The environmental and evolutionary history of Lake Ohrid (FYROM/Albania): Interim results from the SCOPSCO deep drilling project

4

Bernd Wagner¹, Thomas Wilke², Alexander Francke¹, Christian Albrecht², 5 Bertini⁴, Baumgarten³. Adele Nathalie Combourieu-Nebout⁵, Henrike 6 Aleksandra Cvetkoska⁶, Michele D'Addabbo⁷, Timme H. Donders⁶, Kirstin 7 Föller², Biagio Giaccio⁸, Andon Grazhdani⁹, Torsten Hauffe², Jens Holtvoeth¹⁰, 8 Sebastien Joannin¹¹, Elena Jovanovska², Janna Just¹, Katerina Kouli¹², 9 Andreas Koutsodendris¹³, Sebastian Krastel¹⁴, Jack H. Lacey^{15,16}, Niklas 10 Leicher¹, Melanie J. Leng^{15,16}, Zlatko Levkov¹⁷, Katja Lindhorst¹⁴, Alessia Masi¹⁸, 11 Anna M. Mercuri¹⁹, Sebastien Nomade²⁰, Norbert Nowaczyk²¹, Konstantinos 12 Panagiotopoulos¹, Odile Peyron¹¹, Jane M. Reed²², Eleonora Regattieri^{1,8}, Laura 13 Sadori¹⁸, Leonardo Sagnotti²³, Björn Stelbrink², Roberto Sulpizio^{7,24}, Slavica 14 Tofilovska¹⁷, Paola Torri¹⁹, Hendrik Vogel²⁵, Thomas Wagner²⁶, Friederike 15 Wagner-Cremer⁶, George A. Wolff²⁷, Thomas Wonik³, Giovanni Zanchetta²⁸, 16 Xiaosen S. Zhang²⁹ 17

- 18
- 19 [1] Institute of Geology and Mineralogy, University of Cologne, Cologne, Germany
- 20 [2] Department of Animal Ecology & Systematics, Justus Liebig University Giessen, Giessen,
- 21 Germany
- 22 [3] Leibniz Institute for Applied Geophysics (LIAG), Hannover, Germany
- 23 [4] Dipartimento di Scienze della Terra, Università di Firenze, Firenze, Italy
- [5] CNRS UMR 7194, Muséum National d'Histoire Naturelle, Institut de Paléontologie
 Humaine, Paris, France
- [6] Palaeoecology, Department of Physical Geography, Utrecht University, Utrecht, TheNetherlands
- 28 [7] Dipartimento di Scienze della Terra e Geoambientali, University of Bari, Bari, Italy

- 1 [8] Istituto di Geologia Ambientale e Geoingegneria CNR, Rome, Italy
- 2 [9] Faculty of Geology and Mineralogy, University of Tirana, Albania
- 3 [10] School of Chemistry, University of Bristol, Bristol, U.K.
- 4 [11] CNRS UMR 5554, Institut des Sciences de l'Evolution de Montpellier, Université de
- 5 Montpellier, Montpellier, France
- 6 [12] Faculty of Geology and Geoenvironment, National and Kapodistrian University of7 Athens, Athens, Greece
- 8 [13] Paleoenvironmental Dynamics Group, Institute of Earth Sciences, Heidelberg University,
- 9 Heidelberg, Germany
- 10 [14] Institute of Geosciences, Christian-Albrechts-Universität zu Kiel, Kiel, Germany
- 11 [15] Centre for Environmental Geochemistry, School of Geography, University of12 Nottingham, Nottingham, UK
- 13 [16] NERC Isotope Geosciences Facilities, British Geological Survey, Keyworth,
 14 Nottingham, UK
- 15 [17] University Ss Cyril and Methodius, Institute of Biology, Skopje, Macedonia
- 16 [18] Dipartimento di Biologia Ambientale, Università di Roma "La Sapienza", Rome, Italy
- 17 [19] Dipartimento di Scienze della Vita, Laboratorio di Palinologia e Paleobotanica,
 18 Università di Modena e Reggio Emilia, Modena, Italy
- 19 [20] Laboratoire des Sciences du Climat et de l'Environnement, UMR 8212,
 20 CEA/CNRS/UVSQ et Université Paris-Saclay 91198 Gif-Sur-Yvette, France
- 21 [21] Helmholtz Centre Potsdam, GFZ German Research Centre for Geosciences, Potsdam,
- 22 Germany
- 23 [22] Geography, School of Environmental Sciences, University of Hull, Hull, UK
- 24 [23] Istituto Nazionale di Geofisica e Vulcanologia, Rome, Italy
- 25 [24] IDPA-CNR, via M. Bianco 9, Milan, Italy
- 26 [25] Institute of Geological Sciences & Oeschger Centre for Climate Change Research,
- 27 University of Bern, Bern, Switzerland

- 1 [26] The Lyell Centre, Heriot-Watt University, Edinburgh, UK
- 2 [27] Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences,
- 3 University of Liverpool, Liverpool, UK
- 4 [28] Dipartimento di Scienze della Terra, University of Pisa, Pisa, Italy
- 5 [29] Institute of Loess Plateau, Shanxi University, Taiyuan, China
- 6
- 7 Correspondence to: B. Wagner (wagnerb@uni-koeln.de)
- 8
- 9
- 10

11 Abstract

12 This study reviews and synthesises existing information generated within the SCOPSCO 13 ('Scientific Collaboration on Past Speciation Conditions in Lake Ohrid') deep drilling project. 14 The four main aims of the project are to infer (i) the age and origin of Lake Ohrid (Former 15 Yugoslav Republic of Macedonia/Republic of Albania), (ii) its regional seismotectonic 16 history, (iii) volcanic activity and climate change in the central northern Mediterranean 17 region, and (iv) the influence of major geological events on the evolution of its endemic 18 species. The Ohrid basin formed by transtension during the Miocene, opened during the 19 Pliocene and Pleistocene, and the lake established *de novo* in the still relatively narrow valley 20 between 1.9 and 1.3 Myr ago. The lake history is recorded in a 584 m long sediment 21 sequence, which was recovered within the framework of the International Continental 22 Scientific Drilling Program (ICDP) from the central part (DEEP site) of the lake in spring 23 2013. To date, 54 tephra and crypto-tephra horizons have been found in the upper 460 m of this sequence. Tephrochronology and tuning biogeochemical proxy data to orbital parameters 24 25 revealed that the upper 247.8 m represent the last 637 kyr. The multi-proxy dataset covering 26 these 637 kyr indicates long-term variability. Some proxies show a change from generally 27 cooler and wetter to drier and warmer glacial and interglacial periods around 300 ka. Short-28 term environmental change caused, for example, by tephra deposition or the climatic impact 29 of millennial-scale Dansgaard-Oeschger and Heinrich events are superimposed on the long-30 term trends. Evolutionary studies on the extant fauna indicate that Lake Ohrid was not a

refugial area for regional freshwater animals. This differs from the surrounding catchment, 1 2 where the mountainous setting with relatively high water availability provided a refuge for temperate and montane trees during the relatively cold and dry glacial periods. Although Lake 3 4 Ohrid experienced significant environmental change over the last 637 kyr, preliminary 5 molecular data from extant microgastropod species do not indicate significant changes in diversification rate during this period. The reasons for this constant rate remain largely 6 7 unknown, but a possible lack of environmentally induced extinction events in Lake Ohrid and/or the high resilience of the ecosystems may have played a role. 8

- 9
- 10

11 **1 Introduction**

Systematic limnological studies started in the early 20th century and were first carried out in 12 Europe, for example, at Lake Geneva (e.g., Forel, 1901), a number of lakes in Germany (e.g., 13 14 Thienemann, 1918), and at Lake Ohrid on the Balkan Peninsula (reviewed in Stanković, 1960). These initial studies focused on hydrological data, such as temperature, dissolved 15 oxygen and bottom morphology, and on biological data, such as the distribution and ecology 16 of lake biota. Analytical and technological advances in the following decades facilitated a 17 18 more comprehensive understanding of the interactions between catchment dynamics, hydrology, and the living world of lakes. This led to the establishment of new institutions, 19 20 such as the Hydrobiological Institute at Lake Ohrid in 1935 (Stanković, 1960).

21

22 Besides analyses in extant lakes, early scientists were also interested in studying past changes 23 in lake systems, and paleolimnology, a sub-discipline of limnology, was established in the 1920s. This field started with the collection of sediment cores from lakes to interpret 24 25 stratigraphic data on plant and animal fossils as a record of the lake's history (National 26 Research Council, 1996). Particularly with the establishment of radiometric dating methods in 27 the 1950s and 1960s, paleolimnological studies developed into a powerful tool for long- and short-term reconstructions of the climatic and environmental history of lakes and their 28 catchments. 29

One of the most important developments in paleolimnological work has been the formation of a multi-national continental drilling program – the International Continental Scientific Drilling Program (ICDP). The 'Potsdam Conference', conducted in 1993, defined the scientific and management needs for the ICDP and declared Lake Ohrid, Europe's oldest freshwater lake, as an ICDP target site.

6

One of the most outstanding characteristics of Lake Ohrid, besides its presumed old age, is its 7 8 high degree of endemic biodiversity. With more than 300 described eukaryotic endemic taxa 9 (Föller et al., 2015), Lake Ohrid belongs to the most biodiverse ancient lakes, i.e., lakes that 10 have continuously existed for >100 kyr (Albrecht and Wilke, 2008). If its surface area is taken into account, it may have the highest endemic biodiversity amongst all lakes worldwide. 11 12 Though Lake Ohrid has long been considered to be of Tertiary age, estimates vary 13 considerably, between ca. 2 and 10 Ma (reviewed in Albrecht and Wilke, 2008). Likewise, its 14 limnological origin remains poorly understood, and hypotheses include paleogeographical connections to former marine or brackish water systems and a de novo formation from springs 15 16 and/or rivers (see also Albrecht and Wilke, 2008 for further information and references 17 therein).

18

19 The unique characteristics of Lake Ohrid, together with the lack of knowledge regarding its 20 origin, precise age, and limnological/biological evolution, provided the main motivation to 21 establish an international scientific deep drilling project. Its continuous existence over a long 22 timescale together with an extraordinary degree of endemic biodiversity made Lake Ohrid an ideal 'natural laboratory' to study the links between geological and biological evolution and 23 to unravel the driving forces of speciation, leading to the interdisciplinary project 'Scientific 24 25 Collaboration on Past Speciation Conditions in Lake Ohrid' (SCOPSCO). The four major 26 aims of the SCOPSCO project are to (i) obtain more information on the age and origin of 27 Lake Ohrid, (ii) unravel the regional seismotectonic history including effects of major 28 earthquakes and associated mass-wasting events, (iii) obtain a continuous record containing 29 information on Quaternary volcanic activity and climate change in the central northern 30 Mediterranean region, and (iv) evaluate the influence of major geological events on biotic evolution and the generation of the observed extraordinary degree of endemic biodiversity 31 32 (Wagner et al., 2014). Based on several site surveys and studies conducted between 2004 and 2011, an ICDP drilling campaign at Lake Ohrid was carried out in spring 2013 using the
'Deep Lake Drilling System' (DLDS) from the 'Drilling, Observation and Sampling of the
Earths Continental Crust' (DOSECC) consortium. In total, more than 2100 m of sediments
were recovered from four drill sites, with a maximum penetration of 569 m below lake floor
(blf) at the main drill site (DEEP) in the central part of Lake Ohrid (Fig. 1).

6

Subsampling and analyses are ongoing, but initial, detailed results of geological and 7 biological investigations of the upper 247.8 m (637 ka) of the DEEP sediment sequence and 8 9 newer results from biological studies on the extant fauna of Lake Ohrid were recently published in a special issue in the journal 'Biogeosciences' ('Integrated perspectives on 10 biological and geological dynamics in ancient Lake Ohrid', edited by Wagner et al.). The aim 11 12 of this paper is to review and synthesise the results of the 14 individual papers of this special 13 issue and to complement them with information from former and new studies in order to 14 provide a comprehensive overview on progress towards achieving the four main aims defined 15 for SCOPSCO.

16

17

18 2 Site information

19 Lake Ohrid is a transboundary lake shared between the Former Yugoslav Republic of 20 Macedonia (FYROM) and the Republic of Albania (Fig. 1). The lake is located at 693.5 m above sea level (a.s.l.) and has a maximum length of 30.4 km (N-S), a maximum width of 21 14.7 km (W-E), a surface area of 358 km², and a tub-shaped bathymetry with a maximum 22 water depth of 293 m, a mean water depth of \sim 151 m, and a total volume of 50.7 km³ (Fig. 1; 23 Popovska and Bonacci, 2007; Lindhorst et al., 2012). Water loss occurs by evaporation (13.0 24 $m^3 s^{-1}$) and by the artificially controlled surface outflow in the northern part of the lake, River 25 Crni Drim, which flows into the Adriatic Sea. Outflow rates vary between 22.0 m³ s⁻¹ 26 (Popovska and Bonacci, 2007) and 24.9 m³ s⁻¹ (Matzinger et al., 2006 and references therein), 27 depending on seasonal and long-term variations in water level of up to ~1.5 m between 1950 28 and 2000 (Popovska and Bonacci, 2007). The total water loss can be averaged to \sim 36.5 m³ s⁻¹ 29 30 and is balanced by water input from surface and sublacustrine springs, direct precipitation, as 31 well as rivers. Published data of the annual precipitation in the watershed of Lake Ohrid vary

between 698.3 and 1194.0 mm yr⁻¹, with higher precipitation at higher altitudes and an 1 2 average of 907 mm vr⁻¹ (Popovska and Bonacci, 2007). The average monthly rainfall is highest in winter, with a maximum in November and December, and lowest between June and 3 4 September. The lake level, however, is highest in June due to snowmelt input and lowest in 5 October and November, before the start of autumn rainfall (Popovska and Bonacci, 2007). The seasonal and long-term variations in water budget allow only an approximation of the 6 7 water input from the various sources. Direct precipitation and river inflows (45%) as well as 8 surface and sublacustrine karst springs (55%) contribute to the overall water input (Matzinger 9 et al., 2006). The River Sateska, which was previously a direct tributary of the Crni Drim, was artificially diverted into Lake Ohrid in 1962 and is today the largest surface river inflow with 10 11 a contribution of ~15% of the total inflow of Lake Ohrid (Matzinger et al., 2006; Poposka and Bonnacci, 2007). The karst springs are located primarily along the eastern shoreline of the 12 13 lake (Fig. 1) and karst waters originate in almost equal proportions from mountain range 14 precipitation and via outflow from Lake Prespa, located ~10 km to the east and ~155 m higher in altitude (Matzinger et al., 2006). Calculating the ratio between the volume of Lake Ohrid 15 (50.7 km^3) and its outflow (~23.5 m³ s⁻¹) results in a theoretical water residence time of ~70 16 17 years (Matzinger et al., 2006; Popovska and Bonacci, 2007). This theoretical residence time is 18 reduced to ~45 years, when evaporation is taken into account and calculated with the total water output or input (\sim 36.5 m³ s⁻¹). However, the real water residence time is probably much 19 20 higher, as sporadic mixing intervals or incomplete mixing, variations in wind stress, or kinetic 21 effects of inflow water entering may affect the lake's hydrology (Ambrosetti et al., 2003). For example, Lago Maggiore in Italy was classified as a holo-oligomictic lake prior to 1970, when 22 the upper 150-200 m of the water column mixed every winter and complete mixing occurred 23 irregularly every few years (Ambrosetti et al., 2003). This is similar to Lake Ohrid today 24 25 (Matzinger et al., 2006) and the real residence time at Lago Maggiore is higher by a factor of 26 3 to 4 than the theoretical residence time (Ambrosetti et al., 2003).

27

28 Physical and chemical characteristics of Lake Ohrid have been provided in several 29 publications and annual reports (e.g., Watzin et al., 2002; Matzinger et al., 2006; Jordanoski 30 et al., 2004, 2005; Naumoski et al., 2007; Schneider et al., 2014). Average total phosphorous 31 (TP) concentrations of <10 mg m⁻³ and Secchi depths ranging between 7 and 16 m 32 characterise the pelagic zone of Lake Ohrid as oligotrophic. These oligotrophic conditions

explain why bottom water oxygen concentrations of above 4 mg L^{-1} are recorded even in 1 2 years without complete overturn (Matzinger et al., 2006). The surface water temperature varies between $\sim 25^{\circ}$ C in summer and $\sim 7^{\circ}$ C in winter, while bottom water temperatures are 3 4 ~6°C throughout the year. The boundary between epilimnion and hypolimnion is between 30 and 50 m, depending on the season. The pH decreases from 8.6-8.9 in surface waters to 7.9-5 8.4 in bottom waters. The specific conductivity is around 200 μ S cm⁻¹ in surface waters, 6 around 150 µS cm⁻¹ at 50–200 m water depth and increases again in deeper waters. The 7 8 concentration of Si is lowest in the trophogenic surface waters, where it is taken up by diatoms, and increases gradually to $<2 \text{ mg L}^{-1}$ in bottom waters (Stanković, 1960). The littoral 9 part of the lake exhibits a slightly higher trophic state (Schneider et al., 2014). These meso- to 10 11 slightly eutrophic conditions in relatively shallow waters might be due to a direct input of nutrients from the catchment, higher temperatures, and increasing anthropogenic pollution 12 13 over the last several decades (Kostoski et al., 2010; Schneider et al., 2014). The macrophytic 14 flora in the littoral part of Lake Ohrid can be subdivided into different belts, with Chara species in water depths between 3 and 30 m, Potamogeton species in shallow waters, and a 15 discontinuous belt of *Phragmites australis* along the shore (Albrecht and Wilke, 2008; Imeri 16 17 et al., 2010).

18

19 The vegetation in the catchment of Lake Ohrid can be categorized along altitudinal belts (cf., 20 Filipovski et al., 1996; Matevski et al., 2011). Grasslands and agricultural land are 21 encountered in the littoral zone and the lowlands surrounding the lake, followed by forests 22 dominated by different species of both deciduous and semi-deciduous oaks (Quercus cerris, *O. frainetto*, *O. petraea*, *O. pubescens*, and *O. trojana*) and hornbeams (*Carpinus orientalis*, 23 24 Ostrya carpinifolia) up to 1600 m a.s.l. Mesophilous/montane species such as Fagus sylvatica, Carpinus betulus, Corylus colurna, Acer obtusatum, and Abies borisii-regis 25 26 dominate at higher altitudes up to 1800 m a.s.l. Due to intense grazing, the timberline is between 1600 and 1900 m a.s.l. Reforestation is now slowly replacing the existing alpine 27 pasture lands and grasslands at and above this altitude (Matevski et al., 2011). Sparse 28 populations of several Pinus species, considered to be Tertiary relics, are located in the wider 29 30 region of Lake Ohrid (Sadori et al., 2016). Em et al. (1985) considered the Ohrid-Prespa region to be a refugial area with remains of vegetation of other species (e.g., Pinus 31 32 heldreichii, Quercus trojana, Juniperus excelsa, Aesculus hippocastanum, Genista radiata).

The highest mountains in the Lake Ohrid watershed, which encompasses 1002 km² sensu 2 stricto and 2393 km² including the Lake Prespa catchment, reach 1532 m a.s.l. in the Mocra 3 Mountains to the west, and 2288 m a.s.l. in the Galičica Mountains to the east of the lake. The 4 5 average altitude of the Lake Ohrid watershed is 1109 m a.s.l. About 12% of its watershed is 6 located at an altitude above 1500 m a.s.l. (Popovska and Bonacci, 2007). Intensely karstified 7 Triassic limestones and Devonian siliciclastic bedrock dominate in the southeastern, eastern, 8 and northwestern catchment (e.g., Wagner et al., 2009; Lindhorst et al., 2015). Ultramafic 9 metamorphic and magmatic rocks including ophiolites of Jurassic and Cretaceous age crop 10 out in the west. The plains at the northern, northeastern, and southern lake shore are covered by Quaternary sediments. 11

12

1

- 13
- 14 **3** Material and methods

15 **3.1 Field work**

16 3.1.1 Seismic and hydro-acoustic surveys

Seismic and hydro-acoustic surveys were carried out on Lake Ohrid between 2004 and 2009. 17 18 Parametric sediment echosounder profiles span >900 km in length and were collected at operating frequencies between 6 and 12 kHz (SES-96 light in 2004 and SES 2000 compact in 19 20 2007 and 2008, Innomar Co.). These frequencies allowed up to 60 m of penetration into the 21 sediments at a vertical resolution of ~20 cm. Over 500 km of profiles were collected by multichannel seismic surveys using a Mini GI Air Gun (0.2 L in 2007 and 0.1 L in 2008) and 22 23 a 16-channel 100 m long streamer. The Mini GI Air Gun operated at frequencies between 150 24 and 500 Hz and allowed a maximum penetration of several hundred metres at a vertical 25 resolution of ~2 m. A multibeam survey in 2009, using an ELAC Seabeam 1180 sonar 26 system, was used to acquire detailed bathymetric information of the lake floor below ~20 m 27 water depth. More detailed information on the technical specifications of the seismic and hydro-acoustic systems, their settings, the location of the individual profiles, and the 28 29 operational logistics can be found in Wagner et al. (2014) and Lindhorst et al. (2015).

1 3.1.2 Coring and onsite analyses

2 Several gravity and piston coring campaigns were carried out from local research vessels or 3 small floating platforms (UWITEC Co.) on Lake Ohrid between 2004 and 2011. Whereas 4 surface sediments collected by gravity corer throughout the basin were used to reconstruct the 5 recent settings and the most recent history of Lake Ohrid (e.g., Matzinger et al., 2007; Wagner 6 et al., 2008a; Vogel et al., 2010c), piston cores with a maximum penetration of ~15 m blf 7 were collected from the lateral parts of the lake, where the water depth did not exceed 150 m 8 (e.g., Wagner et al., 2008b, 2009; Belmecheri et al., 2009; Vogel et al., 2010a, 2010b). These 9 piston cores enabled a reconstruction of the environmental, climatic, and tephrostratigraphic 10 history of the lake back to ~140 ka and provided fossil records of pollen (Wagner et al., 11 2009), molluscan faunas (Albrecht et al., 2010), and diatom floras (Reed et al., 2010).

12

Based on the site surveys, five primary target sites in Lake Ohrid were proposed for the SCOPSCO ICDP project. One of these sites, Lini (Co1262; Fig. 1), was cored in 2011 using a UWITEC platform and piston corer at 260 m water depth. Although the Co1262 sediment sequence reached only 10.08 m blf, this is the most complete Holocene sequence retrieved to date. Studies on the core material contributed to a better understanding of the tectonic activity (Wagner et al., 2012) and the Late Glacial to Holocene environmental history of the region (Lacey et al., 2015; Zhang et al., 2016).

20

The remaining four sites were cored in spring 2013 using the DLDS (Wagner et al., 2014; Francke et al., 2016). At the main site, the DEEP site in the central part of the Lake Ohrid basin, six holes (5045-1A to 5045-1F) were drilled with a maximum depth of ~569 m blf (Fig. 1) and an average distance of ~40 m between the individual holes (for details see Francke et al., 2016). In total, ~1500 m of sediment cores were recovered, cut into up to 1 m long segments, and stored in a reefer at 4°C before being shipped to the University of Cologne, Germany, for further processing.

28

Onsite analyses during the 2013 deep drilling campaign included borehole logging, core scanning for magnetic susceptibility, and sedimentological and palaeobiological core catcher analyses. Borehole logging was carried out with various probes at all four drill sites. The logging tools comprised magnetic susceptibility (MS), dipmeter, resistivity, borehole televiewer, spectral gamma ray (SGR), and sonic. While SGR was run through the drill pipe in order to prevent caving of sediments into the drill hole, all other tools were run in 40–50 m long open-hole sections, except for the uppermost 30 m blf, which were kept open with drill pipes to allow re-entry of other probes. Details of the borehole logging tools, logging speed, and vertical resolution are given in Baumgarten et al. (2015). Check shots were recorded for hole 5045-1C, allowing a very good seismic-to-core correlation for the DEEP-site.

8

9 In order to determine volume-specific MS on the sediment cores and to carry out preliminary
10 core correlation, all cores were scanned onsite at a resolution of 2 cm with a Bartington
11 MS2C loop sensor (10 cm internal diameter) mounted on a multi sensor core logger (MSCL,
12 Geotek, UK). Smear slide analyses of core catcher material (~3 m resolution) from holes
13 5045-1B and 5045-1C were used for onsite diatom analyses (Wagner et al., 2014).

14

15 3.1.3 Biological sampling

Biological field sampling within the SCOPSCO project focused on the collection of living invertebrates from the lake and its surroundings in order to conduct phylogenetic and metacommunity analyses. The collection methods for gastropods followed those described in Hauffe et al. (2011) and Schreiber et al. (2012), and included hand collecting, snorkeling, sieving, and dredging from small boats or the research vessel of the Hydrobiological Institute Ohrid. Samples were preserved in 80% ethanol for subsequent analyses.

22

In order to improve the interpretation of changes in sedimentary lipid biomarker composition,
samples from main modern terrestrial organic matter pools, i.e., soils and leaf litter, as well as
macroalgae and macrophytes (*Characeae* spp., *Cladophora* spp., *Potamogeton* spp., *Phragmites* spp.) were collected from the eastern and southern realm of the Ohrid Basin (for
details see Holtvoeth et al., 2016). All samples were oven-dried shortly after collection (70°C,
48 hours) and kept frozen prior to biomarker analysis.

29

1 3.2 Laboratory work

2 The geological work carried out on the gravity and piston cores from the site surveys and on the cores obtained during the ICDP drilling campaign comprises a broad suite of analytical 3 methods. It includes lithological description after core opening, measurement of the 4 geophysical properties, and granulometric, geochemical, mineralogical, and rock-magnetic 5 6 analyses. These analyses are carried out on whole core sections, on split core surfaces, and on discrete samples (cf., Wilke et al., 2016) and are described in detail in several individual 7 8 publications (Matzinger et al., 2007; Wagner et al., 2008a, 2008b, 2009, 2012; Belmecheri et 9 al., 2009, 2010; Holtvoeth et al., 2010, 2016; Leng et al., 2010; Lindhorst et al., 2010; Matter et al., 2010; Vogel et al., 2010a, 2010b; Lacey et al., 2015, 2016; Francke et al., 2016; Just et 10 al., 2016; Leicher et al., 2016). Dating of the sediment successions was mainly based on 11 12 radiocarbon dating as well as tephrostratigraphic and tephrochronological work. Tuning of 13 sediment proxies to orbital parameters, such as summer insolation and winter season length, 14 or to other records has only been carried out on the sediment sequence from the DEEP site (Baumgarten et al., 2015; Francke et al., 2016; Zanchetta et al., 2016). Optical and 15 geochemical information was used for a correlation of the DEEP core sequences and led to a 16 17 composite profile of 584 meters composite depth (mcd) (Francke et al., 2016 and unpublished data). Some of the sediment sequences were also studied for their fossil diatom, pollen, 18 19 ostracod, or mollusc compositions. The sample preparation for the micro- and macrofossil analyses and the determination of the taxa are described in detail in the individual 20 publications (Belmecheri et al., 2009, 2010; Wagner et al., 2009, 2014; Albrecht et al., 2010; 21 22 Reed et al., 2010; Cvetkoska et al., 2016; Sadori et al., 2016; Zhang et al., 2016).

23

Information on interspecific relationships between Ohrid endemics and Balkan species, and on the drivers of speciation processes and community changes was derived from extant taxa by conducting molecular phylogenetic, lineage-through-time plot, and diversification-rate analyses (for details see Föller et al., 2015 and references therein), as well as modeling of community assembly processes (see Hauffe et al., 2016).

29

1 4 Results and discussion

2 4.1 Age and origin

3 4.1.1 Age

4 At the start of the SCOPSCO project, the age and origin of Lake Ohrid were poorly 5 constrained. Previous geological and biological age estimates varied from 2 to 10 Ma 6 (summarised in Albrecht and Wilke, 2008). Our new results allow for more precise age 7 estimation. Based on SGR from borehole logging, MS from core logging, and total inorganic carbon (TIC) analyses on core catcher samples from the DEEP site, and by comparing these 8 9 data with global climate records, such as the benthic isotope stack LR04 (Lisiecki and Raymo, 2005), a minimum age of 1.2 Ma has been proposed for the permanent lake phase of Lake 10 Ohrid (Wagner et al., 2014). This minimum age is supported by the results from more detailed 11 studies of the uppermost 247.8 mcd of the DEEP site sequence, which cover the last 637 kyr, 12 13 according to an age model derived from tephrochronology and tuning of bio-geochemical proxy data to orbital parameters (Francke et al., 2016). The high-resolution data allow a better 14 15 understanding of proxy variation over time and show that high TIC characterises interglacial periods and very low TIC represents glacial periods, as previously inferred from studies on 16 core catcher material (Wagner et al., 2014). Indeed, a prominent TIC maximum at ~368 m blf 17 18 in the core catcher samples from the DEEP site was presumed to represent the Marine Isotope 19 Stage (MIS) 31 at 1.081–1.062 Ma (Wagner et al., 2014), which is regarded as one of the warmest interglacials during the Mid Pleistocene Transition (MPT; e.g., Melles et al., 2012) 20 21 between 1250 and 700 ka (Clark et al., 2006). The lithology of the DEEP site sediment 22 sequence indicates that lacustrine, hemi-pelagic sediments comprise the upper ~ 430 m blf. 23 whereas littoral and fluvial sediments dominate below (Wagner et al., 2014). The transition 24 from fluvial or littoral facies to hemi-pelagic sediments most likely indicates the onset of full 25 lacustrine conditions in Lake Ohrid. Five TIC maxima below the presumed MIS 31 maximum and above the fluvial or littoral facies (cf., Wagner et al., 2014) could represent five additional 26 27 interglacials, which would place the onset of hemi-pelagic sedimentation within MIS 41 and 28 refines the minimum age of Lake Ohrid to ca. 1.3 Ma.

29

30 An age estimation for the onset of lacustrine sedimentation in the Lake Ohrid basin has been 31 derived from comparing seismic and chronological information from core Co1202 recovered

in the north-eastern part of the lake (Fig. 1). Tracking seismic reflectors from this coring 1 2 location (~ 2 km from the DEEP site) to the central part of the lake allowed for the transfer of 3 chronological information of the core into the basin centre (Lindhorst et al., 2015). In 4 addition, the strength of the reflectors was correlated with chronological information and 5 glacial/interglacial cycles derived from pollen analyses at Lake Ioannina (Tzedakis, 1994), 200 km to the South of Lake Ohrid. Based on this information, an average sedimentation rate 6 of 0.43 mm yr⁻¹ was calculated for the last 450 kyr in the basin centre (Lindhorst et al., 2015). 7 8 Using this sedimentation rate for the maximum sediment fill of ~800 m blf observed in the 9 basin centre, resulted in an age of 1.9 Ma for the onset of sedimentation (Lindhorst et al., 2015). At the DEEP site a somewhat lower average sedimentation rate of 0.39 mm yr⁻¹ can be 10 calculated for the upper 247.8 mcd or for the last 637 kyr (Francke et al., 2016). Sediment 11 compaction with increasing sediment depth (cf. Baumgarten et al., 2015) may have caused 12 13 further lowering of the calculated sediment accumulation rate downward and also would lead 14 to older ages compared to those based on a constant sedimentation rate of 0.43 mm yr⁻¹. However, lacustrine, hemi-pelagic sediments only form the upper ~430 m blf of sediments at 15 16 the DEEP site, which represents only half of the maximum sediment fill equivalent to ~800 m 17 blf. As the underlying littoral and fluvial sediments most likely have significantly higher 18 sedimentation rates, the extrapolated age of 1.9 Ma for the onset of hemi-pelagic 19 sedimentation can be regarded as a tentative maximum age, assuming there were no major phases of erosion and/or non-deposition. 20

21

Overall, based on this new geological information, the minimum and maximum age of Lake Ohrid can be restricted to ca. 1.3 and 1.9 Ma, respectively. More precise age estimation will be obtained by ongoing tephrostratigraphic work and paleomagnetic analyses, which may reveal the existence of major reversals in the Earth's magnetic field, such as the Jaramillo (1.075-0.991 Ma), Cobb Mountain (1.1938-1.1858 Ma), or Olduvai (1.968-1.781 Ma) subchrons (Nowaczyk et al., 2013 and references therein).

28

These estimates of 1.3–1.9 Ma correspond well to evolutionary data for endemic Lake Ohrid species obtained prior to the drilling campaign. Based on genetic information from extant endemic species and molecular-clock analyses, the onset of intralacustrine speciation in various groups of Lake Ohrid endemics (='ancient lake species flocks') started between 1.4

Ma for the limpet genus Acroloxus (Albrecht et al., 2006) and 2.0 Ma for the endemic Salmo 1 2 trutta trout complex (Sušnik et al., 2006) and the Dina leech flock (Trajanovski et al., 2010). 3 Assuming that the origin of Lake Ohrid predates the onset of intralacustrine speciation events, 4 the latter authors suggested that the minimum age of Lake Ohrid is approximately 2.0 Ma. 5 However, they were not able to explain why the species flocks investigated differed in their time of origination and why some of the flocks were as young as 1.3 Ma. A potential 6 7 explanation is now provided by the initial results of the SCOPSCO deep drilling campaign, 8 which indicate that persisting lacustrine conditions with pelagic or hemi-pelagic 9 sedimentation established between 1.9 Ma and 1.3 Ma ago. The period of lake establishment 10 and persisting lacustrine conditions may have comprised up to several hundred thousand 11 years, which in turn might have given rise to most species flocks in Lake Ohrid.

12

13 4.1.2 Origin

There is a broad consensus that the 40 km long and N-S-trending Ohrid graben basin 14 15 developed as part of the Alpine orogeny during a transfersional phase in the Late Miocene, followed by an extensional phase since the Pliocene (e.g., Cvijić 1911; Aliaj et al., 2001; 16 17 Dumurdzanov et al., 2004; Reicherter et al., 2011; Lindhorst et al., 2015). There is little consensus on the limnological origin of the lake itself, however. Albrecht and Wilke (2008) 18 19 summarized four related hypotheses. Three of these hypotheses favour an origin as part of a 20 marine ingression or a brackish-water lake system during the Miocene: the Mesohellenic 21 Trough hypothesis, the Tethys hypothesis, and the Lake Pannon hypothesis. A fourth hypothesis postulates a *de novo* origin, i.e., that Lake Ohrid formed in a dry polje fed by 22 23 springs during the Pliocene or Pleistocene. The latter is supported, in part, by the known existence of substantial active karst aquifers (Matzinger et al., 2006) and the seismic data, 24 25 which indicate that Lake Ohrid formed in a relatively narrow and elongated valley (Lindhorst 26 et al., 2015). Moreover, sediments at the base of the DEEP site sequence are formed by 27 gravel, which is overlain by alternating peat layers, sand horizons, and fine-grained sediments, and contain a relatively shallow, obligate fresh water diatom flora (Wagner et al., 28 29 2014). These sediments indicate very dynamic environments, ranging from fluvial to slack 30 water conditions, with varying shallow water conditions, and support, in combination with the presumed Pleistocene age of Lake Ohrid, the *de novo* hypothesis of lake formation. 31

- 1
- 2

3 4.2 Sediment architecture and basin development

In addition to information on the formation of the Ohrid basin, the hydro-acoustic data sets
from Lake Ohrid can also provide knowledge on mass transport deposits (MTDs) and on
long-term lake level change.

7

8 The evaluation of the seismic and hydro-acoustic data sets indicated that MTDs are only 9 observed during the last ca. 340 ka in Lake Ohrid (Lindhorst et al., 2016). Older MTDs are 10 not covered by the seismic profiles or may be masked by multiple reflections below 250-300 m sediment depth in the central part of the basin. Five major MTDs are detected during MIS 11 12 9, 7, and 6. Since ca. 80 ka, the number of MTDs increased, however this is accompanied by a trend of decreasing MTD volume. Due to the restricted vertical resolution of the seismic data 13 14 sets, the age control of the MTDs is relatively imprecise. Nevertheless, it seems that the 15 occurrence of MTDs is not driven by or a response to glacial/interglacial cyclicity, as they 16 occur during glacials, interglacials, and their respective transitions. Although MTDs are 17 detected throughout the entire basin (Lindhorst et al., 2016), they cluster along the major 18 faults in the southeastern and northwestern part of the basin and are probably the result of 19 fault activity and major earthquakes (Lindhorst et al., 2012; Wagner et al., 2012). Hence, 20 MTDs in the Ohrid basin apparently have a rather limited spatial extent and are not 21 accompanied by basin-wide suspension clouds or turbidites. MTDs with a maximum 22 thickness of <3 cm are observed in the DEEP site record, with clusters in MIS 8, late MIS 6, 23 and MIS 2 (Francke et al., 2016). The thickness of these MTDs is significantly below the 24 vertical resolution of the seismic data.

25

The hydro-acoustic data can also provide information about the tectonic history of the basin with respect to lake-level fluctuations. The minimum water depth can be estimated from measuring the depth difference of individual reflectors between their largest depth in the basins and the minimal depth of occurrence at the lake margins. The minimal depth of occurrence for individual reflectors maybe a real reflection termination but in most cases,

1 individual reflectors cannot be traced further up because the shallowest areas of the lake basin 2 are not covered by the seismic and hydro-acoustic survey or reflectors could not be traced to 3 the shallower parts due to faults (Fig. 2). In a second step, linking these reflectors to the 4 chronological information from the DEEP site provides chronological information for the 5 minimum water depth. Tracing a reflector from ~275 m blf at the DEEP site, i.e., a reflector located below the existing age model, supposes a minimum water depth of 300 m (Fig. 2). 6 7 Reflectors at the MIS 16/15 (~240 m blf) and the MIS13/12 boundaries (~190 m blf) suggest 8 minimum water depths of 300 m as well, thus exceeding the present day water depth of 293 m 9 (Fig. 2). The minimum water depth was reduced to 225 m at the MIS 9/8 boundary (~140 m 10 blf), to 200 m during MIS 8 (~100 m blf), and to 175 m during MIS 5 (47 m blf). In MIS 4 11 (20 m blf), the minimum water depth increased to 250 m, returning to a level similar to that 12 observed in the lower half of the record. Note that this method for estimating water depth 13 contains several sources of uncertainties. The actual water depth during each period may have 14 been much higher, as individual reflectors may continue to shallower water depths or even 15 above the present lake level but cannot be mapped due to missing data coverage in shallow 16 water depth, or reflectors may have been eroded during a following period of a lower lake level. Ongoing subsidence might also have affected the shape of the individual reflectors and 17 18 potentially increased the maximum depth difference of individual reflectors. Nonetheless, the 19 data suggest a general trend from deeper waters from prior to MIS 16 through to MIS 13/12, 20 followed by decreasing water depths with a minimum in MIS 5 and a subsequent deepening to present day lake level. As a result, the deepening of the Lake Ohrid basin was apparently 21 22 not a continuous and gradational process; we assume that short or mid-term changes reflect 23 changes in water budgets while subsidence is a much slower process. However, already at or 24 shortly after the end of the MPT at 700 ka (Clark et al., 2006), the lake showed similar or even higher water depths compared to present lake level. The seismic data do indicate periods 25 26 of very low lake levels or even a completely desiccated lake since that time.

27

Mapping of the hydro-acoustic reflectors indicates that the shape of the Ohrid basin slightly altered over time. Based on the isopleths, the deeper part of the basin changed from a more elongated shape to a roundish shape during the last ca. 700 kyr, with a formation of a secondary basin in the northwestern part of the lake after the MIS 13/12 boundary at 478 ka (Fig. 2). This also reflects the extension of the lake basin.

- 1
- 2

3 4.3 Tephrostratigraphic and environmental history

4 4.3.1 Tephrostratigraphy

5 The DEEP site sequence drilled in 2013 provides the most complete tephrostratigraphic 6 record obtained from Lake Ohrid. A total of 39 tephra layers have been identified in the upper 7 247.8 mcd so far (Fig. 3; Leicher et al., 2016 and unpublished data). Major element analyses 8 (SEM-EDS/WDS; see Leicher et al., 2016 for details) on juvenile glass fragments suggest an 9 origin exclusively from Italian volcanic provinces. Of these tephra layers (OH-DP-0027 to 10 OH-DP-2060), 13 could be identified and correlated with known and dated widespread 11 eruptions (Leicher et al., 2016 and references therein). They include the Mercato tephra (OH-12 DP-0027, 8.43-8.63 cal ka BP) from Somma-Vesuvius, the Y-3 (OH-DP-0115, 26.68-29.42 cal ka BP), the Campanian Ignimbrite/Y-5 (OH-DP-0169, 39.6 ± 1.6 ka), and the X-6 (OH-13 14 DP-0404, 109 ± 2 ka) from the Campanian volcanoes, the P-11 (OH-DP-0499, 129 ± 6 ka) from Pantelleria, the Vico B (OH-DP-0617, 162 ± 6 ka) from the Vico volcano, the Pozzolane 15 16 Rosse (OH-DP-1817, 457 ± 2 ka) and the Tufo di Bagni Albule (OH-DP-2060, 527 ± 2 ka) from the Colli Albani volcanic district, and the Fall A (OH-DP-2010, 496±3 ka) from the 17 18 Sabatini volcanic field. Furthermore, a comparison of the Ohrid record with 19 tephrostratigraphic records of mid-distal Mediterranean archives enabled the identification of 20 less well-known tephra layers, such as the TM24-a/POP2 (OH-DP-0404, 101.8 ka; Regattieri et al., 2015) from Lago Grande di Monticchio and the Sulmona basin, the SC5 (OH-DP-1955, 21 22 493.1 \pm 10.9 ka) from the Mercure basin, and the A11/12 (OH-DP-2017, 511 \pm 6 ka) from the 23 Acerno basin, whose specific volcanic sources are still poorly constrained. OH-DP-0624 was 24 tentatively correlated to the CF-V5/PRAD3225 layers from the Campo Felice basin/Adriatic 25 Sea and thus to the Pitigliano Tuff from the Vulsini volcanic field (ca. 163 ka; Leicher et al., 2016). However, recent tephrochronological results including ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ of a tephra from the 26 27 Fucino Basin, central Italy, suggest that these tephras correspond to an un-known eruption from the Neapolitan volcanic area at 158.8 ± 3.0 ka (Giaccio et al., 2016). In order to obtain a 28 consistent set of ages all 40 Ar/ 39 Ar were calculated by using the same flux standard (1.194 Ma 29 30 for ACs, which corresponds to FCs at 28.02 Ma). The chronological information of 11 of the well-identified tephras from Lake Ohrid was used as 1st order tie points for the age-depth 31

model of the composite core, and complemented by tuning of sediment proxies to orbital
parameters, such as summer insolation and winter season length (Francke et al., 2016).

3

Fifteen additional tephra horizons have been identified within the lower hemi-pelagic section of the DEEP site sequence between 248 and 450 mcd (Fig. 3) and are the subject of on-going work. Although knowledge of tephrostratigraphy for the period >637 ka is restricted, a combination of tephrochronological with paleomagnetic information should provide a robust chronology for this part of the sequence.

9

With a total of at least 54 tephra layers intercalated in a continuous sediment succession of > 10 1.3 Ma, the tephrostratigraphic record from Lake Ohrid is a strong candidate to become the 11 12 template for central Mediterranean tephrostratigraphy, especially for the poorly-known and explored Lower and Middle Pleistocene period. The tephrostratigraphic record may also help 13 14 to allow re-evaluation and improvement of the chronology of dated and undated tephra layers from other key sites, such as the age of the Fall A tephra (Leicher et al., 2016). Moreover, the 15 tephras constitute valuable, independent tie points that resolve leads and lags between 16 changes in different components of the climate system and allow a synchronisation of the 17 18 Lake Ohrid record with other regional records (Zanchetta et al., 2016).

19

20 4.3.2 Environmental history

The examination of the environmental history of Lake Ohrid over the last 637 kyr focuses
both on long-term changes over several glacial/interglacial periods, and short-term changes on
the sub-orbital scale.

24

25 Long-term changes

26

The study of the long-term environmental history of Lake Ohrid and its surrounding area includes the reconstruction of minimum lake levels based on hydro-acoustic information, by vegetation changes in the catchment, and by internal lake proxies. According to the

established age model (Francke et al., 2016), hvdro-acoustic (Lindhorst et al., 2015), and 1 borehole logging data (Baumgarten et al., 2015), the sediments deposited at 637 ka are now 2 3 located ~240 m blf at the DEEP site. If the altitude of the Lake Ohrid outlet or the bedrock 4 gap used by the river Crni Drim would have been the same as it is today (693.5 m a.s.l.), the 5 water depth of Lake Ohrid at 637 ka would have been more than 480 m. There is no evidence in the seismic or sedimentological data for such a great water depth at that time, which 6 7 implies that subsidence or other tectonic activity affected the sediment succession in the lake 8 basin or the altitude of the outlet. Nevertheless, the hydro-acoustic data suggest a fairly deep 9 lake at the end of the MPT, with a water depth similar or even deeper than today (Figs 2 and 10 4). Shallower minimum water depths are tentatively indicated between MIS 9 and MIS 3, 11 with an absolute minimum during MIS 6 or MIS 5. Tectonic activity and the relative altitude 12 of the outlet are probably the most significant contributors to water depth variations in Lake 13 Ohrid. A comparison of the minimum water depth data with pollen data shows some differences, but suggests that climate change may also have triggered water-depth 14 15 fluctuations. Although the Lake Ohrid watershed was a refugial area for both temperate and 16 montane trees during the glacial periods of the last 500 kyr, high amounts of herbs (grasses, chenopods, Cichorioideae and Cyperaceae) are found in the earlier glacials MIS 12, MIS 10, 17 18 and MIS 8 and indicate the presence of open formations and grassland (Sadori et al., 2016). 19 Such vegetation requires relatively humid conditions, whereas steppe vegetation with 20 unexpected high amounts of Artemisia and pioneer taxa typical of dry conditions dominated during MIS 6, MIS 4, and MIS 2 (Fig. 4; Sadori et al., 2016). The pollen data suggest that in 21 22 addition to glacials, a drying trend is also observed in interglacials. This is mainly based on 23 the reduction of montane trees, particularly Abies and Picea values in MIS 5 and the 24 Holocene (Sadori et al., 2016), which may indicate a rearrangement of vegetation in altitudinal belts. The overall progressive change from cooler and wetter conditions recorded 25 26 during both interglacial and glacial periods prior to 288 ka to subsequently warmer and drier 27 interglacials and glacials (Sadori et al., 2016) broadly matches with the generally shallower 28 minimum water levels reconstructed by tracing hydro-acoustic reflectors throughout the basin. Moreover, driest conditions and a maximum in steppe vegetation between 160-129 ka 29 30 (Sadori et al., 2016) correspond to a prominent lake-level lowstand and the formation of a 31 subaguatic terrace ~ 60 m below the present lake level in the northeastern Ohrid basin (Fig. 4; 32 Lindhorst et al., 2010). This lowstand was reconstructed based on hydro-acoustic studies and tephrochronological information from two short sediment cores. Two tephras deposited on the 33

terrace were previously correlated with MIS 5 tephras C-20 (ca. 80 ka) and X5 (105 ± 2 ka) 1 2 (Sulpizio et al., 2010), and it was supposed that the formation of this terrace took place during MIS 6 (Lindhorst et al., 2010). However, new tephrostratigraphic results suggest that the two 3 tephras instead correspond with Vico B (OH-DP-0617, 162 ± 6 ka) and CF-V5/PRAD3225 4 5 (OH-DP-0624, ca. 163 ka; Leicher et al., 2016). This constrains the formation of this terrace to the earlier part of MIS 6 and the subsequent lake-level increase to late MIS 6 or early MIS 6 7 5, with a secondary lowstand around 100 ka (Fig. 4). The lake level curve from northeastern 8 Lake Ohrid is only partly in phase with the minimum lake level curve based on the new 9 hydro-acoustic reconstruction (Figs 2 and 4). Whereas the terraces in the northeastern basin provide relatively precise water depths, the reconstruction based on hydro-acoustic 10 11 information (Fig. 2) can give only minimum water depths and is certainly biased by 12 subsidence.

13

14 Internal lake proxies support the long-term trend seen in pollen from generally wetter and 15 cooler interglacial and glacial periods between 637 ka and ca. 300 ka to drier and warmer stages between 300 ka and the Present. The oxygen isotope composition of lake water 16 $(\delta^{18}O_{lakewater})$, calculated from $\delta^{18}O$ of endogenic calcite, shows only moderate variability 17 between interglacial periods with a relatively stable climate from MIS 15 to MIS 13, 18 19 progressively wetter conditions during MIS 11 and MIS 9, and increasingly evaporated, drier conditions in more recent interglacials (Fig. 4; Lacey et al., 2016). In particular, higher 20 $\delta^{18}O_{lakewater}$ through MIS 5 and the Holocene indicate higher evaporation due to dry and warm 21 conditions prevailing under a Mediterranean-type climate. During glacials calcite is typically 22 absent, however $\delta^{18}O_{lakewater}$ reconstructed from early diagenetic siderite shows a more 23 24 pronounced long-term shift, with values being consistent with the adjacent interglacials during MIS 14, MIS 12, and MIS 10, a transition to lower values through MIS 8, and very 25 low $\delta^{18}O_{lakewater}$ during MIS 6, MIS 4, and MIS 2 (Fig. 4). The similarity between interglacial 26 and glacial lake water prior to ca. 300 ka suggests that Lake Ohrid may have experienced 27 regular and complete mixing, as calcite and siderite form in different environments; calcite in 28 surface waters during summer months and siderite as a product of early diagenesis in the 29 surface sediments. Lower average $\delta^{18}O_{lakewater}$ before ca. 300 ka indicates moderate summer 30 temperatures (reduced seasonality). It may also suggest higher activity of the karst system due 31 32 to more precipitation and/or a higher lake level of neighbouring Lake Prespa. Subsequently, a

1 trend to higher $\delta^{18}O_{lakewater}$ during interglacials indicates stronger rates of summer evaporation 2 and drier conditions, and lower $\delta^{18}O_{lakewater}$ in glacial periods suggests isotopically fresh 3 conditions most likely due to low evaporation. Increasing summer aridity towards present is 4 also backed by the gradual increase of Mediterranean taxa pollen percentages.

5

6 A transition from generally wetter and cooler to drier and warmer conditions is also indicated by a shift from relatively invariant and low TOC prior to ca. 300 ka towards more fluctuating 7 and higher TOC, particularly during the more recent interglacials (Fig. 4; Francke et al., 8 9 2016). Wetter and cooler conditions after the MPT drive a high activity of the karst system 10 and intense mixing of the water column, thus promoting decomposition of organic matter. This would, in turn, increase the supply of sulphur to the sediments and allow for the 11 12 formation of greigite (Fig. 4; Just et al., 2016). A greater activity of the karst system and associated high ion (Ca^{2+}, HCO_3) input is further supported by the relatively high TIC during 13 14 MIS 15, MIS 14, and MIS 13 (Fig. 4; Francke et al., 2016). Pollen data suggest moderate summer temperatures, i.e., conditions that would have favoured mixing and, hence, increased 15 16 organic matter degradation. Conversely, drier and warmer conditions after ca. 320 ka likely reduced mixing of the water column during the interglacials, which would lead to anoxic 17 18 bottom waters and a better preservation of organic matter. Just et al. (2016) proposed a 19 decrease in sulfide availability, either by lower sulfate concentration in lake water or ceased 20 upward migrating fluids, changing the geochemical regime in Lake Ohrid. Such conditions 21 are indicated by a shift from predominant glacial formation of Fe-sulfides to siderite around 22 320 ka, when higher Fe concentrations and limited sulphur content of sediments may have 23 prevented the formation of greigite (Fig. 4; Just et al., 2016).

24

25 The maximum sedimentation rate during early MIS 6 (Francke et al., 2016) correlates well 26 with the formation of the subaquatic terrace located at 60 m below the present lake level (Fig. 27 4; Lindhorst et al., 2010). The lower lake level during early MIS 6 led to exposure and erosion 28 of formerly shallow parts of the lake and a lower distance from inlets to the central part of the 29 lake. However, there is no indication, e.g., in isotope or redox sensitive data, for an endorheic 30 lake at that time or any other time during the last 637 kyr. It thus seems that the outlet was active most of the time and climate driven lake-level change may have existed only for 31 32 relatively short periods or has been compensated at least partly by tectonic activity.

Significant variations in TOC and isotope data during early MIS 6 imply a higher variability of the climate compared to the latter period of MIS 6 (Fig. 4). These observations correspond well with palynological studies from the Ioannina basin, where distinct vegetation changes between 185–155 ka indicate a high climate variability, whereas a greater abundance of steppe taxa and other herbaceous elements, combined with lower tree pollen percentages, during the latter MIS 6 after 155 ka indicate that the landscape was predominantly open in character and more stable (Roucoux et al., 2011).

8

9 <u>Sub-orbital changes</u>

10

11 On a sub-orbital scale, prominent environmental changes in the Northern Hemisphere that 12 potentially affected Lake Ohrid include Dansgaard-Oeschger (D/O) and Heinrich events (HE) (e.g., Bond et al., 1992, 1993; Dansgaard et al., 1993; Raymo et al., 1998; McManus et al., 13 1999). D/O events are a pervasive feature of the last glacial (e.g., Wolff et al., 2010) and also 14 of older glacial periods (Stein et al., 2009; Naafs et al., 2014). They are likely related to 15 16 variations in the Atlantic Meridional Overturning Circulation (AMOC) and are recorded as climatic perturbations in many marine and terrestrial records (e.g., Genty et al., 2002; Rohling 17 18 et al., 2003; Margari et al., 2009; Fletcher et al., 2013; Naafs et al., 2014; Seierstad et al., 2014; Stockhecke et al., 2016). In the eastern Mediterranean, D/O events may have influenced 19 20 regional hydrology and led to large-scale droughts during the past four glacial cycles (Stockhecke et al., 2016). HE are distinctively represented by deposition of ice rafted debris 21 22 (IRD) in North Atlantic marine cores (e.g., Hemming et al., 2004), and are also well documented to have had an imprint on marine and terrestrial records for the last glacial and 23 beyond (e.g., Shackleton et al., 2000; Roucoux et al., 2001, 2011; Sanchez-Goni et al., 2002; 24 25 Martrat et al., 2004; Margari et al., 2010; Naafs et al., 2013). At the IODP drill site U1308 in 26 the North Atlantic, HE are first indicated during MIS 16 and are represented by ice-rafted 27 debris (IRD) layers that are rich in detrital carbonate and poor in biogenic carbonate (Hodell et al., 2008). It has been speculated that ice volume and the duration of glacial conditions 28 29 surpassed a critical threshold during MIS 16 and activated the dynamic processes responsible 30 for Laurentide Ice Sheet instability in the region of Hudson Strait, which led to increased iceberg discharge and weakening of thermohaline circulation in the North Atlantic (Hodell et 31 32 al., 2008).

2 MIS 12 is considered to be one of the most severe glacials during the Quaternary, with the 3 lowest summer sea surface temperatures (SST) recorded across multiple records (e.g., 4 Shackleton 1987; Naafs et al., 2013, 2014; Rohling et al., 2014). Abrupt sea surface warming 5 events of 3–6°C in the mid-latitude North Atlantic during MIS 12 likely reflect the imprint of 6 D/O events and probably had a substantial impact on global climate (Naafs et al., 2014). In 7 contrast to the observations from MIS 16, a temporal lag between the occurrence of IRD and 8 surface water cooling during MIS 12 implies that HE were not the cause for a weakening of 9 the thermohaline circulation in the North Atlantic at this time (Naafs et al., 2014).

10

11 High-resolution records from the Mediterranean region, which can be used to test a larger 12 regional or even global impact of D/O and HE during MIS 16 or MIS 12, are scarce (e.g., 13 Hughes et al., 2006; Tzedakis et al., 2006; Girone et al., 2013; Capotondi et al., 2016). A 14 multi-proxy record with lithological, geochemical, and isotope data from the Sulmona basin 15 in central Italy covering MIS 12 shows pronounced hydrological variability at orbital and millennial time scales, which replicates North Atlantic and western Mediterranean SST 16 fluctuations (Fig. 5; Regattieri et al., 2016). Several short-term fluctuations in the MIS 12 17 Sulmona record most likely reflect sub-orbital scale hydrological variations, and are 18 19 apparently related to reduced precipitation sourcing from the North Atlantic due to episodes 20 of iceberg melting, and IRD deposition at the west Iberian margin (Regattieri et al., 2016 and 21 references therein). However, as the timing of these IRD events at the western Iberian margin 22 was used to improve the chronology of the Sulmona record, the correlation of hydrological 23 variations in central Italy and IRD deposition in the North Atlantic is not fully independent.

24

25 At Lake Ohrid and further to the East, the arboreal pollen concentration in the Tenaghi 26 Philippon record from Greece correlates well with the general pattern of the sea surface 27 temperatures in the North Atlantic during MIS 12 (Fig. 5; Tzedakis et al., 2006). The 28 resolution of the existing record is too low yet to allow a clear identification of D/O or HE 29 related climate change. The high-resolution record from Lake Van in eastern Turkey also 30 cannot be used for testing the climatic impact of D/O or HE on the eastern Mediterranean, as 31 the sediments of MIS 12 and the onset of MIS 11 are disturbed and lack independent age 32 control (Stockhecke et al., 2014).

2 The new high-resolution record from the DEEP site in Lake Ohrid now offers the possibility 3 to assess the impact of D/O or HE during MIS 12 on a broader regional scale, particularly as 4 it provides two absolute tephra age control points with ages centred at 493.1 \pm 10.9 and 457 \pm 5 2 ka (Fig. 5; Francke et al., 2016; Leicher et al., 2016). During MIS 12, potassium (K) shows 6 a long-term increase, which supports the overall trend towards colder temperatures, such as 7 can be inferred from other marine, terrestrial, or synthetic climate records (Fig. 5). K 8 represents the proportion of clastic, terrigenous matter relative to the content of carbonate 9 (reflected by TIC) and organic matter (reflected by TOC and bSi). TOC was used to infer the 10 severity of glacials at Lake Ohrid (Francke et al., 2016) and shows a remarkable saw tooth 11 pattern during MIS 12, which resembles fluctuations in SST related to D/O variability from the North Atlantic marine record U1313 (Fig. 5; Naafs et al., 2014). Higher TOC is favoured 12 13 by both increased overall productivity (on land and in the water column) as well as increased 14 organic matter preservation, with the latter resulting from oxygen depletion of the bottom 15 water due to enhanced thermal stratification, decreased mixing, and higher temperatures. These higher temperatures at Lake Ohrid likely correlate with higher SST in the North 16 17 Atlantic. The TOC record from Lake Ohrid thus would be the first terrestrial record to indicate D/O cycle-related teleconnections between the North Atlantic thermohaline 18 19 circulation and the climate in the northeastern Mediterranean region during MIS 12. 20 Interestingly, the dominant *Pinus* pollen abundance in the vegetation record indicates a 21 regular ~8 kyr variability during MIS 12 and 10, for which a high-resolution analysis is now 22 being performed (Figure 2 in Sadori et al., 2016).

23

24 The environmental impact of HE or other short-term climate events has been studied in detail 25 for the last glacial cycle in several records from the Balkans (e.g., Tzedakis et al., 2004; 26 Müller et al., 2011). Based on pollen and diatom analyses from lakes Prespa and Ohrid, HE in 27 the North Atlantic during MIS 4 to MIS 2 led to short spells of very dry and cold conditions 28 superimposed on the glacial conditions (Panagiotopoulos et al., 2014; Cvetkoska et al., 2015). 29 Moreover, there is an increased formation of Fe and Mn concretions in Lake Prespa 30 sediments, most likely driven by a significant shift in the bottom water redox conditions 31 (Wagner et al., 2010). According to diatom studies spanning the last 92 ka, Lake Prespa 32 experienced significant regime shifts that are correlated with lake level fluctuations and

changes between (oligo-) meso- and eutrophic conditions (Cvetkoska et al., 2016). Lake 1 2 Ohrid seems to be less sensitive to short-term climate change due to its higher volume-to-3 surface area ratio (e.g., Wagner et al., 2010; Leng et al., 2013). It does not indicate sub-orbital 4 time scale lake-level changes and shifted between ultra oligo- and oligotrophic conditions 5 during the last 92 kyr (Cvetkoska et al., 2016). However, the formation of Fe and Mn concretions and the occurrence of siderite indicate that Lake Ohrid is also sensitive to shifts in 6 7 the bottom water redox conditions (Lacey et al., 2016). During MIS 12, Fe peaks in XRF data 8 are positively correlated with TIC and indicate the formation of early-diagenetic siderite in 9 response to a shift in bottom water redox conditions towards a more oxic environment (Fig. 5; 10 Francke et al., 2016; Lacey et al., 2016). The Fe peaks during the coldest period of this glacial 11 match particularly well with the number of IRD grains and with maxima in the quartzite- or 12 dolomite-calcite ratio in the U1313 record from the North Atlantic (Fig. 5). The latter are 13 interpreted as millennial ice-rafting driven events (Voelker et al., 2010; Naafs et al., 2011, 14 2013) and thus demonstrate that North Atlantic HE may have caused changes in internal lake 15 conditions, such as bottom water redox conditions.

16

17 One of the HE, the H4 event at 40.4–38.4 ka, is superimposed by another short-term event, 18 the eruption from the Campi Flegrei volcanoes 39.6 ± 1.6 ka. This eruption is one of the most 19 severe volcanic eruptions during the Pleistocene and left a 15 cm thick tephra known as 20 Campanian Ignimbrite or Y-5 marine tephra layer in the records from lakes Ohrid and Prespa (e.g., Wagner et al., 2009; Vogel et al., 2010b; Damaschke et al., 2013). High-resolution 21 22 studies of diatoms in both lake sediment records indicated little evidence for a response of the 23 diatom community related to the H4 event, but a clear and rapid change following tephra 24 deposition (Jovanovska et al., 2016). This strong change is likely due to fertilisation and the availability of nutrients, particularly silica, such as it was shown in laboratory studies and 25 26 leaching experiments of tephra with Lake Ohrid water (D'Addabbo et al., 2015). After the initial response, diatom community compositions in lakes Ohrid and Prespa returned to their 27 quasi pre-disturbance state. In Lake Ohrid, the recovery time was ca. 1100 years vs. ca. 4000 28 years in Lake Prespa (Jovanovska et al., 2016). Although both lakes are resilient to short-term 29 30 environmental change, it seems that Lake Ohrid is even more resilient than Lake Prespa, likely due to differences in geology, lake age, limnology, and intrinsic parameters of the 31 32 diatom proxies (Jovanovska et al., 2016).

2

3 4.4 Drivers of biodiversity change

One of the major interdisciplinary goals of the SCOPSCO project is to infer the drivers of the 4 5 extraordinary endemic biodiversity in Lake Ohrid, in general, and to evaluate the influence of major environmental events on evolutionary processes, in particular. Lake Ohrid thus serves 6 7 as a model system to address questions that have puzzled evolutionary biologists for decades. 8 These questions include the problem whether the high number of endemic species is mainly a 9 result of an accumulation of relict species ('reservoir function') and/or of a high rate of intralacustrine speciation ('cradle function'). Moreover, if intralacustrine speciation plays a 10 11 significant role, is it primarily driven by geographic or environmental gradients during periods of relatively constant environmental conditions, possibly supported by a high 12 ecosystem resilience of the lake, or does ongoing environmental change lead to an increase 13 14 (or decrease) in rates of species diversification? Finally, what role do potentially 15 'catastrophic' environmental fluctuations play, such as lake level change or significant 16 changes in the trophic state?

17

18 4.4.1 Reservoir vs. cradle function of Lake Ohrid

19 As discussed in Föller et al. (2015), ancient lakes have often been considered to serve as 20 evolutionary or geographic refugia, either harboring old and distinct lineages or enabling the 21 accumulation of species from extralimital areas during periods of adverse environmental 22 changes, respectively ('reservoir function'). However, previous evolutionary studies in Lake 23 Ohrid on selected animal taxa could not demonstrate the existence of such relict species 24 (sensu Grandcolas et al., 2014), either because ancestral distribution ranges are largely 25 unknown (e.g., Schultheiß et al., 2008) or the native species are not extraordinarily old (e.g., Albrecht et al., 2008; Hauswald et al., 2008). Instead, intralacustrine speciation after 26 27 immigration events prevails. Most endemic animal species in Lake Ohrid are considerably younger than the lake itself and form monophyletic clades (also see Section 4.1.2.). This 28 29 suggests that the high endemic species richness in Lake Ohrid invertebrates is predominantly 1 a result of intralacustrine diversification ('cradle function', e.g., Albrecht et al., 2006, 2008;

2 Wilke et al., 2007; Schultheiß et al., 2008; Wysocka et al., 2014; Föller et al., 2015).

3

Interestingly, the situation is different for plant species inhabiting the surrounding of Lake
Ohrid. For example, the existing pollen record from the DEEP site sequence, which covers
the last 500 kyr, indicates that the Lake Ohrid catchment has indeed been a refugial area for
both temperate and montane trees during glacial periods (Sadori et al., 2016), comparable to
the Lake Ioannina catchment (Tzedakis et al., 2002).

9

10 4.4.2 Impact of environmental change on species diversification

11 Ancient lakes are often considered to be comparatively stable systems, potentially resulting in 12 constant diversification rates (i.e., speciation minus extinction rates) over time. Nonetheless, 13 several factors, often related to environmental, geological, or climatic changes, and depending on the genetic features of the species, have been suggested to affect the tempo of 14 15 diversification in ancient lake species flocks. Accordingly, phases of rapid environmental fluctuations may lead to net evolutionary change. Diversification rates may be higher in the 16 initial phase of lake colonisation and may decline once niche space is increasingly occupied. 17 18 Alternately, there might be a pronounced lag phase between the colonization of a lake and the 19 onset of subsequent diversification (reviewed in Föller et al., 2015).

20

21 Although high-resolution sediment-core analyses, covering the last 637 kyr, indicate that 22 Lake Ohrid experienced several environmental changes, phylogenetic studies on a 23 microgastropod group using lineage-through-time plots and diversification-rate analyses did 24 not reveal significant changes in this rate over time (Föller et al., 2015). Moreover, diatom 25 community analyses conducted from the DEEP sediment cores could not show extinction 26 events due to major environmental events such as tephra deposition (Jovanovska et al., 2016; for details see section 4.3.2) and climate change over the last 92 kyr (Cvetkoska et al., 2016). 27 28 However, the potential for a regime shift increases with recent human impact on the diatom 29 flora of both lakes Ohrid (Zhang et al., 2016) and Prespa (Cvetkoska et al., 2015) although, 30 again, Ohrid appears to be more well-buffered from eutrophication than Prespa.

2 The reasons for the relatively constant diversification rate over time observed in 3 and the lack of diatom extinction events microgastropods during the Late 4 Pleistocene/Holocene remain largely unknown. However, the lack of environmental induced 5 extinction events in Lake Ohrid and/or the high resilience of its ecosystems may have played 6 a role (Föller et al., 2015; Cvetkoska et al., 2016; Jovanovska et al., 2016). Local buffering 7 from extreme environmental effects in a refugial area, such as Lake Ohrid, may have not only 8 led to reduced extinction rates, but also allowed divergence of lineages to proceed. Refugia 9 thus may have acted both as 'museums' for the conservation of diversity and as 'cradles' for 10 the production of new diversity (Tzedakis et al., 2002; Tzedakis, 2009). Nonetheless, though 11 environmental changes may have had only a minor direct effect on diversification processes 12 in endemic taxa of Lake Ohrid during the last 637 kyr, these changes potentially altered the 13 abundance and community compositions of diatoms and ostracods (e.g., Belmecheri et al., 14 2010; Reed et al., 2010; Zhang et al., 2016), thus indirectly affecting speciation processes. In 15 fact, the analysis of the gastropod community in Lake Ohrid implied the presence of both geographical and ecological speciation due to physical barriers and divergence across 16 17 environmental or life history gradients, respectively (Hauffe et al., 2016).

18

1

19 Another aspect of environmental change is the impact of anthropogenic activity on species 20 composition, diversity, and diversification. As previously suggested, Lake Ohrid is facing a 21 "creeping biodiversity crisis", as increasing human impact in and around the lake already 22 jeopardises endemic species (Kostoski et al., 2010). For example, the presence of globally 23 invasive species has been recently demonstrated for Lake Ohrid (Albrecht et al., 2014). 24 Moreover, human-mediated environmental change is also predicted to alter the trophic state 25 of the lake (e.g., Matzinger et al., 2006). Given the small size of both the lake and its catchment, increasing negative effects on the endemic biodiversity of Lake Ohrid and the 26 27 respective habitats are foreseeable and will likely foster extirpation. Only concerted and 28 international conservation activities might help mitigating the human impact on the sensitive 29 and highly biodiverse ecosystem of Lake Ohrid.

30

5 Conclusions and outlook

2 The SCOPSCO deep drilling project was initiated in 2004 and aimed at inferring (i) the age and origin of Lake Ohrid (Former Yugoslav Republic of Macedonia/Republic of Albania), (ii) 3 4 its regional seismotectonic history, (iii) volcanic activity and climate change in the central northern Mediterranean region, and (iv) the influence of major geological events on the 5 6 evolution of its endemic species. The project included phylogenetic and metacommunity analyses of living invertebrates and sampling from main modern terrestrial organic matter 7 8 pools from the lake and its surroundings, seismic and hydro-acoustic surveys of the lake's internal sediment architecture, and the recovery of surface sediments and sediment cores. 9 Within the framework of the International Continental Scientific Drilling Program (ICDP) a 10 deep drilling in Lake Ohrid took place in spring 2013 and provided, among others, a 584 m 11 long sediment sequence from the central part (DEEP site) of the lake. Initial results of the 12 study of this sediment sequence in combination with the results of the biological and 13 14 geophysical as well as former sedimentological studies reveal that the Ohrid basin formed 15 during the Miocene and Pliocene. Lake Ohrid established between 1.9 and 1.3 Myr ago and provides a continuous record of distal tephra deposition and climatic and environmental 16 17 change in the central northern Mediterranean region. With its geographical location, the Lake Ohrid record provides a unique opportunity to align marine records from the North Atlantic 18 19 with long-term and independently dated terrestrial archives in the northern and eastern Mediterranean, such as the records from the Sulmona basin, Tenaghi Philippon, Lake Van, or 20 21 Dead Sea. This is a major precondition to disentangle longitudinal climate gradients and 22 investigate leads and lags circumventing age model uncertainties.

23

More detailed studies exist meanwhile on the upper 247.8 m of the DEEP site sediment 24 sequence and indicate that this part represents the last 637 kyr. Over this period, Lake Ohrid 25 experienced significant environmental change, which is related to orbital-scale climate forcing 26 27 and regional geological events. These changes apparently did not cause major extinction 28 events in Lake Ohrid, as evident from both the microgastropod phylogeny and the diatom 29 fossil record. The potential high resilience of the ecosystem to past climatic and 30 environmental changes together with relatively low extinction rates may explain the 31 extraordinary degree of endemic biodiversity in the lake. Ongoing biological studies and more detailed analyses of the early stages of Lake Ohrid basin, based on the now accessible 32

sediment records, will help to better understand the drivers of biological diversification and endemism. Lake Ohrid is thus a key site to further resolve the link between biological and geological evolution and should centre our attention on protecting the endemic community from a substantial biodiversity crisis due to the increasing anthropogenic impact.

5

6 Acknowledgements. The SCOPSCO Lake Ohrid drilling project was funded by ICDP, the German Ministry of Higher Education and Research, the German Research Foundation, the 7 8 University of Cologne, the British Geological Survey, the INGV and CNR (both Italy), and 9 the governments of the Republics of Macedonia (FYROM) and Albania. The Hydrobiological 10 Institute in Ohrid (S. Trajanovski and G. Kostoski) and the Hydrometeorological Institute in Tirana (M. Sanxhaku and B. Lushaj) provided logistic support for presite surveys and the 11 12 deep drilling campaign. Drilling was carried out by Drilling, Observation and Sampling of the Earth's Continental Crust (DOSECC) and using the Deep Lake Drilling System (DLDS). We 13 14 also would like to thank P. Tzedakis and an anonymous reviewer for the positive feedback and valuable suggestions to improve the manuscript. 15

16

17

18 **References**

19

Albrecht, C., Trajanovski, S., Kuhn, K., Streit, B., and T. Wilke: Rapid evolution of an
ancient lake species flock: freshwater limpets (Gastropoda: Ancylidae) in the Balkan lake
Ohrid, Organisms, Diversity and Evolution, 6, 294–307, doi:10.1016/j.ode.2005.12.003,
2006.

24

Albrecht, C. and Wilke, T.: Ancient Lake Ohrid: biodiversity and evolution, Hydrobiologia,
615, 103–140, doi:10.1007/978-1-4020-9582-5 9, 2008.

27

Albrecht, C., Wolf, C., Glöer, P., and Wilke, T.: Concurrent evolution of ancient sister lakes
and sister species: The freshwater gastropod genus *Radix* in lakes Ohrid and Prespa,
Hydrobiologia, 615, 157–167, doi:10.1007/s10750-008-9555-1, 2008.

- 1 2 Albrecht, C., Vogel, H., Hauffe, T., and Wilke, T.: Sediment core fossils in ancient Lake 3 Ohrid: testing for faunal change since the Last Interglacial, Biogeosciences, 7, 3435-3446, 4 doi:10.5194/bg-7-3435-2010, 2010. 5 6 Albrecht, C., Föller, K., Hauffe, T., Clewing. C., and Wilke, T.: Invaders versus endemics: 7 alien gastropod species in ancient Lake Ohrid, Hydrobiologia, 739, 163-174, 8 doi:10.1007/s10750-013-1724-1, 2014. 9 Aliai, S., Baldassarre, G., and Shkupi, D.: Quaternary subsidence zones in Albania: some case 10 11 studies, B. Eng. Geol. Environ., 59, 313-318, doi:10.1007/s100640000063, 2001. 12 Ambrosetti, W., Barbanti, L., and Sala, N.: Residence time and physical processes in lakes, J. 13 14 Limnol., 62, 1–15, doi:10.4081/jlimnol.2003.s1.1, 2003. 15 16 Barker, S., Knorr, G., Edwards, R. L., Parrenin, F., Putnam, A. E., Skinner, L. C., Wolff, E., and Ziegler, M.: 800,000 years of abrupt climate variability, Science, 334, 347-351, 17 18 doi:10.1126/science.1203580, 2011. 19 20 Baumgarten, H., Wonik, T., Tanner, D. C., Francke, A., Wagner, B., Zanchetta, G., Sulpizio, 21 R., Giaccio, B., and Nomade, S.: Age depth-model of the past 630 kyr for Lake Ohrid 22 (FYROM/Albania) based on cyclostratigraphic analysis of downhole gamma ray data, 23 Biogeosciences, 12, 7453-7465, doi:10.5194/bg-12-7453-2015, 2015. 24 25 Belmecheri, S., Namiotko, T., Robert, C., von Grafenstein, U., and Danielopol, D. L.: Climate controlled ostracod preservation in Lake Ohrid (Albania, Macedonia), Palaeogeogr., 26 Palaeoclimatol., Palaeoecol., 277, 236–245, doi:10.1016/j.palaeo.2009.04.013, 2009. 27
- 28

Belmecheri, S., von Grafenstein, U., Andersen, N., Evmard-Bordon, A., Régnier, D., Grenier, 1 2 C., and Lézine, A.-M.: Ostracod-based isotope record from Lake Ohrid (Balkan Peninsula) 3 the Ouaternary over last 140 ka. Sci. Rev., 29. 3894-3904. 4 doi:10.1016/j.quascirev.2010.09.011, 2010.

5

Bond, G., Heinrich, H., Huon, S., Broecker, W., Labeyrie, L., Andrews, J., McManus, J.,
Clasen, S., Tedesco, K., Jantschik, R., Simet, C., and Klas M.: Evidence for massive
discharges of icebergs into the Northern Atlantic, Nature, 360, 245–249, 1992.

9

Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., and Bonani, G.:
Correlations between climate records from North Atlantic sediments and Greenland ice,
Nature, 365, 143–147, 1993.

13

Capotondi, L., Girone, A., Lirer, F., Bergami, C., Verducci, M., Vallefuoco, M., Afferri, A.,
Ferraro, L., Pelosi, N., and De Lange, G. J.: Central Mediterranean Mid-Pleistocene
paleoclimatic variability and its association with global climate, Palaeogeogr. Palaeoclimatol.
Palaeoecol., 442, 72–83, doi:10.1016/j.palaeo.2015.11.009, 2016.

18

Clark, P. U., Archer, D., Pollard, D., Blum, J. D., Rial, J. A., Brovkin, V., Mix, A. C., Pisias,
N. G., and Roy, M.: The middle Pleistocene transition: characteristics, mechanisms, and
implications for long-term changes in atmospheric pCO2, Quaternary Sci. Rev., 25, 3150–
3184, doi:10.1016/j.quascirev.2006.07.008, 2006.

23

Cvetkoska, A., Levkov, Z., Reed, J. M., Wagner, B., Panagiotopoulos, K., Leng, M. J., and
Lacey, J.: Quaternary climate change and Heinrich events in the southern Balkans: Lake
Prespa diatom palaeolimnology from the last interglacial to present, J. Paleolimnol., 53, 215–
231, doi:10.1007/s10933-014-9821-3, 2015.

1	Cvetkoska, A., Jovanovska, E., Francke, A., Tofilovska, S., Vogel, H., Levkov, Z., Donders,
2	T., Wagner, B., and Wagner-Cremer, F.: Ecosystem regimes and responses in a coupled
3	ancient lake system from MIS 5b to present: the diatom record of lakes Ohrid and Prespa,
4	Biogeosciences, 13, 3147-3162, doi:10.5194/bg-13-3147-2016, 2016.
5	
6	Cvijić, J.: L'ancient Lac Égéen, Ann. Geographicae, 20, 233–259, 1911.
7	
8	D'Addabbo, M., Sulpizio, R., Guidi, M., Capitani, G., Mantecca, P., and Zanchetta, G.: Ash
9	leachates from some recent eruptions of Mount Etna (Italy) and Popocatépetl (Mexico)
10	volcanoes and their impact on amphibian living freshwater organisms, Biogeosciences, 12,
11	doi:10.5194/bg-12-7087-2015, 7087-7106, 2015.
12	
13	Dansgaard, W., Johnsen, S. J., Clausen, H. B., Hvidberg, C. S., and Steffensen, J. P.:
14	Evidence for general instability of past climate from a 250-kyr, Nature, 364, 15, 1993.
15	
16	Damaschke, M., Sulpizio, R., Zanchetta, G., Wagner, B., Böhm, A., Nowaczyk, N.,
17	Rethemeyer, J., and Hilgers, A.: Tephrostratigraphic studies on a sediment core from Lake
18	Prespa in the Balkans, Climate of the Past, 9, 267–287, doi:10.5194/cp-9-267-2013, 2013.
19	
20	Em, H., Dzhekov, S., and Rizovski, R.: Refugial forest vegetation in SR Macedonia,
21	Contributions, 6(1-2), 5–20, Skopje, 1985.
22	
23	Filipovski, G., Rizovski, R., and Ristevski, P.: The characteristics of the climate-vegetation-
24	soil zones (regions) in the Republic of Macedonia, Macedonian Academy of Sciences and
25	Arts, Skopje, 178, 1996.
26	
27	Fletcher, W. J., Müller, U. C., Koutsodendris, A., Christanis, K., and Pross, J.: A centennial-
28	scale record of vegetation and climate variability from 312 to 240 ka (Marine Isotope Stages

1	9c-a, 8 and 7e) from Tenaghi Philippon, NE Greece, Quaternary Sci. Rev., 78, 108-125
2	doi:10.1016/j.quascirev.2013.08.005, 2013.

4 Forel, F. A.: Handbuch der Seenkunde, 249 S.; Stuttgart, Verlag J. Engelhorn, 1901.

5

Föller, K., Stelbrink, B., Hauffe, T., Albrecht, C., and Wilke, T.: Constant diversification rates
of endemic gastropods in ancient Lake Ohrid: ecosystem resilience likely buffers
environmental fluctuations, Biogeosciences, 12, 7209–7222, doi:10.5194/bg-12-7209-2015,
2015.

10

Francke, A., Wagner, B., Just, J., Leicher, N., Gromig, R., Baumgarten, H., Vogel, H., Lacey,
J. H., Sadori, L., Wonik, T., Leng, M. J., Zanchetta, G., Sulpizio, R., and Giaccio, B.:
Sedimentological processes and environmental variability at Lake Ohrid (Macedonia,
Albania) between 640 ka and modern days, Biogeosciences, 13, 1179–1196, doi:10.5194/bgd12-15111-2015, 2016.

16

Genty, D., Blamart, D., Ouahdi, R., Gilmour, M., Baker, A., Jouzel, J., an Van-Exter, S.:
Precise dating of Dansgaard–Oeschger climate oscillations in western Europe from stalagmite
data, Nature, 421, 833–837, doi:10.1038/nature01391, 2003.

20

21 Giaccio, B., Niespolo, E., Pereira, A., Nomade, S., Renne, P. R., Albert, P. G., Arienzo, I., Regattieri, E., Wagner, B., Zanchetta, G., Gaeta, M., Galli, P., Mannella, G., Peronace, E., 22 23 Sottili, G., Florindo, F., Leicher, N., Marra, F., and Tomlinson, E. L.: First integrated tephrochronological record for the last ~190 kyr from the Fucino Quaternary lacustrine 24 25 succession, central Italy, Quaternary Sci. Rev., 158, 211 - 234, 26 doi:10.1016/j.quascirev.2017.01.004, 2017.

27

Girone, A., Maiorano, P., Marino, M., and Kucera, M.: Calcareous plankton response to orbital and millennial-scale climate changes across the Middle Pleistocene in the western

- 1Mediterranean,Palaeogeogr.Palaeoclimatol.Palaeoecol.,392,105–116,2doi:10.1016/j.palaeo.2013.09.005, 2013.
- 3

Goñi, M. S., Cacho, I., Turon, J. L., Guiot, J., Sierro, F., Peypouquet, J., Grimalt, J., and
Shackleton, N.: Synchroneity between marine and terrestrial responses to millennial scale
climatic variability during the last glacial period in the Mediterranean region, Climate
Dynamics, 19, 95–105, doi:10.1007/s00382-001-0212-x, 2002.

- 8
- 9 Grandcolas, P., Nattier, R., and Trewick, S.: Relict species: a relict concept?, Trends Ecol.
 10 Evol., 29, 655–663, doi:10.1016/j.tree.2014.10.002, 2014.

11

Hauffe, T., Albrecht, C., Schreiber, K., Birkhofer, K., Trajanovski, S., and Wilke, T.:
Spatially explicit analysis of gastropod biodiversity in ancient Lake Ohrid, Biogeosciences, 8,
175–188, doi:10.5194/bg-8-175-2011, 2011.

15

Hauffe, T., Albrecht, C., Wilke, T.: Assembly processes of gastropod community change with
horizontal and vertical zonation in ancient Lake Ohrid: a metacommunity speciation
perspective, Biogeosciences, 13, 2901–2911, doi:10.5194/bg-13-2901-2016, 2016.

19

Hauswald, A. K., Albrecht, C., and Wilke, T.: Testing two contrasting evolutionary patterns
in ancient lakes: species flock versus species scatter in valvatid gastropods of Lake Ohrid,
Hydrobiologia, 615, 169–179, doi:10.1007/978-1-4020-9582-5 12, 2008.

23

Hemming, S. R.: Heinrich events: Massive late Pleistocene detritus layers of the North
Atlantic and their global climate imprint, Reviews Geophys., 42,
doi:10.1029/2003RG000128, RG1005, 2004.

27

Hodell, D. A., Channell, J. E. T., Curtis, J. H., Romero, O. E., and Röhl, U.: Onset of "Hudson Strait" Heinrich events in the eastern North Atlantic at the end of the middle

Pleistocene transition (~640 ka)? Paleoceanography, 23, PA4218, 2 doi:10.1029/2008PA001591, 2008. 3 Holtvoeth, J., Vogel, H., Wagner, B., and Wolff, G. A.: Lipid biomarkers in Holocene and

4 5 glacial sediments from ancient Lake Ohrid (Macedonia, Albania), Biogeosciences, 7, 3473-6 3489, doi:10.5194/bg-7-3473-2010,2010.

7

8 Holtvoeth, J., Rushworth, D., Copsey, H., Imeri, A., Cara, M., Vogel, H., Wagner, T., and 9 Wolff, G. A.: Improved end- member characterisation of modern organic matter pools in the 10 Ohrid Basin (Albania, Macedonia) and evaluation of new palaeoenvironmental proxies, Biogeosciences, 13, 795-816, doi:10.5194/bg-13-795-2016, 2016. 11

12

Hughes, P. D., Gibbard, P. L., and Woodward, J. C.: Middle Pleistocene glacier behaviour in 13 14 the Mediterranean: sedimentological evidence from the Pindus Mountains, Greece, J. Geol. 15 Soc. 163, 857-867, doi:10.1144/0016-76492005-131, 2006.

16

17 Imeri, A., Mullaj, A., Gjeta, E., Kalajnxhiu, A., Kupe, L., Shehu, J., and Dodona, E.: Preliminary results from the study of flora and vegetation of Ohrid lake, Natura 18 19 Montenegrina, 9, 253-264, 2010.

20

Jovanovska, E., Cvetkoska, A., Hauffe, T., Levkov, Z., Wagner, B., Sulpizio, R., Francke, A., 21 22 Albrecht, A., and Wilke, T.: Differential resilience of ancient sister lakes Ohrid and Prespa to 23 environmental disturbances during the Late Pleistocene, Biogeosciences, 13, 1149-1161, doi:10.5194/bg-13-1149-2016, 2016. 24

25

26 Just, J., Nowaczyk, N., Sagnotti, L., Francke, A., Vogel, H., Lacey, J.H., and Wagner, B.: 27 Climatic control on the occurrence of high-coercivity magnetic minerals and preservation of 28 greigite in a 640 ka sediment sequence from Lake Ohrid (Balkans), Biogeosciences, 13, 29 1179-1196, doi:10.5194/bg-13-2093-2016, 2016.

Kostoski, G., Albrecht, C., Trajanovski, S., and Wilke, T.: A freshwater hotspot under
pressure – assessing threats and identifying conservation needs for ancient Lake Ohrid,
Biogeosciences, 7, 3999–4015, doi:10.5194/bg-7-3999-2010, 2010.

5

Lacey, J., Francke, A., Leng, M. J., Vane, C. H., and Wagner, B.: A high resolution Late
Glacial to Holocene record of environmental change in the Mediterranean from Lake Ohrid
(Macedonia/Albania), Int. J. Earth Sci., 104, 1623–1638, doi:10.1007/s00531-014-1033-6,
2015.

10

Lacey, J. H., Leng, M. J., Francke, A., Sloane, H. J., Milodowski, A., Vogel, H., Baumgarten,
H., and Wagner, B.: Mediterranean climate since the Middle Pleistocene: a 640 ka stable
isotope record from Lake Ohrid (Albania/Macedonia), Biogeosciences, 13, 1801–1820,
doi:10.5194/bg-13-1801-2016, 2016.

15

Leicher, N., Zanchetta, G., Sulpizio, R., Giaccio, B., Nomade, S., Wagner, B., and Francke,
A.: First tephrostratigraphic results of the DEEP site record in Lake Ohrid, Macedonia,
Biogeosciences, 13, 2151–2178, doi:10.5194/bg-13-2151-2016, 2016.

19

Leng, M. J., Baneschi, I., Zanchetta, G., Jex, C. N., Wagner, B., and Vogel, H.: Late
Quaternary palaeoenvironmental reconstruction from Lakes Ohrid and Prespa
(Macedonia/Albania border) using stable isotopes, Biogeosciences 7, 3109–3122,
doi:10.5194/bg-7-3109-2010, 2010.

24

Leng, M. J., Wagner, B., Aufgebauer, A., Panagiotopoulos, K., Vane, C., Snelling, A.,
Haidon, C., Woodley, E., Vogel, H., Zanchetta, G., Sulpizio, R., and Baneschi, I.:
Understanding past climatic and hydrological variability in the Mediterranean from Lake
Prespa sediment isotope and geochemical record over the last glacial cycle, Quaternary Sci.
Rev., 66, 123–136, doi:10.1016/j.quascirev.2012.07.015, 2013.

Lindhorst, K., Vogel, H., Krastel, S., Wagner, B., Hilgers, A., Zander, A., Schwenk, T.,
Wessels, M., and Daut, G.: Stratigraphic analysis of lake level fluctuations in Lake Ohrid: an
integration of high resolution hydro-acoustic data and sediment cores, Biogeosciences, 7,
3531–3548, doi:10.5194/bg-7-3531-2010, 2010.

6

Lindhorst, K., Gruen, M., Krastel, S., and Schwenk, T.: Hydroacoustic Analysis of Mass
Wasting Deposits in Lake Ohrid (FYR Macedonia/Albania), in: Submarine Mass Movements
and Their Consequences, edited by: Yamada, Y., Kawamura, K., Ikehara, K., Ogawa, Y.,
Urgeles, R., Mosher, D., Chaytor, J., and Strasser, M., Springer, the Netherlands, 245–253,
2012.

12

Lindhorst, K., Krastel, S., Reicherter, K., Stipp, M., Wagner, B., and Schwenk, T.:
Sedimentary and tectonic evolution of Lake Ohrid (Macedonia/Albania), Basin Res., 27, 84–
101, doi:10.1111/bre.12063, 2015.

16

Lindhorst, K., Krastel, S., and Baumgarten, H.: Mass Wasting history within Lake Ohrid
Basin (Macedonia/Albania) over the last 600 ka, Submarine Mass Movements and their
Consequences: 7th International Symposium. G. Lamarche, J. Mountjoy, S. Bull et al. Cham,
Springer International Publishing: 291–300, 2016.

21

22 Lisiecki, L. E. and Raymo, M. E.: A Pliocene-Pleistocene stack of 57 globally distributed

- 23 benthic ∂^{18} O records, Paleoceanography, 20, PA1003, doi:10.1029/2004PA001071, 2005.
- 24

Margari, V., Gibbard, P. L., Bryant, C. L., and Tzedakis, P. C.: Character of vegetational and
environmental changes in southern Europe during the last glacial period; evidence from
Lesvos Island, Greece, Quaternary Sci. Rev., 28, 1317–1339,
doi:10.1016/j.quascirev.2009.01.008, 2009.

29

30 Margari, V., Skinner, L. C., Tzedakis, P. C., Ganopolski, A., Vautravers, M., and Shackleton,

1	N. J.: The nature of millennial-scale climate variability during the past two glacial periods,
2	Nature Geoscience, 3, 127-131, doi:10.1038/ngeo740, 2010.
3	
4	Matevski, V., Carni, A., Avramovski, O., Juvan, N., Kostadinovski, M., Košir, P., Marinšek,
5	A., Paušic, A., and Šilc, U.: Forest Vegetation of the Galicica Mountain Range in Macedonia,
6	Založba ZRC, Ljubljana, 2011.
7	
8	Martrat, B., Grimalt, J. O., Lopez-Martinez, C., Cacho, I., Sierro, F. J., Flores, J. A., Zahn, R.,
9	Canals, M., Curtis, J. H., and Hodell, D. A.: Abrupt temperature changes in the Western
10	Mediterranean over the past 250,000 years, Science, 306, 1762-1765,
11	doi:10.1126/science.1101706, 2004.
12	
13	Matter, M., Anselmetti, F. S., Jordanoska, B., Wagner, B., Wessels, M., and Wüest, A.:
14	Carbonate sedimentation and effects of eutrophication observed at the Kališta subaquatic
15	springs in Lake Ohrid (Macedonia), Biogeosciences, 7, 3755-3767, doi:10.5194/bg-7-3755-
16	2010, 2010.
17	
18	Matzinger, A., Spirkovski, Z., Patceva, S., and Wüest, A.: Sensitivity of ancient Lake Ohrid
19	to local anthropogenic impacts and global warming, J. Great Lakes Res., 32, 158-179,
20	doi:10.3394/0380-1330(2006)32[158:SOALOT]2.0.CO;2, 2006.
21	
22	Matzinger, A., Schmid, M., Veljanoska-Sarafiloska, E., Patceva, S., Guseska, D., Wagner, B.,
23	Müller, B., Sturm, M., and Wüest, A.: Eutrophication of ancient Lake Ohrid: Global warming
24	amplifies detrimental effects of increased nutrient inputs, Limnol. Oceanogr., 52, 338-353,
25	doi:10.4319/lo.2007.52.1.0338, 2007.
26	
27	McManus, J. F., Oppo, D. W., and Cullen, J. L.: A 0.5-million-year record of millennial-scale
28	climate variability in the North Atlantic, Science, 283, 971-975,
29	doi:10.1126/science.283.5404.971, 1999.
30	
31	Müller, U. C., Pross, J., Tzedakis, P. C., Gamble, C., Kotthoff, U., Schmiedl, G., Wulf, S.,

and Christanis, K.: The role of climate in the spread of modern humans into Europe,
Quaternary Sci. Rev., 30, 273–279, doi:10.1016/j.quascirev.2010.11.016, 2011.

1	
2	Naafs, B. D. A., Hefter, J., Ferretti, P., Stein, R., and Haug, G. H.: Sea surface temperatures
3	did not control the first occurrence of Hudson Strait Heinrich Events during MIS 16,
4	Paleoceanography 26, PA4201, doi:10.1029/2011PA002135, 2011.
5	
6	Naafs, B. D. A., Hefter, J., and Stein, R.: Millennial-scale ice rafting events and Hudson Strait
7	Heinrich(-like) events during the late Pliocene and Pleistocene: A review, Quaternary Sci.
8	Rev., 80, 1–28, doi:10.1016/j.quascirev.2013.08.014, 2013.
9	
10	Naafs, B. D. A., Hefter, J., and Stein, R.: Dansgaard-Oeschger forcing of sea surface
11	temperature variability in the midiatitude North Atlantic between 500 and 400 ka (MIS 12),
12	Paleoceanography, 29, 1024–1030, doi:10.1002/2014PA00269/, 2014.
13	National Research Council · Freshwater ecosystems: Re-vitalizing educational programs in
14	limpology National Academy Press Washington D.C. 364 p. 1996
16	minology. National Academy Press, washington, D.C. 504 p., 1990.
17	Nowaczyk N R Haltia E M Ulbricht D Wennrich V Sauerbrey M A Rosén P
18	Vogel, H., Francke, A., Meyer- Jacob, C., Andreev, A. A., and Lozhkin, A. V.: Chronology of
19	Lake El'gygytgyn sediments – a combined magnetostratigraphic, palaeoclimatic and orbital
20	tuning study based on multi-parameter analyses, Clim. Past, 9, 2413–2432, doi:10.5194/cp-9-
21	2413-2013, 2013.
22	
23	Panagiotopoulos, K., Böhm, A., Leng, M. J., Wagner, B., and Schäbitz, F.: Climate variability
24	over the last 92 ka in SW Balkans from analysis of sediments from Lake Prespa, Clim. Past,
25	10, 643–660, doi:10.5194/cp-10-643-2014, 2014.
26	
27	Popovska, C. and Bonacci, O.: Basic data on the hydrology of Lakes Ohrid and Prespa,
28	Hydrol. Proc., 21, 658–664, 2007.
29	
30	Raymo, M. E., Ganley, K., Carter, S., Oppo, D. W., and McManus, J.: Millennial-scale
31	climate instability during the early Pleistocene epoch, Nature, 392, 699-702,
32	doi:10.1038/33658, 1998.
33	

- Reed, J. M., Cvetkoska, A., Levkov, Z., Vogel, H., and Wagner, B.: The last glacial interglacial cycle in Lake Ohrid (Macedonia/Albania): testing diatom response to
 climate, Biogeosciences, 7, 3083–3094, doi:10.5194/bg-7-3083-2010, 2010.
- 4

Regattieri, E., Giaccio, B., Zanchetta, G., Drysdale, R. N., Galli, P., Nomade, S., Peronace, E.,
and Wulf S.: Hydrological variability over Apennine during the Early Last Glacial
precession minimum, as revealed by a stable isotope record from Sulmona basin, central Italy,
J. Quat. Sci., 30, 19–31, doi:10.1002/jgs.2755, 2015.

- 9
- Regattieri, E., Giaccio, B., Galli, P., Nomade, S., Peronace, E., Messina P., Sposato, A.,
 Boschi, C., and Gemelli, M.: A multi-proxy record of MIS 11-12 deglaciation and glacial
 MIS 12 in-stability from the Sulmona Basin (central Italy), Quaternary Sci. Rev., 132, 129–
 145, doi:10.1016/j.quascirev.2015.11.015, 2016.
- 14

Reicherter, K., Hoffmann, N., Lindhorst, K., Krastel, S., Fernandez-Steeger, T., Grützner, C.,
and Wiatr, T.: Active Basins and Neotectonics: Morphotectonics of the Lake Ohrid Basin

17 (FYROM and Albania), Z. Dtsch. Ges. Geowiss., 162, 217–234, 2011.

18

22

Roucoux, K. H., Shackleton, N. J., de Abreu, L., Schönfeld, J., and Tzedakis, P. C.:
Combined marine proxy and pollen analyses reveal rapid Iberian vegetation response to North
Atlantic millennial-scale climate oscillations, Quatern. Res., 56, 128–132,
doi:10.1006/qres.2001.2218, 2001.

27

Roucoux, K. H., Tzedakis, P. C., Lawson, I. T., and Margari, V.: Vegetation history of the penultimate glacial period (Marine isotope stage 6) at Ioannina, north-west Greece. Journal

- 30 Quatern. Sci., 26, 616–626, doi:10.1002/jqs.1483, 2011.
- 31

32 Sadori, L., Koutsodendris, A., Panagiotopoulos, K., Masi, A., Bertini, A., Combourieu-33 Nebout, N., Francke, A., Kouli, K., Joannin, S., Mercuri, A. M., Peyron, O., Torri, P.,

<sup>Rohling, E. J., Mayewski, P. A., and Challenor, P.: On the timing and mechanism of
millennial-scale climate variability during the last glacial cycle, Clim. Dynam., 20, 257–267,
doi:10.1007/s00382-002-0266-4, 2003.</sup>

- Wagner, B., Zanchetta, G., Sinopoli, G., and Donders, T. H.: Pollen-based
 paleoenvironmental and paleoclimatic change at Lake Ohrid (SE Europe) during the past 500
 ka, Biogeosciences, 13, 1423–1437, doi:10.5194/bg-13-1423-2016, 2016.
- 4
- Schneider, S., Cara, M., Eriksen, T. E., Budzakoska Goreska, B., Imeri, A., Kupe, L.,
 Loshkoska, T., Patceva, S., Trajanovska, S., Trajanovski, S., Talevska, M., and Veljanovska
 Sarafilovska, E.: Eutrophication impacts littoral biota in Lake Ohrid while water phosphorus
 concentrations are low, Limnologica, 44, 90–97, doi:10.1016/j.limno.2013.09.002, 2014.
 Schreiber, K., Hauffe, T., Albrecht, C., and Wilke, T.: The role of barriers and gradients in
 differentiation processes of pyrgulinid microgastropods of Lake Ohrid, Hydrobiologia, 682,
 61–73, doi:10.1007/s10750-011-0864-4, 2012.
- 13

14 Schultheiß, R., Albrecht, C., Bößneck, U., and Wilke, T.: The neglected side of speciation in

15 ancient lakes: phylogeography of an inconspicuous mollusc taxon in lakes Ohrid and Prespa,

16 Hydrobiologia, 615, 141–156, doi:10.1007/978-1-4020-9582-5_10, 2008.

17

18 Seierstad, I. K., Abbott, P. M., Bigler, M., Blunier, T., Bourne, A.J., Brook, E., Buchardt, S. 19 L., Buizert, C., Clausen, H. B., Cook, E., Dahl-Jensen, D., Davies, S. M., Guillevic, M., Johnsen, S. J., Pedersen, D. S., Popp, T. J., Rasmussen, S. O., Severinghaus, J. P., Svensson, 20 21 A., and Vinther, B. M.: Consistently dated records from the Greenland GRIP, GISP2 and 22 NGRIP ice cores for the past 104 ka reveal regional millennial-scale d18O gradients with 23 possible Heinrich event imprint, Quaternary Sci. Rev., 106, 29--46, 24 doi:10.1016/j.quascirev.2014.10.032, 2014.

- 25
- Shackleton, N. J.: Oxygen isotopes, ice volume and sea level, Quaternary Sci. Rev., 6, 183–
 190, doi.org/10.1016/0277-3791(87)90003-5, 1987.
- 28

Shackleton, N. J., Hall, M. A., and Vincent, E.: Phase relationships between millennial-scale
events 64,000–24,000 years ago, Paleoceanography, 15, 565–569,
doi:10.1029/2000PA000513, 2000.

³³ Stanković, S.: The Balkan Lake Ohrid and its living world, Dr. W. Junk, The Hague, 1960.

1	
2	Stockhecke, M., Kwiecien, O., Vigliotti, L., Anselmetti, F. S., Beer, J., Çagatay, M. N.,
3	Channell, J. E. T., Kipfer, R., Lachner, J., Litt, T., Pickarski, N., and Sturm, M.:
4	Chronostratigraphy of the 600,000 year old continental record of Lake Van (Turkey),
5	Quaternary Sci. Rev., 104, 8–17, doi:10.1016/j.quascirev.2014.04.008, 2014.
6	
7	Stockhecke, M., Timmermann, A., Kipfer, R., Haug, G. H., Kwiecien, O., Friedrich, T.,
8	Menviel, L., Litt, T., Pickarski, N., Anselmetti, F. S.: Millennial to orbital-scale variations of
9	drought intensity in the Eastern Mediterranean, Quaternary Sci. Rev., 133, 77-95,
10	doi:10.1016/j.quascirev.2015.12.016, 2016.
11	
12	Sulpizio, R., Zanchetta, G., D'Orazio, M. D., Vogel, H., and Wagner, B.: Tephrostratigraphy
13	and tephrochronology of the lakes Ohrid and Prespa, Balkans, Biogeosciences 7, 3273-3288,
14	doi:10.5194/bg-7-3273-2010, 2010.
15	
16	Sušnik, S., Knizhin, I., Snoj, A., and Weiss, S.: Genetic and morphological characterization of
17	a Lake Ohrid endemic, Salmo (Acantholingua) ohridanus with a comparison to sympatric
18	Salmo trutta, J. Fish Biol., 68, Supplement A, 2–23, doi:10.1111/j.0022-1112.2006.00902.x,
19	2006.
20	
21	Thienemann, A.: Untersuchungen über die Beziehung zwischen dem Sauerstoffgehalt des
22	Wassers und der Zusammensetzung der Fauna in norddeutschen Seen, A. Hydrobiol., 12, 1-
23	65, 1918.
24	
25	Trajanovski, S., Albrecht, C., Schreiber, K., Schultheiß, R., Stadler, T., Benke, M., and Wilke,
26	T.: Testing the spatial and temporal framework of speciation in an ancient lake species flock:
27	the leech genus <i>Dina</i> (Hirudinea: Erpobdellidae) in Lake Ohrid, Biogeosciences, 7, 3387–
28	3402, doi:10.5194/bg-7-3387-2010, 2010.
29	
30	Tzedakis, P.: Vegetation change through glacial-interglacial cycles: a long pollen sequence
31 22	perspective, Phil. Irans. K. Soc. B, 345, 403–432, doi:10.1098/rstb.1994.0118, 1994.
32 22	Tradelie D. C. Museums and are dies of Meditemannen his discussion I. 20
33	izeuakis, r. C.: Museums and cradies of Mediterranean biodiversity, J. Biogeography, 36,

1 2	1033–1034, doi:10.1111/j.1365-2699.2009.02123.x, 2009.
3	Tzedakis, P.C., Hooghiemstra, H., and Pälike, H.: The last 1.35 million years at Tenaghi
4	Philippon: revised chronostratigraphy and long-term vegetation trends, Quaternary Sci. Rev.,
5	25, 3416–3430, doi:10.1016/j.quascirev.2006.09.002, 2006.
6	
7	Tzedakis, P. C., Lawson, I. T., Frogley, M. R., Hewitt, G. M., and Preece, R. C.: Buffered tree
8	population changes in a Quaternary refugium: evolutionary implications. Science, 297, 2044–
9	2047, doi:10.1126/science.1073083, 2002.
10	
11	Tzedakis, P. C., Frogley, M. R., Lawson, I. T., Preece, R. C., Cacho, I., and De Abreu, L.:
12	Ecological thresholds and patterns of millennial-scale climate variability: the response of
13	vegetation in Greece during the last glacial period, Geology, 32, 109-112,
14	doi:10.1130/G20118.1, 2004.
15	
16	Voelker, A. H. L., Rodrigues, T., Billups, K., Oppo, D. W., McManus, J. F., Stein, R., Hefter,
17	J., and Grimalt, J. O.: Variations in mid-latitude North Atlantic surface water properties
18	during the mid-Brunhes (MIS 9-14) and their implications for the thermohaline circulation,
19	Clim. Past, 6, 531-552, doi:10.5194/cp-6-531-2010, 2010.
20	
21	Vogel, H., Wagner, B., Zanchetta, G., Sulpizio, R., and Rosén, P.: A paleoclimate record with
22	tephrochronological age control for the last glacial-interglacial cycle from Lake Ohrid,
23	Albania and Macedonia, J. Paleolimnol., 44, 295-310, doi:10.1007/s10933-009-9404-
24	x,2010a.
25	
26	Vogel, H., Zanchetta, G., Sulpizio, R., Wagner, B., and Nowaczyk, N.: A tephrostratigraphic
27	record for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia, J.
28	Quatern. Sci., 25, 320-338, doi:10.1002/jqs.1311, 2010b.
29	
30	Vogel, H., Wessels, M., Albrecht, C., Stich, H. B., and Wagner, B.: Spatial variability of
31	recent sedimentation in Lake Ohrid (Albania/Macedonia), Biogeosciences, 7, 3333-3342,
32	doi:10.5194/bg-7-3333-2010, 2010c.
33	

Wagner, B., Reicherter, K., Daut, G., Wessels, M., Matzinger, A., Schwalb, A., Spirkovski,
 Z., and Sanxhaku, M.: The potential of Lake Ohrid for long-term palaeoenvironmental
 reconstructions, Palaeogeogr. Palaeoclimatol. Palaeoecol., 259, 341–356,
 doi:10.1016/j.palaeo.2007.10.015, 2008a.

5

Wagner, B., Sulpizio, R., Zanchetta, G., Wulf, S., Wessels, M., Daut, G., and Nowaczyk, N.:
The last 40 ka tephrostratigraphic record of Lake Ohrid, Albania and Macedonia: a very distal
archive for ash dispersal from Italian volcanoes, J. Volcanol. Geotherm. Res., 177, 71–80,
doi:10.1016/j.jvolgeores.2007.08.018, 2008b.

10

Wagner, B., Lotter, A. F., Nowaczyk, N., Reed, J. M., Schwalb, A., Sulpizio, R., Valsecchi,
V., Wessels, M., and Zanchetta, G.: A 40,000-year record of environmental change from
ancient Lake Ohrid (Albania and Macedonia), J. Paleolimnol., 41, 407–430,
doi:10.1007/s10933-008-9234-2, 2009.

15

Wagner, B., Vogel, H., Zanchetta, G., and Sulpizio, R.: Environmental changes within the
Balkan region during the past ca. 50 ka recorded in sediments form lakes Prespa and Ohrid,
Biogeosciences, 7, 3187–3198, doi:10.5194/bg-7-3187-2010, 2010.

19

Wagner, B., Francke, A., Sulpizio, R., Zanchetta, G., Lindhorst, K., Krastel, S., Vogel, H.,
Rethemeyer, J., Daut, G., Grazhdani, A., Lushaj, B., and Trajanovski, S.: Possible earthquake
trigger for 6th century mass wasting deposit at Lake Ohrid (Macedonia/Albania), Clim. Past,
8, 2069–2078, doi:10.5194/cp-8-2069-2012, 2012.

24

Wagner, B., Wilke, T., Krastel, S., Zanchetta, G., Sulpizio, R., Reicherter, K., Leng, M. J.,
Grazhdani, A., Trajanovski, T., Francke, A., Lindhorst, K., Levkov, Z., Cvetkoska, A., Reed,
J., Zhang, X., Lacey, J., Wonik, T., Baumgarten, H., and Vogel, H.: The SCOPSCO drilling
project recovers more than 1.2 million history from Lake Ohrid, Sci. Drill., 17, 19–29,
doi:10.5194/sd-17-19-2014, 2014.

Wijmstra, T. A.: Palynology of the first 30m of a 120m deep section in northern Greece, Acta
 Bot. Neerl., 18, 511–527, 1969.

3

Wijmstra, T. A. and Smit, A.: Palynology of the middle part (30- 78 m) of a 120m deep
section in northern Greece (Macedonia), Acta Bot. Neerl., 25, 297–312, doi:10.1111/j.14388677.1976.tb00241.x, 1976.

7

Wilke, T., Albrecht, C., Anistratenko, V. V., Sahin, S. K., and Yildirim, Z.: Testing
biogeographical hypotheses in space and time: faunal relationships of the putative ancient
Lake Egirdir in Asia Minor, J. Biogeogr., 34, 1807–1821, doi:10.1111/j.13652699.2007.01727.x, 2007.

12

Wilke, T., Wagner, B., Albrecht, C., Ariztegui, D., Van Bocxlaer, B., Delicado, D., Francke,
A., Harzhauser, M., Hauffe, T., Holtvoeth, J., Just, J., Leng, M. J., Levkov, Z., Penkman, K.,
Sadori, L., Skinner, A., Stelbrink, B., Vogel, H., Wesselingh, F., and Wonik, T.: Scientific
drilling projects in ancient lakes: Integrating geological and biological histories, Glob. Planet.
Change, 143, 118–151, doi:10.1016/j.gloplacha.2016.05.005, 2016.

18

Wolff, E. W., Chappellaz, J., Blunier, T., Rasmussen, S. O., and Svensson, A.: Millennialscale variability during the last glacial: The ice core record, Quaternary Sci. Rev., 29, 2828–
2838, doi:10.1016/j.quascirev.20 09.10.013, 2010.

22

Wysocka, A., Grabowski, M., Sworobowicz, L., Mamos, T., Burzy'nski, A., and Sell, J.:
Origin of the Lake Ohrid gammarid species flock: ancient local phylogenetic lineage
diversification, J. Biogeogr., 41, 1758–1768, doi:10.1111/jbi.12335, 2014.

26

Zanchetta, G., Regattieri, E., Giaccio, B., Wagner, B., Sulpizio, R., Francke, A., Vogel, H.,
Sadori, L., Masi, A., Sinopoli, G., Lacey, J. H., Leng, M. L., Leicher, N.: Aligning and
synchronization of MIS5 proxy records from Lake Ohrid (FYROM) with independently dated

Mediterranean archives: implications for DEEP core chronology, Biogeosciences, 13, 2757–
 2768, doi:10.5194/bg-13-2757-2016, 2016.

3

Zhang, X. S., Reed, J. M., Lacey, J. H., Francke, A., Leng, M. J., Levkov, Z., Wagner, B.:
Complexity of diatom response to Lateglacial and Holocene climate and environmental
change in ancient, deep, and oligotrophic Lake Ohrid (Macedonia/Albania), Biogeosciences,
13, 1351–1365, doi:10.5194/bg-13-1351-2016, 2016.

8

9 Figure captions

10

11 Figure 1: (a) Location of Lake Ohrid (black rectangle) on the Balkan Peninsula at the border 12 of the Former Yugoslav Republic of Macedonia (FYROM) and the Republic of Albania. Other records mentioned in the text are indicated by red dots (core U1313 in the North 13 14 Atlantic, Sulmona basin in Italy, Tenaghi Philippon (TP) in Greece). (b) Map of the area of lakes Ohrid and Prespa and bathymetric map of Lake Ohrid (from Lindhorst et al., 2015). 15 Coring locations of piston core Co1202 (red; Vogel et al., 2010) and ICDP sites (white) are 16 shown, with DEEP and Lini sites mentioned in the text. Secondary ICDP sites P (Pestani), G 17 (Gradiste), and C (Cerava) are not mentioned in the text. (c) Geological map of the Lake 18 19 Ohrid catchment (modified from Lindhorst et al., 2015).

20

Figure 2: Selected seismic profiles and calculated water depths at different times (see text for details). The arrow of the reflector at 140 m blf (MIS 8/9) indicates the existence of a secondary basin in the northwestern part of the lake. Please note that the lake was probably larger for most periods but individual reflectors cannot be traced to the shallower water depth due to faults. This also explains, why the estimated water depth is not zero at the edges of the shown lake coverage.

27

Figure 3: Lithostratigraphy of the upper 247.8 mcd and tephra and crypto-tephra horizons in the DEEP sediment sequence. For nomenclature and details see Leicher et al. (2016). Tephra in bold was used as tie points for the age-depth model for the upper 247.8 mcd spanning the last 637 kyr (Francke et al., 2016; Leicher et al., 2016). Tephrostratigraphic work on tephra
 from below 247.8 mcd is ongoing.

3

Figure 4: Lake-level reconstructions (modified from Lindhorst et al., 2010; for details see chapter 4.3.2 of this study), pollen (Sadori et al., 2016), sedimentological, and geochemical data over the last 637 kyr (Francke et al., 2016; Just et al., 2016; Lacey et al., 2016) indicate a long-term shift from cooler and wetter to drier and warmer glacial and interglacial periods around 300 ka. Pollen curves have been corrected with respect to those reported in Sadori et al. (2016). MIS boundaries are according to Lisiecki and Raymo (2005).

10

Figure 5: Geochemical data from the DEEP site sequence with sub-orbital changes during 11 12 MIS 12 in comparison with other records from a similar latitude (for location of North Atlantic core U1313, the pollen record from Tenaghi Philippon and the isotope record from 13 14 Sulmona basin see Fig. 1). Arboreal pollen (AP) records are excluded of *Pinus*, *Juniperus*, and Betula (Sadori et al., 2016); the record from Tenaghi Philippon is based on pollen data 15 from Wijmstra (1969) and Wijmstra and Smit (1976), and the age model from Tzedakis et al. 16 (2006); see also Sadori et al. (2016). Red bars and black dots at the bottom age axis indicate 17 18 tephrochronological tie points and tuning points used for the age model of the DEEP site 19 sequence (Francke et al., 2016).

- 20
- 21
- 22
- 23
- 24
- 25
- 26
- 27







Fig. 2







Fig. 4

