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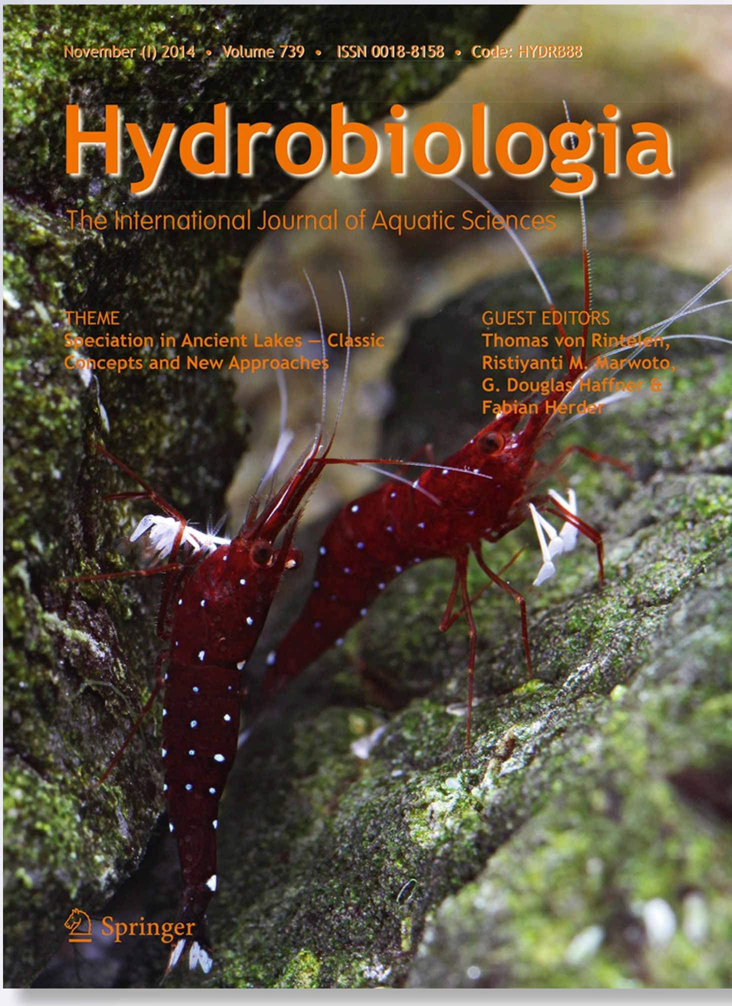

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SPECIATION IN ANCIENT LAKES 6

Preface: Speciation research in ancient lakes – classic concepts and new approaches

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Ancient lakes harbor some of the most formidable aquatic ecosystems on earth. Most of the long-term stable lakes are large and extraordinarily deep, and their biotas have evolved under more or less pronounced isolation. This isolation, and the often restricted number of lineages of organisms that successfully invaded their waters, have set the stage for some of the most impressive cases of adaptive radiation, local endemism, and highly adapted organismal communities.

It has for long been recognized that the biotas of ancient lakes offer outstanding opportunities for testing hypotheses in evolutionary biology, ecology, climatic history, and geology (Brooks, 1950). In the continuously expanding field of speciation research, much of the knowledge available to date rests upon studies performed in radiations restricted to isolated lakes of varying ages (Martens, 1997; Rossiter & Kawanabe, 2000).

This present Special Issue of *Hydrobiologia* is devoted to recent progresses in the field of speciation in ancient lakes, arising from the 6th SIAL Conference ("Speciation in Ancient Lakes: Classic concepts and new approaches"), held in Cibinong, Indonesia, in August 2012. Beyond its extraordinarily rich riverine freshwater faunas, distributed over thousands of islands, Indonesia harbors on Sulawesi two ancient water bodies, namely Lake Poso and the Malili Lakes system. It is hence little surprising that several contributions at SIAL 6 were devoted to Indonesia's native lakes and to the evolution of their endemic species flocks. The range of research presented was however much broader, highlighting the patterns of speciation, and its temporal as well as abiotic context, in ancient lakes from Baikal and Ohrid to Tanganyika. It is in the nature of the topic that the need for definitions stipulated some discussion on the question of the age of so-called "ancient lakes".

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Guest editors: T. von Rintelen, R. M. Marwoto, G. D. Haffner & F. Herder / Speciation in Ancient Lakes – Classic Concepts and New Approaches

T. von Rintelen (✉)
Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, 10115 Berlin, Germany
e-mail: thomas.vonrintelen@mfn-berlin.de

R. M. Marwoto
Museum Zoologicum Bogoriense, Research Center for Biology, LIPI, 17911 Cibinong, Indonesia

G. D. Haffner
Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada

F. Herder
Zoologisches Forschungsmuseum Alexander Koenig, Sektion Ichthyologie, Adenauerallee 160, 53113 Bonn, Germany

Brook's (1950) pragmatic border of >1 Ma is obviously of limited use when aiming at a joint discussion of the mechanisms underlying diversification in ancient lake species flocks. Contributions focusing on substantially younger lakes such as Victoria or Malawi highlighted that syntheses including isolated lakes of various ages are especially promising (see also Genner et al., 2007; Wagner et al., 2012).

Here we highlight some of the major topics discussed at this meeting and covered by the papers submitted to this special issue. We also hint at some emerging perspectives for speciation research in the oldest open freshwater bodies of our planet.

The geography of ancient lake research

The seminal review of Brooks (1950) mentions eight ancient lakes or lake systems (Tanganyika, Malawi, Victoria, Baikal, Titicaca, Ohrid, Lanao, and Malili Lakes system). Research efforts have since been devoted quite unequally to these (and other) systems. Among the lakes listed by Brooks, the most heavily studied ones, in terms of active research groups and publications, have traditionally been the large and old lakes of the African rift valley (Tanganyika, Malawi) and Lake Baikal in Russia. Southeast European Lake Ohrid has only moved (back) onto the stage during the last decade, and Lake Biwa in Japan, which was not considered by Brooks, also received a fair amount of study. Baikal and Biwa are the only ancient lakes which boast permanent research institutions (since 1928 and 1982, respectively) devoted to the study of their ecology and limnology. However, the contributions presented at SIAL 6 (see SIAL 6 abstract volume, electronic supplementary material) as well as those included in this Special Issue confirm a comparatively recent trend towards more research on the lesser well-known ancient lakes, in particular the Sulawesi lakes (Bramburger et al., 2014; Poettinger & Schubart, 2014; Pfaender et al., 2014 in this issue). Much progress has been made in establishing the taxonomic and phylogenetic backbone for the major species flocks in almost all confirmed or putative ancient lakes with the exception of Lake Lanao on Mindanao which is still off-limits for security reasons. As the ongoing research on Ohrid and now the Sulawesi lakes has shown, the smaller size and lower diversity of these previously somewhat neglected ancient lakes are actually an advantage when it comes to gaining a holistic perspective of evolution in the entire system (Cristecu et al., 2010), and research on these lakes is often highly integrated among research groups (see e.g., Vaillant et al., 2011; von Rintelen et al., 2012, for the Sulawesi lakes).

The lost world of ancient paleo-lakes

Ancient lakes are not just featuring in research on the speciation and adaptation of extant organisms. A number of well-known paleo-lakes with extinct species flocks (of easily fossilizing molluscs and ostracods in particular) have been known for a long time and provided insights into major evolutionary phenomena such as punctuated equilibrium (East African Lake Turkana, Williamson, 1981) or spawned the first phylogenetic tree of fossil taxa (Lake Steinheim in Germany, Hilgendorf 1867). In recent years, these classical examples have been revisited using modern concepts and methods (see e.g., Van Bocxlaer et al., 2008 for Lake Turkana), and other Paleo lakes such as Lake Pebas in South America (Wesselingh et al., 2002), or Lake Makgadikgadi in southern Africa (Joyce et al., 2005) have been added to the list. This is reflected in this special issue by two papers with a very different focus: Rasser (2014) reviews the taxonomy and evolution of the *Gyraulus* species flock in the Miocene Lake Steinheim, while Riedel et al. (2014) describe the dynamics of limnological and hydrological change during the late Pleistocene in the Makgadikgadi basin. Both papers provide a valuable background for future studies on the evolution of the extinct species flocks in these paleo-lakes. Kavembe et al. (2014) focus on the saline remnants of Pleistocene Lake Orolonga where populations of a small cichlid fish species persist in the disconnected less-hostile lagoons of the basin. The surprisingly pronounced genetic differentiation among these populations highlights the strong abiotic isolation of these lake fragments, and the need for accurate species delimitation incorporating genetic and morphological data.

The taxonomy and phylogeny of ancient lake species flocks

The ultimate aim of research on the occasionally spectacular endemic organisms in ancient lakes obviously is to uncover patterns of diversification and adaptation, and infer universal processes from these patterns (see e.g., Cristecu et al., 2010). Understanding speciation processes requires a robust underlying taxonomic and phylogenetic framework (e.g., Rohde, 1996); however, and despite the huge progress made in many systems (compare above), much still needs to be done in almost every species flock (see e.g., Fryer et al., 2000; von Rintelen et al., 2012). The four respective studies in this issue nicely demonstrate the differences in the level of detail for the three taxa and lakes involved: Poettinger & Schubart (2014) use a mitochondrial phylogeny to unravel the history of lake colonization and trophic specialization of the entire gecarcinid freshwater crab species flock in the ancient lakes of Sulawesi. While there is some mismatch between morphospecies and mitochondrial data, all species from the lakes in the study have been formally described, contrasting with a large number of undescribed species from rivers and streams of Sulawesi. Using similar methods, Albrecht et al. (2014b) look into the relationships and ancestry of the enigmatic lymnocardiid clams of the Caspian Sea and Black Sea. This study recovered an extremely shallow tree topology for the 'true' lymnocardiids (to the exclusion of one genus traditionally assumed to belong to the group) and no geographic structure. Both findings suggest that common assumptions of an ancient lineage do not hold, at least for its recent representatives. Schön et al. (2014) and Daneliya & Väinölä (2014) operate at a lower taxonomic level, looking into the phylogenetic and phylogeographic structure of supposedly widespread species in Lake Tanganyika ostracods (Schön et al., 2014; nuclear and mtDNA data) and Lake Baikal amphipods (Daneliya & Väinölä, 2014; mtDNA, barcoding fragment), respectively. Both studies reveal a significant genetic and geographic structure. Schön et al. (2014) consider the presence of cryptic species, while Daneliya & Väinölä (2014) include morphological data to describe five new amphipod subspecies.

New insights from experimental approaches

The understanding of widely discussed evolutionary processes and mechanisms such as ecological speciation (Schluter, 2009), escalation (predator–prey arms race; Vermeij & Covich, 1978; Covich, 2010), or sexual selection (Maan & Seehausen, 2011) have received much impetus from ancient lake research (for escalation, e.g., see West et al., 1991; West & Cohen, 1996; von Rintelen et al., 2004; Rasser & Covich, 2014). Increasingly, the common approach of looking at patterns at various levels (genetic, ecological, and geological) to understand and explain these phenomena is complemented by experimental projects. This is neatly demonstrated in this special issue by three respective papers. Bramburger et al. (2014) simulate an upwelling event and examine the response of a community of endemic diatom species from Sulawesi's Lake Matano to this perturbation. Their results indicate that community function is maintained through shifts in competitive dynamics rather than, as commonly assumed in (microbial) community ecology (Allison & Martiny, 2008), community resistance and resilience. Weigand et al. (2014) use food choice experiments to determine feeding preferences of the only freshwater crab species in Lake Malawi. They can partly falsify the assumption of non-molluscivory in this species and also show that fish is a preferred food for this crab species when it can get hold of it. The third experimental study in this issue does not involve simulations or manipulations, but Pfaender et al. (2014) nevertheless move beyond classic approaches by measuring cryptic spectral coloration in living individuals of sailfin silverside fishes from Lake Matano. Pfaender et al. (loc.cit.) found that there are indeed differences (cryptic to the human eye) in female coloration that corresponds to the conspicuous male color morphs, albeit with a lesser intensity. All three studies neatly demonstrate the usefulness of complementing standard systematic and ecological approaches with innovative experiments, and their potential to challenge existing paradigms.

Alien species invasions and its consequences

Unfortunately, not all topics gaining eminence in ancient lake research in recent years present a welcome addition to research methodology or general knowledge. The conservation of ancient lake biota is an ever more pressing issue (see Kostoski et al., 2010 for Lake Ohrid), and in addition to the usual suspects (habitat degradation, population pressure, overfishing) introductions of alien species are increasingly posing a problem. While this is not exactly a new issue, (see the disastrous introduction of Nile perch in Lake Victoria in 1954, Goudswaard et al., 2008), it is an expanding problem, both in terms of the number of alien species and the lakes subject to intentional or accidental introductions. Basically, all ancient lakes are now affected to a varying degree; an example of a very recent introduction is the flowerhorn cichlid in Sulawesi's Lake Matano (introduced between 2006 and 2010; Herder et al., 2012). Albrecht et al. (2014a) in this issue present data for another recent introduction, the case of the globally invasive pulmonate species (*Physa acuta* and *Ferrissia fragilis*) in Lake Ohrid. While they do not (yet) find evidence for competitive replacement of endemic gastropod species in that lake, the increasing occurrence of the invader in disturbed habitats, in combination with the predicted increase in habitat degradation, shed light on the need to carefully monitor the situation. Sadly, such studies will foreseeably (need to) become common in the future.

Perspectives arising from genomics and transcriptomics in speciation research

The ten reviews or research papers in this issue very much represent the current state-of-the-art of ancient lake research in many aspects. However, the SIAL 6 meeting in Indonesia and also some first recent publications offer a perspective on the increasing influence of genomic approaches (including transcriptomics) in ancient lakes research. Cichlids from the East African lakes are, once again, leading the pack (Fan et al., 2012; Colombo et al., 2013; Wagner et al., 2013). However, we expect that genomics will replace much of the 'classical' molecular phylogenetics and population genetics as state-of-the-art tools at the next SIAL meeting in Windsor, Ontario, Canada in 2015. Based on the authors personal experience, nearly all major research groups working on the evolution of ancient lake species flocks either are using genomic approaches or are in the process of implementing them (like the authors of this preface). As in speciation research, in general (Seehausen et al., 2014), the great promise of a wealth of informative data providing unprecedented insights at a fraction of the costs will transform the field.

Perspectives arising from the integration of biological and geological data

Evolutionary biologists have always been keen to obtain and use insights from the geosciences in the widest sense (geology, paleolimnology, and geochemistry), given their eminent influence on the environment of evolving ancient lake species flocks. Over the next few years, new methods and new data will provide a much more detailed window into the past of ancient lakes with percussions far beyond intralacustrine diversification. Biogeochemistry, for example, provides new perspectives on the 'co-evolution' for e.g., microbial communities and water chemistry (Crowe et al., 2008) offering insights into biota often neglected over the spectacular species flocks of animals in ancient lakes. Major drilling campaigns in ancient lakes through the *International Continental Drilling Program* (ICDP) now provide a wealth of data on lake age, fluctuations, paleoclimate, surrounding vegetation, or catastrophic events like volcanic eruptions. Lake Malawi for e.g., has been cored in 2005, and analyses of the cores have provided insights far beyond the evolution of the lake biota themselves such as late Pleistocene climate fluctuations (Cohen et al., 2007; Scholz et al., 2011), and their impact on the origin of modern humans (Scholz et al., 2007) or vegetation changes (Beuning et al., 2011) in East Africa and globally. However, from a speciation in ancient lakes perspective, well-resolved records of past lake level fluctuations of changes in drainage connections, and of course the age of the continuous lacustrine environment are most interesting. In 2013, Lake Ohrid was successfully drilled (Wagner et al., 2014), with one explicit aim being the provision of such data for evolutionary biology (Wagner & Wilke, 2011) as exemplified in the project name ("Scientific Collaboration On Past Speciation Conditions in Lake Ohrid", SCOPSCO); Lake Towuti in Sulawesi is scheduled to be cored in 2015 (Russell & Bijaksana, 2012). The involvement of research groups actively researching organismic diversification in these lakes will ensure a maximum integration of biological (including genomic) and geological data for a truly holistic perspective on ancient lake evolution.

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