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Commentary

Speciation in Ancient Lakes 8 – Celebrating 25 years and moving towards the future

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Hypotheses in evolutionary biology, ecology, climatology and geology are often tested in insular ecosystems. Ancient lakes, i.e. lakes that have existed since at least the Last Glacial Maximum and typically for longer periods of time, provide such study systems (Brooks, 1950), and a wide range of knowledge in the field of biotic diversification stems from the examination of ancient lakes and their biota (Cristescu et al., 2010; Martens, 1997; Rossiter and Kawanabe, 2000, Sturmbauer et al., 2012; von Rintelen et al., 2014). Scientists first formalized "Speciation in Ancient Lakes (SIAL)" as a society during an initial workshop held in Belgium in 1993 (Martens et al., 1994). Ever since, SIAL meetings have been organized at various places, not always but often at the shores of the ancient lakes that interest this scholarly community.

Prior to 2018 and after seven previous meetings, the African Great Lakes had not hosted a SIAL conference despite their recognition as globally outstanding hotspots of aquatic biodiversity and figuring prominently in ancient lake discussions (e.g., Salzburger et al., 2014).

This Special Section is the result of the international conference "SIAL 8 – Speciation in Ancient Lakes" that was jointly organized by the Justus Liebig University Giessen, Germany, and Mbarara University of Science and Technology, Uganda. It took place in Entebbe (Uganda) from 29 July until 3 August 2018 and was thus the first SIAL conference to be hosted in Africa, at the shore of Lake Victoria. At the same time, this conference celebrated the 25th anniversary of SIAL. The main goal of this conference and its eponymous society has always been to bring together scientists from different research fields that deal with speciation processes in a broader context in ancient lakes. Accordingly, a wide range of topics were covered by SIAL 8 including evolutionary biology, biogeography, (paleo)-limnology, health issues, and conservation. In total, 181 authors from 23 countries worldwide contributed to SIAL 8 (http://www.sial-online.org/index.php/conferences/sial8), and more than 50 delegates from 13 countries worldwide were welcomed to Entebbe (Fig. 1.).

In the present Special Section, many of the aspects discussed at SIAL 8 have been addressed, including, among others, biodiversity patterns and population genetics of extant and extinct invertebrates, systematics and anthropogenic impacts on ancient lake biota as well as conservation issues. Some topics, such as parasitology, are relatively new in ancient lake research. Almost all ancient lake systems of the world are covered in a truly interdisciplinary context that spans the past, the present and bridges to the future of ancient lakes and their biota.

Biodiversity patterns and community ecology

It is the remarkable biodiversity and the outstanding degree of endemism that make ancient lakes so famous and attractive for scientists from various disciplines (Salzburger et al., 2014). Arguably one of the most renowned groups of organisms that have diversified in ancient lakes are the species flocks of cichlid fishes in the African Great Lakes. Consequently, SIAL regularly obtains contributions on the diversity of cichlids. In the current issue, Ronco et al. (2020) summarize the taxonomic status of the hyper-diverse cichlid fish fauna of Lake Tanganyika, one of the most species rich and eco-morphologically diverse adaptive radiations on Earth, By providing a complete list of all valid taxa and a discussion of more than 50 undescribed taxa, Ronco et al. (2020) provide the most comprehensive and up to date account of this remarkable assemblage of fishes. Cichlid fish diversity of a less spe-

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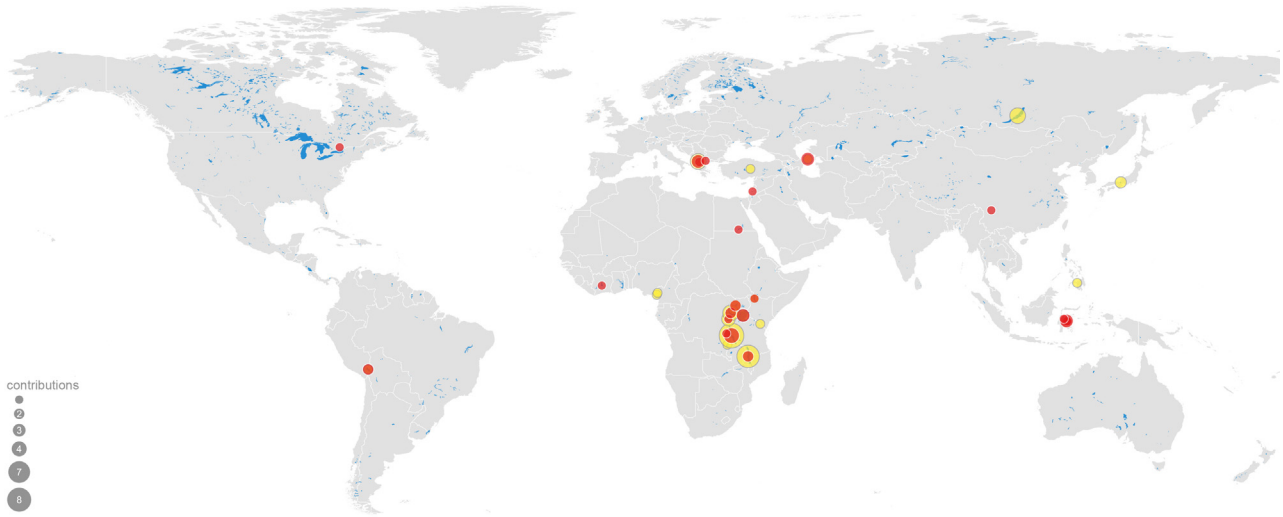

Fig. 1. Map showing ancient (and other) lakes studied in SIAL 8 conference contributions (talks and posters; yellow dots) and in publications of this Special Section (red dots). Circle sizes are proportional to the number of contributions in which the respective lake was discussed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cies-rich, but still important lake in the African rift system, is the topic of a study by Vranken et al. (2020), who investigated the evolutionary significance of thickened lips in a *Haplochromis* species in Lake Edward. They detected a case of cryptic diversity where a presumably single species turned out, in fact, to be two species.

Less biodiverse lakes with lower degrees of endemicity have traditionally received less scientific attention compared to the hyper-diverse ones, but they should not be dismissed. In fact, there are a number of forgotten, overlooked or unrecognized ancient lakes in the world (e.g., Albrecht et al., 2012; Stelbrink et al., 2019; Wilke et al., 2007). Smaller and younger lake systems with less complex biota can provide study systems that are easier to access, facilitating the study of biodiversity and the processes leading to it. Among the largely neglected lakes in this context is Lake Skadar (Scutari) in the Balkans. Zawal et al. (2020) studied water mites and found that environmental conditions in the various zones of the lake determine the distribution of the 53 species of mites in that lake. Another lake that has only very occasionally been mentioned in the context of ancient lakes is Lake Lugu (Yunnan, China). Wiese et al. (2020) evaluated existing speculations and assesses the molluscan fauna for its diversity and endemism as well as morphological peculiarities of a genus of gastropods in this lake. The authors conclude that Lake Lugu is indeed putatively an ancient lake.

Unlike during previous SIAL meetings, we saw an increasing number of invertebrate studies compared to studies dealing with fish taxa. This Special Section contains two contributions on cichlid fishes (Ronco et al., 2020; Vranken et al., 2020) and their monogenean parasites (Kmentová et al., 2020), whereas all remaining papers deal with invertebrates, with the exception of Bramburger et al. (2020), who studied diatoms. For the invertebrates, molluscs dominate in the number of publications, but the studies range from monogeneans (Kmentová et al., 2020), nematodes and rotifers (Wilden et al., 2020), leeches (Stelbrink et al., 2020), sponges (Erpenbeck et al., 2020), to crustaceans such as ostracodes (Gravina et al., 2020), gammarids and asselids (Stelbrink et al., 2020).

Community structures and assembly processes in ancient lakes are occasionally studied and include, for example, fish (Janzen et al., 2017), molluscs (Hauffe et al., 2016) but also diatom communities (Jovanovska et al., 2016). This SIAL Special Section contains a study that compares factors regulating composition and structure of diatom communities in Sulawesi's Lake Matano with analogues in the Canadian Mazinaw Lake (Bramburger et al., 2020). Another contribution examines Lake Ohrid's meiobenthic fauna with the aim of comparing littoral and profundal communities (Wilden et al., 2020).

Evolutionary patterns and processes

The processes shaping biodiversity, and the speciation process in particular, have always been a core topic of the SIAL community. Various studies in the current Special Section therefore can be arranged under this thematic umbrella. Molluscs in African lakes have featured in two studies. Whereas Ndeo et al. (2020) provide the first evidence that Lake Tanganyika endemic gastropods occur naturally far outside the lake, in the Lukuga River system, Clewing et al. (2020a) report on the first occurrence of an unusual corkscrew shell from pulmonate snails in Lake Malawi. These snails are potential intermediate hosts for schistosome parasites causing the bilharzia disease. Diversity of parasites is a relatively new and largely neglected topic in ancient lakes. Kmentová et al. (2020) focused on whether diplectanid parasites of *Lates* spp. fishes of African large lakes underwent extensive diversification as their hosts did. Apparently, they largely failed to diverge and potential reasons for this are discussed.

Ancient lakes on Sulawesi have been widely recognized as outstanding ancient systems only during the last two decades (von Rintelen et al., 2014). Some molluscan taxa were not previously studied in a phylogenetic framework. Here, the diversity and biogeography of bivalves of the family Sphaeriidae are studied by Clewing et al. (2020b); whereas, Albrecht et al. (2020) investigated a potential case of co-evolution of members of the pachychilid gastropod species flock and their unique epizoic limpets. A long recognized lake system that did not receive much attention lately is Lake Titicaca and adjacent systems on the South American Altiplano. Wolff et al. (2020) found that the diversification processes in the most important gastropod species flock of that lake were likely triggered by recovery from interglacial-related bottlenecks. This study exemplifies how knowledge on the lakes' history can help elucidating evolutionary patterns. Ancient Lake Ohrid is the oldest and biologically most diverse freshwater lake in Europe (Albrecht and Wilke, 2008). Information obtained from the recent deep-drilling campaign SCOPSCO helped interpreting time-calibrated

molecular phylogenies for eight invertebrate groups endemic to Lake Ohrid. Stelbrink et al. (2020) show that diversification was triggered by an increased ecological opportunity arising from massive environmental changes in the course of the lake deepening. Lake Ohrid is also home to endemic sponge lineages. Sponges occur in basically all ancient lakes; and their systematics, which is mostly based on morphological features, has been challenging. Erpenbeck et al. (2020) study a large global phylogenetic dataset and discuss general implications for freshwater sponge evolution.

Environmental changes and impacts

Ancient lakes have experienced various changes in their limnology and general settings throughout their long histories. These changes are often archived in their sediments (Cohen, 2012; Wilke et al., 2016). This circumstance allows linking geological history revealed by environmental history data from sediments and biological evolution. An example was outlined by the study of Lake Titicaca's gastropods (Wolff et al., 2020). In an epoch termed Anthropocene, it is often challenging to disentangle (natural) ongoing environmental change and man-made ecological changes. These changes can be abrupt or steadily occurring and potentially lead to extinction events (Cohen, 1994) and even biodiversity crises (Hampton et al., 2018). Even though these developments might be partly documented or recognized at least by the scientific community, many lakes remain unstudied or data are outdated for many critical lakes. If conservation or management efforts are implemented, which is often hampered by the multi-national settings in ancient lakes, benthic taxa and primarily invertebrates typically remain neglected. Decline and loss of endemic diversity is evident or at least suspected in parallel to ongoing major (anthropogenic) environmental changes. Deforestation along the shores and escarpments of lakes cause substantial changes in the limnological systems. Gravina et al. (2020) use ostracode assemblages to test the sensitivity to sediment discharge in Lake Tanganyika. The results gave insights on how the deforestation effects on the benthic ecosystem could be mitigated by conservation and management projects.

The Caspian Sea, the world's largest lake by area and volume, currently faces tremendous environmental changes. Lattuada et al. (2020) use a modelling approach to differentiate the effects anthropogenic pressure factors have on the endemic Caspian Sea molluscan fauna. They found that the factors significantly differ among hotspot and non-hotspot areas of impact and then discuss implications of these findings for conservation and management strategies.

The study of van de Velde et al. (2020) provides a baseline of the native molluscan fauna of pre-anthropogenic, i.e. Late Pleistocene times. Only such studies allow an assessment of the magnitude and rate of biodiversity change. The authors demonstrate that the species-rich Selitrennoye fauna is significantly different from the fauna found today in similar settings around the Caspian Sea.

New avenues

The topics covered by SIAL have changed over the past 25 years. New research directions or new approaches to old questions are appropriate and are thus being implemented in various science directions. Although the selection of papers in the SIAL Special Section represents the state-of-the-art in ancient lake studies, we will increasingly see modelling and particularly *omics* approaches used in upcoming studies. In addition, we expect to see more applications of new technical advances to model systems in ancient lakes. A new horizon is certainly the exploration of the profundal of lakes, including the use of environmental DNA (eDNA) approaches. Studies on research questions that are currently not primarily related to ancient lakes such as studies on parasites and water-borne diseases as well as species invasions will likely increase in the near future. We also foresee more truly interdisciplinary research programs. A particularly promising development is the inclusion of biological aims in deep-drilling programs in ancient lakes. These scientific campaigns allow ecosystem and environmental reconstruction over whole lifespans of the lakes, which in turn, enables the detailed study of the evolution of communities, historical biogeography, the impact of global climate change and many other topics which can otherwise not adequately be targeted.

The need for interdisciplinary and comparative approaches has been advocated several times (e.g. Martens, 1997; Wilke et al., 2016). To date, most studies are single-lake (case) studies. However, regional or even global studies are needed in order to disentangle extrinsic and intrinsic drivers of biodiversity. Moreover, studies focusing on various processes within single lakes are also needed. The SIAL Special Section contains papers representing truly comparative approaches that target a single taxon supra-regionally (Kmentová et al., 2020) or even globally (Erpenbeck et al., 2020). Another comparative approach advancing our understanding of general patterns and processes includes comparing several taxa co-occurring in one lake and its watershed as exemplified by the study of Lake Ohrid's invertebrate species flocks by Stelbrink et al. (2020). Despite such progress, world-wide ancient lakes have to be considered widely understudied. This is particularly unfortunate given the pressing anthropogenic pressures all of them are suffering from (Hampton et al., 2018). Current and future challenges facing ancient lakes in Africa are identified in the Commentary by Obiero et al. (2020), who also provide a new way forward by introducing an international initiative called ACARE as a response to the call for harmonized, long-term, collaborative networks and partnerships. This initiative aims at advancing Africa's Great Lakes research and academic potential. The lessons learnt from this example can be instrumental for other, if not all, worldwide ancient lakes.

The next SIAL 9, again to be held in Africa, will tell us about the developments in the field of ancient lakes studies in all its facets. This upcoming conference in July 2021 will take place at the shores of one of the most outstanding lakes on earth, Lake Tanganyika. This major rift lake is also the next targeted for a continental deep-drilling campaign (Russell et al., 2020) which will tremendously boost our understanding of the history of this iconic lake.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Albrecht, C., Hauffe, T., Schreiber, K., Wilke, T., 2012. Mollusc biodiversity in a European ancient lake system: lakes Prespa and Mikri Prespa in the Balkans. Hydrobiologia 682, 47–59.

Albrecht, C., Stelbrink, B., Gauffre-Autelin, P., Marwoto, R.M., von Rintelen, T., Glaubrecht, M. (2020). Diversification of epizoic freshwater limpets in ancient lakes on Sulawesi, Indonesia: coincidence or coevolution? J. Great Lakes Res. 46 (5), 1187–1198.

Albrecht, C., Wilke, T., 2008. Ancient Lake Ohrid: biodiversity and evolution. Hydrobiologia 615, 103–140. https://doi.org/10.1007/s10750-008-9558-y.

Bramburger, A.J., Hamilton, P.B., Haffner, D.G., Hehanussa, P.E. (2020). Variable niche breadth in benthic diatoms: Implications of ecological specialization and generalization for community structure. J. Great Lakes Res. 46 (5), 1131–1139.

Brooks, J.L., 1950. Speciation in ancient lakes. Q. Rev. Biol. 25 (30–60), 131–176.

Clewing, C., Van Bocxlaer, B., Albrecht, C., (2020a). First report of extraordinary corkscrew gastropods of the genus Bulinus in Lake Malawi. J. Great Lakes Res. 46 (5), 1168–1175.

Clewing, C., Stelbrink, B., Bößneck, U., Neubauer, T.A., von Rintelen, T., Köhler, F., Marwoto, R.M., Albrecht, C., (2020b). Freshwater biogeography in Wallacea: the case of sphaeriid bivalves in the Malili lake system (Sulawesi, Indonesia). J. Great Lakes Res. 46 (5), 1176–1186.

Cohen, A.S., 1994. Extinction in ancient lakes: biodiversity crises and conservation 40 years after JL Brooks. Ergebnisse der Limnologie 44, 451–479.

Cohen, A.S., 2012. Scientific drilling and biological evolution in ancient lakes: lessons learned and recommendations for the future. Hydrobiologia 682, 3–25.

Cristescu, M.E., Adamowicz, S.J., Vaillant, J.J., Haffner, G.D., 2010. Ancient lakes revisited: from the ecology to the genetics of speciation. Mol. Ecol. 19, 4837–4851. https://doi.org/10.1111/j.1365-294X.2010.04832.x.

Erpenbeck, D., Galitz, A., Wörheide, G., Albrecht, C., Pronzato, R., Manconi, R., (2020). Having the balls to colonize–The Ephydatia fluviatilis group and the origin of (ancient) lake "endemic" sponge lineages. J. Great Lakes Res. 46 (5), 1140–1145.

Gravina, A., Soreghan, M., Bogan, M.T., Busch, J., Kimirei, I., McGlue, M., McIntyre, P., Cohen, A. (2020). Relationship of sediment influx to ostracode populations on the variably deforested Luiche and Mahale platform coasts of Lake Tanganyika, Tanzania. J. Great Lakes Res. 46 (5), 1207–1220.

Hampton, S.E., McGowan, S., Ozersky, T., Virdis, S.G.P., Vu, T.T., Spanbauer, T.L., Kraemer, B.M., Swann, G., Mackay, A.W., Powers, S.M., Meyer, M.F., Labou, S.G., O'Reilly, C.M., DiCarlo, M., Galloway, A.W.E., Fritz, S.C., 2018. Recent ecological change in ancient lakes. Limnol. Oceanogr. 63, 2277–2304. https://doi.org/10.1002/lno.10938.

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

Janzen, T., Alzate, A., Muschick, M., Maan, M.E., van der Plas, F., Etienne, R.S., 2017. Community assembly in Lake Tanganyika cichlid fish: quantifying the contributions of both niche-based and neutral processes. Ecol. Evol. 7, 1057–1067.

Jovanovska, E., Cvetkoska, A., Hauffe, T., Levkov, Z., Wagner, B., Sulpizio, R., Francke, A., Albrecht, C., Wilke, T., 2016. Differential resilience of ancient sister lakes Ohrid and Prespa to environmental disturbances during the Late Pleistocene. Biogeosciences.

Kmentová, N., Koblmüller, S., Van Steenberge, M., Artois, T., Bukinga, F.M., N'sibula, T.M., Risasi, D.M., Mulungula, P.M., Gelnar, M., Vanhove, M.P., (2020). Failure to diverge in African Great Lakes: The case of Dolicirroplectanum lacustre gen. nov. comb. nov. (Monogenea, Diplectanidae) infecting latid hosts. J. Great Lakes Res. 46 (5), 1113–1130.

Lattuada, M., Albrecht, C., Wesselingh, F.P., Klinkenbuß, D., Vinarski, M.V., Kijashko, P., Raes, N., Wilke, T., (2020). Endemic Caspian Sea mollusks in hotspot and non-hotspot areas differentially affected by anthropogenic pressures. J. Great Lakes Res. 46 (5), 1221–1226.

Martens, K., Coulter, G., Goddeeris, B., 1994. Speciation in ancient lakes-40 years after Brooks. Ergebnisse der Limnologie 44. 75–75.

Martens, K., 1997. Speciation in ancient lakes. Trends Ecol. Evol. 12, 177–182. https://doi.org/10.1016/S0169-5347(97)01039-2.

Ronco, F., Büscher, H.H., Indermaur, A., Salzburger, W., (2020). The taxonomic diversity of the cichlid fish fauna of ancient Lake Tanganyika, East Africa. J. Great Lakes Res. 46 (5), 1067–1078.

Obiero, K., Lawrence, T., Ives, J., Smith, S., Njaya, F., Kayanda, R., Waidbacher, H., Olago, D., Miriti, E., Hecky, R.E., (2020). Advancing Africa's great lakes research and academic potential: Answering the call for harmonized, long-term, collaborative networks and partnerships. J. Great Lakes Res. 46 (5), 1240–1250.

Rossiter, A., Kawanabe, H., 2000. Ancient lakes: biodiversity, ecology and evolution (Vol. 31).

Russell, J.M., Barker, P., Cohen, A., Ivory, S., Kimirei, I., Lane, C., Leng, M., Maganza, N., McGlue, M., Msaky, E., Noren, A., 2020. ICDP workshop on the Lake Tanganyika Scientific Drilling Project: a late Miocene–present record of climate, rifting, and ecosystem evolution from the world's oldest tropical lake. Sci. Drill. 27, 53–60.

Salzburger, W., Van Bocxlaer, B., Cohen, A.S., 2014. Ecology and evolution of the African Great Lakes and their faunas. Annu. Rev. Ecol. Evol. Syst. 45, 519–545. https://doi.org/10.1146/annurev-ecolsys-120213-091804.

Stelbrink, B., von Rintelen, T., Albrecht, C., Clewing, C., Naga, P.O., 2019. Forgotten for decades: Lake Lanao and the genetic assessment of its mollusc diversity. Hydrobiologia 843, 31–49.

Stelbrink, B., Wilke, T., Albrecht, C., (2020). Ecological opportunity enabled invertebrate radiations in ancient Lake Ohrid. J. Great Lakes Res. 46 (5), 1156–1161.

Sturmbauer, C., Albrecht, C., Trajanovski, S., Wilke, T., 2012. Preface: Speciation in ancient lakes. Hydrobiologia 682, 1–2.

Ndeo, O.W., Clewing, C., Stelbrink, B., Albrecht, C., (2020). Lake Tanganyika endemic gastropods also occur in the Lukuga River. J. Great Lakes Res. 46 (5), 1162–1167.

Wiese, R., Clewing, C., Albrecht, C., Rabethge, C., Zhang, H., Riedel, F., (2020). How ancient is Lake Lugu (Yunnan, China)? The gastropods' viewpoint with focus on Radix (Lymnaeidae). J. Great Lakes Res. 46 (5), 1099–1112.

Wilden, B., Tasevska, O., Traunspurger, W., (2020). A comparison of benthic meiofaunal communities in the oldest European lake. J. Great Lakes Res. 46 (5), 1146–1155.

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

Wilke, T., Wagner, B., Van Bocxlaer, B., Albrecht, C., Ariztegui, D., 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., Wonik, T., 2016. Scientific drilling projects in ancient lakes: integrating geological and biological histories. Glob. Planet. Change 143, 118–151. https://doi.org/10.1016/j.gloplacha.2016.05.005.

Wolff, C., Albrecht, C., Wilke, T., (2020). Recovery from interglacial-related bottleneck likely triggered diversification of Lake Titicaca gastropod species flock. J. Great Lakes Res. 46 (5), 1199–1206.

van de Velde, S., Yanina, T.A., Neubauer, T.A., Wesselingh, F.P., (2020). The Late Pleistocene mollusk fauna of Selitrennoye (Astrakhan province, Russia): A natural baseline for endemic Caspian Sea faunas. J. Great Lakes Res. 46 (5), 1227–1239.

von Rintelen, T., Marwoto, R.M., Haffner, G.D., Herder, F., 2014. Preface: Speciation research in ancient lakes–classic concepts and new approaches. Hydrobiologia 739, 1–6.

Vranken, N., Van Steenberge, M., Kayenbergh, A., Snoeks, J., (2020). The lobed-lipped species of Haplochromis (Teleostei, Cichlidae) from Lake Edward, two instead of one. J. Great Lakes Res. 46 (5), 1079–1089.

Zawal, A., Bańkowska, A., Michoński, G., Grabowski, M., Szlauer-Łukaszewska, A., Czernicki, T., Stępień, E., Płóciennik, M., Pešić, V., (2020). Environmental determinants of water mite (Acari: Hydrachnidia) distribution in the ancient Lake Skadar system. J. Great Lakes Res. 46 (5), 1090–1098.