Ante Jurilj's evolutionary hypothesis and its implication for diatom research on Lake Ohrid

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The diatom flora of Lake Ohrid has been under investigation for more than a century and has resulted in the recognition of around 900 different taxonomic entities. Although several floristic studies have been published, one of the more important studies was undertaken by Ante Jurilj (1910-1981), a Croatian diatomist, who published his observations in four publications (Jurilj 1948, 1954, 1956, 1957). In these, Jurilj provided several important results on the taxonomy, biogeography, phylogeny and evolution of Lake Ohrid diatoms. According to his studies the diatom flora of Lake Ohrid is characterized by its high diversity, endemism and abundance of relict taxa. However, besides just describing many new diatom taxa (genera and species), Jurilj proposed some important ideas concerned the phylogeny and evolution of the Surirelloid diatoms. Jurilj proposed that species in the genera *Surirella* and *Campylodiscus* were the ultimate members of a phylogenetic lineage that had several transitional forms. The Lake Ohrid Surirelloids represent a complete series of those transitional taxa and provide evidence that the evolutionary process of speciation is a result of cladogenesis. Thus, for example, *Campylodiscus* is not the result of a direct line of descent, but only a branch. It is important to point out that this evolutionary process began in the Miocene, but not in Lake Ohrid, while the transitional forms still exist in the lake. These finding suggest several important questions concerning the age, origin, phylogeny, evolution and speciation of diatoms in Lake Ohrid. Answers to these questions might be obtained by examination of the fossil record and molecular/genetic analyses of extant populations.

Recently, the deep-drilling project SCOPSCO (Scientific Collaboration On Past Speciation Conditions in Lake Ohrid) was initiated to investigate the influence of past geological and environmental events on the biological evolution of the lake biota. According to geochemical analyses and extrapolation of average sedimentation rates, the age of the lake is estimated at ca. 2 million year (Myrs). The data from the core sequence also implies that Lake Ohrid did not experience any major catastrophic events, such as extreme lake level low stands or desiccation events. Lake Ohrid, however, did experience a number of environmental disturbances during its ca. 2.0 Myrs history. These comprised of disturbances that lasted over longer periods of time ("press events"), such as glacial–interglacial cycles and Heinrich events, as well as sudden and short disturbances ("pulse events"), like the deposition of landslides, earthquakes and volcanic ash depositions. Depending on the magnitude of the disturbance and the resilience of the ecosystem, the lake biota may react with extinction events and/or changes in community structures and function. Data from core sequences suggest that the communities in Lake Ohrid probably did not experience regime shifts and the lake show a high resilience to environmental

disturbances. This might accord with the constant diversification rate of species, but also with the lack of an abundance of extinction events. Examples of anagensis and cladogenesis in the genera *Cyclotella* (planktonic) and *Surirella* (benthic) might be observed in the core sequence. It is supposed that evolution of planktonic species is anagenetic (phyletic transformation), while the evolution of benthic species is cladogenetic.

Molecular analyses (multilocus phylogeny) of selected diatom genera has shown that intralacustrine speciation very likely occurred in Lake Ohrid. Molecular data on the Surirelloids show that the genus *Spirodiscus* is sister to a *Scoliodiscus*/*Campylodiscus hibernicus* clade, and also the genera *Iconella* and *Helissella*, which have species with apical torsion to their valves, were found to be sister to one another. Such data provide support for hypothesising the evolutionary steps leading to *Campylodiscus* by both morphological and molecular data.

Few endemic species from Lake Ohrid related to *Diploneis elliptica* form a monophyletic clade, supporting the hypothesis of intralacustrine speciation. However, data show that *Diploneis* taxa (lineages) from Lake Ohrid form a paraphyletic assemblage that might be the result of multiple colonization events or the colonization of different evolutionary lineages. The age estimates obtained from molecular-clock analysis reveals that the species flocks from Lake Ohrid potentially started to diversify before the extant lake came into existence. The species were present in a pre-lake/paleo-lake phase or in other waterbodies of the Ohrid Graben system, such as rivers or springs, and continued to exist in the extant lake. The evidence for such hypothesis might be found in the core sequences, where the deepest (oldest) parts of the core are dominated by the benthic species with almost the same morphology as contemporary species.

Finally, the high diversity and endemism of diatoms in Lake Ohrid is very likely not the result of a single process, but of multiple factors including several colonizations, the presence of relicts and speciation, all of which can contribute to the high diversity. Alternatively, the presence of relict species in the lake may have been caused by two factors: (i) a lack of catastrophic environmental events in Lake Ohrid; and/or (ii) high ecosystem resilience, buffering any environmental changes. The occurrence of Surirelloid species observed and described by Jurilj from Lake Ohrid provides support of these hypotheses.

Ante Jurilj, in his extraordinary work on Lake Ohrid, noticed events that are now gaining support from fossil (core sequences) and molecular data.