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SPECIATION IN ANCIENT LAKES

Ancient Lake Ohrid: biodiversity and evolution

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Abstract Worldwide ancient lakes have been a major focal point of geological, biological, and ecological research, and key concepts in, for example, evolutionary biology are partly based on ancient lake studies. Ancient lakes can be found on most continents and climate zones with most actual or putative ancient lakes in Europe being restricted to the Balkan Region. The arguably most outstanding of them is the oligotrophic and karstic Lake Ohrid, a steep-sided graben of rift formation origin situated in the central Balkans. Here, an attempt is made to summarize current knowledge of the geological, limnological, and faunal history of Lake Ohrid. Additionally, existing data on biodiversity and endemism in Lake Ohrid are updated and evaluated, and patterns and processes of speciation are reviewed in the context of the Ohrid watershed, including its sister lake, Lake Prespa. Whereas the geological history of the Ohrid Graben is relatively well studied, there is little knowledge about the limnological and biotic history of the actual lake (e.g., the age of the extant lake or from where the lake first received its water, along with its first biota). Most workers agree on a time frame of origin for Lake Ohrid of 2–5 million years ago (Mya). However, until now, the exact limnological origin and the origin of faunal or floral elements of Lake Ohrid remain uncertain. Two largely contrasting opinions either favour the theory of de novo formation of Lake Ohrid in a dry polje with a spring or river hydrography or a palaeogeographical connection of Lake Ohrid to brackish waters on the Balkan Peninsula. Whereas neither theory can be rejected at this point, the data summarized in the current review support the de novo hypothesis. An assessment of the fauna and flora of Lake Ohrid confirms that the lake harbours an incredible endemic biodiversity. Despite the fact that some biotic groups are poorly studied or not studied at all, approximately 1,200 native species are known from the lake, including 586 animals, and at least 212 species are endemic, including 182 animals. The adjusted rate of endemicity is estimated at 36% for all taxa and 34% for Animalia. In terms of endemic biodiversity, Lake Ohrid is with these 212 known endemic species and a surface area of 358 km^2 probably the most diverse lake in the world, taking surface area into account. Preliminary phylogeographical analyses of endemic Lake Ohrid taxa indicate that the vast majority of respective sister taxa occurs in the Balkans and that therefore the most recent common ancestors of Ohrid- and non-Ohrid species likely resided in the region when Lake Ohrid

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came into existence. These data also indicate that there is relatively little faunal exchange and overlap between Lake Ohrid and its sister lake, Lake Prespa, despite the fact that the latter lake is a major water supplier for Lake Ohrid. Studies on selected species flocks and scatters, mostly in molluscs, point towards the assumption that only few lineages originally colonized Lake Ohrid from the Balkans and that the majority of endemic species seen today probably started to evolve within the lake during the early Pleistocene. Within the Ohrid watershed, endemism occurs at different spatial and taxonomic scales, ranging from species endemic to certain parts of Lake Ohrid to species endemic to the whole watershed and from subspecies to genus level and possibly beyond. Modes of speciation in the Ohrid watershed are largely affected by its degree of isolation. Observational evidence points towards both allopatric (peripatric) and parapatric speciation. Though sympatric speciation within a habitat is conceivable, so far there are no known examples. Today, the lake suffers from increasing anthropogenic pressure and a "creeping biodiversity crisis". Some endemic species presumably have already gone extinct, and there are also indications of invasive species penetrating Lake Ohrid. The comparatively small size of Lake Ohrid and the extremely small range of many endemic species, together with increasing human pressure make its fauna particularly vulnerable. It is thus hoped that this review will encourage future research on the ecology and evolutionary biology of the lake's taxa, the knowledge of which would ultimately help protecting this unique European biodiversity hot spot.

Keywords Ancient lake · Lake Ohrid · Lake Prespa · Balkans · Sister lakes · Geology · Limnology · Biodiversity · Endemism · Speciation

Introduction

Evolutionary patterns in ancient lakes is a topic that has fascinated biologists for decades, and a number of landmark publications have resulted from studies of ancient lake taxa, significantly increasing our knowledge about evolutionary processes in these unique ecosystems and beyond. Basic concepts of sympatric speciation (e.g., Genner et al., 2007), sexual selection (e.g., Seehausen, 2006), adaptive radiation (e.g., von Rintelen et al., 2004; Herder et al., 2006), hybridization (e.g., Seehausen, 2004), and punctuated equilibrium (e.g., Williamson, 1981; Gould, 1992) are, at least partly, based on studies of ancient lake taxa.

Moreover, ancient lakes, i.e., extant lakes that have continuously existed for hundred thousand or even million years (see Glossary), have long been recognized as centres of biodiversity and endemism (Brooks, 1950; Martens et al., 1994; Martens, 1997; Rossiter & Kawanabe, 2000) and are a major focal point for systematic, ecological, and conservation research (Coulter et al., 2006).

A principal problem in ancient lake studies is that due to their prominence, some workers narrowly focus on these systems, whereas the closer or wider surroundings often receive less attention, potentially leading to an overestimation of degree of endemism in ancient lakes. Other problems include lack of knowledge and/or controversy about the limnological history of many ancient lakes and the unknown origin of respective faunal and floral elements.

Although ancient lakes undisputedly differ in their origins and characteristics, it is their diversity and endemism that typically distinguish them from short-lived, post-glacial lakes. In fact, these parameters often serve as proxies for the recognition of ancient lakes (Martens, 1997), and it has recently been demonstrated that species diversity in modern and fossil records of lake faunas correlates with lake longevity (Gierlowski-Kordesch & Park, 2004). Most workers, however, consider longevity to be the only objective criterion for ancient lakes as there is a considerable number of worldwide lakes that are presumably old but lack a high degree of diversity and endemism. Reasons for that are, for example, recent extinction events as in Lake Kivu (Degens et al., 1973; Martens, 1997) or harsh climate conditions as in Lake Tahoe (Gardner et al., 2000). On the other hand, there are lakes with incredible biotic diversity that are considered to be relatively young (e.g., Lake Victoria, Seehausen, 2006). An unclear limnological history and often poor faunal knowledge also partly account for the uncertain status of a number of putative ancient lakes in the world that are outshone by their more famous counterparts (Albrecht et al., 2006a; Wilke et al., 2007). Though studies on ancient lake biota are ongoing for a number of taxa and lakes, no unifying theory on patterns and