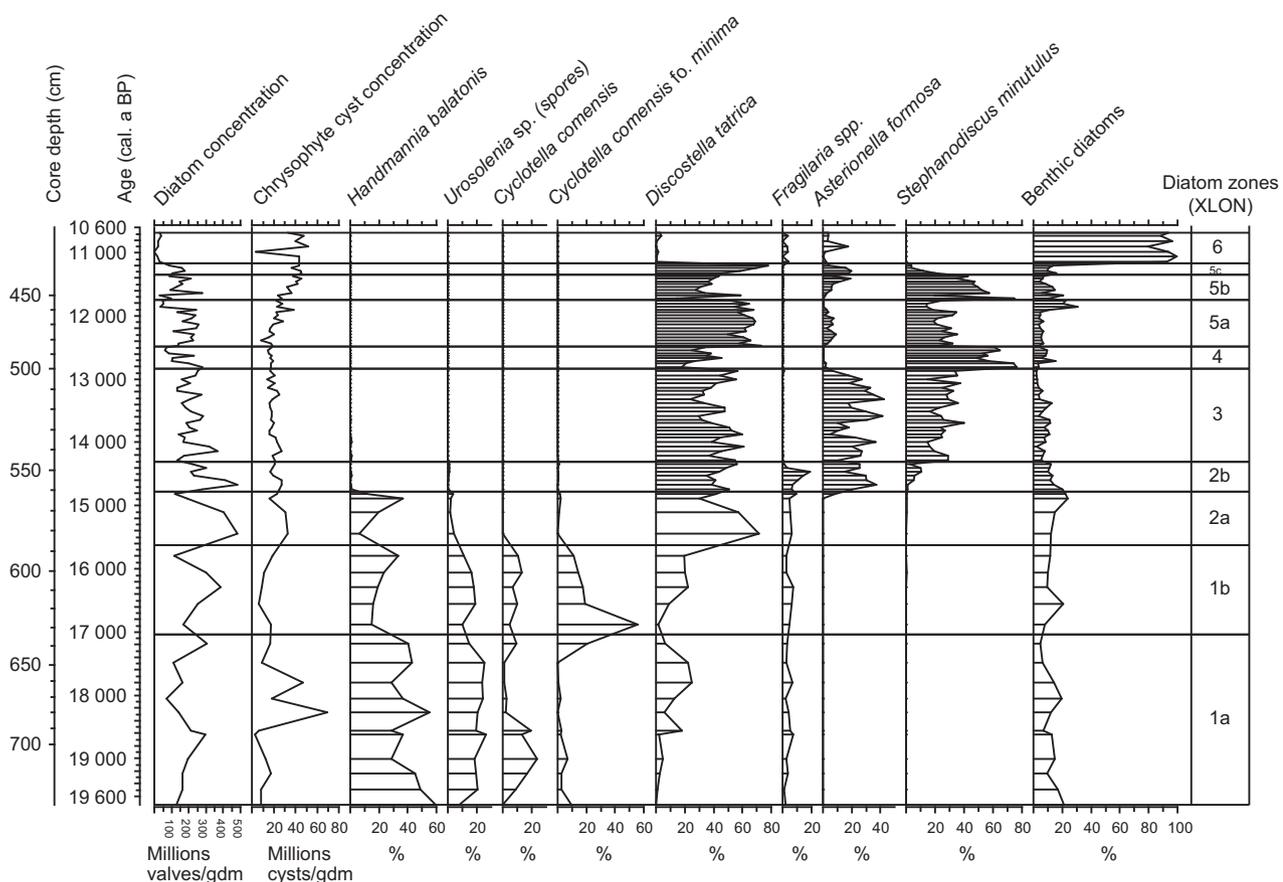


Fig. 3. Summary diatom diagram of the Lateglacial and early Holocene sequence of Lake Xiaolongwan. Only the relative percentages for the major planktonic species are plotted along with the sum of all benthic species. Diatom concentrations ($\times 10^6$ valves per gram dry matter) are plotted on the left-hand side. Diatom assemblage zones were determined by optimal partitioning.

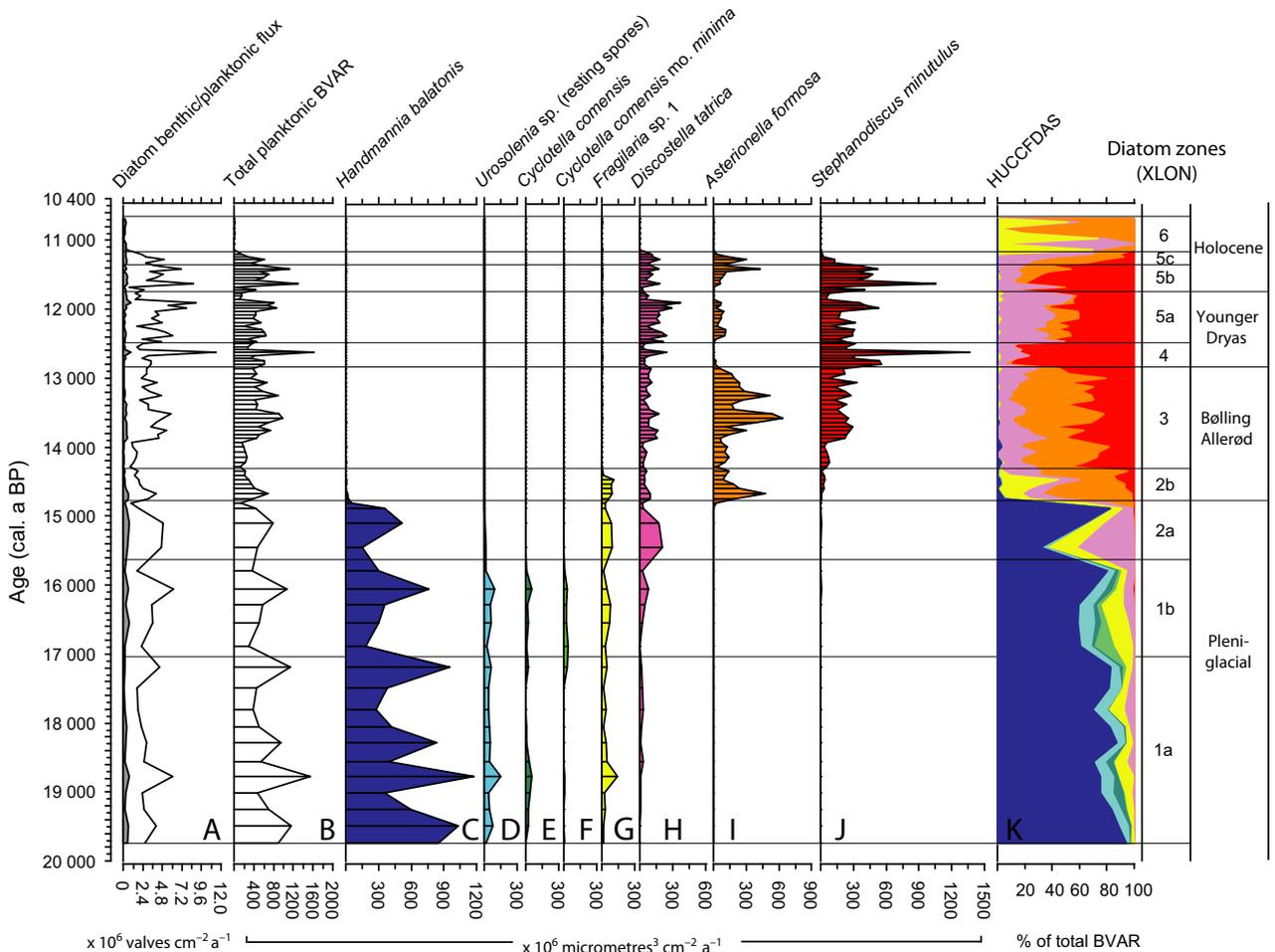


Fig. 4. A. Planktonic and benthic diatom flux in the Xiaolongwan sediment record. B. Total planktonic diatom biovolume accumulation rate (BVAR). C–J. Variation in BVAR for the main diatom species. K. Contribution in terms of relative percentages to the total BVAR of the main diatom species.

to this taxonomic confusion, there are few mentions of this species in the literature and knowledge on its distribution and ecology is very incomplete.

Discostella tatrica. – Like the other members of this recently erected genus, this species is difficult to identify consistently under a light microscope (Fig. S1: 1–7). In a previous study on Lake Xiaolongwan, Panizzo *et al.* (2013) identified this taxon as *Discostella woltereckii* (Hustedt) Houk & Klee. However, further analyses under a scanning electron microscope (SEM) revealed that this taxon is better identified as *D. tatrica*, a taxon recently described from lakes in the Tatra Mountain (Slovakia/Poland) by Procházková *et al.* (2012).

Cyclotella comensis morphotypes *comensis* and *minima*. – Following the work of Scheffler and colleagues (Scheffler & Morabito 2003, Scheffler *et al.* 2003, 2005), we distinguished two morphotypes of *C. comensis*: the nominal morphotype and the very small-sized

morphotype *minima* (valve diameter 3.5–4.9 μm ; Fig. S1: 8–14 and 15–31).

Urosolenia sp., resting spores. – As stated by Edlund & Stoermer (1993), diatom resting spores are often an overlooked and misconstrued component of siliceous microfossil assemblages (Fig. S1: 48–53). The spores from Lake Xiaolongwan varied in size from 2.9 to 11.8 μm in apical length and 3.1 to 6.7 μm in the perivalvar axis. The current taxonomy of this genus is extremely uncertain and we cannot attribute these spores to any described species.

Fragilaria sp. 1. – The ranges for valve length, width and stria density are 72–135 μm , 2.0–2.9 μm and 18.6–21.1 striae in 10 μm , respectively (Fig. S1: 61–63). The characteristics of this taxon are intermediate between those of *Fragilaria tenera* (W. Smith) Lange-Bertalot and *Fragilaria nanana* Lange-Bertalot as given in Hofmann *et al.* (2011).

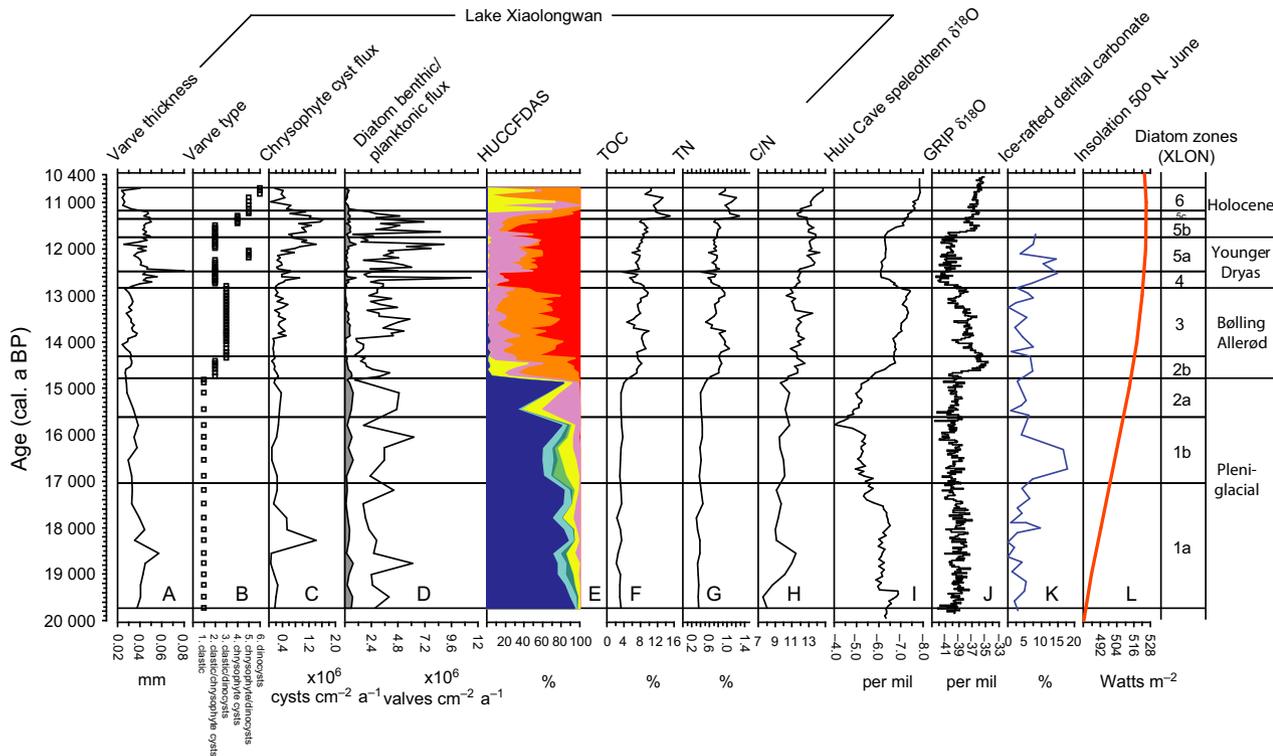


Fig. 5. Summary results of the diatom and geochemical analyses of the Lake Xiaolongwan sequence and comparison with climate records and forcings during the last deglaciation. A. Varve thickness (mm). B. Varve types. C. Chrysophyte cyst flux ($\times 10^6$ cysts $\text{cm}^{-2} \text{a}^{-1}$). D. Flux of planktonic and benthic diatoms (filled grey time series) ($\times 10^6$ cysts $\text{cm}^{-2} \text{a}^{-1}$). E. Contribution in terms of relative percentages to the total BVAR of the main diatom species. F–H. Geochemical data from Lake Xiaolongwan including total organic carbon (%), total nitrogen (%) and the carbon: nitrogen atomic ratio. I. Oxygen isotope speleothem record from Hulu Cave in central China (Wang *et al.* 2001). J. The oxygen isotope record from the Greenland Ice Core Project (GRIP) (Rasmussen *et al.* 2014; Seierstad *et al.* 2014). Note that the chronology was shifted to AD 1950 instead of AD 2000 as in the original data file. K. Record of ice-rafted detrital carbonates (%) from North Atlantic core VM23–81 identifying times of Heinrich events H1 and H0 (Bond *et al.* 1999). L. Mid-month insolation at 50°N for June (orange line) (Berger & Loutre 1991).

Diatom, varve and geochemical analyses

The sequence was divided into six diatom assemblage zones. The results of the geochemical analyses are only briefly reported as a detailed interpretation of these data will be published elsewhere.

DAZ XLON-1, 740–585 cm, 19 730–15 620 a BP. – This first zone can be subdivided into two subzones, mainly according to the percentages of *Cyclotella comensis* morphotype *minima*. The lowermost part of the sequence, DAZ XLON-1a from 19 730 to 17 040 a BP, is dominated by *Handmannia balatonis*, both in terms of relative percentage and planktonic BVAR. Owing to the large biovolume of this species, the average planktonic BVAR for XLON-1a is the largest of all the zones of the sequence ($\sim 800 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$). The other abundant diatoms are *Urosolenia* resting spores, *Cyclotella comensis* morphotype *comensis* and *Discostella tatica*. DAZ XLON-1b from 17 040 to 15 620 a BP is characterized by a sharp increase in the percentages of *Cyclotella comensis* mo. *minima*, whereas those of *H. balatonis* decline. Although the average total

diatom flux increases ($\sim 3.5 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$), the small biovolume of morphotype *minima* causes a decrease in the average BVAR ($\sim 575 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$). The varves are of the clastic type for the whole zone. The peak in chrysophyte flux between 18.3–17.8 ka BP corresponds to a high abundance of chrysophyte cysts of very small size ($< 5 \mu\text{m}$ in diameter) that could not be seen in the thin sections used to define the varve types. TOC and TN are low throughout XLON-1.

DAZ XLON-2, 585–546 cm, 15 620–14 310 a BP. – DAZ XLON-2 is dominated by *D. tatica* and can be divided into two subzones that are characterized by the subdominant species. In DAZ XLON-2a, from 15 620 to 14 780 a BP, *H. balatonis* is still abundant, whereas in DAZ XLON-2b from 14 780 to 14 310 a BP *Asterionella formosa* increases sharply. In DAZ XLON-2b, the averages for both the total diatom flux and the planktonic BVAR decrease, to $\sim 2.4 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$ and $\sim 380 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$, respectively. Varves in XLON-2a are of the clastic type, whereas in XLON-2b they are of the clastic-chrysophyte cysts

type. XLON-2b is also characterized by a sharp increase in TOC, TN and C/N ratio.

DAZ XLON-3, 546–500 cm, 14 310–12 840 a BP. – XLON-3 is dominated by *D. tatrlica*, *A. formosa* and *Stephanodiscus minutulus*. The averages for both the total diatom flux and the planktonic BVAR increase, to $\sim 3.1 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$ and $\sim 480 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$, respectively. In XLON-3, all varves are of the clastic-dinocyst type.

DAZ XLON-4, 500–484 cm, 12 840–12 490 a BP. – The assemblages in this zone are almost exclusively composed of the two species *S. minutulus* and *D. tatrlica*. *S. minutulus* is largely dominant (up to 76%). The averages for both the total diatom flux and the planktonic BVAR increase further, to $\sim 3.7 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$ and $\sim 565 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$, respectively. This zone is also characterized by a sharp increase in varve thickness. All varves are of the clastic-chrysophyte cysts type.

DAZ XLON-5, 484–427 cm, 12 490–11 170 a BP. – The assemblages of this zone differ from that of the previous zone by the return of *A. formosa*. It can be divided into three subzones according to the fluctuations in the percentages of *D. tatrlica* and *S. minutulus*. XLON-5a from 12 490 to 11 740 a BP is largely dominated by *D. tatrlica*. In this subzone, the average total diatom flux increases but the average planktonic BVAR decreases and varves are of the clastic-chrysophyte cyst or the chrysophyte cyst-dinocyst types. XLON-5a is also characterized by an increase in the C:N ratio (Fig. 5). XLON-5b from 11 740 to 11 350 a BP is dominated by *S. minutulus*. This causes an increase of the average planktonic BVAR ($\sim 630 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$), whereas the average total diatom flux remained constant at $\sim 4.2 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$. In that subzone varves are of the clastic-chrysophyte cyst or chrysophyte cyst types. Chrysophyte cyst flux is the highest of the whole sequence. In XLON-5c from 11 350 to 11 170 a BP, the percentages of *S. minutulus* collapse and the averages for both the total diatom flux and planktonic BVAR also decline. Varves are of the chrysophyte cyst or the chrysophyte cyst-dinocyst types. In XLON-5c TOC and TN values sharply increase.

DAZ XLON-6, 427–414 cm, 11 170–10 690 a BP. – The last zone is characterized by a collapse in the percentage of planktonic diatoms. Benthic diatoms represent over 90% of the assemblages in most samples of this zone. The averages for both the total diatom flux and planktonic BVAR drop to $\sim 0.2 \times 10^6$ valves $\text{cm}^{-2} \text{a}^{-1}$ and $\sim 5 \times 10^6 \mu\text{m}^3 \text{cm}^{-2} \text{a}^{-1}$, respectively. Varve thickness decreases sharply in the first part of this zone when the varves are of the chrysophyte cyst-dinocyst

type. In the last three samples of the sequence, varves are of the dinocyst type and varve thickness increases. The C/N values increase.

Discussion

The changes in diatom assemblages are consistent with the 'classic' Lateglacial climate periods established in many records from the Northern Hemisphere. To make comparison easier, the terminology derived from the northern European pollen sequences such as Bølling, Allerød and Younger Dryas, Rasmussen *et al.* (2014). In Fig. 5, the Xiaolongwan record is compared with the synchronized Greenland ice-core records, especially the GRIP record plotted with the GICC05modelext chronology (Rasmussen *et al.* 2014; Seierstad *et al.* 2014), with the Hulu cave speleothem record from central China (Wang *et al.* 2001), with the record of ice-rafted detrital carbonate from the North Atlantic that identifies times of Heinrich events H1 and H0 (Bond *et al.* 1999) and with the insolation at 50°N for June (Berger & Loutre 1991).

The pleniglacial

The geochemical analyses gave low values for total organic carbon (TOC) and total nitrogen (TN) for the pleniglacial part of the sediment core, whereas the thin sections revealed that the varves were mainly of the clastic type. Pollen analyses from the neighbouring Sihailongwan Lake indicate that at that time the vegetation was composed of taiga-like woodland patches, permafrost conditions were likely and the climate cold and dry (Stebich *et al.* 2009). It is also important to consider that the basin of Lake Xiaolongwan would have been 6–7 m deeper than it is nowadays. Thus, it is most likely that Lake Xiaolongwan was deep and oligotrophic as the supply of nutrients from the frozen catchment soils would have been limited. Nevertheless, the lake was not a substerile environment but already productive as indicated by the high BVAR values. This finding confirms the air-temperature reconstruction of Peterse *et al.* (2011) based on the paleosol-loess sequence from central China that indicated that deglacial warming started at 19 ka BP, i.e. 3000 years earlier than the strengthening of the East Asian summer monsoon. The onset of Northern Hemisphere deglaciation was also constrained at 19 ka BP by Clark *et al.* (2009), who drew their results from a very large data set of ^{14}C and cosmogenic nuclide ages.

The first diatom subzone, XLON-1a (19 730–17 040 a BP) is characterized by high percentages and BVAR of *H. balatonis* (Figs 3, 4). Houk *et al.* (2010) reported this species as a pelagic diatom in mesotrophic to eutrophic lakes in Europe. Budzynska & Wojtal (2011) found it in abundance in a small, shallow, eutrophic lake in Poland where its maximum development is in

the winter–spring period and finishes with the onset of stratification. The same taxon is currently very abundant in Lake Sihailongwan, located a few kilometres away from Lake Xiaolongwan. In this deep (50 m maximum depth), clear-water, mesotrophic lake *H. balatonis* is most abundant in early spring (just after ice break-up) and in autumn when thermal stratification breaks down (P. Rioual, unpublished data). The other planktonic species that contribute significantly to the assemblages and BVAR are *Urosolenia* spp., *Cyclotella comensis* in the lower part of the subzone and *Fragilaria* sp. and *D. tatrlica* in the upper part of the subzone. *Urosolenia* spp. are associated with clear, deep, base-poor lakes (Padisák *et al.* 2009) and with seasonal mixing of the water column (Souza *et al.* 2008), and therefore most probably have a seasonal distribution similar to that of *H. balatonis*. *C. comensis* morphotype *comensis* can be present in the water column throughout the year but reaches its peak during the summer period of thermal stratification (Scheffler *et al.* 2003). This species is more abundant in alkaline lakes with low phosphorus concentrations, moderate nitrate concentrations and a moderate mixing depth (Saros & Anderson 2015 and references therein).

Interestingly, between *c.* 18.5 and *c.* 17.3 ka BP *C. comensis* declines sharply (in percentages and BVAR), whereas the contribution of *Fragilaria* sp. 1 increases. Needle-shape planktonic araphid diatoms such as *Fragilaria teneralnanana* (previously included in the genus *Synedra*) are generally considered to have similar ecological requirements (Tolotti *et al.* 2007; Wang *et al.* 2012). In a temperate lake of the Italian Alps Tolotti *et al.* (2007) found that this type of *Fragilaria* species mostly develops from mid-summer to autumn. They also found a strong positive relationship between this taxon abundance and concentrations in nitrate–nitrogen and silica that were positively associated, in that lake, with high summer rainfall. It is well established that the wetter the climate, especially in humid, cool, temperate areas, the higher the amount of nitrogen supplied to the lake via terrestrial runoff and directly from precipitation (Clair & Ehrman 1996; Wetzel 2001; Kane *et al.* 2008). By causing nitrogen enrichment, wet summer conditions may therefore be more favourable to *Fragilaria* sp. 1 than to *C. comensis*. This assemblage shift occurs simultaneously with a significant increase in varve thickness and a peak in chrysophyte cysts. In their review of varves in lake sediments, Zolitschka *et al.* (2015) showed that in situations where vegetation and soils are not efficient for runoff control, varve thickness is highly correlated with variations in summer precipitation. Under such conditions, rainfall is transferred to the varves via enhanced sediment flux, resulting in thicker and more siliciclastic varves. Interestingly, this time interval corresponds to a strong East Asian Summer Monsoon

event in the speleothem records of central China (Zhang *et al.* 2014).

The subzone XLON-1b (17 040–15 620 ka BP) is differentiated from XLON-1a by a significant decrease in the percentages and BVAR of *H. balatonis* and a shift in the proportions of the two different morphotypes of *C. comensis*. In XLON-1b, *C. comensis* morphotype *minima* is more abundant. Detailed investigations of the life cycle of these *Cyclotella* populations have confirmed that *C. comensis* fo. *minima* is a winter ecotype of *C. comensis* and that the morphological transition between the two occurs during sexual reproduction (Scheffler & Morabito, 2003; Scheffler *et al.* 2003). In alkaline lakes of northern Germany *C. comensis* fo. *minima* occurs in October in the plankton and blooms from January to March, whilst being completely absent from the plankton during the summer period. Therefore, XLON-1b suggests an interval with longer, colder winter periods. These conditions would delay and reduce the length of spring and would be favourable for *C. comensis* fo. *minima* to dominate the winter and early spring plankton whilst being detrimental to *H. balatonis*. The simultaneous increase in BVAR of *Fragilaria* sp. 1 also suggests weak spring circulation that may not have extended to the bottom of the lake and low phosphorus supply rates (Bradbury 1988). This is because *Fragilaria* (*Synedra*) species have consistently been found to be extremely good P-competitors (Sommer 1983; Grover 1988), having the lowest growth requirements for P of any species tested in culture (Kilham 1986). All together, these diatom shifts suggest that this interval of the Xiaolongwan record corresponds with a climate cooling event. Its timing overlaps with that of the ice-rafted debris event recorded in the North Atlantic at 17.0 ka BP (Heinrich event H1; Bond *et al.* 1999).

Zone XLON-2a (15 620–14 780 a BP) is characterized by the dominance of *D. tatrlica* and the decreased relative abundance of *H. balatonis*. Simultaneously, the C:N ratio rose (Fig. 5), suggesting an increase in the input of organic matter from the catchment. TOC, however, did not increase significantly. In the Tatra Mountain lakes from where it was originally described, *D. tatrlica* appears to be tolerant to different levels of nutrients as it was observed in ultra-oligotrophic to mesotrophic lakes (Procházková *et al.* 2012). Ecological information more relevant to our study is provided by sediment trap data from Lake Xiaolongwan (Chu *et al.* 2008; P. Rioual & G.Chu, unpublished data). The trap data show that *D. tatrlica* is currently the most abundant planktonic species in the lake. It is abundant during the spring and autumn periods of turnover but is also present during summer stratification (P. Rioual, unpublished data). The relatively high DOC concentrations and low Secchi depth observed in recent years suggest that this small, wind-sheltered forest lake has a shallow mixing depth (Fee *et al.* 1996;

Von Einem & Granéli 2010). This shift from *H. balatonis* to *D. tetrica* may therefore indicate a shallower mixing depth. This is consistent with the study of Saros *et al.* (2012), who observed a much lower mixing depth optimum for *Discostella* spp. than for *Handmannia* spp.

The last two diatom zones overlap with the ‘Mystery Interval’ (17.5–14.5 ka BP) that is characterized in the speleothem records of central China by a weak summer monsoon (Zhang *et al.* 2014).

The Bølling – Allerød interstadial

In their list of recommendations, Rasmussen *et al.* (2014) suggested that the Bølling – Allerød could be used as a non-archive-specific name for the generally mild climate period from approximately 14.6 to 12.9 ka BP. In the pollen record of Lake Sihailongwan, Stebich *et al.* (2009) determined that the interstadial lasted 1770 years, from 14 450 to 12 680 a BP. In the Xiaolongwan diatom record, the equivalent interval is found to have lasted a little longer, starting at *c.* 14.8 and ending at *c.* 12.8 ka BP, and to include two diatom zones.

The first of these, XLON-2b (14 780–14 310 a BP), is characterized by the sharp increase in *A. formosa* and the simultaneous collapse in *H. balatonis* (both in terms of relative percentages and BVAR). *A. formosa* is a definite spring species (Simola *et al.* 1990; Talling 1993; Salmaso *et al.* 2003) and a very good early indicator of nutrient enrichment, especially nitrogen. Consistent with the increase of the nitrophilous *A. formosa* (Saros *et al.* 2005; Michel *et al.* 2006; Hundey *et al.* 2014), there is a sharp rise in TN concentrations (Fig. 5). TOC concentrations also increase and suggest a general increase in lake productivity and in the input of organic matter from the catchment. Consistent with an increase in the productivity of the lake, the varve type changes from clastic to clastic-chrysophyte cysts.

The next zone, XLON-3 (14 310–12 840 a BP), is marked by further increase in TOC and TN concentrations in the sediment whereas the varve type changed to the clastic-dinocyst type. All these indicate a more productive lake system. Simultaneously, in the diatom assemblages *S. minutulus* and *A. formosa* expanded further whilst *H. balatonis* disappeared. Like *A. formosa*, *S. minutulus* is a typical late-winter and/or early spring-blooming species associated with cold water and low light conditions, when the water column is mixing (Druart *et al.* 1987; Kilham *et al.* 1996). These two species are reported to have higher requirements for nutrients than *Handmannia* and *Discostella* species. Their development indicates a longer and stronger spring period of mixing of the water column that extended to the sediment surface at the bottom of the lake and caused an increase in the rate of nutrient supply. Such long spring periods are associated with

earlier break-up of the winter ice cover. Nutrient enrichment may have also been caused by higher water inflow and associated nutrient delivery. In the sediment record from Lake Sihailongwan, the increase in pollen production and the initial expansion of *Ulmus* and *Fraxinus* (Stebich *et al.* 2009) started at 14.4 ka BP, indicating climatic amelioration.

The Younger Dryas stadial

Rasmussen *et al.* (2014) suggested that the Younger Dryas chronozone can be used as a non-archive-specific synonym for the stadial period between the Bølling – Allerød and the Holocene that lasted approximately between 12.9 and 11.7 ka BP. In the Sihailongwan pollen record, the Younger Dryas cooling event begins at 12 680 a BP but lacks an abrupt termination as gradual changes took place between 11 600 and 12 250 a BP. The Younger Dryas was therefore estimated to have lasted between 1000–1300 years (Stebich *et al.* 2009). In the Lake Xiaolongwan diatom sequence, the Younger Dryas event corresponds to XLON-4 and XLON-5a and has a duration of *c.* 1100 years.

The short zone XLON-4 (12 840–12 490 a BP) is marked by a sharp increase in varve thickness, a switch back to the clastic-chrysophyte cyst varve type, a rise in the clastic content and a modest increase in the flux of benthic diatoms. In the diatom assemblage the main feature is the large increase in *S. minutulus* concomitant with the sharp decline in *A. formosa*. The ecology of these two spring-blooming diatoms essentially differs by their nutrient requirements. *S. minutulus* has high P demands and very low Si requirements, which makes it a specialist of conditions with a low silicon to phosphorus ratio (Si:P) (Interlandi *et al.* 1999; Lynn *et al.* 2000). By contrast *A. formosa* has relatively high silicon requirements (and also low requirements for growth under phosphorus limitation), which implies that it can often dominate the plankton at high Si:P ratios (Sommer 1983; Van Donk & Kilham 1990). Therefore, the high abundance of *S. minutulus* and the decrease in the percentages of *A. formosa* can be interpreted as a shift towards low Si:P conditions. This shift may be caused by an increased supply of P, a decreased supply of Si or both.

In Lake Xiaolongwan, a drier climate would promote *Stephanodiscus* by lowering the Si:P ratio as the loading of silica to the lake is closely linked to the amount of precipitation in these maar lakes (Schettler *et al.* 2006). Simultaneously, in the Lake Sihailongwan pollen record a reduction in vegetation density and the re-expansion of *Larix* and *Picea* were interpreted as indicating a colder and drier climate (Stebich *et al.* 2009). Generally weak monsoon conditions, starting at 12 850 a BP, were also reported from the speleothem record of Kulishu Cave in northern China (Ma *et al.*

2012). Park *et al.* (2014), however, reported from Han-non maar palaeolake in South Korea that conditions remained humid until 12.6 ka BP. Hong *et al.* (2010) also reported wet conditions during the Younger Dryas from analysing peat cellulose $\delta^{13}\text{C}$ from the Hani peat, located near Lake Xiaolongwan. Hong *et al.*'s (2010) interpretation is however very controversial and was refuted by Schettler (2011) and Stebich *et al.* (2011).

Alternatively, the increase in *Stephanodiscus* may have been caused by an increased loading of P not related to a change in precipitation. Interestingly, in the varved sequence of Meerfelder Maar (Germany) Brauer *et al.* (1999a,b) reported that the start of the Younger Dryas was also characterized by a large increase in varve thickness. Varves in that interval were composed by monospecific spring/summer layers of *Stephanodiscus* and autumn/winter layers enriched in allochthonous minerogenic matter, plant detritus and abundant epiphytic diatoms. They interpreted these changes as a significant eutrophication event caused by soil erosion and reworking of littoral sediments. Soil erosion was caused by the demise of forest vegetation, whereas reworking of littoral sediments was linked to a lowering of the lake level owing to drier conditions. More recently, however, Lane *et al.* (2013) proposed that the *Stephanodiscus* blooms observed in the Meerfelder Maar sequence were wind-driven. In Lake Suigetsu, in Japan, the onset of the Younger Dryas is characterized by a diatom shift that indicates an intensified winter monsoon bringing stronger winds (more turbulence to the water column) and thicker snow cover (increase surface runoff associated with meltwater in spring) (Kossler *et al.* 2011). Therefore, the diatom changes observed in Lake Xiaolongwan at *c.* 12.8 ka BP may have been caused by a combination of windier and/or drier climate that caused an increase in P loading and/or a decline in the supply of Si. In any case it is very unlikely that these diatom shifts were caused by an increase in summer precipitation. Therefore, the Xiaolongwan diatom record does not support the assertions of Hong *et al.* (2010) for a wet Younger Dryas, at least not from the onset.

The start of XLON-5a (12 490–11 740 a BP) is marked by a peak in varve thickness caused by an increase in clastic content of the sediment. Following this short event both TOC and TN increase. The rise in the C:N ratio (Fig. 5) suggests an increase in the input of organic matter from the catchment. An increase in benthic diatoms (both in terms of percentages and flux) at the top of this zone may indicate some reworking of the littoral sediments. The appearance of varve of the dinocyst-chrysophyte cysts between 12.2 and 12 ka BP also suggests an increased input of allochthonous organic matter and may match with one of the centennial warming/wetting fluctuations observed in several Chinese speleothem records (Ma *et al.* 2012; Liu *et al.* 2013) and in other Eurasian

records such as Meerfelder Maar (Rach *et al.* 2014). Simultaneously in the diatom assemblages, *S. minutulus* declines whereas *D. tatrlica* and to a lesser extent *A. formosa* increase. As seen earlier, *D. tatrlica* would be favoured by less transparent water (higher DOC content) and a shallower mixing depth (less windy conditions).

From the above it seems that the Younger Dryas in Xiaolongwan has two distinct phases (XLON-4 and XLON-5a). A similar bipartite structure has been observed in several European lake records (Neugebauer *et al.* 2012; Lane *et al.* 2013). Basing their studies on several very well-dated northern European sediment records, Lane *et al.* (2013) and Muschitiello & Wohlfarth (2015) showed that the onset of the Younger Dryas was asynchronous at the continental scale. Considering the limitation of our age model and the time resolution of our record, we refrain from evaluating how the timing of the Younger Dryas at Lake Xiaolongwan compares with these records.

The early Holocene

In the Lake Sihailongwan pollen record the start of the Holocene is characterized by an increase in *Betula* and increasing forest cover density occurring at 11 650 a BP (Stebich *et al.* 2009). For Lake Xiaolongwan, the zone XLON-5b (11 740–11 350 a BP) is marked by a return to high percentages of the spring-blooming *S. minutulus*. There are no large changes in varve type, varve thickness or geochemical proxies associated with this diatom shift. This suggests that this was caused by a direct effect of climate on the seasonal diatom succession (earlier and longer springs as seen earlier) rather than a catchment-mediated change in nutrient and/or light conditions as seen for the start of the Younger Dryas.

The following zone, XLON-5c (11 350–11 170 a BP), is characterized by abrupt rises in TOC and TN and a change of varve type from chrysophyte cysts to 'chrysophyte cysts-dinocysts'. In the diatom assemblages, the collapse in *S. minutulus* numbers is associated with a rise in *A. formosa* and then *D. tatrlica*. As seen above, the increase in *D. tatrlica* was maybe caused by increasingly coloured waters. It is approximately at that time that carbon started to accumulate in peatlands of the LGVF, such as the Hani peat located nearby Lake Xiaolongwan (Xing *et al.* 2015). Long time series data sets have shown that light availability is the main factor governing *A. formosa*'s rate of cell increase in spring. The greater rates of increase are caused by a late start of the growth period (owing to a late date of ice-cover break-up) and hence growth under higher light conditions (Maberly *et al.* 1994). It is noticeable that during this time interval late spring (June) insolation was at its maximum (Fig. 5). This taxon, unlike *S. minutulus*, would therefore benefit

from a longer period of ice cover and high light conditions in late spring. This short zone, marked by the end of *S. minutulus*' dominance, may correspond with the 11.4 ka BP cold event reported in the Greenland ice-core records (Rasmussen *et al.* 2014). It is also called the Pre-Boreal oscillation and was reported in South Korea (Park *et al.* 2014) but not in the pollen record from Lake Sihailongwan (Stebich *et al.* 2009).

In XLON-6 (11 170–10 690 a BP), an increase in the C:N ratio (Fig. 5) indicates further input of organic matter from the catchment. The diatom assemblages are largely dominated by benthic diatoms as the BVAR of planktonic diatoms collapses. Simultaneously, there is a change of varve type from chrysophyte cyst-dinocyst to dinocyst. Therefore, planktonic diatoms would appear to have been out-competed by Dinophyceae. This shift to dominance of Dinophyceae may have been caused by increased dissolved organic matter of terrestrial origin in the lake water (Purina *et al.* 2004; Chu *et al.* 2008). At Sihailongwan this time interval is marked by a sharp increase in dust accumulation that indicates a shift towards drier conditions in northern China (Zhu *et al.* 2013). Reduced snow cover under drier conditions may have also been a factor in shifting the phytoplankton composition as Weyhenmeyer *et al.* (1999) showed that Dinophyceae are favoured over diatoms when the spring phytoplankton peak occurs below the ice cover, i.e. before ice break-up, when light conditions are sufficient (i.e. if the ice is clear, without thick snow cover). Allelopathic substances released by Dinophyceae have also been observed to inhibit nutrient acquisition by centric diatoms, especially those of small size (Lyczkowski & Karp-Boss 2014). These effects may have contributed to reducing the growth of planktonic diatoms once Dinophyceae started to dominate.

Conclusions

The diatom and geochemical data presented here for the Xiaolongwan Lateglacial and early Holocene sedimentary sequence provide a detailed record of environmental and climatic change during the last deglaciation. Lake Xiaolongwan appears to have recorded some shifts of lower amplitude that were not reported in the pollen results from the neighbouring Lake Sihailongwan (Stebich *et al.* 2009). In particular, the two diatom assemblage zones that characterize the Younger Dryas suggest a bipartite division of this stadial event as already reported in some studies from eastern Asia (Park *et al.* 2014) and Europe (Lane *et al.* 2013). Interestingly, subdivision of the Younger Dryas is a common feature in the diatom records from Europe as reviewed by Buczkó *et al.* (2012). There is also a short event at c. 11 350 a BP that most likely matches with the Pre-Boreal oscillation. The quasi-synchronicity of these events with the oscillations

described in the North Atlantic realm demonstrates a strong control of the climate in northeastern China by North Atlantic dynamics at centennial and millennial time scales.

This sequence is also useful as it illustrates the complexity of interpreting shifts in diatom assemblages as these may be caused by either the direct effects of seasonal climate on the limnology of the lake (in particular on the duration and timing of ice cover, and length and strength of spring mixing) and/or catchment-mediated effects on the concentrations of nutrients (P and Si) and on the light conditions (via input of dissolved organic matter). This is most obvious with the shifts in abundance of *S. minutulus*. Unlike in other studies (e.g. Bradbury 1988; Rioual *et al.* 2007), in which increases of the spring-blooming *S. minutulus* were unequivocally associated with warmer conditions (shorter ice cover), in the Lateglacial sequence of Lake Xiaolongwan this species is also associated with the start of a cold event, as in that case its growth was stimulated by windier, drier conditions as well as increased input of nutrients from the catchment and/or the littoral zone of the lake.

This sequence also highlights the importance of considering biotic interactions (e.g. competition, allelopathy) between the various groups of phytoplanktonic algae (diatoms, chrysophytes and Dinophyceae in the case of Lake Xiaolongwan) when interpreting the shifts in assemblages observed in the fossil record.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at <http://www.boreas.dk>.

Fig. S1. Light microscope photographs of the main planktonic diatom species. 1–7: *Discostella tatrlica*; 8–14: *Cyclotella comensis*; 15–31: *Cyclotella comensis* morphotype *minima*; 32–38: *Stephanodiscus minutulus*; 39–47: *Handmannia balatonis*; 48–53: *Urosolenia* sp. resting spores; 54–60: *Asterionella formosa*; 61–63: *Fragilaria* sp. 1. Scale bars = 10 μm .