

# Recent environmental history of the desert oasis lakes at Ounianga Serir, Chad

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**Abstract** The Sahara desert oasis of Ounianga Serir in northern Chad comprises seven shallow but perennial lakes, which are maintained against an extremely negative local moisture balance by continuous inflow of fossil groundwater from the Nubian Sandstone Aquifer. Here we analyze the lithostratigraphy, charcoal, and fossil mollusks in short, dated sediment cores from three of these lakes (Edem, Hogou, and Agouta) to assess the hydrological and environmental stability of these unique aquatic ecosystems over the last few centuries. Our results indicate that the studied lakes remained relatively stable and fresh over the past 200–600 years, confirming the dominant and constant nature of groundwater input, preventing desiccation.

Modest lake-level fluctuations did occur but were not synchronous between the lakes, arguing against climate variability being their primary cause. Likely, their site-specific history was determined by variations in groundwater through-flow, influenced by migration of sand dunes separating the lakes. The desert setting is responsible for characteristic lacustrine sediments comprised of carbonate mud with silt and sand. The associated fossil assemblages of freshwater mollusks suggest that the present-day mollusk fauna of Ounianga Serir may be more species-rich than previously thought. Our data expand the known distribution of the Palearctic snail *Valvata nilotica* markedly south and westward into the central Sahara.

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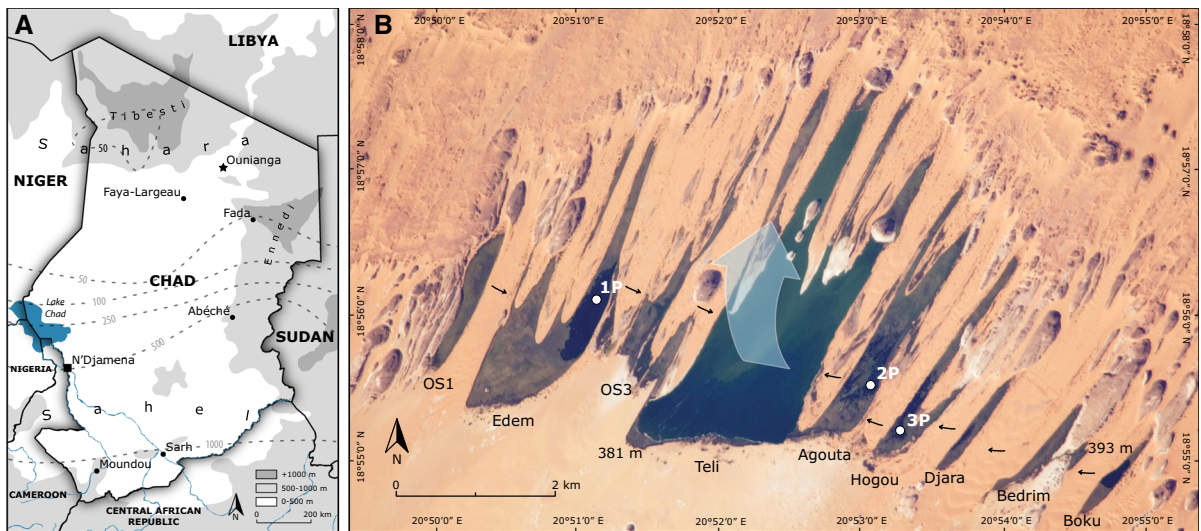
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## Introduction

The Ounianga region of northeastern Chad contains the largest permanent aquatic ecosystems in the Sahara desert (Fig. 1). The lakes and swamps of Ounianga persist in the arid core of the Sahara desert, where rainfall is erratic and annual evaporation can exceed 6000 mm (Direction des Ressources en Eau et de la Météorologie, N'Djamena, Chad). The paradoxical existence of this protected UNESCO World Heritage site is due to a significant inflow of fossil



**Fig. 1** **a** Map of Chad with the Ounianga area located in the northeast between the Tibesti Mountains and the Ennedi Plateau. The *dashed contour lines* show annual rainfall, in mm. **b** Modified real-colour photograph of Ounianga Serir taken from the International Space Station ([www.earthobservatory.nasa.gov](http://www.earthobservatory.nasa.gov)), with indication of the three core sites (OUNIS12-1P, -2P and -3P) and schematic representation of the hydrological pump mechanism which keeps most lakes relatively fresh (George 1999). All lakes receive inflow of fresh fossil groundwater at their northeastern end, near the foot of the sandstone escarpment. All lakes, except the central Lake Teli, are hydrologically

open, with outflow towards their more centrally located neighboring lake, either at the surface (e.g., from OS3 to Lake Teli) or below the surface through the sand dunes that separate the lakes (*black arrows*). Due to its large size (6.5 km<sup>2</sup>) and restricted marginal vegetation, more than half of the evaporation at Ounianga Serir occurs from the water surface of Lake Teli (*large blue arrow*), which is hypersaline because of this evaporation and closed hydrology. Over time this ‘hydrological pump’ has resulted in a strong water-chemistry gradient between the dilute peripheral lakes and Lake Teli, creating a diverse range of aquatic and sedimentary environments. (Color figure online)

groundwater from the Nubian Sandstone Aquifer, which was last recharged in the early Holocene (Hissene 1986), under the wetter climate conditions of the so-called African Humid Period (deMenocal et al. 2000). The lakes lie in two clusters, Ounianga Kebir and Ounianga Serir, and range from shallow to deep (0.4–26 m) and from fresh to hypersaline (330–157,000  $\mu\text{S cm}^{-1}$ ; Van Bocxlaer et al. 2011). They are surrounded to varying degree by reed swamp (*Phragmites*) and date palms (*Phoenix*), as is typical for desert oases. Sediment cores from Lake Yoa at Ounianga Kebir produced a continuous, high-resolution 6100-year paleoenvironmental record (Kröpelin et al. 2008; Francus et al. 2013) which shows that mid-to late-Holocene desiccation of the Sahara occurred gradually, rather than abruptly. How the aquatic fauna of the Ounianga lakes evolved in response to this increasing aridity and salinity was studied in detail for chironomids (Eggermont et al. 2008) and mollusks (Van Bocxlaer et al. 2011), in a comparative framework that included the lakes at Ounianga Serir.

Here we focus on the recent environmental history of lakes Edem, Hogou, and Agouta at Ounianga Serir, which thus far remain poorly explored. Specifically, we analyze their shallow sedimentary record to assess the ecosystem stability of these shallow lakes (depth  $\leq 6.8$  m) and the probability of long-term persistence. The principal paleohydrological proxies explored here are sediment lithostratigraphy and texture, and the composition of sub-recent aquatic mollusk communities.

A major challenge is the construction of precise age models for the studied lacustrine deposits. <sup>210</sup>Pb and <sup>137</sup>Cs dating was not attempted because these methods rely on the delivery of the radioisotope (or its parent isotope) to the lakes by rainfall, which is erratic in this hyper-arid desert environment. With virtually no vegetation on the surrounding landscape and absence of crop agriculture, there is also little potential for historical cultural indicators in the pollen record. In order to optimize sediment chronology, we constructed high-resolution records of macro-charcoal

abundance at all three sites, in search of shared signatures of (natural or human-lit) fire events in the relatively recent past that would allow temporal cross-correlation between the sediment sequences, in turn helping to constrain age models based on  $^{14}\text{C}$ -dating.

### Study area

The Ounianga region of northeastern Chad is situated between the Tibesti Mountains to the northwest and the Ennedi Plateau to the southeast (Fig. 1a; Schiffers 1952; Arkell 1964). The lakes of Ounianga Serir (18°54'N, 20°53'E) are situated 40 km to the southeast of Ounianga Kebir (19°03'N, 20°29'E). Much of the surrounding relief is thought to have been formed by fluvial erosion when the Ounianga region was located at the putative outlet of Neogene Lake Chad (Griffin 2006), and was modified during the Quaternary by aeolian processes (Castañeda et al. 2009). The region experiences a subtropical hyperarid climate with <5 mm annual rainfall on average, high daytime temperatures, and dry northeasterly trade winds blowing almost year-round through the Tibesti-Ennedi corridor (Kröpelin et al. 2008). The extremely high rate of evaporation is balanced by the inflow of fresh groundwater from the world's largest fossil groundwater basin, the Nubian Sandstone Aquifer System (NSAS) (Thorweihe 1986).

The Ounianga Serir basin comprises seven fresh or saline lakes plus several depressions (such as OS1 and OS3; Fig. 1b) completely covered with reed (*Phragmites australis*). The hypersaline Lake Teli (6.5 km<sup>2</sup>) is the largest natural lake (Pesce 1968), and Lake Edem (2.0 km<sup>2</sup>) the largest permanent freshwater lake in the Sahara. All lakes at Ounianga Serir, except Lake Teli, are sufficiently fresh (maximally 2680  $\mu\text{S cm}^{-1}$ ) to allow the development of floating reed mats, which partly (e.g., Edem) or almost completely (Bedrim) cover the lake surface (Van Bocxlaer et al. 2011). Vegetation surrounding the lakes is limited to reed (*Phragmites*) and cattail (*Typha*), date palm (*Phoenix*) plantations and a few isolated *Acacia*; other plants in the larger Ounianga region are confined to dry river beds (Kröpelin et al. 2008). The most dilute and transparent lakes harbor patches of submerged water plants, such as *Utricularia* and *Ceratophyllum* in Lake Bedrim, *Chara* in Lake Edem, and *Potamogeton* in Lake Boku. The slightly brackish lakes Hogou (1900  $\mu\text{S cm}^{-1}$ ) and Agouta (2680  $\mu\text{S cm}^{-1}$ ) lack

submerged vegetation, despite adequate transparency (Van Bocxlaer et al. 2011). Lakeshore reed belts limit the influx of windblown sand and slow the progression of sand dunes on the lakes, whereas floating reed mats diminish surface evaporation.

The large gradient of physico-chemical characteristics between the lakes is maintained by a peculiar natural evaporation pump (George 1999; Kröpelin 2007). Inflow of fossil groundwater at the northeastern end of each lake (at the foot of the sandstone escarpment) balances extreme lake-surface evaporation most effectively in the smaller, marginal lakes of the basin, creating a hydraulic gradient from the peripheral lakes (e.g., Lake Boku, situated at 393 m elevation) to the centrally located Lake Teli (at 381 m elevation). Evaporation from the large surface of shallow Lake Teli draws water from the other lakes through the permeable sand dune barriers separating them. As a result, all freshwater lakes of Ounianga Serir have a subsurface outflow which removes dissolved salts. Most salts eventually accumulate in Lake Teli, the only lake lacking subsurface outflow.

## Materials and methods

### Collection of sediment cores

The studied short sediment cores were recovered from the deepest parts of Lake Edem (2.0 km<sup>2</sup>, 6.8 m deep), Hogou (0.6 km<sup>2</sup>, 4.6 m deep) and Agouta (1.3 km<sup>2</sup>, 3.6 m deep) in January 2012, using a single-drive piston corer with polycarbonate tubes (Wright 1980). The deepest point of each lake was found by depth-sounding along transects through the lake, guided by surrounding topography. Bottom water was siphoned off, and the cores were allowed to dry upright until the sediment–water interface was sufficiently stable to enable capped transport without disturbance. In the laboratory the polycarbonate tubes were cut lengthwise, upon which one half of each core was used for non-destructive scanning analyses and archival, the other for sedimentological, charcoal, and mollusk analyses.

### Sedimentological analyses

Immediately after opening the sediment cores, high-resolution images were taken with a fixed-mount

Nikon digital camera. The images were stitched together to one continuous image using Adobe Photoshop. The profiles' lithostratigraphy was described according to the classification system of Schnurrenberger et al. (2003), supplemented with petrographic smear-slide analyses to identify carbonate minerals and to qualitatively estimate the mean grain size and diatom abundance. Water content, porosity, and the bulk organic, carbonate and (other) inorganic components of the sediment were measured via the loss-on-ignition (LOI) technique (Dean 1974; Bengtsson and Enell 1986). We used a fixed amount of 0.5 cm<sup>3</sup> sediment, sampled every centimeter throughout each sediment core. In these lakes, the inorganic component can be assumed to only contain siliciclastic mineral matter and biogenic Si derived from diatoms. Since the abundance of the latter was assessed qualitatively from our smear-slide analyses, we could estimate the fraction of non-carbonate clastic mineral matter in selected samples by adding 2 M sodium carbonate (Na<sub>2</sub>CO<sub>3</sub>) to the rest fractions of LOI analysis and placing them in a warm water bath (90 °C) until all diatoms were dissolved; the process was monitored by intermittent smear-slide scanning. Afterwards, the samples were rinsed with deionized water, dried and weighed again to determine weight loss.

Similarly, textural assessments based on smear-slide analysis were calibrated by grain-size measurements performed on selected samples using a Malver Mastersizer 2000 laser particle counter. These samples were pre-treated with 30 % HCl to eliminate calcium carbonate, 30 % H<sub>2</sub>O<sub>2</sub> to remove organic material, and Na<sub>2</sub>CO<sub>3</sub> to remove biogenic Si; all reactions were performed in a warm water bath and samples were centrifuged and rinsed with demineralized water between every step. To prepare the samples for grain-size measurement, we added 5 % sodium hexametaphosphate to deflocculate the remaining sediment, and sonicated for 5 min to disperse small aggregates.

Magnetic susceptibility (MS) was measured contiguously at 2-mm intervals along the length of the archival core halves, using a Bartington MS2E point sensor with spatial resolution of 3.8 mm mounted on a Geotek Multi-Sensor Core Logger (MSCL). Dry mass data from LOI analysis were used to determine mass-specific magnetic susceptibility ( $\chi$ ), i.e. MS corrected

for variability in sediment compaction (i.e., water content).

#### Macrofossil analyses

Macroscopic charcoal was extracted from 1 cm<sup>3</sup> of wet sediment, sampled contiguously at 1-cm intervals along the complete sequences, and processed using the method of Whitlock and Larsen (2001). Sieved charcoal particles (>100  $\mu$ m) were counted using a Leica Wild M10 binocular microscope, after which the counts were converted to mass-specific abundance using water-content data. Fossil mollusks were extracted from 10 cm<sup>3</sup> of wet sediment in 1-cm intervals, i.e. a volume sufficiently large to limit stochasticity in the presence/absence of species. These samples were also sieved at 100  $\mu$ m, after which the mollusks were picked and identified with a Leica Wild M10 binocular microscope using Brown (1994) and Van Bocxlaer et al. (2011) as principal references. Mollusk counts were also converted to dry mass-specific abundances. Throughout this paper, charcoal and mollusk abundances (expressed as particles or specimens g<sup>-1</sup>) refer to counts per gram of dry sediment, to avoid the spurious trends that might otherwise be created by changes in water content, i.e. the degree of sediment compaction, down-core. Ostracods were occasionally encountered but only in very low abundance and with erratic distribution, not allowing a meaningful paleoecological analysis.

#### Chronology

Given the impracticality of <sup>210</sup>Pb and <sup>137</sup>Cs dating in this desert setting, we used AMS radiocarbon (<sup>14</sup>C) dating to constrain the period during which the studied sediments were deposited. We avoided dating bulk organic carbon or mollusk shells, considering that dissolved inorganic carbon in these fossil groundwater-dominated lakes may cause a substantial old carbon age offset (Björk and Wohlfarth 2001). Instead we used terrestrial plant matter such as charred and unburned reed fragments, and charred seeds. For each core one sample near the bottom was dated, and for the cores from lakes Hogou and Agouta also one sample each at intermediate depth. The <sup>14</sup>C dates obtained were calibrated using INTCAL13 (Reimer et al. 2013).

**Results**

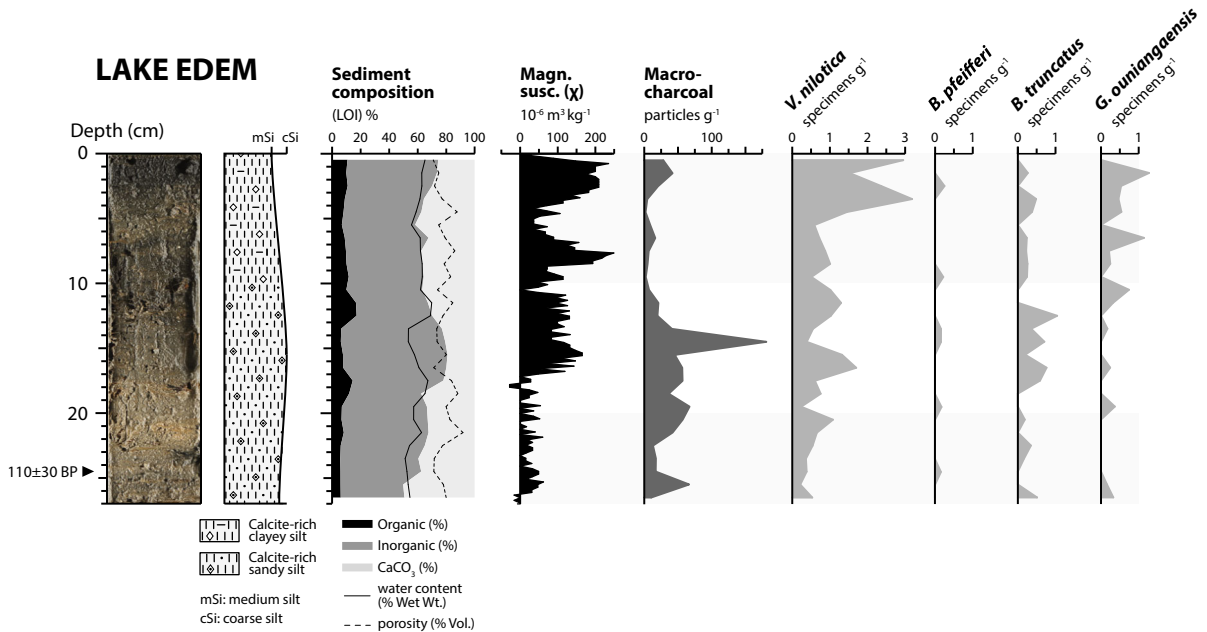
Lake Edem

*Sediment composition*

The sediment sequence of Lake Edem (core OUNIS12-1P, 27 cm; Fig. 2) mainly consists of calcite-rich clayey to sandy silt. The abundant primary calcite crystals are present mostly as aggregates of up to 60 μm diameter. Laminations or other conspicuous sedimentary structures are lacking, but coarse debris of plant material is visually present throughout the core. The median siliciclastic grain size increases slightly from medium silt at the base of the core to coarse silt at around 15 cm, and decreases back to medium silt at the top (Fig. 2; Table 1). Organic-matter content displays a slightly increasing trend from 8 % at the bottom to 10 % at the top, but with pronounced maxima at 11–13 and 17–18 cm. Carbonate content varies between 20 and 50 %, with maxima at the base and at 3–11 cm, and minima at 14–17 cm and at the top. Biogenic Si (diatom) content varies between 9 and 17 %. Weight-

specific MS of the Lake Edem sediment is low in general ( $<250 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ ), but increases abruptly from  $\sim 20 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$  below 17 cm depth to  $\sim 120 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$  above it, and values become more variable in the upper 10 cm of the core. The very low (and occasionally negative) MS values reflect the dominance of diamagnetic materials such as calcite and quartz. The slightly higher values at the top indicate presence of some paramagnetic materials such as iron-bearing carbonates or silicates, but ferromagnetic minerals are lacking.

Macrocharcoal in the Lake Edem core averages 33 particles  $\text{g}^{-1}$ . In the lower half of the sequence they average 51  $\text{g}^{-1}$  and show one pronounced peak of 180  $\text{g}^{-1}$  at 14–15 cm depth, above which the abundance drops to 16  $\text{g}^{-1}$  on average (Fig. 2). The unburned plant macrofossils are all pieces of grass epidermis, here most likely *Phragmites* remains. Also *Chara* oogonia were recovered from most charcoal samples, indicating the continuous occurrence of this rooted alga in Lake Edem throughout the period covered by OUNIS12-1P, as it does today (Van Bocxlaer et al. 2011).



**Fig. 2** Lithostratigraphy, bulk composition, magnetic susceptibility, charcoal abundance and mollusk biostratigraphy of core OUNIS12-1P from Lake Edem (6.8 m water depth). Particle and

specimen abundances are expressed in number per gram of dry sediment mass

**Table 1** Results of quantitative grain-size analysis on the siliciclastic mineral fraction of Ounianga Serir sediments

Lake	Core code	Depth (cm)	Total			Silt				Sand			
			Clay (%)	Silt (%)	Sand (%)	Very fine (%)	Fine (%)	Medium (%)	Coarse (%)	Very fine (%)	Fine (%)	Medium (%)	Coarse (%)
Edem	OUNIS12-1P	9–10	22.1	67.4	10.6	8.3	8.9	21.1	29.1	10.6	0.0	0.0	0.0
		15–16	15.4	45.9	38.6	6.6	5.2	10.6	23.5	34.0	4.7	0.0	0.0
		24–25	14.3	50.7	34.4	7.7	10.3	15.7	17.0	25.3	9.1	0.6	0.0
Hogou	OUNIS12-3P	15–16	9.1	36.7	54.2	3.2	3.0	8.2	22.3	42.2	11.6	0.4	0.0
		33–34	9.6	35.6	54.8	3.6	3.6	8.0	20.4	41.7	12.6	0.5	0.0
		49–50	8.7	32.6	58.8	3.0	2.7	7.2	19.7	39.0	17.3	2.4	0.0
		53–54	8.9	32.8	58.2	3.7	3.4	6.8	19.0	41.7	15.6	0.9	0.0
Agouta	OUNIS12-2P	9–10	9.2	30.1	61.9	3.2	2.8	6.0	16.9	42.6	18.3	1.0	0.0
		34–35	9.9	33.5	53.4	3.0	2.7	6.1	22.1	46.0	7.4	0.0	0.0
		59–60	7.7	24.8	68.4	2.3	2.1	4.5	15.1	45.9	21.2	1.2	0.0

### Sub-recent fossil mollusks

The sub-recent mollusk fauna of Lake Edem as represented by the collection of specimens obtained from core OUNIS12-1P consists of *Valvata nilotica* (Fig. 5a), *Biomphalaria pfeifferi* (Fig. 5b), *Bulinus truncatus* (Fig. 5c) and *Gabbiella ouniangaensis* (Fig. 5d). Positive identification of the latter species was aided by the occasional recovery of opercula, which consistently displayed the diagnostic features of *G. ouniangaensis*, rather than those of its regional congeners *G. tchadiensis* or *G. senaariensis* (Van Bocxlaer et al. 2011). *Valvata nilotica* is the most abundant species (119 specimens in total), and is continuously present with fluctuating but upwardly increasing abundances (from 0.5 to 3.2 specimens  $g^{-1}$ ). *Bulinus truncatus* is almost continuously present as well (31 specimens in total), but generally less common than *V. nilotica*, except between 12 and 18 cm depth (0.5–1.0  $g^{-1}$ ). *Gabbiella ouniangaensis* (30 specimens) is scarce in the lower half of the core but replaces *B. truncatus* as the second-most common species from a depth of 12 cm upwards (up to 1.2  $g^{-1}$ ). *Biomphalaria pfeifferi* occurs sporadically (six specimens in total, <0.3  $g^{-1}$ ).

### Chronology

Unburned reed fragments at 25–26 cm depth yielded a radiocarbon age of  $110 \pm 30$  year BP, corresponding

to calibrated age ranges of 13–148 cal year BP (95 % confidence interval) or 60–137 cal year BP (68 %); the latter age range corresponds to the period 1813–1890 AD (Table 2).

### Lake Hogou

#### Sediment composition

The faintly banded sediment sequence of Lake Hogou (core OUNIS12-3, 57 cm; Fig. 3) consists of sandy calcite mud ('marl' or 'lake chalk') with four intercalated lenses of up to 90 % calcite content. In this context the term mud refers to all sediments composed predominantly of silt- and clay-sized particles (Schunrenberger et al. 2003); here these fine particles are predominantly calcite crystals, and crystal aggregates of up to 60  $\mu m$  diameter. The few siliciclastic mineral grains present are mainly quartz, and their median size decreases slightly from very fine sand at the base to coarse silt at around 34 cm, after which the grain size remains constant towards the top (Fig. 3; Table 2). No coarse plant fragments are visible on the split core surface. The content of organic matter averages a constant 7–9 % from the base of the core until 12 cm depth, after which it first slowly increases to values >10 %, and then rapidly to 38 % at the sediment surface. Carbonates are generally the most abundant sediment component (on average 64 % of dry mass, excluding the calcite lenses), except at the sediment

**Table 2** Results of accelerator mass spectrometric (AMS) <sup>14</sup>C dating on five samples of plant macrofossils

Lake	Core code	Depth (cm)	Lab code	<sup>14</sup> C age BP	95 % (2σ) cal. age range BP	68 % (1σ) cal. age range BP	Age range AD	
Edem	OUNIS 12-1P	25–26	Poz-60096	110 ± 30	13–148 (69.3 %)	32–41 (8.1 %)	1909–1918	
					188–198 (1.9 %)	60–137 (64.6 %)	1813–1890	
					212–269 (28.6 %)	223–234 (10.0 %)	1716–1727	
Hogou	OUNIS 12-3P	27	Poz-62072	115 ± 30	12–148 (67.8 %)	25–40 (12.1 %)	1910–1925	
					188–205 (3.7 %)	60–118 (47.9 %)	1832–1890	
					211–269 (28.5 %)	122–140 (14.7 %)	1810–1828	
						222–232 (8.8 %)	1718–1728	
						240–260 (16.5 %)	1690–1710	
			55–56	Poz-60063	155 ± 30	–2–38 (18.6 %)	5–31 (21.3 %)	1919–1945
					64–118 (16.3 %)	85–86 (1.0 %)	1864–1865	
					124–154 (11.8 %)	95–95 (0.6 %)	1855–1855	
					166–231 (35.8 %)	138–152 (11.9 %)	1798–1812	
					243–284 (17.4 %)	170–223 (45.9 %)	1727–1780	
Agouta	OUNIS 12-2P	21–23	Poz-62071	380 ± 30	319–384 (33.6 %)	334–349 (20.3 %)	1601–1616	
					386–391 (1.6 %)	437–498 (79.6 %)	1452–1513	
					426–504 (64.7 %)			
			69–71	Poz-60061	395 ± 30	323–376 (23.3 %)	336–348 (15.9 %)	1602–1614
						428–511 (76.6 %)	456–504 (84.0 %)	1446–1494

All obtained <sup>14</sup>C dates correspond with multiple calendar-age windows; indicated are the respective probability of each calendar-age interval (in cal year BP) at both 2σ and 1σ; and the most likely age intervals (in years AD) at 1σ

surface (~30 %, due to high organic content) and in some core sections directly adjacent to calcite lenses (~40 %).

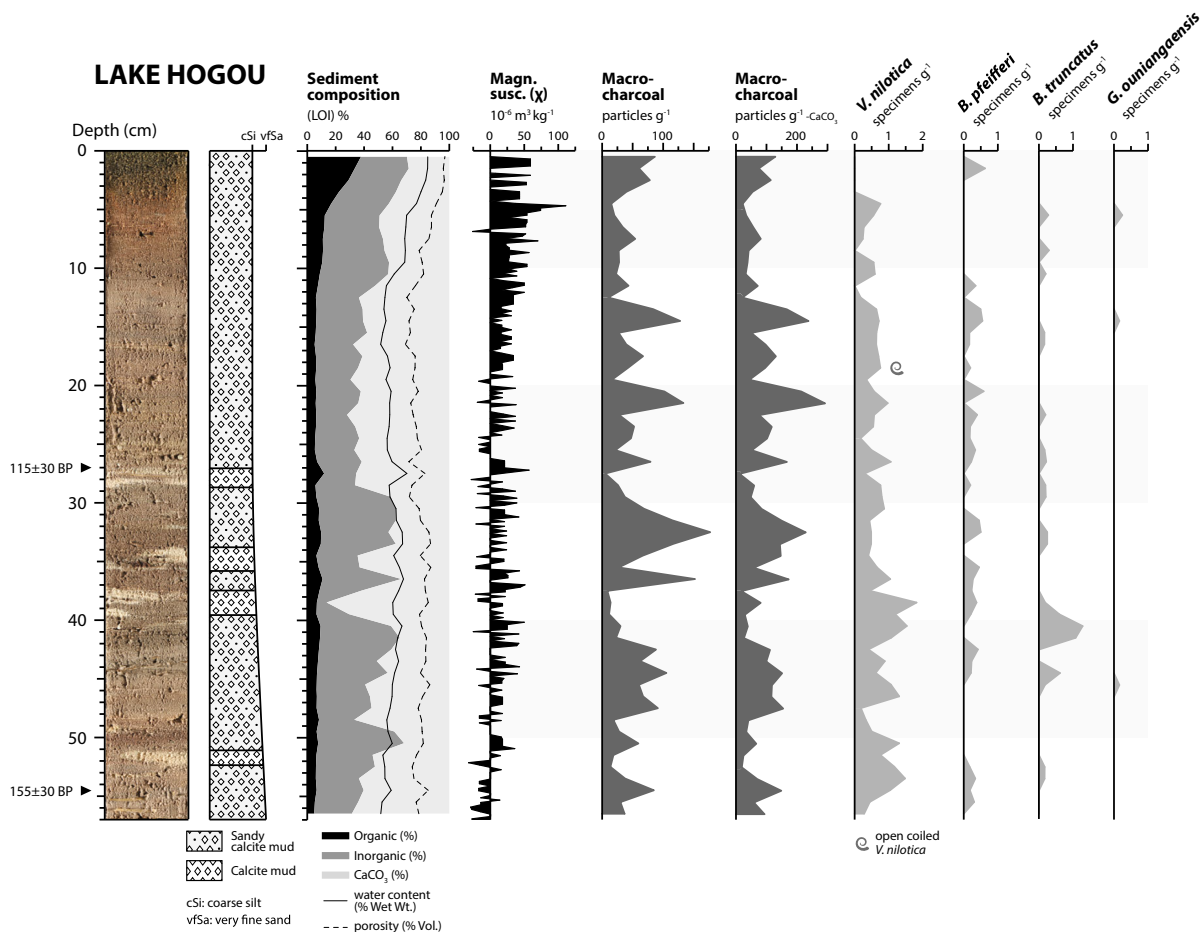
Biogenic Si content is stable at 7–12 %, except for pronounced minima of ~2 % within calcite lenses. Weight-specific MS is low (~15 × 10<sup>-6</sup> m<sup>3</sup> kg<sup>-1</sup>) and often negative, again reflecting predominance of diamagnetic calcite and quartz. Only a very slight positive trend is evident from the bottom to the top of the core, with values averaging ~23 × 10<sup>-6</sup> m<sup>3</sup> kg<sup>-1</sup> in the lower half of the core and ~7 × 10<sup>-6</sup> m<sup>3</sup> kg<sup>-1</sup> in the upper half.

Substantial variation in the abundance of charcoal particles throughout the Lake Hogou sequence creates a saw-tooth pattern with no singularly pronounced peaks. Charcoal particles are consistently more limited within the calcite lenses (on average 24 g<sup>-1</sup>) than in between them (87 g<sup>-1</sup>). Suspecting that dilution played an effect, we recalculated charcoal abundance per gram dry mass excluding carbonates. However, although this roughly doubles all charcoal values the

overall stratigraphic pattern of charcoal peaks and valleys remains unaltered (Fig. 3; average density 57 g<sup>-1</sup>). At four levels, charcoal abundance exceeds 100 g<sup>-1</sup>; the most recent of these occurs at 14–15 cm depth.

### Mollusks

The sub-recent mollusk fauna of Lake Hogou obtained from core OUNIS12-3P consists of the same species as those found in Lake Edem. *Valvata nilotica* is again the most abundant species (185 specimens in total), and has been present continuously except for its absence in the top 4 cm of the core. This species was slightly more abundant in the lower third of the core (on average >1 specimen g<sup>-1</sup>) than in more recent sediments (~0.5 g<sup>-1</sup>). One open-coiled specimen (Fig. 5a) was found at 18–19 cm depth. *Biomphalaria pfeifferi* and *B. truncatus* are less common (44 and 32 specimens in total, respectively), so that the



**Fig. 3** Lithostratigraphy, bulk composition, magnetic susceptibility, charcoal abundance and mollusk biostratigraphy of core OUNIS12-3P from Lake Hogou (4.6 m water depth). Particle

persistence of their local populations throughout the covered period is uncertain. However, *B. pfeifferi* is the second-most common species in sediments of Lake Hogou, whereas *B. truncatus* is always found as single specimens, except for a greater concentration (up to  $1.2 \text{ g}^{-1}$ ) at 40–42 cm depth. *Gabbiella ouniangaensis* is with a total count of three specimens rare in Lake Hogou.

### Chronology

Mixed samples of unburned reed fragments and charcoal particles collected at 27 and 55–56 cm depth yielded radiocarbon ages of  $115 \pm 30$  and  $155 \pm 30$  year BP, respectively (Table 1). The upper dated interval corresponds to calibrated age ranges of

and specimen abundances are expressed in number per gram of dry sediment mass

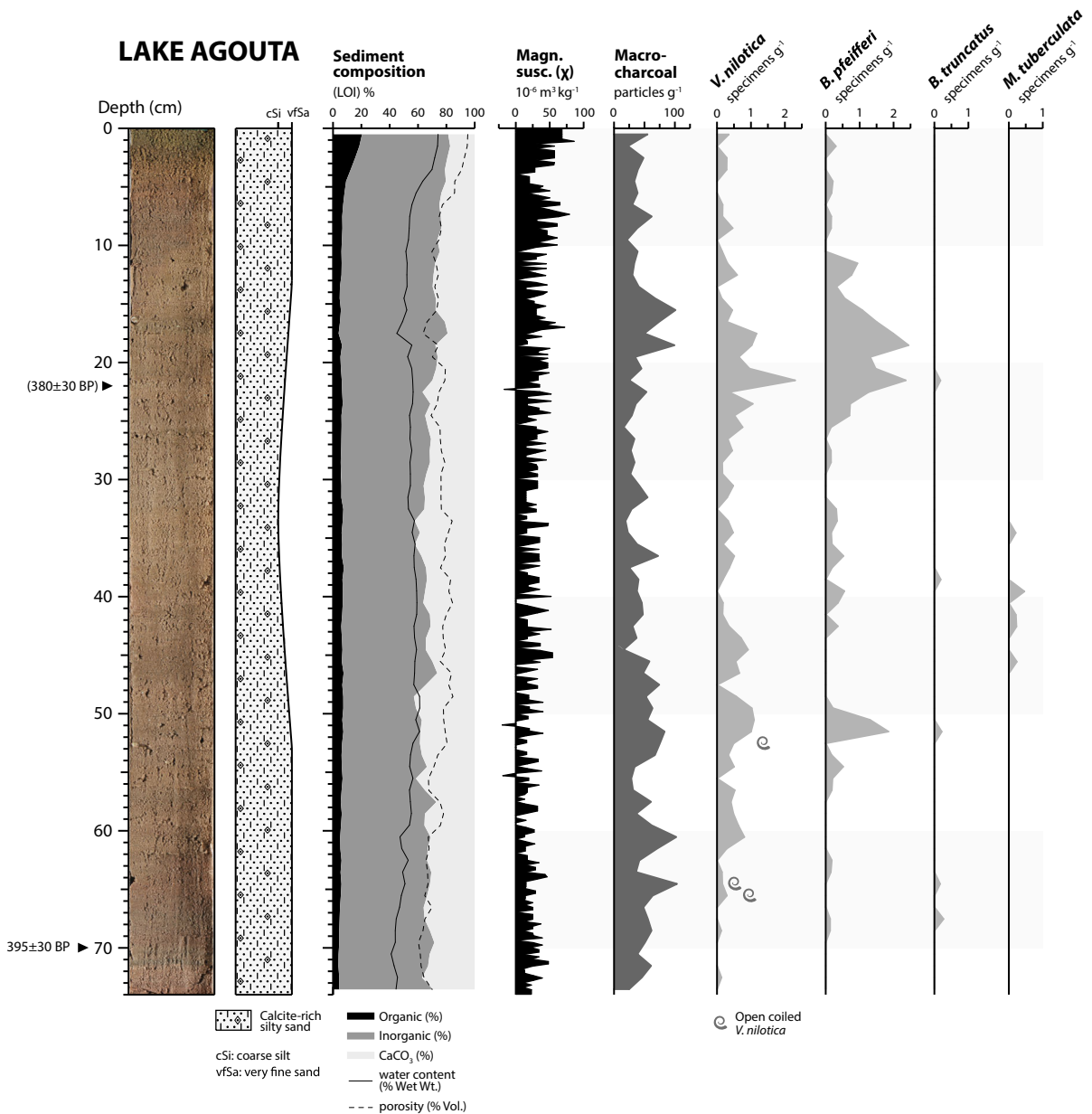
12–148 cal year BP (95 % confidence interval) and 60–118 cal year BP (68 %), broadly the period 1832–1890 AD. The lower dated interval has a wide calibrated age range with highest probabilities around 166–231 cal year BP (95 %) and 170–223 cal year BP (68 %), or broadly the period 1727–1780 AD.

### Lake Agouta

#### Sediment composition

The sediment sequence of Lake Agouta (OUNIS 04-2P, 74 cm; Fig. 4) consists of faintly banded, calcite-rich silty sand. No conspicuous sedimentary structures or plant fragments were observed on the split core surface. The siliciclastic mineral component





**Fig. 4** Lithostratigraphy, bulk composition, magnetic susceptibility, charcoal abundance and mollusk biostratigraphy of core OUNIS12-2P from Lake Agouta (3.6 m water depth). Particle

and specimen abundances are expressed in number per gram of dry sediment mass

consists mainly of quartz, with a median grain size of very fine sand at the base and top of the sediment sequence, and coarse silt in the section between 50 and 20 cm of depth (Fig. 4; Table 2). The organic-matter content is constant at ~5 % throughout the sequence except at the sediment surface where it increases to

20 %. Carbonate content is lower than in Lake Hogou and fairly constant at 30–40 % up to 23 cm depth, from where it decreases toward values below 20 % at the top. Calcite crystals again occur most often as aggregates of up to 60 μm. Biogenic Si content is also fairly constant throughout, averaging ~6 %. Like in

the other lakes, weight-specific MS is low ( $\sim 26 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ ) throughout most of the sequence, increasing to values averaging  $37.5 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$  above 20 cm. However, compared to Lake Hogou, a smaller fraction of the MS measurements yielded negative (diamagnetic) values.

The average abundance of macrocharcoal particles in the Lake Agouta sequence is 47 particles  $\text{g}^{-1}$ . Mean charcoal abundance is higher in the lower third of the sequence ( $56 \text{ g}^{-1}$ ) than higher up ( $37 \text{ g}^{-1}$ ), and single peaks are poorly pronounced. Only two intervals, 60–61 and 15–16 cm, contain abundances exceeding  $100 \text{ g}^{-1}$ .

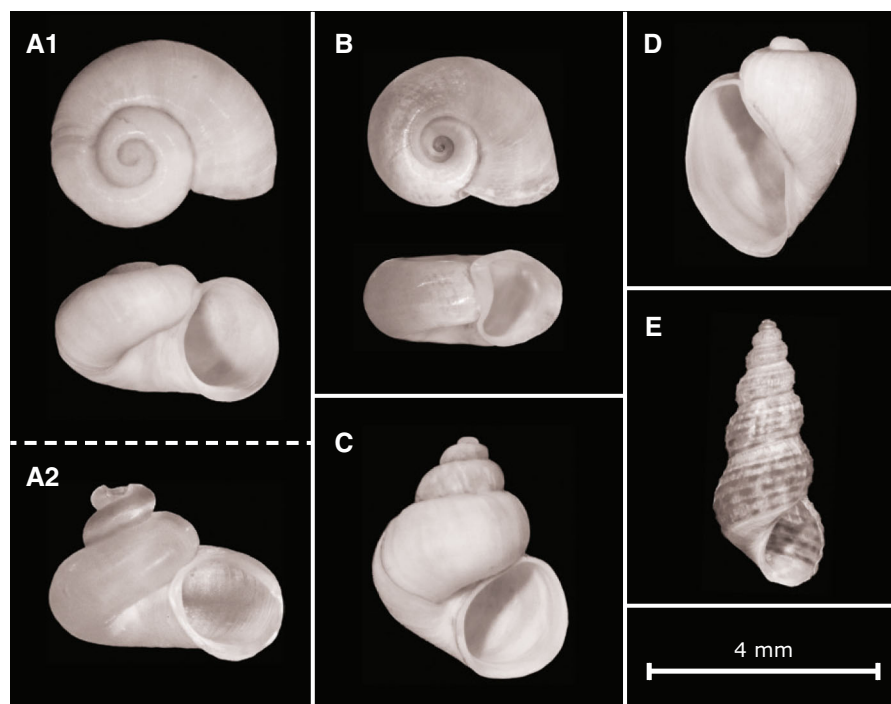
### Mollusks

The sub-recent mollusk fauna of Lake Agouta obtained from core OUNIS12-3P consists of *V. nilotica*, *B. pfeifferi*, *B. truncatus* and *Melanoides tuberculata* (Fig. 5e); *Gabbiella ouniangaensis* is absent. *Valvata nilotica* is abundant (174 specimens in total), but given that 161 specimens of *B. pfeifferi* were recovered, it is not as dominant in Lake Agouta as it is in lakes Edem

and Hogou. *V. nilotica* is again (almost) continuously present, reaching its highest abundances ( $>1.0 \text{ g}^{-1}$ ) at 49–52 cm and 17–21 cm. Several open-coiled specimens were recovered from the lower third of the sequence. Overall *B. pfeifferi* has a depth distribution similar to *V. nilotica*, but with more pronounced maxima at 50–52 cm and 15–23 cm, combined with more frequent absences. *Bulinus truncatus* is only sporadically present (six specimens in total), and two of its occurrences coincide with the two maxima shared by *V. nilotica* and *B. pfeifferi*. We further recovered six specimens of *M. tuberculata*, all within the depth interval of 34–46 cm.

### Chronology

Two mixed samples of charred seeds and charcoal fragments collected at 21–23 and 69–71 cm yielded similar radiocarbon ages of  $380 \pm 30$  and  $395 \pm 30$  year BP (Table 1). The upper dated interval corresponds to calibrated age ranges of 426–504 (95 % confidence interval) or 437–498 cal year BP (68 %), broadly the period 1452–1513 AD. The lower



**Fig. 5** Aquatic mollusk species found in the studied sediment sequences from Ounianga Serir. **A1** *Valvata nilotica* Jickeli 1874, **A2** open-coiled *V. nilotica* specimen, **B** *Biomphalaria*

*pfeifferi* (Krauss 1848), **C** *Gabbiella ouniangaensis* Van Bocxlaer, 2011, **D** *Bulinus truncatus* (Audouin 1827), **E** *Melanoides tuberculata* (O.F. Müller 1774)

dated interval has a calibrated age range with highest probability for 428–511 (95 %) and 456–504 cal year BP (68 %), broadly the period 1446–1494 AD.

## Discussion

### Time frame represented by the studied sequences

With a calibrated bottom age situated between AD 1801 and 1883, core OUNIS12-1P (27 cm) covers about 130–210 years of the recent environmental history of Lake Edem. This age range translates into a mean linear sedimentation rate between 1.3 and 2.1 mm year<sup>-1</sup>, and a mean dry-sediment accumulation rate (dSAR) of 0.06–0.10 g cm<sup>-2</sup> year<sup>-1</sup>.

Core OUNIS12-3P from Lake Hogou (57 cm) has a calibrated bottom age between AD 1722 and 1774, and thus covers about 240–290 years. This age range translates into a mean linear sedimentation rate between 2.0 and 2.4 mm year<sup>-1</sup>, and a mean dSAR of 0.10–0.12 g cm<sup>-2</sup> year<sup>-1</sup>. The most likely age range of the upper dated interval (AD 1832–1890 at 27 cm depth) is consistent with similar sedimentation rates in the lower (mean dSAR: 0.14 g cm<sup>-2</sup> year<sup>-1</sup>) and upper (0.07–0.10 g cm<sup>-2</sup> year<sup>-1</sup>) parts of the sequence, reflecting a stable sedimentation regime at least in the deepest area of the lake throughout the period of its deposition. However, the four calcite lenses in the lower half of the Hogou core are probably event deposits. If so, then the sedimentation rate between the dated levels must be corrected by excising the 7 cm combined thickness of the calcite lenses. The revised dSAR value for the lower part of the sequence (0.11 g cm<sup>-2</sup> year<sup>-1</sup>) brings it closer still to that of the upper part.

Core OUNIS12-2P from Lake Agouta (74 cm) has a calibrated bottom age of AD 1414–1464, and thus covers about 550–600 years. However, the most likely age range of the upper dated interval (AD 1452–1513 at 21–23 cm depth) is inconsistent with a hypothesis of similar sedimentation rates in the upper and lower parts of the sequence. Interpreting the data at face value would imply that both the mean linear sedimentation rate and the dSAR below 21–23 cm were more than an order of magnitude higher than above it. Considering the low probability that changes in sedimentation rate of this magnitude could have occurred without a clear change in bulk sediment

composition (e.g., organic and carbonate content), or the densities of fossils contained within the sediments, we reject the upper <sup>14</sup>C date as erroneous. Most likely the charred seed extracted for dating at 21–23 cm has been reworked from older sediments. Retaining only the date at the base of the core translates into a mean linear sedimentation rate between 1.2 and 1.4 mm year<sup>-1</sup>, and a mean dSAR of 0.08–0.09 g cm<sup>-2</sup> year<sup>-1</sup>, which is very similar to the values obtained in lakes Edem and Hogou.

Based on these exploratory age models, we find that the deepest parts of lakes Edem, Hogou and Agouta experienced largely similar accumulation rates of dry sediment (dSAR) and of non-carbonate inorganic matter (iSAR, with long-term mean values of 0.05, 0.04 and 0.05 g cm<sup>-2</sup> year<sup>-1</sup>, respectively). This overall similarity in sedimentation rates is perhaps not surprising, given that aeolian processes dominate sediment input to these three neighboring lakes, which lack river inflow and surface run-off. Furthermore, iSAR values are more similar between the lakes than dSAR values, which confirms the autochthonous, rather than detrital nature of their sedimentary carbonate.

### Frequency and between-site correlation of past fire events

At this sub-tropical hyper-arid desert location, wild-fires may be started by occasional lightning strikes from a rare thunderstorm, the spontaneous combustion of marsh methane accumulating inside rotting *Phragmites* reed mats, or by humans (Frandsen 1987). Within the time frame of the last few centuries, natural fires at Ounianga Serir probably occurred at random intervals and locations in any patch of burnable reed vegetation. Large reed fires can easily jump and spread to adjacent lakes (Fig. 1), but given the lack of vegetation on the surrounding landscape, fires must have been restricted to the basin of Ounianga Serir. The amount of charcoal produced per unit area depends on the type and biomass of the vegetation (Pyne et al. 1996). In the reed swamps of Ounianga Serir both the type and density of vegetation are rather uniform, as it is determined by access to fossil groundwater in interdunal depressions. Hence we assume that the amount of charcoal produced by individual wildfires primarily reflects the affected area.

Charcoal deposition in lake sediments is a function of the total amount of charcoal produced, proximity of the fire to a specific lake's coring site, and the ratio between the areas of open water and surrounding reed swamp, including floating but dry reed mats (e.g., compare Lake Agouta with Lake Teli, Fig. 1). Therefore, past lake-level fluctuation may have influenced both the frequency of fires and the total amount of charcoal deposited in the sediment record within a given period, via the effects of lake-level change on the abundance of riparian vegetation, and on the distance between that vegetation and the core site. However, in the groundwater-dominated setting of Ounianga Serir, this effect is dampened because the lakes' reduced hydrological sensitivity allowed the development of large floating *Phragmites* mats along wind-sheltered and leeward areas of lakeshore (Fig. 1). Thus, within a certain amplitude of lake-level fluctuation, *Phragmites* marsh simply rises and settles rather than changing in surface area (and hence, burnable biomass).

In this study, individual samples analyzed for charcoal at contiguous 1-cm intervals cover between about 4 and 8 years of charcoal deposition. At this resolution, only the largest and/or closest fires would result in the deposition of sufficient charcoal to create a distinct peak in charcoal abundance (Whitlock and Larsen 2001). After deposition the charcoal signatures of individual wildfires may be blurred by bioturbation; the rather massive, unlaminated appearance of all three lakes' sediments suggests that such effects may be significant. Another process potentially reducing the amplitude of charcoal peaks is the 'background' input of secondary charcoal, i.e. the charcoal which is eroded from catchment soils and deposited in lakes as part of the clastic sediment matrix (Whitlock and Larsen 2001). We estimate such background signals to be limited, however, because the barren surroundings of Ounianga lack real soils, the lakes have no river input, and any charcoal settling on dunes and rock surfaces is quickly remobilized into the air to either be carried off beyond the catchment or become part of wind-blown input to the lake shortly after the fire event. Consequently, this latter type of 'background' deposition is likely to strengthen the sedimentary signature of recent wildfires rather than providing a longer-lasting source of 'contaminating' charcoal.

The nearly continuous deposition of charcoal at concentrations of between 30 and 60 particles  $\text{g}^{-1}$  dry

mass, or a preserved charcoal flux of 2.7–5.9 particles  $\text{cm}^{-2} \text{year}^{-1}$  in all three of the studied lakes reflects a frequent (i.e., yearly or inter-annual) occurrence of reed fires at Ounianga Serir, which mostly remained restricted to relatively small areas before expiring. The few charcoal peaks approaching or exceeding 100 particles  $\text{g}^{-1}$  dry mass can be interpreted to reflect fires that affected an unusually large patch of vegetation and/or occurred directly at the shores of the cored lake. If a fire was widespread we would expect it to create a synchronous charcoal signature in the cores of several lakes, which may then serve as a correlative time-marker horizon. In the studied sequences, one possible candidate for this shared status is the most recent singular charcoal peak situated around 15 cm depth in all three cores. Based on our radiocarbon-based age models, the age of this peak is constrained to AD 1905–1946 in the sediment record of Lake Edem, AD 1929–1956 in Lake Hogou, and AD 1895–1905 in Lake Agouta. Given the sizable age uncertainty in all three records, we must accept rather than reject a hypothesis of simultaneous deposition. Judging from the relative magnitude of this charcoal peak across all three records, this fire may have occurred either at Lake Edem or within the western sector of Ounianga Serir, but it was large enough to deliver charcoal to the eastern sector of the basin. A number of other charcoal peaks deeper down in the sedimentary sequences of neighboring lakes Hogou and Agouta may also represent shared signatures of individual fires. However, considering the generally different appearance of each lake's charcoal profile, matching individual peaks between them is subjective.

Although Ounianga Serir is a relatively pristine environment, it is not unlikely that some of the charcoal in the recovered cores derives from human-induced fires in the recent past. Reed and date palms are harvested by a small settlement of goat herders nearby, who also grow vegetables in small clearings of reed marsh (which are traditionally cleared by hand, not fire). Based on the first appearance of date palm (*Phoenix dactylifera*) in regional pollen records, humans have frequented the Ounianga oases for at least  $\sim 1500$  years (AM Lézine, pers. comm.), i.e. well before the start of our sediment records. Whether human pressure on either the terrestrial or aquatic ecosystem of Ounianga Serir has increased in recent times cannot be ascertained at this time. In any case, the charcoal records provide no evidence for a recent increase in biomass burning.

## Sediment stratigraphy, and evidence for past lake-level fluctuation

In all three sediment cores, calcite-crystal aggregates within the silt size range are present in high concentrations. The crystals themselves are formed because the Nubian Aquifer provides a steady inflow of dissolved  $\text{Ca}^{2+}$ , and high evaporation causes permanent oversaturation of calcite. Significant temporal variation in nutrient fluxes and therefore phytoplankton productivity may, in principle, have induced changes in carbonate deposition through time, because biogenic removal of carbon dioxide through photosynthesis alters surface-water pH (Kalff 2002). However, the phytoplankton productivity of these shallow desert lakes is unlikely to have varied much during the studied period, because new external input of nutrients such as phosphorus and nitrogen has been low (as it depended on the rate of fresh bedrock erosion upwind from Ounianga), and because local nutrients from organic matter decaying on the lake bottom are frequently recycled by turbulent and convective mixing. Only major changes in lake level (and hence mixing regime) could have substantially affected this internal nutrient cycling.

The calcite lenses interrupting conformable sedimentation in Lake Hogou may have resulted from slumping of uncompacted carbonate deposits at the sediment surface, under the influence of wind-induced turbulence; their irregular thickness across the core's cross-section seems to support this scenario. Alternatively, the lenses may represent episodes of enhanced precipitation following (extreme) super-saturation, as may have been driven by an abrupt pH shift (Kalff 2002). Thin horizons of slightly higher organic content, and thus darker sediment color, immediately above three of the lenses suggest that, in these cases, the putative pH shift may have been of biological origin.

Magnetic susceptibility is low throughout the cores of all three lakes, as can be expected in sediments mainly composed of the diamagnetic minerals calcite and quartz (Thompson and Oldfield 1986). Negative values were most frequent in the lower part of the Hogou sequence, where the carbonate fraction often exceeds 50 % of bulk composition and siliciclastic mineral particles are mostly coarse silt or sand-sized; clay-sized particles are scarce (<10 %). The slightly higher MS values in Lake Edem ( $\sim 120 \times 10^{-6} \text{ m}^3 \text{ kg}^{-1}$ ) are associated with lower carbonate values, and clay-sized mineral

particles representing 14–22 % of the total siliciclastic component. Presumably, these particles contain some paramagnetic minerals.

The dominant siliciclastic mineral in all three cores is quartz, with a median grain size ranging from medium silt to very fine sand (16–125  $\mu\text{m}$ ), and in all intervals that we analyzed quantitatively (except the uppermost sample from Lake Edem; Table 1) a significant component of fine and medium (125–500  $\mu\text{m}$ ) sand. The proximate source of these largest quartz grains (perhaps also part of the very fine sand) is sand dunes constituting the shores of all three lakes, and their deposition on the lake bottom mainly results from dune slope instability under water and/or by sand grains floating on the water surface, being trapped in surface tension after saltation from the dune into the lake during sand storms (Simonds 1896). The greater contribution of fine and medium sand grains in lakes Agouta (7–22 %) and Hogou (12–20 %) than in Edem (0–10 %) can be explained by variation in the distance of the core location to the shore (Edem:  $\sim 150$  m; Hogou and Agouta:  $\sim 80$ –100 m). The common source of all clay-, silt-, and very fine sand-sized quartz grains is ultimately the aeolian mobilization of particles originating from fresh sandstone weathering, or blown out of remnant early-Holocene lacustrine deposits situated upwind from Ounianga. Once in the lakes, coarse and fine particles are affected differently by the focusing of sediment (Davis and Ford 1982; Hilton et al. 1986) from wind-stressed shallow-water bottoms near-shore to more quiet deeper bottoms offshore. This eventually results in the well-known gradient from coarser to finer median grain size with increasing distance from shore (Håkanson and Jansson 1983; Dearing 1997).

Two feasible mechanisms exist to cause changes in the median grain size of the quartz deposited over time at a core site. First, changes in wind strength may cause variation in the mobilization of siliciclastic mineral particles. However, in this scenario the stratigraphic changes in our three lakes' sediment records are expected to be synchronous, which does not fit our observations. The second, more likely explanation is that the size distribution of sediment grains reaching the offshore core sites is influenced by lake-level fluctuations. During episodes of low lake level, zones of sediment resuspension and transport (Håkanson 1982), which are limited to waters shallower than the mud boundary depth (Rowan et al.

1992), move closer to the core site; hence, more large grains are deposited towards the center of the basin (Dearing 1997). Judging from the overall quite limited variation in median grain size throughout the studied sediment sequences, as well as their lack of stiff clay horizons reflecting episodes of (intermittent) desiccation, all three lakes are certain to have never dried out during the two (Edem) to six (Agouta) past centuries covered by our cores. The sequences also contain no obvious textural unconformities such as would be created by re-suspension and redistribution of surface sediment in shallow remnant pools. The combined sedimentological evidence, hence, indicates that these lakes have experienced at most only moderate lake-level fluctuation throughout the covered periods. This result demonstrates the long-lived rather than ephemeral nature of these aquatic ecosystems, despite their extremely negative local water balance.

Importantly, the timing of the lake-level fluctuations, albeit modest, which grain-size variation does suggest to have occurred appears dissimilar among the three studied lakes. Allowing for significant chronological uncertainty, grain-size stratigraphy suggests that the early-twentieth century fire responsible for peak charcoal deposition around 15 cm depth in all three lake cores occurred when Lake Edem experienced a relative lowstand, followed by a trend of increasing lake depth towards the present (Fig. 2). In Lake Agouta, this fire occurred around the start of a relative lowstand which continued throughout the 20th century until the present (Fig. 4). Lake Hogou, finally, had its last lowstand in the 18th century after which the lake experienced relatively high lake level continuously for the past ~200 years (Fig. 3). This lack of coherence among neighboring lakes argues against those fluctuations having been driven by a common climatic cause, such as a change in rainfall (at present, there is hardly any) or lake-surface evaporation (which is extreme in any case). Therefore, we consider it more parsimonious that the asynchronous lake-level changes result from small variations through time in the balance between subsurface flow into and out of each lake through the dunes separating them (Fig. 1b). As the hydraulic head between the peripheral and central parts of Ounianga Serir draws water towards the central Lake Teli, dune migration and changes in the amount of dune-stabilizing vegetation at the shores of the lakes continually influence the permeability of each barrier dune, affecting the cascade-like connection between the lakes.

#### Aquatic mollusk ecology, faunistics and biogeography

In total over 800 mollusk specimens were obtained from the three studied cores, belonging to five species of freshwater snails (gastropods). Three snail species belong to the lung-breathing Heterobranchia (*V. nilotica*, *B. pfeifferi*, *B. truncatus*), the other two are gill-breathing Caenogastropoda (*G. ouniangaensis* and *M. tuberculata*). Only *B. pfeifferi* and *M. tuberculata* have been recorded alive at Ounianga Serir, but all of them were present during the early Holocene. Mollusk species richness at that time was much higher (11 species), reflecting the existence then of a stable aquatic ecosystem with greater habitat diversity (Van Bocxlaer et al. 2011). The early Holocene fauna also included one bivalve species (*Pisidium ovampicum*), but none were found in the three short cores studied here.

*Valvata nilotica* was found abundantly in the sediments of all three lakes. Lakes Hogou and Agouta currently experience conductivities at the high end of the freshwater range (1900 and 2680  $\mu\text{S cm}^{-1}$ ), which suggests that *V. nilotica* can tolerate moderate salinity stress. In these two slightly brackish lakes, but not in the more dilute Lake Edem (620  $\mu\text{S cm}^{-1}$ ), some open-coiled *Valvata* shells were found (Fig. 5a), meaning that the whorls are detached from one another. Open-coiling is a relatively rare and still poorly understood phenomenon in freshwater snails (Scholz and Glaubrecht 2010), but it seems to occur more frequently in habitats with elevated salinity and few natural predators. The current known distribution of *V. nilotica* is limited to northern Egypt, northern Sudan and the Ethiopian highlands (Brown 1994). During the early Holocene this species occurred much further west in the present-day Sahara (Van Damme 1984), including Ounianga Serir (Van Bocxlaer et al. 2011). We found *V. nilotica* to be abundant in all three short sediment cores and up to the sediment surface in lakes Edem and Agouta. Our results hence indicate that *V. nilotica* may have a viable population at Ounianga Serir today, which would represent a sizable westward extension of its known modern-day distribution.

*Biomphalaria pfeifferi* was dominant in all early Holocene samples from Ounianga Serir studied by Van Bocxlaer et al. (2011), and these authors also found one living specimen in Lake Boku (Fig. 1b).

Although present in all three short sequences studied here, it was relatively uncommon in the cores from lakes Edem and Hogou. In the Agouta core the total abundance of *B. pfeifferi* roughly equals that of *V. nilotica*. However half of the specimens were recovered from a short section of the core (11–25 cm) dated to the 19th century.

*Bulinus truncatus* is the third snail species found in all three studied cores. This is not surprising given that it has greater tolerance for fluctuating chemical and thermal conditions than *B. pfeifferi* (and *V. nilotica*), and can even withstand intermittent desiccation (Appleton 1978; McCullough 1962). Yet no living specimens of this species have been found at Ounianga so far (Van Bocxlaer et al. 2011). This apparent absence of the eurytopic *B. truncatus* from the modern lakes was an important argument to consider faunal persistence throughout the Holocene unlikely (Van Bocxlaer et al. 2011). Our present evidence indicates that the species has maintained viable populations throughout the past 2–3 centuries in lakes Hogou and Edem, and it may still live in Lake Edem today (Figs. 2, 3).

*Gabbiella ouniangaensis* (Van Bocxlaer et al. 2011) was recovered from lakes Edem and Hogou but not Agouta, suggesting that its upper salinity tolerance is situated around 2000  $\mu\text{S cm}^{-1}$ . However it was only abundant in the core from Lake Edem, which is a larger, deeper and more dilute lake than the other two. Edem also has extensive beds of submerged macrophytes (here the macro-alga *Chara*), which by analogy with *G. tchadiensis* may be the preferred habitat of *G. ouniangaensis* (Van Bocxlaer et al. 2011). Previously known only from the early Holocene lake deposits at Ounianga, our record of this species throughout the Edem sediment sequence suggests that, as for *B. truncatus*, a living population of *G. ouniangaensis* may still exist in Edem today.

*Melanioides tuberculata* was recovered only from the sediment sequence of Lake Agouta, and only from a short core section dated to around 300 years ago. *M. tuberculata* occurs in almost any type of flowing and standing water in warm temperate to tropical regions (Brown 1994), and is known to withstand a wide variety of environmental stresses (Brown 1994; Samadi et al. 1999; Facon et al. 2003). In present-day Ounianga Serir, *M. tuberculata* has been found only on sandy near-shore bottoms in Lake Boku, in line with published information on its preferred

substrate (Lévêque et al. 1983). Its occurrence in the Agouta sequence is not linked to the presence of coarser grain sizes, however. Therefore, no specific inferences can be made, besides noting that the occurrence of *M. tuberculata* in Lake Agouta coincided with somewhat reduced abundances of *V. nilotica* and *B. pfeifferi*.

Overall our study of sub-recent aquatic mollusk assemblages in three short sediment cores suggests that the modern-day mollusk fauna of Ounianga Serir may be more diverse than currently known. We note, however, that specimens of another species, *Lymnaea natalensis*, have been found alive in Lake Djara at Ounianga Serir, and also in the Girki spring at Ounianga Kebir (Van Bocxlaer et al. 2011), but this species was not found among the sub-recent material studied here.

The composition and stratigraphic distribution of sub-recent mollusk assemblages in the studied sediment sequences indicates that the aquatic environment of all three studied lakes has been relatively stable throughout the past two to six centuries. Lake Edem has continuously been a fairly dilute and clear freshwater lake with both emergent and submerged aquatic macrophytes, and diatoms contributing prominently to (relatively modest) aquatic productivity. Lakes Hogou and Agouta have continuously been slightly brackish but never truly saline, and cyanobacteria rather than diatoms were likely responsible for their higher aquatic productivity (although this remains unquantified at present).

## Conclusions

Results of our analyses of the sedimentology and fossil mollusk assemblages of short sediment sequences from three lakes, supported by  $^{14}\text{C}$ -based age models anchored in a shared charcoal signature of past reed fire, indicate that the aquatic environments of Ounianga Serir have been relatively stable over the past few centuries. Given that evaporation exceeds 6 m annually and that the examined lakes are only between 3.6 and 6.8 m deep, our finding highlights the importance of constant groundwater inflow for these desert aquatic ecosystems to persist. Changes in lake conditions that did occur were minor, and caused by variation in the balance between local inflow and outflow depending on dune migration and the variable presence of stabilizing vegetation. Sand dunes and *Phragmites*

swamp give the Ounianga lakes their typical oasis character; a continuous supply of carbonate-rich fossil groundwater and lack of soil in the surrounding desert landscape are responsible for the sandy carbonate mud accumulating on their bottom.

Our analysis of the sub-recent mollusk assemblages likely adds *V. nilotica*, *B. truncatus* and *G. ouniangaensis* to the extant fauna of Ounianga Serir. A living population of *V. nilotica* at Ounianga Serir would represent a major westward extension of the taxon's modern distribution into the Sahara. The presence of *B. truncatus* and *B. Pfeifferi* in sub-recent sediments at Ounianga is notable because of their role as intermediate hosts for blood flukes of the genus *Schistosoma*, which cause urinary and intestinal schistosomiasis, respectively, in humans (Gryseels et al. 2006; Useh 2013). The finds of *G. ouniangaensis* in recently deposited surface sediments are significant because thus far this species was known only from the early-Holocene lacustrine deposits at Ounianga, and hence it was presumed to be extinct.

Van Bocxlaer et al. (2011) suggested that the species-poor modern fauna of aquatic mollusks at Ounianga Serir was likely established via relatively recent colonization events following one or more episodes of complete desiccation (or intolerably high salinity), sometime during the past four millennia when the region's present-day hyper-arid climate regime became established (Hoelzmann et al. 2004; Kröpelin et al. 2008). Considering the higher mollusk species richness documented here from sub-recent sediments, and that *G. ouniangaensis* is likely endemic to the Ounianga region, we cannot exclude the possibility that freshwater aquatic habitat, however small, may have persisted at Ounianga Serir from the wetter early Holocene until the present day. The results presented here show that at least three of lakes at Ounianga Serir have been permanent and relatively stable aquatic environments over the last few centuries.

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