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Paleolimnological features of a mega-lake phase in the Makgadikgadi Basin (Kalahari, Botswana) during Marine Isotope Stage 5 inferred from diatoms

Mareike Schmidt · Markus Fuchs · Andrew C. G. Henderson · Annette Kossler · Melanie J. Leng · Anson W. Mackay · Elisha Shemang · Frank Riedel

Abstract The Makgadikgadi–Okavango–Zambezi basin (MOZB) is a structural depression in the south-western branch of the East African Rift System of the northern and middle Kalahari, central southern Africa. In the present day, the mainly dry subbasins of the MOZB are part of a long-lived lacustrine system that has likely existed since Early Pleistocene and from which an extant freshwater fish radiation emerged seeding all major river systems of southern Africa. During hydrologically favourable periods the subbasins were connected as a single mega-lake termed Lake Palaeo-Makgadikgadi. Previous geomorphological studies and OSL dates have provided evidence for repeated mega-lake periods since approximately 300 ka. The environmental and climatic implications of such large scale late Quaternary lake-level fluctuations are controversial, with the duration of mega-lake phases poorly constrained. Here, we present the first evidence for a Marine Isotope Stage (MIS) 5 mega-lake period (about 935–940 m a.s.l.) reconstructed from a diatom-rich, 30-cm-thick lacustrine sediment section, exposed close to a palaeo-shoreline of the Makgadikgadi Basin. Based upon the environmental setting and in comparison with sedimentation rates of other similar lake environments, we tentatively estimated that the highstand lasted approximately 1 ka during MIS 5d–b. The 30-cm section was sampled in 0.5-cm steps. Diatom species diversity ranges from 19 to 30 through

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the section. The dominant species are *Pseudostaurosira brevistriata*, *Rhopalodia gibberula*, *Cyclotella meneghiniana* and *Epithemia sorex*. The total of 60 sediment samples provide us with a record at decadal to bi-decadal resolution. Based on diatom assemblages and their oxygen isotope composition ($\delta^{18}O$) we infer an alkaline and mostly oligohaline lake with shallow water conditions prevailing in MIS 5, and is potentially analogous to a Heinrich event. The climate over southern Africa during MIS 5 has been considered very arid but the hydromorphological context of our sediment section indicates that we captured a mega-lake period providing evidence that short-term excursions to significantly higher humidity existed. A hydrologically more favourable environment during MIS 5 than formerly presumed is in line with the early human occupation of the Kalahari.

Introduction

Geomorphological studies of the northern and middle Kalahari in northern Botswana have provided evidence of a former mega-lake system (Passarge 1904; Grove 1969; Ebert and Hitchcock 1978; Cooke 1979; Heine 1982; Thomas and Shaw 1991; Burrough et al. 2009a; Podgorski et al. 2013; Riedel et al. 2014; Fig. 1), which developed within the Makgadikgadi–Okavango–Zambezi basin (MOZB). The structural depression of the MOZB belongs to the south-western branch of the East African Rift System (Ringrose et al. 2005; Kinabo et al. 2007; Shemang and Molwalefhe 2011; Riedel et al. 2014). Grey and Cooke (1977) termed highstands in this lacustrine system Lake Palaeo-Makgadikgadi (referring to the Makgadikgadi Basin, the largest and deepest of the depressions), which likely comprised of several lacustrine basins (Fig. 1) and exhibited a maximum expansion of about 66,000–90,000 km^2 (Eckardt et al. 2008; Podgorski et al. 2013). There is geological and phylogeographical evidence that the mega-lake system may have existed since the Early Pleistocene (Genner et al. 2007; Moore et al. 2012; Riedel et al. 2014; Schultheiß et al. 2014). An OSL (optical stimulated

luminescence) date of *c.* 290 ka (Burrough et al. 2009a) provides only a minimum age of the palaeolake system as this is at the limit of the OSL dating technique (Cordier et al. 2012).

Burrough et al. (2009a) presented a large number of OSL dates in order to illuminate the chronology of mega-lake periods. Apart from two dates that fall within MIS 8 (*c.* 290 and *c.* 270 ka) they dated highstands during MIS 5–MIS 1. Their OSL samples were taken from palaeo-shorelines of the Makgadikgadi Basin which represents the dominant water body during Lake Palaeo-Makgadikgadi highstands. Burrough et al. (2009a) inferred seven periods of lake highstands in the Makgadikgadi Basin during the past approximately 105 ka. Two of these occurred during MIS 5 (104.6 ± 3.1 and 92.2 ± 1.5 ka) and the next youngest one is of MIS 4 age (64.2 ± 2.0 ka).

Today, the Makgadikgadi Basin (Fig. 1) is characterized by several salt pans. The largest are the central Ntwetwe Pan (about 4700 km^2) and the eastern Sua Pan (about 3000 km^2), which are occasionally filled with water in modern times, but these temporary infills are not high enough to link the pans together (Riedel et al. 2012). The bottoms of the pans lie generally below an altitude of 950 m a.s.l. (Grove 1969; Grey and Cooke 1977; Cooke 1980; Mallick et al. 1981), with the deepest point (also of the MOZB) located in the northern part of the Sua Pan at an altitude of 890 m a.s.l. (Cooke 1980; Thomas and Shaw 1991; Eckardt et al. 2008).

The western margin of the Makgadikgadi Basin is sharply bordered by the prominent Gidikwe Ridge (Fig. 1), which stretches about 250 km from north to south and exhibits a series of palaeo-shorelines. Here, two distinct palaeo-shorelines were determined at an altitude of 945 and 936 m a.s.l. (Cooke and Verstappen 1984; Thomas and Shaw 1991; Burrough et al. 2009a, b). Lacustrine sediments recorded west to the Gidikwe Ridge (Fig. 1) were interpreted to be of lagoon origin (Cooke 1980; Thomas and Shaw 1991). The backside of the Gidikwe Ridge, however, was considered a second ridge (Moremaoto) by Gumbricht et al. (2001; personal observations FR), delimiting the Makalamabedi Basin (Fig. 1) to the east, which exhibits a curvilinear morphology interpreted as palaeo-shorelines at approximately 930–940 m a.s.l. (Gumbricht et al. 2001; Riedel et al. 2014). Near the Moremaoto Ridge about 2-m-thick diatom-rich
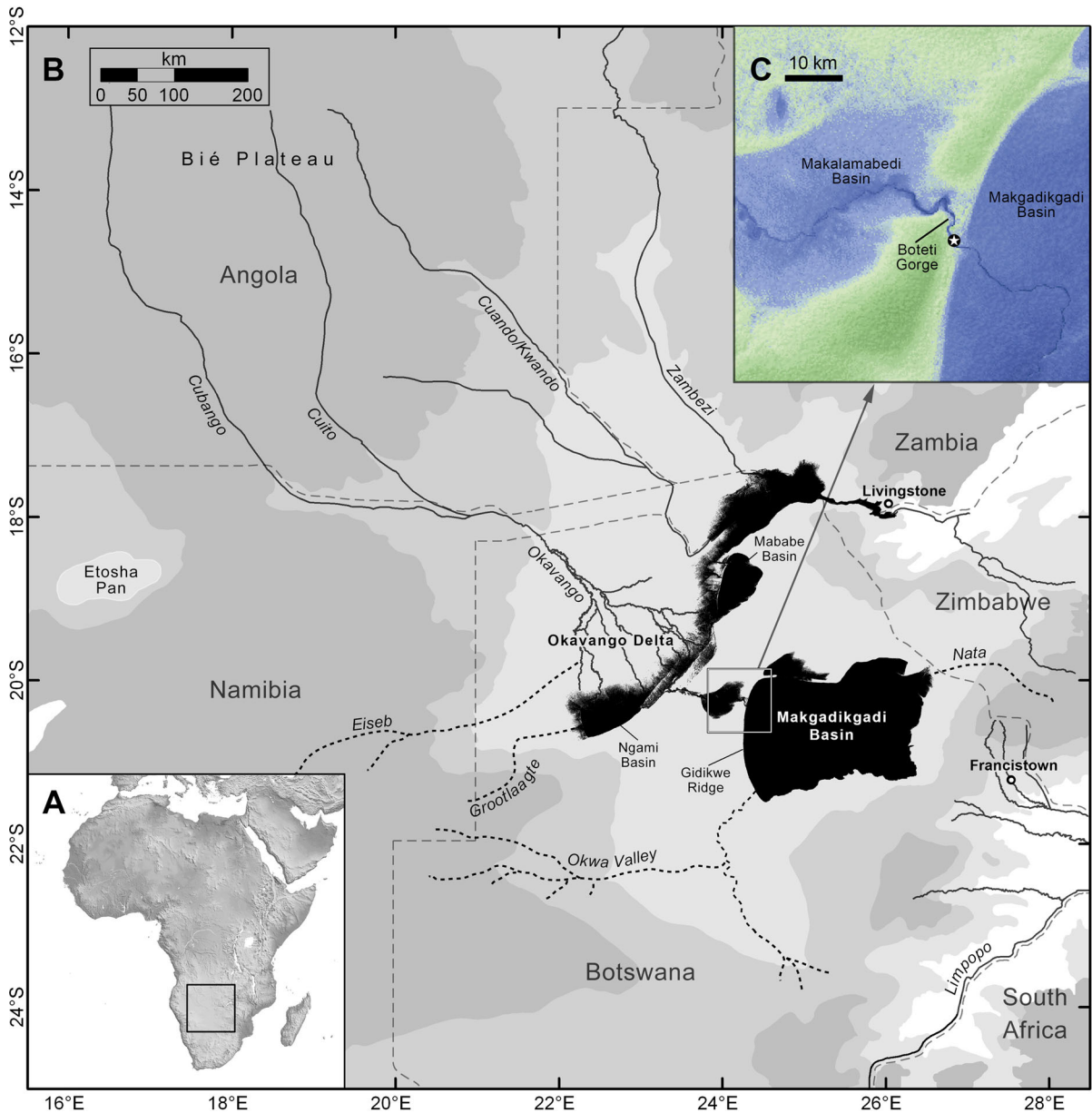
Fig. 1 **a** General location of study area. **b** Map of Makgadik-gadi–Okavango–Zambezi basin (MOZB) of the south-western branch of the East African Rift System and the major tributaries. *Black dashed lines* indicate valleys of palaeo-rivers. Major subbasins of MOZB *shaded black*. During late Quaternary hydrologically favourable periods these subbasins may have been part of a mega-lake. Due to tectonics and hydromorphological processes the modern setting can be used only tentatively for simulating past mega-lake sizes and shapes. **c** A digital elevation model (modified from Riedel et al. 2014) exhibits the location of the studied geological section at the western edge of the Makgadikgadi Basin where palaeo-shorelines can be found on the structural Gidikwe Ridge

sediments (personal observation MS and FR) are exposed, which were originally described in Passarge (1904) who considered an Eemian (MIS 5e) lake period. Shaw et al. (1997) re-studied the diatom-rich sediments, established a MIS 3 age and related them to a lake highstand of the Makgadikgadi Basin. These sediments however are located in the Makalamabedi Basin (Riedel et al. 2014).

There are currently no palaeontological records from lacustrine sediments in the MOZB older than MIS 3 (Riedel et al. 2014) that could be used to characterise mega-lake periods. Joyce et al. (2005) concluded an extant cichlid radiation emerged from Lake Palaeo-Makgadikgadi during the Middle Pleistocene seeding all major river systems of southern Africa. These fish require freshwater habitats, which could be sustained over longer periods only when the lake had an outlet (Riedel et al. 2014). The Zambezi, which transverses the northern extension of the lacustrine system, could have acted as an outflow during highstands when all basins where connected into a single mega-lake. It has been suggested that the inflow of the Okavango River, and possibly of the Zambezi, controlled mega-lake periods (Nugent 1990). There are, however, several fossil river systems entering the Makgadikgadi Basin (Riedel et al. 2014) of which the Okwa Valley is the largest (Fig. 1). Riedel et al. (2014) suggested that the Okwa River was fully active for the last time during the Last Glacial Maximum and ceased flowing during Heinrich event 1. So far it can only be speculated whether during periods of enhanced Okwa River inflow the Makgadikgadi Basin became exorheic, with an outflow to the west, and freshwater conditions prevailed (Riedel et al. 2014).

On the one hand the environmental and climatic implications of such large scale late Quaternary lake-level fluctuations and the dynamics of aeolian activity are mainly controversial and on the other hand the discussion has focussed especially on the period MIS 3–MIS 1 (Street and Grove 1976; van Zinderen Bakker 1976; Heine 1981, 1987, 1988; Stokes et al. 1997; Gasse et al. 2008; Burrough and Thomas 2009; Burrough et al. 2009a, b; Hürkamp et al. 2011; Riedel et al. 2014). There has been limited work on MIS 5 sediments, and some climate interpretations do exist although these rely heavily on marine sediments (from off Namibia: Shi et al. 2001; Stuut et al. 2002) at a low temporal resolution (Urrego et al. 2015). It is noteworthy that Urrego et al. (2015) reported increased aridity in south-western Africa (neighboring our study area) during the warmest periods of MIS 5 (5e, 5c, 5a), but they also identified short increases in humidity during warm-cold and cold-warm transitions. Geyh and Heine (2014) reported MIS 5 speleothem growth from the Namib Desert. In south-eastern Africa, MIS 5 was characterized by episodes of

extremely arid conditions leading to dramatic low-stands of Lake Malawi (Cohen et al. 2007; Scholz et al. 2007).

These tropical African MIS 5 "megadroughts" (Scholz et al. 2007) are discussed to have facilitated human expansions across Africa and ultimately out of Africa (Rito et al. 2013). Genetic data suggest that anatomically modern humans (Balter 2002) originated in Africa during MIS 6 (Ingman et al. 2000) and there is archaeological evidence that they populated the southern tip of Africa as early as ∼165 ka (Marean et al. 2007). Genomic diversity of extant hunter-gatherer populations is in agreement with this early occupation of southern Africa and tentatively suggests even the orgin of modern humans from this region (Henn et al. 2011). Symbolic and thus modern behaviour of such southern African human populations may have first appeared during MIS 5a (Henshilwood et al. 2002) or early MIS 4 (Jacobs and Roberts 2009). In the Kalahari, archaeological sites at the Tsodilo Hills indicate human occupation since at least 90 ka (Robbins et al. 2016). Burrough (2016) discussed the environmental contributions to early human dispersal in the Kalahari and emphasised the contrast between MIS 5 lake highstands in the Makgadikgadi Basin and extreme lowstands of Lake Malawi.

The modern climate setting over semi-arid southern Africa is complex (Peel et al. 2007; Gasse et al. 2008; Chase et al. 2012; Riedel et al. 2014) and comprises moisture transport from the West and East African monsoons (including convective moisture from the Congo Basin) to the Okavango catchment and the Kalahari during austral summer. Rainfall variability in Botswana is described by Batisani and Yarnal (2010). During austral winter, moisture from the south-eastern Atlantic triggers rainfall (mainly) over the Western Cape Province. South-western Indian Ocean (Agulhas Current) derived moisture triggers rainfall over southern Africa mainly during austral summer but also during winter (Chase and Meadows 2007; Gasse et al. 2008; Burrough et al. 2009b; Chase et al. 2012; Urrego et al. 2015).

The aim of our study is to reconstruct for the first time the palaeohydrological status of a mega-lake phase (about 66,000–90,000 km^2) in the MOZB, which corresponds to a highstand of at least 936–945 m a.s.l. of Lake Palaeo-Makgadikgadi, by analysing diatom assemblages and their oxygen

isotope composition ($\delta^{18}O_{diatom}$). The mega-lake phase adressed here occurred during MIS 5 and is the first attempt to infer the duration of a mega-lake phase in this region. Our findings contribute to the understanding of phylogeographical patterns and climate evolution of southern Africa.

Study site

Our study site (Fig. 1) is located at the Gidikwe Ridge where the ridge is cut by the Boteti River valley forming a 20–22 m deep gorge. Here, a 10-m-thick sedimentary succession was exposed (S20.28672°, E24.26822°), which exhibited 40 cm consolidated, heavily diagenetically altered lacustrine deposits at the base, followed by 9.3 m unfossiliferous, silcrete- and calcrete-rich playa sediments (Riedel et al. 2014). On the top of the succession of sediments, at about 935 m a.s.l., the playa sediments are overlain by a 30-cm-thick unit (Fig. 2), which consists of consolidated, fine-laminated to thin-bedded, finely clastic, light-grey to whitish lacustrine sediments rich in diatoms and deposited during MIS 5 (Riedel et al. 2014). Lithological hiatuses were not identified in the 30-cm unit, suggesting sedimentation was continuous. This sediment unit thins out a few hundred metres west of the section where sandy palaeo-beach features can be found indicating that the former shore was relatively close.

Materials and methods

Sediment samples

The 10-m sediment outcrop within the Boteti Gorge at the western margin of the Makgadikgadi Basin (Figs. 1, 2) was first visited by AK and FR in 2007 and a small number of samples were taken. Samples from a 40-cm-thick unit of white and pale-gray lacustrine sediments at the base of the profile has been strongly affected by diagenesis, and contains only few broken valves of diatoms, while the light-grey to whitish 30-cm-thick deposits at the top of the section (Boteti Top = BT) have abundant diatoms. Although carbonate is contained in BT, remains of ostracod valves were only exceptionally preserved. Except for a few pollen grains, no other fossil remains were identified. When revisiting the section in 2009

samples for OSL dating were taken from the two lacustrine sediment units. MF provided an OSL date suggesting MIS 5 age for BT. OSL dating of the 40-cm unit at the base of the Boteti section failed because the OSL signal was close to saturation and therefore at its upper limit.

In 2011 the outcrop was revisited for high resolution sampling and a fresh surface was exposed and thoroughly cleaned using spade, saw, knife and brush. The sampling of the relatively hard sediments was done in 0.5-cm increments with a knife from the base to the top of the BT unit. 60 sediment samples of about 60 grams each were taken, sample BT_{diatom}-1 corresponding to the lowermost and sample BT_{diatom}-60 to the uppermost layer. In addition, using a saw, a $30 \times 15 \times 15$-cm-sediment block was removed covering the complete BT unit in order to obtain suitable material for optical dating. The sawed surfaces did not exhibit cracks through which light could have penetrated into the internal sediments. The block was immediately wrapped with thick black plastic foil and stored in a sealed box.

OSL dating

Samples were taken from the lower (BT 1055), middle (BT 1054) and upper part (BT 1052) of the sediment block in the OSL lab of Bayreuth University, Germany. A further sample (BT 885) from the middle part of the BT section had been already obtained during field work in 2009 (Fig. 2).

The coarse grain quartz fraction (90–200 µm) of the sediment samples was used for OSL dating. Luminescence measurements were carried out using a Risø-Reader TL/OSL-DA-15 (Bøtter-Jensen 1997), equipped with blue LEDs (470 ± 30 nm) for stimulation, a Thorn-EMI 9235QA photomultiplier combined with one 7.5 mm U-340 Hoya filter (transmission 290–370 nm) for detection and a $^{90}Y/^{90}Sr$ β-source (8.1 ± 0.6 Gy/min) for artificial irradiation.

The equivalent dose (D_e) was determined by applying a single aliquot regenerative (SAR) dose protocol (Murray and Wintle 2000). Shine-down curves were measured for 20 s at elevated temperatures (125 °C) after a preheat for 10 s at 220 and 240 °C respectively for the natural and regenerated signals and a cut-heat of 160 °C for the test doses. The preheat temperatures were chosen after a preheat plateau test, which indicated that the given dose could
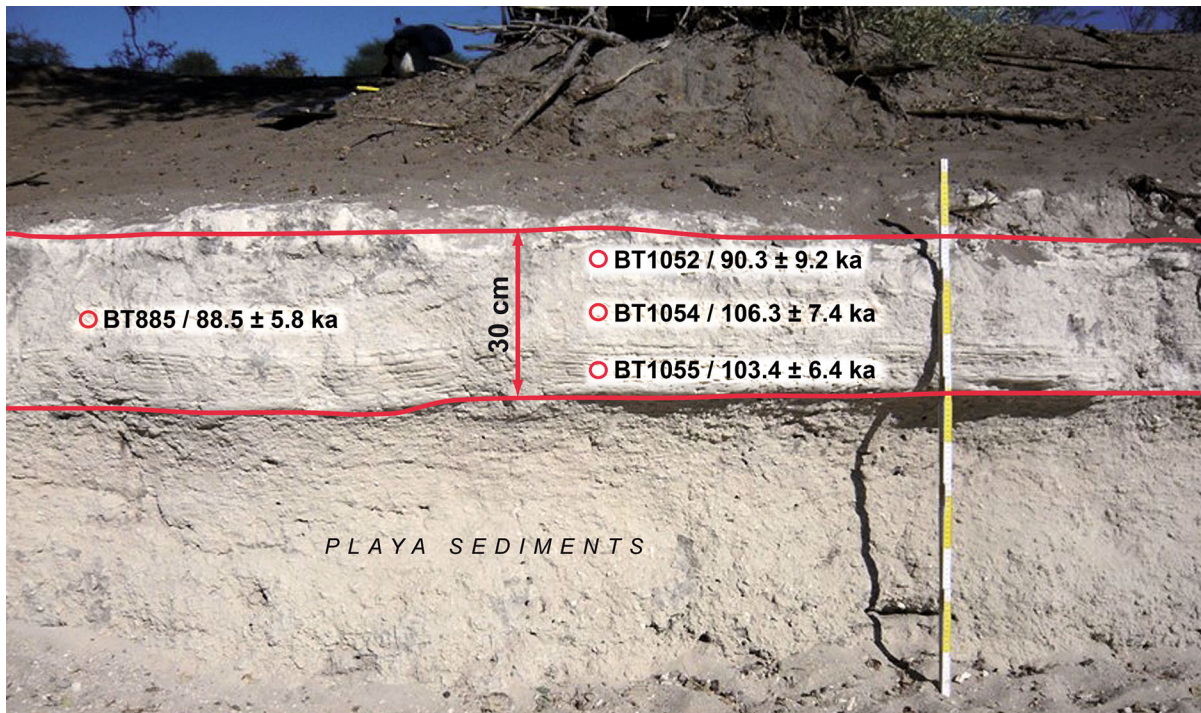
Fig. 2 *Upper part* of the Boteti river valley section with studied 30-cm diatom-rich sediment unit on *top* (BT). Position of samples for OSL dating and OSL dates are indicated

be reproduced within a temperature range of 220–240 °C.

Finally, the D_e was calculated from the integral of the first 0.4 s from the shine-down curves after subtracting the mean background (16–20 s) signal. For each sample, up to 28 small aliquots (steal cups) were measured with 200–500 grains per aliquot. Possible feldspar contamination of the aliquots was checked by stimulating the artificially irradiated samples with infrared (IR-OSL) and detecting in the UV range (290–370 nm). For D_e determination, only those aliquots of a sample were used, which passed the criteria of a recycling ratio of 1 ± 0.1 and a recuperation value of <5% (Murray and Wintle 2000). The standard error was used as D_e error.

The dose rate $\left(\dot{D}\right)$ for OSL age calculation was determined by thick source α-counting and ICP-MS. Cosmic-ray dose rates were calculated according to Prescott and Hutton (1994). The water content of the samples was determined using the average value of the possible water content range, based on the porosity of the samples. An error for the water content value was chosen, which included the possible water content

range. The values used for the water content were checked by measuring the in situ water contents of the samples, showing conformity within errors.

Diatom assemblages

Diatom extraction and slide preparation for microscopic analyses were carried out following Battarbee et al. (2001). Diatom identification and counting were performed using a Meiji Techno 4000 microscope at $1000\times$ magnification with an oil immersion objective. Approximately 500 diatom valves were counted per sample to ensure that effective numbers of taxa were counted. Diatom relative abundances were plotted using Tilia® (Grimm 1991–2011), and planktonic to benthic ratios calculated according to the formula: $\sum(\text{planktonic})/\sum(\text{planktonic} + \text{benthic})$.

For precise identification of the diatom taxa, a Zeiss Supra 40 VP scanning electron microscope (SEM) was additionally used. Diatoms for the SEM analyses were prepared by drying 0.5 ml of the treated sample suspension on a cover slip fixed on a stub. After drying, the diatoms were coated with gold in a sputter

coater and then examined with the SEM. Diatom species were identified using, amongst other keys, Krammer (2002), Krammer and Lange-Bertalot (1997, 1999, 2000, 2004), Levkov (2009) and Kusber and Cocquyt (2012). A list of species and their authorities is provided in ESM 1.

The ecological preferences of identified diatoms concerning salinity, pH and trophic level were taken from the literature (ESM 2), but are unknown in some taxa. The salinity classification follows Schlungbaum and Baudler (2001): freshwater = <0.5 psu; oligohaline = 0.5 to <5 psu; mesohaline = 5–18 psu; euryhaline = fresh to saltwater, indifferent or non-significant.

Ordination analyses were undertaken using Canoco 4.5 (ter Braak and Šmilauer 2002) to reveal major trends in the diatom data. An initial detrended correspondence analysis (DCA) gave an axis 1 gradient of only 0.734, revealing a dataset with very little species turnover, so principal components analysis (PCA) was used instead. Scaling for both samples and species was optimized through symmetric scaling of the ordination scores (Gabriel 2002). Because we have closed relative abundance data, species data were log $(x + 1)$ transformed and both species and samples were centred to give a log-linear contrast PCA (Lotter and Birks 1993). To determine if any of the PCA axes were in themselves significant in explaining variation in the diatom data, a broken stick analyses was undertaken (Jollifer 1986). The diatom stratigraphy was zoned using Constrained Incremental Sum of Squares Cluster Analysis (CONISS) according to Grimm (1991–2011).

Diatom oxygen isotope analysis

From the 60 BT samples studied in respect of diatom assemblages, alternate samples were analysed for their oxygen isotope composition. Following the protocol established by Morley et al. (2004) the 30 sediment samples for $\delta^{18}O_{diatom}$ analysis underwent chemical digestion using 30% H_2O_2 and 5% HCl followed by sieving of samples at 74 and 10 μm. Diatoms were then isolated using a combination of differential settling and heavy liquid separation using sodium polytungstate (SPT). The SPT was then washed out of the purified sample using multiple rinses of deionised distilled water, and dried down prior to analysis. Samples were measured using a step-wise fluorination

procedure using 6 mg of sample (Leng and Sloane 2008) and a Finnigan MAT 253 isotope ratio mass spectrometer. $\delta^{18}O_{diatom}$ were converted to the Vienna Standard Mean Ocean Water (VSMOW) scale using an international laboratory diatom standard (BFC$_{mod}$) calibrated against NBS28. The methology has been verified through an inter-laboratory calibration exercise (Chaplygin et al. 2011). Replicate analyses of sample material from this current study indicating an analytical reproducibility (mean difference) of 0.2‰ ($1\sigma = 0.5$, n = 9).

Results

OSL dating

The suitability of the quartz extracts for OSL dating was evaluated using a combined preheat plateau and dose-recovery test. In ESM 3c, the result of this test is shown, indicating the given dose of 70.2 Gy could be reproduced within a temperature range of 220–260 °C. In addition, ESM 3a shows a typical OSL shine-down curve, displaying a bright OSL signal that is quickly bleached to measurement background. Growth curves could be established with high precision, with recycling ratios of 0.9–1.1 (ESM 3b). Thus, the OSL quartz behavior, the preheat plateau and the dose-recovery tests demonstrate the suitability of the applied SAR protocol.

In Table 1, the analytical data for OSL age calculation, including the data for dose rate determination are given. The results of the OSL age calculation ranging from 106.3 ± 7.4 to 88.5 ± 5.8 ka indicate the studied section can be assigned to MIS 5. The sample BT 1055 from the lower part of the studied sediment unit (Fig. 2) has an OSL age of 103.4 ± 6.4 ka, the following sample BT 1054 from the middle part of the 30-cm unit (Fig. 2) shows an age of 106.3 ± 7.4 ka, which is within errors still consistent with the stratigraphic order. Sample BT 1052 from the upper part (Fig. 2) reveals an age of 90.3 ± 9.2 ka. The sample BT 885, which was previously taken in 2009, shows an age of 88.5 ± 5.8 ka and correlates with the result of BT 1052 (Table 1).

Diatom assemblages and $\delta^{18}O_{diatom}$

The microscopic analyses of the samples reveal the sediments are rich in well-preserved diatom valves

Table 1 Analytical data for OSL age calculation: sample code, ^{238}U, ^{232}Th and ^{40}K-concentrations, total dose rate, equivalent dose and OSL age

Sample	U (ppm)	Th (ppm)	K (%)	$\dot{D}$ (Gy/ka)	D_e (Gy)	OSL age (ka)
BT 885	1.14 ± 0.08	2.20 ± 0.05	0.41 ± 0.01	0.88 ± 0.04	77.6 ± 3.8	88.5 ± 5.8
BT 1052	0.97 ± 010	2.02 ± 0.04	0.32 ± 0.01	0.66 ± 0.03	59.7 ± 5.2	90.3 ± 9.2
BT 1054	0.91 ± 0.07	2.38 ± 0.05	0.34 ± 0.01	0.69 ± 0.33	72.9 ± 3.7	106.3 ± 7.4
BT 1055	0.93 ± 0.09	2.42 ± 0.05	0.33 ± 0.01	0.68 ± 0.33	70.7 ± 2.8	103.4 ± 6.4

(Fig. 3). In total, 50 species could be identified of which 44 species are benthic, that is they prefer littoral rather than planktonic habitats (ESM 1, ESM 2). The number of species per sample ranges from 19 to 30. Generally, most species are represented by a few valves only. Benthic diatoms dominate the whole sequence (70–95%), especially in the uppermost sediments, resulting in very low planktonic/benthic ratios (Fig. 4).

Using broken stick, only PCA axis 1 showed significant variation. PCA axis 1 sample scores are therefore also plotted against depth in Fig. 4. These data show considerable variation, superimposed on a strong directional change from the base of the sediment unit to about 25 cm, before sample scores decline to the top of the profile. A moderate but significant Pearson product moment correlation coefficient exists between PCA axis 1 sample scores and the P/B ratio (r = −0.618; p = 0.0001). CONISS has delimited 3 zones (Kala-1 to Kala-3), with major divisions at 13.75 and 23.25 cm (Fig. 4).

Kala-1: This zone is dominated by *Pseudostaurosira brevistriata* and *Rhopalodia gibberula*, although the planktonic *Cyclotella meneghiniana* is also abundant, resulting in highest P/B ratios for the sequence and lowest PCA axis 1 samples scores. *Halamphora thermalis* is also relatively common. At this time, $\delta^{18}O_{diatom}$ values increase steadily to their highest values of +34.2‰ at 11.5 cm.

Kala-2: This zone is delimited by a small peak in *P. brevistriata*, a P/B minimum and declining $\delta^{18}O_{diatom}$ values. Within this zone, the most notable changes include declining *C. meneghiniana* values and increases in *Epithemia sorex*.

Kala-3: This zone is delimited by very low P/B ratio values and high PCA axis 1 samples, and lowest $\delta^{18}O_{diatom}$ values (+28.2‰ at 23.5 cm). During this zone, *C. meneghiniana* values are generally at their lowest, while *E. sorex* values are at their highest. Towards the top of this zone, P/B ratio values increase slightly, concomitant with declining PCA axis 1 sample scores and increasing $\delta^{18}O_{diatom}$ values to about +31‰.

The inferred hydrological parameters (salinity, trophic status, pH) show little variation throughout the palaeolake-phase. Most diatoms are tolerant to salinity fluctuations but about 15% of the species of the assemblages reflect oligohaline conditions in zones Kala-1 and -2 with an increase to 20% in Kala-3. About 60% of the diatom species indicate eutrophic conditions and 20–30% are nutrient-tolerant. The pH reconstruction indicates alkaline conditions (>7). Approximately 30–40% of the diatom species require pH values of 7–8 and 50–80% of 8–9 with slight decrease of alkalinity during zone Kala-3.

Discussion

Dating

Age calculation of mega-lake phases in the MOZB (Fig. 1) have previously been established using a large set of OSL dates from palaeo-shoreline features (Burrough and Thomas 2009; Burrough et al. 2009a, b). In respect of MIS 5, Burrough et al. (2009a) identified two highstands of Lake Palaeo-Makgadikgadi centred at c. 105 and c. 92 ka respectively, analysed as "events of unknown duration" (Burrough et al. 2009b). In contrast to samples obtained from shoreline sediments (Burrough et al. 2009a), which may have been reworked by waves, we dated quartz grains from a low energy aquatic milieu. The fine lamination of the sediments indicates still water conditions below the wave-line and reworking of the sediments can likely be ruled out. The range of
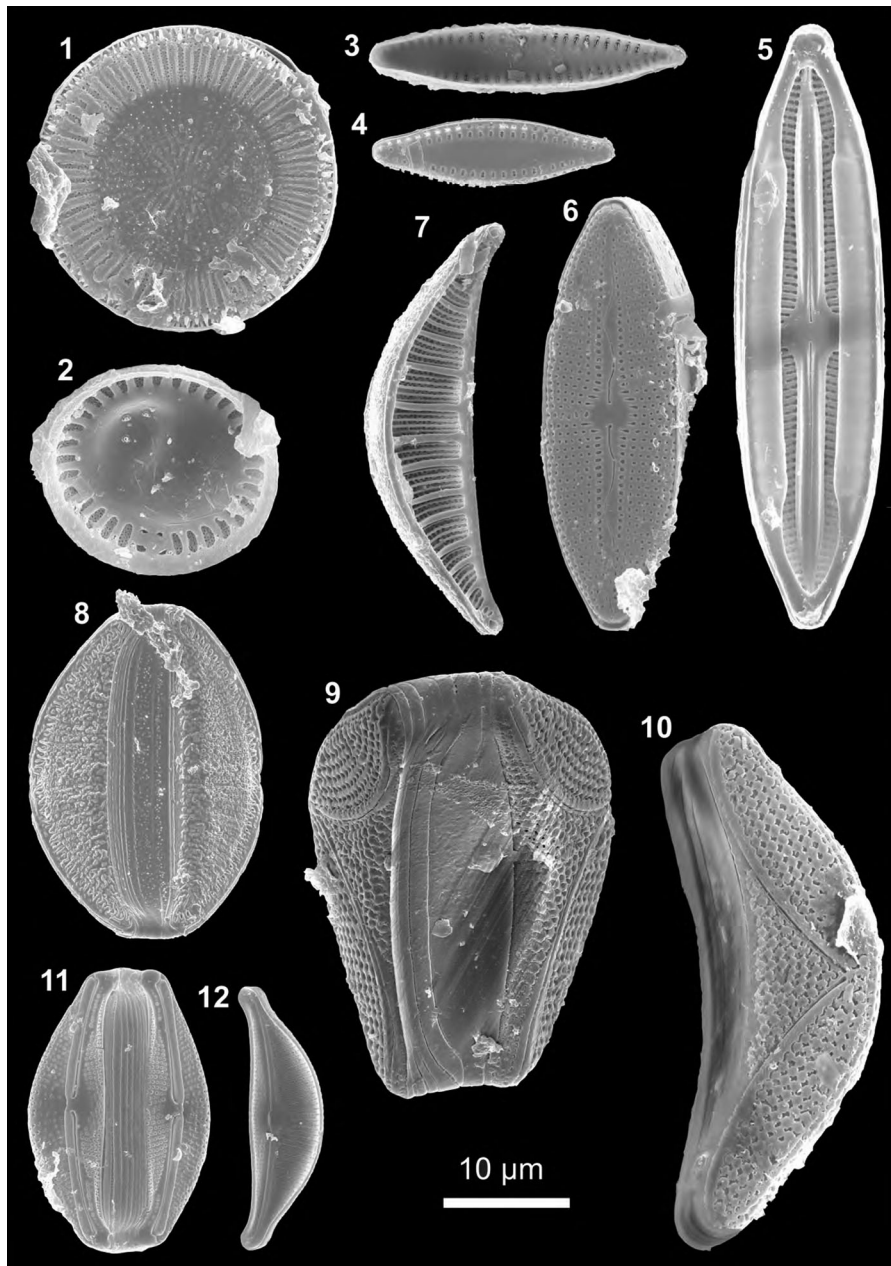
Fig. 3 Scanning electron microscope images of the six most abundant diatom species identified in the Boteti section top unit (BT). *1–2 Cyclotella meneghiniana*, *3–4 Pseudostaurosira brevistriata*, *5–6 Mastogloia elliptica*, *7–8 Rhopalodia gibberula*, *9–10 Epithemia sorex*, *11–12 Halamphora thermalis*

our dates, however, shows large uncertainty remains. Considering the uncertainties of the oldest (106.3 ± 7.4 ka) and the youngest age (88.5 ± 5.8 ka), the max. range is 113.7–82.7 ka, a period of 31 ka covering roughly MIS 5d–b, and the min. range is 98.9–94.3 ka, a period of 4.6 ka.

The range has to be considered in the context of the duration of continuous deposition of 30 cm of lacustrine sediments. In comparision with lake systems showing at least partly similar (palaeo-)environmental settings (Aral Sea: 30 cm ∼650 years, Filippov and Riedel 2009; Lake Titicaca: 30 cm ∼900–1200 years,
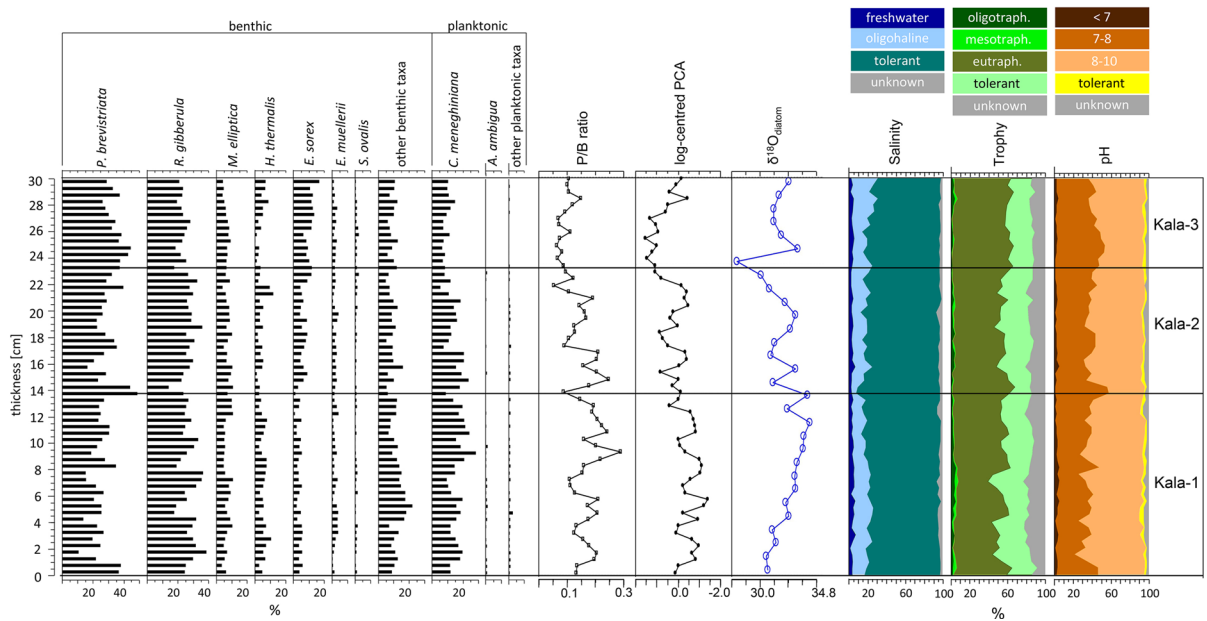
Fig. 4 Composite diagram illustrating percentage abundances of most frequent species separated into benthic and planktonic forms, P/B ratio, log-centred PCA, δ^{18}O$_{diatom}$ variability, and stack diagrams for salinity, trophy and pH inferred from the autecology of the diatom species

Fornace et al. 2014; Tso Moriri, Ladakh, India: 30 cm ~1100 years, Leipe et al. 2014; Lake Kotokel, Buryatia, Russia: 30 cm ~700 years, Kostrova et al. 2016; Lake Teletskoye, Russian Altai: 30 cm ~600 years, Mitrofanova et al. 2016; Lake Van, Turkey: 30 cm ~1000 years, North et al. unpublished data) it can be roughly estimated that the 30-cm sediment unit of the Boteti section had been deposited during a period of approximately 1 ka.

It is possible, but not likely that the terminal highstand is not archived in the 30-cm unit. This could be because of potential deflation processes after the lake level had decreased. Once exposed, sediments of such composition usually harden quickly under a (semi-)arid climate and subsequent weathering and erosion processes are limited. This is also due to the fact that under retreating lake levels, aeolian activity is increasing and consolidated lacustrine sediment sequences are often, instead of being deflated, covered by sand (as can be observed across the MOZB), which protects them from erosion. Moreover, the 40-cm-lacustrine-sediment unit at the base of the Boteti section, which is overlain by playa sediments, appears to be complete and provides an independant example of a relatively short lake highstand. We thus can

provide at least a first idea how long so-called mega-lake phases may have lasted.

The estimation that the 30-cm-sediment unit covers a period of not more than approximately 1 ka allows us to infer a temporal resolution of the analysed samples of 1–2 decades. Dating uncertainties remains a major challenge for an accurate reconstruction of environmental dynamics in the Kalahari, and is probably responsible for most of the controversial discussions related to (Street and Grove 1976; Heine 1981, 1987, 1988; Stokes et al. 1997; Gasse et al. 2008; Burrough and Thomas 2009; Burrough et al. 2009a, b; Chase and Brewer 2009; Hürkamp et al. 2011; Riedel et al. 2014; Burrough 2016).

Significant uncertainties also exist with respect to measured palaeo-shoreline altitudes. In a number of studies the uncertainty is as high or even higher as the 9 m difference between the 936 and 945 m a.s.l. palaeo-shorelines (Riedel et al. 2014). On the other hand, it is unlikely mega-lake highstands reached the same elevation repeatedly, except in exceptional circumstances. The two different lacustrine sediment units of the Boteti section indicate two lake periods at the same position, which means they are of likely similar extension, although the older highstand is

about 9.3 m lower than the younger one. The amount of available water during these two periods may have been similar, pointing at comparable climate settings, but with increased accumulation of sediments in the MOZB raising the lake floor (Haddon and McCarthy 2005). Thus a higher lake level of significant younger age than an earlier lower lake level could have potentially been reached even with less hydrological input.

Diatom assemblages and $\delta^{18}O_{diatom}$

The diatom assemblage presented here is very different from contemporary flora found in the fresh, shallow waters of the Okavango Delta (Mackay et al. 2012). The dominance of benthic taxa (Fig. 4) in the BT unit indicates the persistence of shallow water conditions and extensive littoral regions, especially during the terminal stages of sediment accumulation (zone Kala-3). Patrick (1977) described *E. sorex* as an aerophilous species that can persist in environments characterized by desiccation. Therefore, an increase of the abundance of *E. sorex* within the sediments at this time potentially shows a stronger proximity to the shoreline caused by a drop in lake level during this period of inferred lake level decline. The maximum water depth can be calculated in the hydromorphological context to have been a few metres only (max. depth of palaeolake ∼50 m). The diatom assemblages reveal changes in lake water depth throughout the record. The significant correlation between PCA axis 1 sample scores and P/B ratio suggests varying water levels influenced diatom composition in the shallow lake waters. What is notable is the period of highest P/B ratio is coincident with increasing $\delta^{18}O_{diatom}$ values (increasing effective moisture), indicative of increasing planktonic habitats in this part of the lake (Fig. 4).

These shallow waters were likely freshwater to brackish; qualitative salinity reconstruction indicate oligohaline conditions (0.5 to <5 psu) persisted during the whole period (Fig. 4). For example, the dominant species *P. brevistriata*, *R. gibberula* and *M. elliptica* have wide salinity tolerances (Caljon and Cocquyt 1992; Krammer and Lange-Bertalot 1999; van Dam et al. 1994; Stachura-Suchoples 2001). *E. sorex* is also described from oligohaline waters (Cholnoky 1968; Patrick 1977; Krammer and Lange-Bertalot 1999;

Kelly et al. 2005), while *C. meneghiniana* is often found in brackish water (Hecky and Kilham 1973).

The qualitative oligohaline salinity reconstruction at the study site does not mean that Lake Palaeo-Makgadikgadi was oligohaline in general but exhibited salinity gradients. Filling up and interconnecting the lacustrine basins to a single lake (Fig. 1) required significant inflow from at least one of the major river systems, either from the Okavango River in the (north-)west or from the Okwa River in the southwest. It also cannot be ruled out that both river systems were active simultaneously. If the Okavango was the main source of hydrological input, the main lacustrine depression of the palaeolake-system, the Makgadikgadi Basin, would have acted as a terminal lake with increasing salinity to the east (Fig. 1). The likely outflow in this scenario would be through the Zambezi valley. Therefore, western lake areas between major inflow and outflow would have been under freshwater conditions. An example of a comparator to this behaviour can be found at extant Bosten Lake, Xinjiang, China, where inflow and outflow are located at the western side of the lake and freshwater conditions prevail only there, while the largest part of the water body is oligohaline (Mischke and Wünnemann 2006; Wufuer et al. 2014; personal observation FR). A second scenario considers the Okwa River the main source of water inflow during the highstand. In this case the Makgadikgadi Basin was exorheic and the study site would have been in proximity to the outflow. In both scenarios freshwater areas are limited, and considering the relatively short period of approximately 1 ka, the mega-lake phase likely did not foster evolutionary radiations of freshwater fish or gastropods. This is in agreement with the phylogeographic studies of Joyce et al. (2005) and Schultheiß et al. (2014) who considered Early to Middle Pleistocene age of Lake Palaeo-Makgadikgadi evolutionary radiations, indicating palaeohydrology and hydromorphology differed significantly from our observed MIS 5 setting.

In respect of pH, it can be inferred from the diatoms that the lake was always alkaline (pH ∼8). Whereas *C. meneghiniana*, *E. sorex*, *H. thermalis* and *R. gibberula* occur preferentially in waters with the pH greater than 8 (Cholnoky 1968; Gasse 1986; Gasse et al. 1995; van Dam et al. 1994), *M. elliptica* and *P. brevistriata* predominantly occur in circumneutral to low alkaline waters (pH = 7–8; Cholnoky 1968;

Gasse 1986; van Dam et al. 1994; Stachura-Suchoples 2001; Fig. 4). In addition, *P. brevistriata*, *C. meneghiniana*, and *E. sorex* indicate elevated trophic levels troughout the record (Cholnoky 1968; van Dam et al. 1994; Gasse et al. 1995; Krammer and Lange-Bertalot 2000; Stachura-Suchoples 2001; Kelly et al. 2005).

The $\delta^{18}O_{diatom}$ data reflects the oxygen isotope composition of lake water ($\delta^{18}O_{lake}$), and the water temperature at the time of frustule formation (Leng and Barker 2006; Leng and Henderson 2013). In turn, $\delta^{18}O_{lake}$ is controlled by the isotopic composition of precipitation ($\delta^{18}O_p$) re-charging the lake and the balance of evaporation over precipitation on the lake. Open lake systems that have permanent river inflow and outflow have short residence times, and as a result $\delta^{18}O_{diatom}$ tends to reflect changes in $\delta^{18}O_p$. Whereas in closed lakes that have no discernable outflow, $\delta^{18}O_{lake}$ is usually influenced by evaporation of surface waters, and as a result $\delta^{18}O_{diatom}$ reflects the moisture balance (precipitation over evaporation) of the region (Leng and Marshall 2004; Leng and Barker 2006; Leng and Henderson 2013).

There is scant information about the isotope composition of precipitation ($\delta^{18}O_p$) in Botswana, and southern Africa in general, with much of our understanding of isotope dynamics linked to changes in Late Pleistocene groundwater and speleothem $\delta^{18}O$ records (de Vries et al. 2000; Lee-Thorp et al. 2001; Holmgren et al. 2003; Kulongoski and Hilton 2004). The ^{18}O enrichment of older groundwaters in Uitenhage, South Africa, have previously been interpreted in terms of a change in moisture source, with a northeastward incursion of South Atlantic winter precipitation, which displaces or mixes with monsoonal precipitation from the Indian Ocean in southwestern Africa (Stute and Talma 1998). By comparison, a more recent study from Letlhakeng, southern Botswana, suggests there was no role for Atlantic-sourced moisture and that the Indian Ocean has been the dominant moisture source over the southern Kalahari since the Late Pleistocene through to the present day (Kulongoski and Hilton 2004). The influence of the 'amount effect' on $\delta^{18}O_p$ has also been discounted, as modern $\delta^{18}O_p$ values for the region range from 0 to $-5‰$, but the most depleted $\delta^{18}O_p$ values occur during months with the most amount of rainfall (de Vries et al. 2000). As a result, Kulongoski et al. (2004) concluded that Late Pleistocene groundwater $\delta^{18}O$ variability is caused by

changes in atmosphere-$\delta^{18}O_p$ dynamics driven by changing sea surface temperatures.

A $\delta^{18}O$ speleothem record from Cold Air Cave in the Makapansgat Valley, northern South Africa, was interpreted in terms of $\delta^{18}O_p$ variability caused by changes in the frequency of intense convective storm events during the dry season that bring depleted $\delta^{18}O_p$ (Rozanski et al. 1993), against a background of persistent mid-latitude rain during the wet season (Holmgren et al. 2003). As a result, higher or more positive $\delta^{18}O_p$ values reflect generally warmer, wetter conditions while lower values suggest cooler, drier conditions. This interpretation is supported by a 100-year data set from the region, which demonstrates a positive correlation between measured regional temperatures and speleothem $\delta^{18}O$ (Lee-Thorp et al. 2001). In addition, an observed correlation between regional temperature and precipitation and speleothem colour, layer thickness and $\delta^{18}O$ further supports the interpretation that lighter $\delta^{18}O_p$ is representative of drier, colder conditions over southern Africa (Holmgren et al. 1999).

The $\delta^{18}O_{diatom}$ record from the BT unit spans approximately 1 ka sometime during MIS 5d–b and shows decadal to bi-decadal variability. Based on the interpretative framework for changes in $\delta^{18}O_p$ during the Late Pleistocene set out above, the shift in $\delta^{18}O_{diatom}$ from $+30.5‰$ at the base of the sediment unit to higher values of $+34.2‰$ at 11.5 cm would indicate increasingly warmer and wetter conditions during this period (Fig. 4). The lower $\delta^{18}O_{diatom}$ values would be driven by the enhancement of a wet season over the Kalahari and an subsequent increase in lake level. This observation is consistent with the increase in P/B ratio (Fig. 4), suggesting an increase in planktonic habitats associated with greater lake levels. Moreover, on top of an increasing lake level, the lake water would also be undergoing enhanced evaporation because of the generally warmer conditions, and therefore lake waters would also become further enriched in ^{18}O. Taken together, the shift to a dominant wet season and greater evaporation would both drive $\delta^{18}O_{diatom}$ to the more positive values observed in our record (Fig. 4). However, it is difficult to tease out which would be the dominant mechanism, and the $\delta^{18}O_{diatom}$ record is likely to reflect a combination of both.

After the initial increase there are a number of significant fluctuations in $\delta^{18}O_{diatom}$ from $+34$ to

+30.5‰ between 11.5 and 19.5 cm (Fig. 4), which broadly mirror changes in P/B, and could reflect variability between warm-wet and cold-arid climate, as well as the subsequent changes in evaporative concentration of Lake Palaeo-Makgadikgadi. Following this, the shift to the lowest $\delta^{18}O_{diatom}$ values in our record occurs at 23.5 cm (Fig. 4), which we interpret as a shift to colder and more arid conditions, as well as a lowering of lake level as indicated by the P/B ratio from the diatom assemblages. The return to more positive $\delta^{18}O_{diatom}$ values after this event (Fig. 4) could reflect a shift back to a warm, wet environment, but as the P/B ratios show, lake levels remain low and so could reflect enhanced evaporation of lake water during this arid stage in climate.

The relatively short duration of the mega-lake phase of approximately 1 ka under a generally arid climate over large parts of southern Africa during MIS 5 (Scholz et al. 2007; Urrego et al. 2015) suggests we may have captured a climate event at the scale of a Heinrich event (Bond and Lotti 1995; Broecker 2002). Previous studies have modelled the impact of Heinrich events on South Atlantic sea surface temperatures, which increase abruptly ("Atlantic Heat Piracy Model", Ganopolski and Rahmstorf 2001; Seidov and Maslin 2001). The climatic effect of northern hemisphere triggered Heinrich events on the southern hemisphere has also been identified in Antarctica ice cores (Jouzel et al. 2007). The observation of Urrego et al. (2015) that during climate transitions between warm and cold or cold and warm, humidity during arid MIS 5 temporarily increased, supports the idea of a Heinrich event-like climate period. Our record thus demonstrates the decadal to bi-decadal climate variability during such an event.

Our data cannot contribute to the discussion whether the MIS 5 climate extremes triggered large scale early human migration across and ultimately out of Africa (Carto et al. 2009; Rito et al. 2013). The data, however, can contribute to the discussion why the Kalahari hunter-gatherers, i.e. the Khoisan-speaking Bushmen groups, represent the genetically most divergent population in the world (Tishkoff et al. 2007; Li et al. 2008; Henn et al. 2011). High genetic variation means high adaptation potential (Charlesworth 2009). Semi-arid areas such as the Kalahari are particularly vulnerable because small negative changes in precipitation amount or in rainfall seasonality may trigger major changes in the environment

and thus largely control the habitability. Even under the assumption of large dating uncertainties, it is clear that anatomically modern humans have lived in the Kalahari during MIS 5 and the climate extremes likely triggered migration to environmentally more favourable regions. On the other hand it is evident that Khoisan-speaking groups have adapted to arid climate, exhibiting traits which are absent in other human groups such as the ability to store water and lipid metabolites in body tissues (Schuster et al. 2010). Considering these adaptations in the context of archaeological findings (Robbins et al. 2016), it can be assumed that Khoisan-speaking groups have lived permanently in (semi-)arid environments since MIS 5, that is they probably never left the Kalahari as other human groups did. The environmental history of the Kalahari since MIS 5 appears to be that of a highly dynamic and thus often fragmented ecosystem; habitat fragmentation leading to human population fragmentation. Small populations however are prone to genetic drift, which results in loss of genetic variation (Charlesworth 2009). Against this background it can be suggested that the Khoisan-speaking groups have not been fragmented into small populations but represented a relatively large human population all over the Kalahari. This was possible only if these humans and the animals they hunted had access to potable water.

The here studied MIS 5 lake highstand in the MOZB of approximately 1 ka appears to be a relatively short period, which however, can be compared with the tip of an iceberg. We do not know how far the lake regressed after the highstand. We do not know how the seasonality of MIS 5 rainfall was. We do not know which rivers were active during which period of supposedly extra-arid MIS 5, except that we can assume from the geographical settings of headwaters that Okavango, Orange and Zambezi rivers were likely perennial even during megadroughts. These river systems however cannot have been the only sources of potable water because otherwise the Khoisan-speaking population would have been fragmented, which evidently was not the case. The idea that the Kalahari was even drier than present day during much of the last approximately 100 ka as was postulated for MIS 5 (Urrego et al. 2015) or for the Last Glacial Maximum (LGM; Riedel et al. 2014) must be questioned. Gasse et al. (2008) saw evidence for enhanced humidity over parts of south-western

Africa during LGM. Hürkamp et al. (2011) proposed winter rainfall in addition to summer rainfall over the southern Kalahari during this period and Riedel et al. (2014) suggested that the Okwa River (Fig. 1) was fully active during the LGM. It thus can be speculated that future studies of MIS 5 climate over the Kalahari may exhibit the environment was more favourable for humans than supposed.

Conclusions

OSL ages suggest the identified mega-lake phase in the Kalahari occurred during a period of MIS 5d–b. The climate over southern Africa during MIS 5 was considered to have been (extremely) arid (Scholz et al. 2007; Urrego et al. 2015), although Urrego et al. (2015) identified short excursions to more humid conditions during cold-warm and warm-cold transitions. One of these humid periods triggered a highstand at Lake Palaeo-Makgadikgadi of about 935–940 m a.s.l. for approximately 1 ka, as is tentatively estimated here based on the potential sedimentation rate of the studied section. This short-term hydrologically favorable phase is at the scale of a North Atlantic-driven Heinrich event, and we speculate whether rapid increases of southern Atlantic SSTs could have triggered significantly increased moisture supply over the Kalahari and/or the Bié Plateau (Angola) where the (nowadays) active catchment of the Okavango river system is located (Fig. 1).

The studied section is in close proximity to the palaeo-shore of the mega-lake and based on the P/B ratio of diatom assemblages we infer shallow water conditions prevailed at the site. The analysed diatom assemblages indicate an alkaline and oligohaline lake, although the reconstructed salinity is not representative of the whole mega-lake because the studied section is located about 100–150 km away from the two major inflow systems, the Okavango River in the (north-)west and the Okwa River in the southwest of the lacustrine basins (Fig. 1). As we could not infer which of the inflow systems was active during the highstand, a salinity gradient from freshwater to oligohaline either existed off the Okavango or Okwa river mouths.

Considering the role Pleistocene Lake Palaeo-Makgadikgadi is likely to have played in the phylogeography of freshwater fish (Joyce et al. 2005) or

freshwater gastropods (Schultheiß et al. 2014), we suggest the mega-lake phase in this study is too short a duration that is dominated by oligohaline conditions, and therefore it was not a suitable trigger for evolutionary radiations of freshwater taxa. The comparatively high temporal resolution of 1–2 decades of our studied samples provides valuable insights of climate variability during a mega-lake phase. Albeit significant changes in $\delta^{18}O_{diatom}$ values occurred (Fig. 4), the highstand is considered a hydrologically stable period.

Although the studied mega-lake period was likely a short-term climate anomaly possibly triggered by North-Atlantic iceberg discharges, it is challenging the view that MIS 5 was mostly extremely dry. That the environment may have hydrologically been more favourable, is supported by archaeological and genetic data suggesting permanent human occupation of the Kalahari since MIS 5.

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