

Preface

“Evolutionary and geological history of the Balkan lakes Ohrid and Prespa”

B. Wagner¹ and T. Wilke²

¹University of Cologne, Institute of Geology and Mineralogy, Zùlpicher Str. 49a, 50674 Köln, Germany

²Justus Liebig University Giessen, Heinrich-Buff-Ring 26–32 (IFZ), Department of Animal Ecology & Systematics, 35392 Giessen, Germany

1 Introduction

Worldwide only very few freshwater lakes exist that are characterised by a long geological history, often leading to an outstanding degree of endemic biodiversity. Examples include Lake Baikal located in Siberia, Lake Titicaca in South America, and lakes Tanganyika and Malawi in the East African Rift. Most of such “old” lakes have a tectonic origin and are located in regions, which are still tectonically active.

Two famous representatives of such lakes in Europe are the small “sister lakes” Prespa and Ohrid on the Balkan Peninsula. Lake Ohrid has today a surface area of 358 km², a maximum water depth of 289 m, a mean water depth of 155 m, and a volume of 55 km³ (Matzinger et al., 2006). The surface area of neighbouring Lake Prespa is only 254 km², its maximum and mean water depths are 58 m and 14 m, respectively, and its volume is 3.6 km³ (Matzinger et al., 2006; Albrecht and Wilke, 2008). The shortest straight line distance between the two lakes is 9 km and Lake Prespa (altitude 849 m a.s.l.) is connected hydrologically with Lake Ohrid (altitude 693 m a.s.l.) via underground karstic channels.

2 Ancient lakes Ohrid and Prespa: hotspots of endemic biodiversity

From a geological point of view, the tectonic origin and ongoing tectonic activities of the Prespa and Ohrid basins are confirmed by field observations and recent earthquake data (e.g., Hoffmann et al., 2010¹). Both lakes are believed to have been formed during the Pliocene, roughly two to three, possibly even five million years (Ma) ago (reviewed in Al-

brecht and Wilke, 2008; Trajanovski et al., 2010¹). Therefore, these lakes potentially qualify as ancient lakes. However, the definition for ancient lakes is under debate. Whereas some authors define them as extant lakes that have existed continuously since before the Pleistocene, other authors use a less conservative definition, considering a continuous existence at least since before the last glacial/interglacial cycle (> 120 thousand years (ka)) (Albrecht and Wilke, 2008; also see Gorthner, 1994; Martens et al., 1997). As Lake Ohrid is supposed to have existed continuously after its formation during the Pliocene, its status as ancient lake is not disputed (Salemaa, 1994; also see Albrecht and Wilke, 2008). A Pliocene age of Lake Ohrid is also supported by molecular clock analyses of DNA data derived from several “ancient lake species flocks”, that is, species rich and monophyletic groups of endemic species that have evolved within the lake. By estimating the onset of intralacustrine diversification, these molecular clock approaches allow the establishment of a minimum age of the lake and by estimating the timing of separation from the respective sister taxa outside the lake a potential maximum age (Wilke et al., 2009). Trajanovski et al. (2010)¹, for example, used DNA data from endemic leeches (genus *Dina*) to establish a minimum age of 2.0 ± 0.8 Ma and a maximum age of 8.3 ± 3.6 Ma. By combining these data with the findings for other endemic animal groups (Albrecht et al., 2006; Albrecht and Wilke, 2006; Sušnik et al., 2006; Wilke et al., 2007, 2009; Wysocka et al., 2008), the authors suggested a time frame of approximately 2–3 Ma for the origin of Lake Ohrid, based on evolutionary data.

For the shallower Lake Prespa, however, it is not clear whether it went through one or more desiccation phases during its long hydrological history. Although there is no indication for distinctly lower lake levels during the last ca. 48 ka compared to today (Wagner et al., 2010¹), Wilke et al. (2010)¹ could show by using DNA sequencing data and coalescent approaches that a relative of the zebra mussel



Correspondence to: B. Wagner
(wagnerb@uni-koeln.de)

¹Publication of the Biogeosciences special issue “Evolutionary and geological history of Balkan lakes Ohrid and Prespa”.

in Lake Prespa, *Dreissena presbensis*, showed a major demographic expansion some 110 ka ago. This expansion was possibly a result of a recovery from a significant lake level drop or even complete desiccation. Lake Ohrid apparently also exhibited distinct lake level fluctuations during the last ca. 130 ka (Lindhorst et al., 2010¹), but these lake level and other regional environmental changes may have had less pronounced effects on the population histories of native *Dreissena* spp., as this lake is much deeper and likely has a higher buffer capacity (Wagner et al., 2010¹; Wilke et al., 2010¹).

The differing histories of lakes Ohrid and Prespa might explain qualitative differences in their extant faunas. Lake Ohrid is famous for its large number of (at least 212) endemic species. Although the total number of endemic species is higher in lakes Baikal, Tanganyika, Victoria and Malawi, Lake Ohrid is much smaller and taking its surface area into account, it is possibly the most diverse lake in the world (Albrecht and Wilke, 2008). Biodiversity in the Ohrid Basin is heterogeneously distributed and large scale effects such as the type of water body or water depth are mainly responsible for the main distribution patterns. Recent studies on gastropods show that small scale effects like environmental gradients or biotic interactions also affect species composition within an individual depth zone (Hauffe et al., 2011¹). Compared to Lake Ohrid, the biota of Lake Prespa are inadequately studied and the number of endemic species in the latter lake remains unknown. However, it is assumed that endemic biodiversity in Lake Prespa is much lower with little faunal exchange and overlap to Lake Ohrid, despite their underground hydrological connection (Albrecht and Wilke, 2008). Yet, endemism does exist in groups such as diatoms, oligochaetes, leeches, poriferans, tricladids, molluscs, ostracodes, and fish (Albrecht et al., 2009, 2011).

The ecological importance of both lakes was acknowledged by the declaration of Lake Ohrid as UNESCO world heritage site in 1979 and by the establishment of the Prespa National Park in 1999. Increasing human population in both lake catchments, eutrophication of the lake waters, and ongoing use of lake water for agriculture are adversely affecting the ecosystems today (e.g. Matzinger et al., 2006; Kostoski et al., 2010¹). For example, areas of the highest anthropogenic pressure in Lake Ohrid show an increasing number of widespread gastropod species, although as yet there is no obvious shift in the frequency of endemic species occurrences at individual sites compared to data generated over the past 50 years (Hauffe et al., 2011¹). Kostoski et al. (2010¹) defined nutrient input, habitat conversion and silt load as high-impact threats. They suggested that only concerted international action can stop or at least slow down further degradation of Lake Ohrid and its biodiversity. Similar suggestions for Lake Prespa come from Albrecht et al. (2011). Moreover, the authors argue for a trans-boundary major conservation area of the Ohrid-Prespa region that would allow long-term integration of both humans and nature.

However, the outstanding degree of biodiversity, on one side, and the “creeping biodiversity crises” in lakes Ohrid and Prespa, on the other side, have not only spurred a wealth of biological and ecological studies, they also have promoted intensive interdisciplinary research combining geological, hydrological, sedimentological, and climatic approaches aiming at understanding the evolution of lakes Ohrid and Prespa in general, and climate dynamics and driving forces for the high degree of biodiversity in particular.

3 Sedimentology and tephrostratigraphy

Since 2004, several surface sediment samples and sediment successions have been recovered from lakes Ohrid and Prespa. The surface samples provide valuable information about modern processes and factors controlling sedimentation in each particular lake. They are also of value for better interpreting the long sedimentary records in terms of environmental changes over time. Modern sedimentation in Lake Ohrid is controlled by a complex interaction of multiple processes. Analyses of biogeochemical bulk parameters, selected metals, pigment concentrations as well as grain size distributions revealed a significant spatial heterogeneity in surface sediment composition (Matter et al., 2010¹; Vogel et al., 2010a¹). This implies that modern sedimentation in Lake Ohrid is controlled by an interaction between multiple natural and anthropogenic factors and processes. They are related to geological catchment characteristics, anthropogenic land use, and a counterclockwise surface water current. Subaquatic karst springs play a crucial role for sediment characteristics in Lake Ohrid (Matter et al., 2010¹), but are also discussed as biodiversity hotspots (Hauffe et al., 2011¹; Trajanovski et al., 2010¹). A counterclockwise surface water current is also observed in the northwestern part of Lake Prespa and it leads to subaquatic, trench like structures along several parts of the shore (B. Wagner, unpublished data).

Investigation of sediment records from both lakes allows insights on contemporaneous changes of their hydrology, chemistry, and trophic states and is crucial for the interpretation of climatic and environmental change as trigger for biodiversity change (e.g., Wagner et al., 2009, 2010¹; Albrecht et al., 2010¹; Holtvoeth et al., 2010¹; Leng et al., 2010¹; Lindhorst et al., 2010¹; Reed et al., 2010¹; Vogel et al., 2010b; Wilke et al., 2010¹). A regional tephrostratigraphic framework including tephra layers found in both lakes and marine records in the closer vicinity was established as an important prerequisite for such a comparative study (Sulpizio et al., 2010¹). This tephrostratigraphic framework allows for an absolute correlation of important stratigraphic intervals and indicates that the longest records from lakes Prespa and Ohrid reach back to Marine Isotope Stage (MIS) 6. The location of the lakes at the border of (sub)tropical and mid-latitude atmospheric circulation systems makes them valuable archives of regional and extra-regional climate dynamics.

4 Climate dynamics

The interglacial sediments are characterized by high carbonate, particularly in Lake Ohrid, which is mainly fed by water from karst aquifers (Wagner et al., 2009, 2010¹; Vogel et al., 2010b). In Lake Prespa, interglacial sedimentation is marked by high organic matter content. This indicates that Lake Prespa was under mesotrophic conditions during this period since the lake water warms up faster in spring and summer. Lake Ohrid in contrast, with larger volume and water depth, remained oligotrophic (Wagner et al., 2009, 2010¹; Vogel et al., 2010b). The Pleistocene records from lakes Prespa and Ohrid show relatively stable sedimentation conditions. At least partial ice-cover on the lakes during winter, a well-mixed water column and oligotrophic conditions with a marginal increase of lake productivity at the end of MIS 3 characterize the lakes. Coldest conditions during MIS 2 are documented by the lowest organic matter content in both lakes and the highest abundance of concretionary horizons in Lake Prespa, thus indicating a well-mixed water column (Wagner et al., 2009, 2010¹; Vogel et al., 2010b).

Short-term events are well documented during the Pleistocene and Holocene in both lakes. The most prominent ones during the Pleistocene can tentatively be correlated with Heinrich events. They are characterized by increased aeolian activity, lower temperatures and/or increased aridity in the Balkan region. From an archaeological point of view, these short-term events are of great interest as the Balkan Peninsula was one of the primary gateways for the spread of the modern humans from Africa into Europe during the last glacial (Müller et al., 2011). However, the environmental context, which enabled the first groups of modern humans to enter Europe, is still widely unknown and the detailed framework of climatic and environmental conditions still requires extensive research. The most prominent short-term events during the Holocene occur at 8.2 and 4.2 ka in both lakes, and are characterized by cool and/or dry climate (Holtvoeth et al., 2010¹). Anthropogenic impact is superimposed on the climatic and environmental change during the past 2.5 ka (Wagner et al., 2010¹).

Rapid and/or severe climate changes are likely to have a strong impact on the biotic inventory of lakes. To test the response of Lake Ohrid's biota to climate changes over longer time scales, fossil records of different taxa have been analysed (Wagner et al., 2009; Albrecht et al., 2010¹; Reed et al., 2010¹). For example, the comparison of a fossil mollusc assemblages from the Last Interglacial with a modern one revealed a total of 13 species (9 gastropod and 4 bivalve species) and no taxonomic shift between the faunas. This implies that at this site no mollusc extinctions occurred since the Last Interglacial despite rapid and severe climatic and environmental changes during the last glacial-interglacial cycle (Albrecht et al., 2010¹).

5 Outlook

The results of the recent studies reviewed above constitute a major contribution to our knowledge of the multifaceted and interdependent geological and evolutionary histories of lakes Ohrid and Prespa. At the same time, these studies also raise a number of new questions and they form the basis for future large scale interdisciplinary research projects. They indicate the high sensitivity of lakes Prespa and Ohrid to climatic and environmental change and thus not only emphasize these lakes as world class sites for paleoclimate research but also as some of the few sites worldwide where the impact of geological/climatic events on the lake's biota can be investigated in detail. However, the existing records are too short to provide information about age and origin of the lakes and to unravel the mechanisms controlling the evolutionary processes leading to the extraordinary high degree of endemism. High-resolution hydroacoustic profiles and multichannel seismic studies demonstrate well the interplay between sedimentation and active tectonics and impressively stress the potential of Lake Ohrid for a deep drilling campaign (Lindhorst et al., 2010¹). The maximum sediment thickness in the central basin is ~680 m, with unconformities or erosional features being absent. Thus the complete history of the lake is expected to be recorded.

In order to extend our knowledge about the geological and evolutionary histories of lakes Ohrid and Prespa, a deep drilling campaign within the scope of the International Continental Scientific Drilling Program (ICDP) is envisaged for Lake Ohrid in the near future. This drilling campaign will help (i) to obtain more precise information about the age and origin of the lake, (ii) to unravel the seismotectonic history of the lake area including effects of major earthquakes and associated mass wasting events, (iii) to obtain a continuous record containing information on volcanic activities and climate changes in the central northern Mediterranean region, and (iv) to better understand the impact of major geological/environmental events on shaping the extraordinary degree of endemic biodiversity seen in Lake Ohrid.

Acknowledgements. The pre-site surveys of lakes Ohrid and Prespa were funded by the German Research Foundation (AL 1076/3, DA 563/2, KR 2222/7, RE 1361/10, WA 2109/1, WA 2109/6, WE 2210/3, WI 1902/8, CRC 806), and the Swiss National Science Foundation SCOPES-Grant IB7320-111082. Our special thanks go to the Hydrobiological Institute in Ohrid and the Polytechnic University of Tirana as well as to the local administrative institutions for their outstanding support of fieldwork.

References

Albrecht, C., Hauffe, T., Schreiber, K., and Wilke, T.: Mollusc biodiversity and endemism in the putative ancient Lake Trichonis (Greece), *Malacologia*, 51, 357–375, 2009.

- Albrecht, C., Hauffe, T., Schreiber, H., and Wilke, T.: Assessing mollusc biodiversity in an endangered European ancient lake system: lakes Prespa and Mikri Prespa in the Balkans, *Hydrobiologia*, in press., 2011.
- Albrecht, C., Trajanovski, S., Kuhn, K., Streit, B., and Wilke, T.: Rapid evolution of an ancient lake species flock: freshwater limpets (Gastropoda: Ancyliidae) in the Balkan lake Ohrid, *Org. Div. Evol.*, 6, 294–307, 2006.
- Albrecht, C., Vogel, H., Hauffe, T., and Wilke, T.: Sediment core fossils in ancient Lake Ohrid: testing for faunal change since the Last Interglacial, *Biogeosciences*, 7, 3435–3446, doi:10.5194/bg-7-3435-2010, 2010.
- Albrecht, C. and Wilke, T.: Testing the “old lakes – old taxa assumption”: freshwater limpets (Gastropoda: Acroloxidae) in the European ancient lakes, *Berliner Paläobiol. Abh.*, 9, 7, 2006.
- Albrecht, C. and Wilke, T.: Lake Ohrid: biodiversity and evolution, *Hydrobiologia*, 615, 103–140, 2008.
- Görthner, A.: What is an ancient lake?, in: *Speciation in ancient lakes*, edited by: Martens, K., Gooderis, B., and Coulter, G., *Arch. Hydrobiol. – Ergebnisse der Limnologie*, 44, 97–100, 1994.
- 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.
- Hoffmann, N., Reicherter, K., Fernández-Steeger, T., and Grützner, C.: Evolution of ancient Lake Ohrid: a tectonic perspective, *Biogeosciences*, 7, 3377–3386, doi:10.5194/bg-7-3377-2010, 2010.
- Holtvoeth, J., Vogel, H., Wagner, B., and Wolff, G. A.: Lipid biomarkers in Holocene and glacial sediments from ancient Lake Ohrid (Macedonia, Albania), *Biogeosciences*, 7, 3473–3489, doi:10.5194/bg-7-3473-2010, 2010.
- Kostoski, G., Albrecht, C., Trajanovski, S., and Wilke, T.: A freshwater biodiversity 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.
- Leng, M. J., Banerjee, 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.
- 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.
- Martens, K.: Speciation in ancient lakes (review), *Trends Ecol. Evol.*, 12, 177–182, 1997.
- Matter, M., Anselmetti, F. S., Jordanoska, B., Wagner, B., Wessels, M., and Wüest, A.: Carbonate sedimentation and effects of eutrophication observed at the Kališta subaquatic springs in Lake Ohrid (Macedonia), *Biogeosciences*, 7, 3755–3767, doi:10.5194/bg-7-3755-2010, 2010.
- Matzinger, A., Jordanoski, M., Veljanoska-Sarafiloska, E., Sturm, M., Müller, B., and Wüest, A.: Is Lake Prespa jeopardizing the ecosystem of ancient Lake Ohrid?, *Hydrobiol.*, 553, 89–109, 2006.
- Müller, U. C., Pross, J., Tzedakis, P. C., Gamble, C., Kotthoff, U., Schmiel, G., Wulf, S., and Christanis K.: The role of climate in the spread of modern humans into Europe, *Quat. Sci. Rev.*, 30, 273–279, 2011.
- 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.
- Salemaa, H.: Lake Ohrid, in: *Speciation in ancient lakes*, edited by: Martens, K., Goddeeris, B., and Coulter, G., *Arch. Hydrobiol. – Ergebnisse der Limnologie*, 44, 55–64, 1994.
- Sulpizio, R., Zanchetta, G., D’Orazio, M., Vogel, H., and Wagner, B.: Tephrostratigraphy and tephrochronology of lakes Ohrid and Prespa, Balkans, *Biogeosciences*, 7, 3273–3288, doi:10.5194/bg-7-3273-2010, 2010.
- Sušnik, S., Knizhin, I., Snoj, A., and Weiss, S.: Genetic and morphological characterization of a Lake Ohrid endemic, *Salmo (Acantholingua) ohridanus* with a comparison to sympatric *Salmo trutta*, *J. Fish Biol.*, 68, Supplement A, 2–23, 2006.
- Trajanovski, S., Albrecht, C., Schreiber, K., Schultheiß, R., Stadler, T., Benke, M., and Wilke, T.: Testing the spatial and temporal framework of speciation in an ancient lake species flock: the leech genus *Dina* (Hirudinea: Erpobdellidae) in Lake Ohrid, *Biogeosciences*, 7, 3387–3402, doi:10.5194/bg-7-3387-2010, 2010.
- Vogel, H., Wessels, M., Albrecht, C., Stich, H.-B., and Wagner, B.: Spatial variability of recent sedimentation in Lake Ohrid (Albania/Macedonia), *Biogeosciences*, 7, 3333–3342, doi:10.5194/bg-7-3333-2010, 2010a.
- Vogel, H., Wagner, B., Zanchetta, G., Sulpizio, R., and Rosén, P.: A paleoclimate record with tephrochronological age control for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia, *J. Paleolimnol.*, 44, 295–310, 2010b.
- 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, 2009.
- Wagner, B., Vogel, H., Zanchetta, G., and Sulpizio, R.: Environmental change within the Balkan region during the past ca. 50 ka recorded in the sediments from lakes Prespa and Ohrid, *Biogeosciences*, 7, 3187–3198, doi:10.5194/bg-7-3187-2010, 2010.
- Wilke, T., Albrecht, C., Anistratenko, V. V., Sahin, S. K., and Yildirim, M. Z.: Testing biogeographical hypotheses in space and time: Faunal relationships of the putative ancient lake Egirdir in Asia Minor, *J. Biogeogr.*, 34, 1807–1821, 2007.
- Wilke, T., Schultheiß, R., and Albrecht, C.: As time goes by: A simple fool’s guide to molecular clock approaches in invertebrates, From the symposium “Molluscs as models in evolutionary biology: from local speciation to global radiation” presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium, *American Malacological Bulletin*, 27, 25–45, 2009.
- Wilke, T., Schultheiß, R., Albrecht, C., Bornmann, N., Trajanovski, S., and Kevrekidis, T.: Native *Dreissena* freshwater mussels in the Balkans: in and out of ancient lakes, *Biogeosciences*, 7, 3051–3065, doi:10.5194/bg-7-3051-2010, 2010.
- Wysocka, A., Kostoski, G., Kilikowska, A., Wróbel, B., and Sell, J.: *Proasellus* (Crustacea, Isopoda) species group endemic to the Balkan Lake Ohrid: a case of ecological diversification?, *Fund. Appl. Limnol.*, 172, 301–313, 2008.