

Appendix 2b

## **SUMMARY OF PROFESSIONAL ACCOMPLISHMENTS**

**dr Anna Wysocka**

Department of Genetics and Biosystematics  
Faculty of Biology  
University of Gdansk

Gdańsk, 2018

1. Full name:

**Anna Wysocka**

2. Diplomas and academic or artistic degrees, including their name, place, year of attainment, and title of doctoral thesis:

**2001 - PhD in biological sciences, specialization: biology**, PhD Studies, Faculty of Biology, Geography and Oceanology, University of Gdansk, Poland

Subject: *Genomic DNA hybridization as an attempt to evaluate systematics of Ostracoda* (supervisor: prof. dr hab. Tadeusz Sywula)

**1995 - M.Sc. in biology**, Department of Genetics and Cytology, Faculty of Biology, Geography and Oceanology, University of Gdansk, Poland

Subject: *Genetic variability in populations of ostracod species Candona neglecta Sars* (supervisor: prof. dr hab. Tadeusz Sywula)

3. Previous employment in scientific institutions:

**since 2011**: senior lecturer, Department of Genetics and Biosystematics (earlier: Department of Genetics), Faculty of Biology, University of Gdansk (10/2012-09/2013: health leave)

**10/2001-09/2011**: adjunct, Department of Genetics (earlier: Department of Genetics and Cytology), Faculty of Biology (earlier: Faculty of Biology, Geography and Oceanology, University of Gdansk (03/2002 – 09/2002 maternity leave)

**07/2001-09/2001**: adjunct, Molecular Biology and Marine Biotechnology Laboratory, Marine Biology Center in Gdynia, Polish Academy of Science

**03/2001-07/2001**: research assistant, Molecular Biology and Marine Biotechnology Laboratory, Marine Biology Center in Gdynia, Polish Academy of Science

**11/2000-02/2001**: biologist, Molecular Biology and Marine Biotechnology Laboratory, Marine Biology Center in Gdynia, Polish Academy of Science

**10/1995-04/2001**: doctoral student, Department of Genetics and Cytology, PhD Studies of Environmental Science, Faculty of Biology, Geography and Oceanology, University of Gdansk

4. Scientific accomplishment according to Act on scientific and artistic degrees and title from 14th March 2003 (DZ.U. nr 65, poz.595 ze zm.; article 16, part 2):

a) Title of the scientific accomplishment:

***Evolutionary history of the malacostracan endemic species (Crustacea) from the ancient Lake Ohrid***

Scientific accomplishment includes five articles published in years 2008-2017.

b) The list of publications constituting the scientific achievement:

1. **Wysocka A.**, Kostoski G., Kilikowska A., Wróbel B., Sell J. 2008. The *Proasellus* (Crustacea, Isopoda) species group, endemic to the Balkan Lake Ohrid: a case of ecological diversification? *Fundamental and Applied Limnology (Archiv für Hydrobiologie)*, 172(4): 301-313; DOI: 10.1127/1863-9135/2008/0172-0301 (IF 1,293, IF<sub>5-year</sub> 1,481; MNiSW: 20) – original paper
2. Kilikowska A.\*, **Wysocka A.\***, Burzyński A., Rychlińska J., Kostoski G., Sell J. 2013. Patterns of genetic differentiation and population history of endemic isopods (Asellidae) from ancient Lake Ohrid: combining allozyme and mtDNA data. *Central European Journal of Biology*, 8(9): 854-875; DOI: 10.2478/s11535-013-0204-y (IF 0,633, IF<sub>5-year</sub> 0,748; MNiSW: 20) – original paper
3. **Wysocka A.**, Grabowski M., Sworobowicz L., Burzyński A., Kilikowska A., Kostoski G., Sell J. 2013. A tale of time and depth: intralacustrine radiation in endemic *Gammarus* species flock from the ancient Lake Ohrid. *Zoological Journal of the Linnean Society*, 167(3): 345–359; DOI: 10.1111/j.1096-3642.2012.00878.x (IF 2,658, IF<sub>5-year</sub> 2,574; MNiSW: 40) – original paper
4. **Wysocka A.♦**, Grabowski M., Sworobowicz L., Mamos T., Burzyński A., Sell J. 2014. Origin of the Lake Ohrid gammarid species flock: ancient local phylogenetic lineage diversification. *Journal of Biogeography*, 41(9): 1758–1768; DOI:10.1111/jbi.12335 (IF 4,590, IF<sub>5-year</sub> 5,118; MNiSW: 45) – original paper
5. Grabowski M.\*, **Wysocka A.\*♦**, Mamos T. 2016. Molecular species delimitation methods provide new insight in taxonomy of the endemic gammarid species flock from the ancient Lake Ohrid. *Zoological Journal of the Linnean Society*, 181(2): 272-285; DOI: 10.1093/zoolinnean/zlw025 (IF 2,316, IF<sub>5-year</sub> 2,717; MNiSW: 40) – original paper

\* both authors contributed equally to this work

♦ corresponding author

Summarized IF: 11,49

Summarized IF<sub>5-year</sub>: 12,64

Summarized MNiSW points: 165

Impact factor (IF) and 5-year Impact Factor were obtained from Journal Citation Reports according to the year of publication, except pos. 5, where the last available IF was given (2015); MNiSW points were obtained on the basis of Ministry of Science and Higher Education list of articles, part A, according to the year of publication

### c) Description of the aims and results of the above-mentioned publications

The above-mentioned publications included in the postdoctoral dissertation are further cited in bold, according to the numbering [1-5]. The bibliographical data of other publications cited in the summary are provided in the subsection "Additional Literature". These publications are only selected items, key from the point of view of summary. The entire literature is included in the individual publications included in the habilitation thesis.

The description of the individual contribution in the postdoctoral dissertation can be found in Appendix 3 (List of published scientific papers and information on didactic achievements, scientific cooperation and popularization of science). Statements by all co-authors defining the individual contribution of each of them to the creation of publications can be found in Appendix 5.

Explanation of the causes and mechanisms of evolutionary processes is not a simple task. Indirectly because we have not witnessed evolutionary changes that have taken place in the past, and those occurring today are usually difficult to observe, including at least their slow rate. Nevertheless, some special places on Earth due to their geological history can provide invaluable information about the course of evolution.

Most of the numerous inland water bodies on earth were formed in the Holocene, less than 12,000 years ago (Schön & Martens, 2004). The exception to this rule is a group of only a dozen or so lakes in the world, known as ancient lakes, which have existed continuously for more than 100,000 years (Brooks, 1950; Gorthner, 1994; Martens, 1997). The oldest of them is considered to be Lake Baikal (Siberia), probably originating in the pre-Miocene times, i.e. 30-28 million years ago (Mya) (Sherbakov, 1999, Kaygorodova et al., 2007) and Lake Tanganyika (East Africa), which age is estimated at 9 -12 million years (My) (Cohen et al., 1993). Due to the long-term isolation from external water systems and relatively stable environmental conditions, ancient lakes are a unique testing ground for studying *in situ* the evolutionary processes underlying of the speciation process, mechanisms of colonization, adaptation and diversification (Brooks, 1950; Martens, 1997; Cristescu et al., 2010). The particularly high level of biodiversity and the impressive number of endemic species in most ancient lakes have fascinated researchers for years (Brooks 1950, Martens 1997, Schön & Martens, 2004). It is maintained that the unique nature of the biota of these water bodies may result from their functions. On the one hand, they have served a role as evolutionary reservoirs for preserving ancient lineages, on the other, they may also be a place of local speciation, allo-, para- or sympatric (cradle function) (Martens, 1997; Sherbakov, 1999).

Previous studies emphasized the importance of the first function model (e.g. Rossiter & Kawanabe, 2000; Sell & Spirkovski, 2004), or indicated a combinations of both models (Wilson et al., 2004). At present, with the emerging successive results of molecular research, the importance of intralacustrine speciation in the evolution of taxa living in ancient lakes is more often indicated (e.g. Marijnissen et al., 2006, Schultheiß et al., 2008, Kroll et al., 2012). This process leads to the formation of so-called species flocks: endemic monophyletic groups of closely related taxa, which underwent an

unusually high rate of speciation (Greenwood, 1984). Two of the most well-known examples concern cichlid fish from lakes of eastern Africa (e.g. Sturmbauer et al., 2001, Seehausen, 2006) and Baikal amphipods (e.g. Väinölä & Kamaltynov, 1999, Macdonald et al., 2005).

Although generally the ancient lakes *per se* are characterized as geologically old, isolated and environmentally stable, a detailed analysis shows that most of these lakes have experienced critical moments in the history of their existence. Both geological events and climate changes could have an impact on the stability of their ecosystems (Sturmbauer et al., 2001, Cristescu et al., 2010). Undoubtedly, rapid and/or severe climate changes have been behind significant and repeated fluctuations in water levels (and in extreme cases, even drying out) in the African lakes: Tanganyika, Malawi and Victoria (e.g. Sturmbauer et al., 2001, Cohen et al., 2007; Scholz et al., 2007; Stager & Johnson, 2008; Schultheiß et al., 2011, Van Bocxlaer et al., 2012) or in Lake Titicaca (Lavenu, 1992, Kroll et al., 2012). Consequently, the estimated age of many species flocks may not correlate with the geological age of the lake, and periodic drying may lead, if not to the extinction of entire flocks, at least to seriously deplete their abundance (e.g. Sturmbauer et al., 2001; Kroll et al., 2012). Also the state of complete isolation in such situations may be disturbed by the interaction of biota of ancient lakes with species inhabiting the surrounding rivers, spring lakes or satellite lakes (Coultnner, 1991, Kroll et al., 2012). For example, molecular data suggests that refugia for the present spectacular diversity of cichlid fish from the genus *Haplochromis* Hilgendorf, 1888 from Lake Victoria (after a drastic reduction in the water level 18-15 thousand years ago) probably existed in nearby Lake Kiwu (Elmer et al., 2009).

One of the most outstanding ancient lakes, which during its existence never experienced such drastic climatic and/or geological changes is Lake Ohrid, situated in the western part of the Balkan Peninsula, on the border of two countries, the Former Yugoslav Republic of Macedonia (hereafter, Macedonia) and Albania (Mitic et al., 2002; Albrecht & Wilke, 2008). In comparison to other lakes from this group, Lake Ohrid can be considered as a worldwide unique, because from the beginning of its existence it has formed a single, undivided lake basin (Watzin et al., 2002, Albrecht & Wilke, 2008). Less severe lake-level fluctuations, in comparison to ancient African lakes, allowed maintaining relatively stable zones in the lake itself as well as the surrounding springs (Jovanovska et al., 2015, Lindhorst et al., 2015). Consistently, the relatively stable ecosystem of Lake Ohrid for most of its long history has been also essential for maintaining exceptional high biodiversity (Stankovič, 1960, Watzin et al., 2002, Föllner et al., 2015). For example, the comparison of subfossil mollusk and ostracod assemblages from the Last Interglacial (Eemian) with a modern one did not show any significant differences in species composition, despite serious climate and environmental changes following this period (Belmecheri et al., 2009, Albrecht et al., 2010).

The oligotrophic Lake Ohrid is located in the valley at 693 m a.s.l. and surrounded by mountains ranges of up to 2300 m a.s.l. (Galičica Massif and Mokra Massif) (e.g., Albrecht & Wilke,

2008). It is considered to be the oldest lake in Europe (Albrecht & Wilke, 2008), although the exact geological age and details of its origin remain uncertain. The most probable *de novo* hypothesis suggests the formation of Lake Ohrid from karst springs or rivers in the tectonic collapse field (so-called polje) (Matzinger et al., 2006, Albrecht & Wilke 2008). Based on geological data, it has been assumed that this happened between 5-2 Mya (Albrecht and Wilke 2008), while the molecular clock analyzes made for a number of species flocks narrow the time to the Pliocene/Pleistocene, roughly 3-1,5 Mya (e.g.. Albrecht et al., 2006; Sušnik et al., 2006; Wilke et al., 2009; Trajanovski et al., 2010). The recent results of the sediment cores analyzes obtained as part of the SCOPSCO deep-drilling program (Scientific Collaboration on Past Specification Conditions in Lake Ohrid) indicate that a lake in the form of a deep water basin have existed from at least 1.3 My (Wagner et al., 2014; Wagner et al., 2017), while the oldest sequences of lake sediments estimated by indirect methods, from about 2 My (Jovanovska et al., 2015, Lindhorst et al., 2015). In its early stage of existence, Lake Ohrid was probably a part of the extensive lake system called Dessaretes (Stankovič, 1960). The karst nature of the region and the water supply from the only other extant Dessarete lake, the nearby Lake Prespa (849 m a.s.l.), undoubtedly make the Lake Ohrid basin a unique ecosystem (Watzin et al. 2002).

With an area of 358 km<sup>2</sup>, a capacity of 55 km<sup>3</sup> and a maximum depth of 293 m, Lake Ohrid is considered to be one of the smallest of the ancient lakes in the world (Matzinger et al., 2006; Lindhorst et al., 2015). Nevertheless, taking into account the surface of the lake, it is characterized by the highest endemism rate (36%) adjusted for all taxa of any ancient lake (Albrecht and Wilke 2008). Nearly 350 endemic species have been described so far, of which at least 188 are animals (Albrecht & Wilke, 2008, Pešič, 2015, Stocchino et al., 2013; Hauffe et al., 2015; Stelbrink et al., 2016). Similarly to other ancient lakes, Lake Ohrid is a refugium for old evolutionary lineages (Sell & Spirkovski, 2004) and a place of intralacustrine speciation. However, unlike ancient African lakes, in which known species flocks are formed primarily by vertebrates, in Lake Ohrid (as well as in Bajkal), mostly autochthonic invertebrate species flocks are recorded (Albrecht & Wilke 2008). The most well-known examples are snails of the genus *Ancylus* (Albrecht et al., 2006), snails from the subfamily Pyrgulinae (Wilke et al., 2007), leeches from the genus *Dina* (Trajanovski et al., 2010) and crustaceans [1; 3; 4; 5].

Lake Ohrid with its impressive biodiversity focuses the attention of scientists now, although until recently it remained undervalued and poorly understood. Undoubtedly, it was also a consequence of geopolitical instability in the Balkans in the 1990s, which caused the entire region to be rarely visited, also by carcinologists. Team of the Department of Genetics and Cytology (now the Department of Genetics and Biosystematics) University of Gdansk, under the guidance of prof. dr. hab. Tadeusz Sywula, in 2001, as one of the first research teams began official international scientific cooperation with the Institute of Hydrobiology in Ohrid (Macedonia). The consequence of this ongoing today co-operation is the cycle of papers focused on the faunal diversity and the evolutionary processes in Lake Ohrid (e.g. Sywula et al., 2003; Sell & Spirkovski, 2004 Sywula et al., 2006; 1; 3; 4;

5). After getting the Phd degree, in 2004 I have started research on the genetic diversity of Ohridian malacostracans (Crustacea: Malacostraca) belonging to two poorly known orders: Isopoda and Amphipoda. For both groups, a particularly high level of endemism was noted based on morphological diagnostic characters; for Isopoda, ca. 75%, for Amphipoda - 90% (Karaman, 1953, Stankovič 1960, see: Albrecht & Wilke, 2008). It is worth emphasizing here that the above data come from the age-old but still in use monographies (e.g. Karaman 1929, 1931, 1953, Karaman and Pinkster 1977a, b, 1987), in which, due to the morphological similarity of described species, inaccuracies cannot be excluded in their numbers.

According to the above knowledge, Lake Ohrid is inhabited by four isopod species from the family Asellidae. Three of them are endemic and belong to the genus *Proasellus* Dudich, 1925: *P. remyi* (Monod, 1932), *P. arnautovici* (Remy, 1932) i *P. gjorgjevici* Karaman, 1933, the fourth, is a species widely distributed in Europe, *Asellus aquaticus* (Linnaeus, 1758). Early taxonomic studies (Karaman, 1953, Stankovič 1960) led to the description of several morphological forms/subspecies within particular endemic *Proasellus* species (hereafter, according to the International Codex of Zoological Nomenclature - subspecies) with different ecological preferences related to the vertical zonation of the lake: the littoral (<20 m depth), the sublittoral (20-50 m) and the profundal (>50 m depth). Within *P. arnautovici*: the littoral subspecies *P. arnautovici arnautovici* (Remy, 1932) and the sublittoral/profundal *P. arnautovici elongatus* (Karaman, 1953), within *P. gjorgjevici* - the littoral *P. gjorgjevici litoralis* Karaman, 1933 and the sublittoral/profundal *P. gjorgjevici typicus* Karaman, 1933, while for *P. remyi* - the littoral *P. remyi remyi* (Monod, 1932), the sublittoral *P. remyi acutangulus* (Karaman, 1953) and the profundal *P. remyi nudus* (Karaman, 1953). All taxa associated with the littoral zone prefer the sand-rocky bottom and are found mainly adhered to the stones, shells of *Dreissena polymorpha* (Pallas, 1771) and on the thallus of *Chara ceratophylla* Wallroth 1815. The latter two are also associated mainly with the sublittoral species, preferring the sandy-silty bottom. The profundal taxa live on the bottom covered by mud with organic detritus. In the case of *P. remyi remyi*, it is also found in St. Naum springs, feeding the lake on its southern shore.

In the case of amphipods, Lake Ohrid and its coastal sources inhabit endemic species from three genera representing three different families (Karaman, 1977): *Synurella* Wrześniowski, 1877 (family Crangonyctidae Bousfield, 1973), *Niphargus* Schiodte, 1849 (Niphargidae Bousfield, 1977) i *Gammarus* Fabricius, 1775 (Gammaridae Leach, 1814). Within genus *Gammarus* as many as seven species endemic to Lake Ohrid have been described. There are traditionally referred to as “*Gammarus ochridensis* complex” to highlight their morphological similarities and putative phylogenetic affiliations (Karaman, 1977; Karaman & Pinkster, 1987). Based on the few studies, similarly as in the case of the Ohridian *Proasellus* taxa, species of this complex seem to show at least some characteristic ecological preferences with respect to depth zones and habitat types (Karaman, 1977, Salemaa & Kamal'tynov, 1994). Species *G. ochridensis* (Schäferna, 1926) and *G. salemaai* G.

Karaman, 1985 are associated with the littoral zone, amongst reeds and under stones. The same zone inhabits *G. parechiniformis* G. Karaman, 1977, but occurs amongst underwater mosses and plants in the karstic sources on the lake margins. All three species occasionally can be found in the sublittoral zone. *Gammarus lychnidensis* Schellenberg, 1943 lives in the deeper parts of the lake, but also occurs in the littoral zone. The deeper zones of the lake are also associated with *G. stankokaramani* G. Karaman, 1976, *G. solidus* G. Karaman, 1977 and *G. macedonicus* G. Karaman, 1976. Based on morphological features, all taxa of the *G. ochridensis* complex were included in the group of species commonly referred to as "*balcanicus*", one of the three, next to the "*pulex*" and "*roeselii*" groups, distinguished for the widespread Palearctic and species-rich genus *Gammarus* (Karaman & Pinkster 1977a, b, 1987). Apart from lacustrine species, in a few springs on the lake margin lives endemic *Gammarus sketi* G. Karaman, 1989 (Karaman 1989). The genus *Gammarus* is also represented by species with a wider European range, *G. roeselii* Gervais, 1835, found in the littoral zone of the lake, its larger tributaries and spring areas and *G. balcanicus* Schäferna, 1922, found in the springs and small streams in the lake vicinity (Karaman & Pinkster, 1977b, 1987).

Given the high level of endemism of *Gammarus* and *Proasellus* crustaceans and the fact that animals from both groups inhabit all zones of the lake along the bathymetric gradient and the surrounding springs, they can be an ideal model for studying the process of speciation in the unique ecosystem of Lake Ohrid. This may be supported by poor dispersal ability and limited to specific niches range of occurrence of these crustaceans (Cohen & Johnston, 1987, Cohen, 1994).

To determine the origin of the present-day fauna of Lake Ohrid, gain insight into the processes of taxa differentiation and calculate the time of the major evolutionary events leading to the extraordinary biodiversity and endemism in the area of the lake, in the presented here series of publications that constitute my scientific accomplishment and which concern amphipods of the genus *Gammarus* and isopods of the genus *Proasellus* I wanted to focus on the following specific aims:

- to verify the morphology-based taxonomy [papers: 1, 2, 3, 5];
- to determine the phylogenetic relationships between different taxa from Lake Ohrid and surrounding area [papers: 1, 2, 3];
- to determine the divergence time for particular taxa and their pattern of differentiation in the lake [papers: 1, 2, 3, 4];
- to test whether the Ohridian endemic amphipods and isopods represent an autochthonic species flock [papers: 1, 2, 3];
- to determine the putative origin of the Lake Ohrid fauna and place it within a regional palaeobiogeographical context by the example of *Gammarus* species flock [paper: 4];
- to describe a new to science amphipods species based on morphological and/or molecular features [paper: 5].



Totally, 171 specimens of the genus *Gammarus* and 48 species of *Proasellus* from respectively 91 and 23 locations, from Lake Ohrid, springs supplying the lake and surrounding streams were analysed [1, 2, 3, 4]. For the paleobiogeographical studies, 12 additional taxa representing: *Gammarus*, *Echinogammarus* Stebbing, 1899 and *Laurogammarus* G. Karaman, 1984 genera from 70 sample points located on the Balkan Peninsula were included [4].

I achieved my goals by using a wide range of methods and skills acquired during my scientific work, starting from field works, species identification based on morphological features, by designing experiments and conducting molecular research i.e. sequence analysis of two mitochondrial markers (mtDNA): *cox 1*<sup>1</sup>, *16S rRNA*<sup>2</sup> and one nuclear, *28S rRNA*<sup>3</sup>, and analysis of genetic variability in eight allozymatic loci. Using a wide range of bioinformatic methods I have got an insight into i.e. the genetic population structure, the phylogenetic relationships, the haplotype network, the molecular clock dating, or the species delimitation based on molecular data. Amphipod sequences of *cox 1* and *16S rDNA* obtained within the framework of the DNA barcoding approach, the method widely used for e.g. in search of cryptic/hidden diversity of many animal species, were included in the international project, Barcode of Life Data System (BOLD, <http://boldsystem.org>).

## Results

Below I present a summary description of my results published in a series of five papers submitted for evaluation as part of the scientific achievement:

### *Taxonomic status and phylogenetic relations between endemic species of Gammarus and Proasellus from Lake Ohrid and its surroundings*

The pattern of phylogenetic relationships between endemics from genus *Gammarus* and *Proasellus* obtained in my studies is only partially reflected in the current morphological classification of both groups [1, 2, 3, 5]. Part of species defined on the basis of diagnostic morphological traits (morphospecies) does not form monophyletic groups, thus showing decoupling between morphological and molecular data [1, 2, 3, 5].

The phylogenetic analyses of mtDNA sequences (*cox 1*/*16S rDNA*) of known endemic species from the genus *Gammarus* distinguish eight clades [3]. Seven of them correspond to lacustrine taxa. The eighth lineage is formed by their sister species, *G. sketi*, absent in the lake, but inhabiting sources supplying the lake on its southern and eastern shores. The noted genetic distance ( $D_{TN}$ )<sup>4</sup> amongst these

---

<sup>1</sup> cytochrome c oxidase subunit 1

<sup>2</sup> 16S ribosomal RNA subunit

<sup>3</sup> 28S ribosomal RNA subunit

<sup>4</sup>genetic distance calculated using Tamura-Nei model

seven clades ranges 0.04-0.08, and between each of these clades and *G. sketi* is at the level of 0.08 to 0.10 [3].

Amongst the endemic species, *G. sketi*, *G. solidus*, *G. salemaai* and *G. macedonicus*, are morphologically and molecularly well-defined, representing separate and old lineages [3]. However, it is worth noting that in the case of the last taxon it is difficult to make any reliable conclusion, because among thousands of gammarids collected over the years of fieldwork, only one individual represented this, how it seems, extremely rare species, was found. Of the above, the phylogenetic analyses distinguish also two lineages representing potentially new taxa: *Gammarus* sp. 1 and *Gammarus* sp. 2 [3, 5].

The phylogenetic relationships between the rest of species from the complex: *G. ochridensis*, *G. lychnidensis*, *G. parechiniformis* and *G. stankokaramani* remain unresolved. These morphospecies belong to a group of closely related haplotypes and none of them form a monophyletic lineage [3]. Individuals assigned on the basis of morphological traits to clearly different morphospecies both share the same haplotypes and also have those characteristics only for themselves. The exception is *G. ochridensis* for which no unique haplotype was distinguished. On the other hand, one haplotype appeared to be common for 49 individuals representing as many as three different morphospecies: *G. lychnidensis*, *G. ochridensis* and *G. parechiniformis* [3]. No significant barriers to gene flow between these taxa are consistent with this picture [3]. It is worth emphasizing here that while in the case of *G. ochridensis* and *G. parechiniformis* the significant morphological differences are observed, it is not so obvious for *G. ochridensis* and *G. lychnidensis* [3, 5]. In addition, the latter taxon not only is grouped with representatives of *G. stankokaramani*, but also formed a separate lineage [3]. This situation might have resulted from the lack of well-defined diagnostic features.

Also in the case of endemics from the genus *Proasellus*, the topology of phylogenetic tree of the mtDNA sequence (cox 1) and the results of analyses of 4 allozymatic loci (*Adh*<sup>5</sup>, *Ldh*<sup>6</sup>, *Pgm*<sup>7</sup>, *Pgi*<sup>8</sup>) do not correspond to the current morphological classification of the group, especially due to the lack of confirmed monophyly of *P. remyi nudus* and other subspecies of *P. remyi*, and also *P. arnautovici arnautovici* and *P. arnautovici elongatus* [1, 2]. It seems that the evolutionary history of the Ohridian endemic isopods was slightly different than in the case of the amphipods [1, 2]. Here, in the pattern of branching, two monophyletic clades, distinct genetically are observed ( $D_{HKY}^9 \sim 0.15$ ) [1, 2]. Within the first (G1), lacustrine lineages of *P. remyi* (*P. remyi remyi*, *P. remyi acutangulus*, *P. remyi* indet.) constitute sister clades to *P. remyi remyi* from St. Naum springs and group together with *P. arnautovici arnautovici* ( $D_{HKY}$ : 0.02-0.04). The taxon reported as *P. remyi* indet. responds to

---

<sup>5</sup> alcohol dehydrogenase

<sup>6</sup> lactate dehydrogenase

<sup>7</sup> phosphoglucosmutase

<sup>8</sup> glucose-6-phosphateisomerase

<sup>9</sup> genetic distance calculated using Hasegawa-Kishino-Yano model

individuals associated with the profundal of the lake and which is difficult to clearly assign to one of the known subspecies of *P. remyi* on the basis of morphology [2]. However, despite the differences in morphology, it shares a common haplotype with individuals from sublittoral subspecies *P. remyi acutangulus* [2]. The second group (G2) is formed by two clades, the first with subclades *P. remyi nudus* and *P. arnautovici elongatus* ( $D_{HKY} = 0,026$ ), the second with haplotypes *P. gjorgjevici typicus* and *P. gjorgjevici litoralis* ( $D_{HKY} = 0,017$ ). The results indicate a significant limitation in the gene flow between taxa of the two main groups and a partial restriction or even no barriers within them, respectively (e.g. for the lacustrine *P. remyi*) [2]. Here, in contrast to the situation observed in endemic gammarids, each population has its own unique haplotypes (exception: one common haplotype for *P. remyi acutangulus* and *P. remyi* indet.).

The most probable explanation for the observed inconsistency between morphological and molecular diversity may be the ancestral polymorphism accompanied by the incomplete lineage sorting in young taxa and/or repeated hybridization events and introgression [1, 2, 3]. The contribution of the same mechanisms is also indicated by Trajanovski et al. (2010) regarding the Ohridian endemic leeches of the genus *Dina*. The first mechanism can be explained by the presence of "deepwater" haplotypes in shallow-water taxa, and *vice versa*. The occurrence of the second, the hybridization process may lead to the formation of new species, especially by allopolyploidy. This is not excluded by the karyotype analysis of the *G. ochridensis* complex species, where high diversity in chromosome number were reported, in relation to the most common chromosome number in Western Palearctic gammarids,  $n = 26$  (Salemaa, 1985; Salemaa & Kamal'tynov, 1994). In the case of *G. ochridensis*, *G. parechiniformis*, *G. stankokaramani* and *G. solidus*, the chromosome number is  $n = 25$ , for *G. macedonicus*  $n = 21$ , *G. salemaai*  $n = 12$  and *G. lychnidensis*  $n = 34$ . The nature of this process remains unclear, it can only be hypothesized that the speciation could be induced by auto- or allopolyploidization and the possible chromosome reduction [3, 5]. However, a similar explanation cannot be applied to the endemic *Proasellus* species from the Lake Ohrid. Based on the karyological data no differences in the number of chromosomes ( $n = 11$ ) among species were noted (Salemaa, 1985, Salemaa & Kamal'tynov, 1994). This chromosome number is also characteristic for the part of the other European species of the genus (Salemaa, 1985; Salemaa & Kamal'tynov, 1994), although different from the number of chromosomes reported for *Proasellus coxalis* (Dollfus, 1892),  $n = 6$ , a species considered by some authors to be the closest relative of endemics outside the Lake Ohrid (Karaman, 1953).

It is also possible that the observed inconsistency between molecular and morphological data may be the "overestimation" of the number of species (Funk & Omland, 2003) [2, 5]. Some of the endemic *Gammarus* species could exhibit substantial morphological polymorphism in relation to the occurrence in various habitats along the bathymetric gradient or to the seasonal stage [5]. A similar

situation was observed in the other representatives of the genera: *Gammarus* and *Echinogammarus* [5].

#### *The diversification processes in Lake Ohrid: time and space*

An attempt to determine the pattern of diversification is one of the major challenges in the study of speciation. It seems that the radiation of the Ohridian endemics from the genus *Gammarus* and *Proasellus* was associated with the recurrent lake-level fluctuations – the probable consequence of climate changes that affected the Earth during the Pleistocene [3]. The determination of the evolutionary time frame in ancient lakes is accompanied by a significant question: whether the diversification process of the most ancestral lineage started before the lake formation, along with its beginning or after its formation? The cox 1 molecular clock analysis suggests that the split between *G. sketi* living in the St. Naum springs and the *Gammarus* species flock from the lake occurred approximately 7-5 Mya [3]. The plausible scenario assumes that the radiation within the lake (or the reservoir being its precursor) might have occurred in at least two stages. Older lineages, *G. salemaii*, *G. solidus*, *G. macedonicus* as well as taxa representing potentially new species separated 3-2 Mya [3] – during the period associated with the origin of the lake (Albrecht & Wilke, 2008). The radiation of younger taxa, *G. ochridensis*, *G. parechiniformis*, *G. lychnidensis* and *G. stankokaramani* occurred at less than 1 Mya and could be associated with the lake water-level fluctuations during Pleistocene (Lindhorst et al., 2010).

For the all endemic *Proasellus* species, the last common ancestor dates back to about 7 Mya, however the proper radiation of the two major lineages seems to be more recent [1]. In the case of the G1 lineage grouping taxa *P. remyi* and *P. arnautovici arnautovici*, it is estimated at 1.9-1.5 Mya, and the G2 lineage with *P. remyi nudus*, *P. arnautovici elongatus* and *P. gjorgjevici*, at 2.8-2.3 Mya. Considering the estimated time of the origin of Lake Ohrid, we can presume the intralacustrine radiation of the entire *Proasellus* group. An alternative hypothesis assuming an independent colonization of the lake by two different ancestral lineages seems to be less likely considering, for example, the morphological similarity of all *P. remyi* subspecies. However, it seems that the existence of species complexes in the Ohridian snails of the genus *Valvata* may result from independent colonization events (Hauswald et al., 2008). In the case of two lineages of *P. remyi remyi*, from the lake and from the spring, their separation took place about 1 Mya [1].

The major challenge is to determine the causes for spatial diversification. The observed pattern of vertical distribution of *Gammarus* species in Lake Ohrid and of haplotype groups within the species suggests that their differentiation could be a consequence of adaptive radiation along a depth gradient [3]. The haplotype network shows that the haplotypes are partially shared by individuals collected from littoral and sublittoral as well as sublittoral and profundal zones. There are, however, no haplotypes shared by specimens from all vertical zones and no groups of haplotypes representing both

the littoral and profundal zones. The radiation could be promoted by colonization of formerly empty ecological niches in various depth zones, however, we cannot exclude that it could also be driven by recurrent water level fluctuations during the Pleistocene (Lindhorst et al., 2010). Based on the literature, the latter phenomenon is indicated as significant in the process of the cichlid fish diversification in African lakes (e.g. Sturmbauer & Meyer 1992, Sturmbauer et al., 1997; Rüber et al., 1998; Nagl et al., 2000). As in Lake Ohrid the water fluctuations were incomparably smaller (the maximum level was about 60 m lower, Lindhorst et al., 2010), it seems that the populations living in the littoral zone should be the most affected by them (Rossiter, 1995; Koblmüller et al., 2008). Such a scenario may indicate the lowest haplotype diversity of endemic *Gammarus* species in the littoral zone [3]. Perhaps the lowering water level forced the organisms living in shallower zones to move deeper. At the same time, it seems that the change in the water level has become the cause of the horizontal barrier for populations inhabiting the spring on the southern margin of the lake. Those populations could be temporarily separated, constituting a reservoir for allopatric speciation (Albrecht & Wilke, 2008). Such a scenario may be confirmed by the presence of two divergent lineages, one found in the lake and the other in the springs (St. Naum, St. Drilon) within the *G. parechiniformis* and *G. salemaai* species [3]. Also, individuals of *P. remyi remyi* originating from the St. Naum springs, although the morphological identity to those from the lake, differ genetically ( $D_{HKY} = 0.02$ ) [1, 2]. A similar pattern in which horizontal barriers promote allopatric speciation was demonstrated by Albrecht et al. (2006) for snails of the genus *Ancylus* and by Sywula et al. (2006) for flatworm species of the genus *Dendrocoelum*.

The haplotype network of the *Proasellus* endemic species distinguish two highly divergent groups of haplotypes, analogous to those shown on the phylogenetic tree (G1 and G2) [2]. The first group (G1) is formed mainly by the haplotypes of *Proasellus* found in the littoral/sublittoral of the lake, the second (G2) is dominated by haplotypes characteristic for the sublittoral/profundal zones. As particular taxa are associated with the corresponding zones of the lake, it seems that also here radiation could be resulted from the colonization of new habitats at various depths [2]. Nevertheless, despite the significant morphological diversity and limited mobility, the effect of vertical barriers (biotic and abiotic, described in papers 1, 2) in the lake on the occurrence of *P. remyi* or *P. gjorgjevici* has not been clearly proved [2]. However, this phenomenon cannot be excluded in the case of deep-water populations of *P. remyi nudus* and *P. arnautovici elongatus*, with the limited gene flow between them [2]. The occurrence of barriers in gene flow on a microgeographic scale and the role of vertical environmental zonation in speciation were also noted for the Ohridian hydrobiid snails from the subfamily Pyrgulinae (Schreiber et al., 2012). Considering the possible diversification pattern, the *Proasellus* haplotype network is not conclusive and suggests two alternative scenarios [2]. In the first, the diversification starts from an ancestral lineage originated in the shallow-water, while in the second - from the deeper parts of the lake. The first scenario is congruent with the notion of Karaman (1953)

and Stankovič (1960) and recently supported by Trajanovski et al. (2010) for Ohridian *Dina* spp. In the second variant, due to the presence of troglomorphic features in individuals from the deep-water populations, the contribution of the subterranean karstic waters in this process cannot be excluded.

*Ohridian endemics of the genera Gammarus and Proasellus as the examples of autochthonic species flocks*

The phylogenetic analyses and the molecular clock estimation of major evolutionary events showed that endemic *Gammarus* species from Lake Ohrid constitute a monophyletic group formed likely through rapid intralacustrine speciation [3]. Moreover, *G. sketi* together with all lacustrine endemic taxa also form a monophyletic group whose evolution probably took place in the Lake Ohrid valley [3, 4].

For all endemic isopods of the genus *Proasellus*, the monophyly has not been confirmed based on the analysed data set [1, 2]. It is worth noting that during the extensive sampling over the years in the Lake Ohrid areas, no other freshwater taxa of this genus were identified, only the populations of *A. aquaticus*. However, studies on the genetic differentiation processes in the subterranean isopods of the superfamily Aselloide (Morvan et al., 2013, Eme et al., 2014) extended the cox 1 sequence database of European *Proasellus* representatives and thus allowed me to perform the additional phylogenetic analysis (unpublished data). The results confirm the monophyly of the endemic *Proasellus* species from Lake Ohrid and its surroundings. According to this new data, the Ohridian group forms a separate clade in a large group of species called *Proasellus*-Ibero-Aquitanean *sensu* Morvan et al. (2013). Thus, both endemic *Gammarus* and *Proasellus* species from Lake Ohrid meet the criteria set for a species flock (Greenwood, 1984), the more that in the light of the Schön & Martens definition (2004), the flock can be formed by even 3-4 closely related species, whose ancestor does not have to be endemic to the lake [1, 2, 3]. It should be noted that the *Gammarus* species flock is one of the largest described so far for Lake Ohrid [3, 4].

*The origin of the endemic fauna of Lake Ohrid based on Gammarus species flock: paleobiogeographical context*

The genus *Gammarus* with nearly 30 species on the Balkan Peninsula is much more diverse than other studied animal genera with endemic species flocks in Lake Ohrid, (Karaman & Pinkster, 1977a, b; 1987). Thus it can act as a perfect model not only for the studies upon origin of the Ohridian endemic fauna, but also, in wider context, upon the evolution of Balkan *Gammarus* spp. [4]. According to my results, all the representatives of the genus *Gammarus* from the Balkans form a monophyletic clade, outside *Echinogammarus* spp. and *Laurogammarus* spp. [4]. However, within this genus, despite a few well defined species, the substantial incongruence of morphological and molecular data is observed, particularly for the species that are identified based only on several

morphological features as *G. balcanicus* [4]. According to the molecular clock analysis it seems that the *G. balcanicus* clade, consisted of genetically diverse lineages (Mamos et al., 2016), diverged from the other Balkan *Gammarus* spp. in late Oligocene (ca 23.5 Mya). Further, *G. balcanicus* morphospecies diversified during the continentalization of this region of Europe and the uplift of the Dinaric Alps, the Balkan, Rhodope and Hellenic mountain ranges around 18-19 Mya [4]. The best example of the strength of this diversification process on such limited area are the two genetically distant taxa identified as *G. cf. balcanicus*, co-occurring in one small mountainous stream in the Lake Ohrid basin, for which the time of divergence is estimated to 4 My. One of the old lineages originated in the Hellenides Mts was an ancestor of the endemic gammarids from Lake Ohrid [4]. This lineage colonised the Dinaric Alps from the northern part of the Proto-Balkans, during the Tethys/Paratethys regression and have been diversifying there for the last 18 My of the Dinaric uplift (Alpine orogeny) [4]. It seems that the Ohridian gammarid species flock is a descendant of the lineage once inhabiting the watershed of the the Dessaretis Neogene lake system, of which a remnant is Lake Ohrid. It is also closely affiliated with the biota endemic to the neighboring area of the Galičica Massif and the north-western rivers of Greece [4]. Other closely related taxa are associated with the Vardar and Črni Drim river systems in Macedonia and Albania. These results support the hypotheses concerning the origin of the Ohridian fauna suggesting its close relationship with the fauna from Western Balkans [4].

#### *New insight into taxonomy of the Ohridian endemic gammarid species*

The DNA barcoding approach uses short, standardized DNA fragments to describe biodiversity, not only by identifying known species, but also by looking for hidden diversity (Hebert et al., 2003). Since the congruence of morphological and molecular data was questioned in the *Gammarus* species flock and the existence of potentially new taxa was pointed out [3], I assumed that this flock may be an ideal model to verify the currently used taxonomy with new tools as molecular species delimitation methods and detection of cryptic diversity phenomenon [description of methods: 5]. The analyses of the cox 1 (the marker used as a barcode in animals) and 16S rRNA data set, carried out with five methods, showed that only the older lineages of *G. sketi*, *G. macedonicus* and *G. solidus* species are well defined taxa, morphologically and genetically [5]. However, for another, equally old taxon, *G. salemaai*, clear signals of cryptic diversity have been detected [5]. This taxon was described based on the collection of individuals from the littoral zone of Lake Ohrid (Karaman 1985, Karaman and Pinkster, 1987). In my study, within this morphospecies two molecular operational taxonomic units (MOTU) were distinguished [5]. In addition to this typical littoral form of *G. salemaai*, the existence of another cryptic taxon from a very small spring on the southern coast of the lake was detected (hereinafter: *Gammarus cryptoparechiniformis* sp. nov.) [5]. Another distinct and old lineage is represented by individuals of the taxon referred to in work 3 as *Gammarus* sp.1 (hereinafter:

*Gammarus sywulai* sp. nov.), widely distributed in the sublittoral zone. The most significant lack of congruence of molecular and morphological data was observed in the group of the youngest taxa, being a result of radiation dating for less than 1 Mya [3, 5]. Of these, three MOTUs were identified for *G. parechiniformis* [5]. One of these MOTUs includes individuals from the *locus typicus* situated in the southern part of the St. Naum springs. The second one, previously referred to as *Gammarus* sp.2 [3], represents only three individuals, but from the distant northern and southern parts of the lake (hereinafter: *Gammarus cryptoparechiniformis* sp. nov.). The third lineage includes also the other morphospecies: *G. ochridensis* and *G. lychnidensis*. Unfortunately, in the case of lineages from the lake, representing the aforementioned taxa and *G. stankokaramani*, it is difficult to make conclusions because it is not clear which of these lineages represents the type material.

Although the presence of cryptic species is nowadays often reported for many animal groups, also among the Ohridian molluscan species flock of genus *Pisidium* (Schultheiß et al., 2008), *Valvata* (Hauswald, et al., 2008) and *Radix* (Albrecht et al., 2008 ) or the leeches *Dina* (Trajanovski et al., 2010), these new taxa often remain formally undescribed, which does not systematize our knowledge at all. In the article 5, following Jörger & Schrödle (2013), for the first time the diagnostic molecular characters as the significant nucleotide substitutions of DNA sequences [description of procedure: 5] were used in the formal description of new species from the Lake Ohrid [5].

The scientific description of the taxon defined as *G. sywulai* sp. nov. was performed both on the basis of morphological and molecular characteristics. However, in the case of cryptic taxa *G. cryptoparechiniformis* sp. nov. and *G. cryptosalemaai* sp. nov. description of species was conducted exclusively on the basis of molecular characters. [5]. In the new key for identification of endemic *Gammarus* species from the Lake Ohrid, both morphological and molecular diagnostic characters were included. Holotypes and paratypes (with DNA samples) have been deposited at the Museum and Institute of Zoology PAS. The cox 1 and 16S rRNA sequences, as well as all the additional information about the project, have been deposited in the international Barcode of Life Data Systems database ([www.boldsystems.org](http://www.boldsystems.org)).

### **Summary:**

Since 1979, Lake Ohrid has been on the UNESCO World Heritage List. Each year, the group of people interested in studying its unique character is also expanding. Unfortunately, the eutrophication of the Lake Ohrid waters combined with the growing anthropogenic impact is a serious problem, and threatens the subtle balance of the entire ecosystem of the lake (e.g. Sell & Spirkovski, 2004; 2). Until we make a real assessment of the richness of endemic fauna, we will not understand the evolutionary processes that accompanied its origin; we will not have the tools to manage the



biodiversity resources hidden in this or any other ancient lake. The scientific works included in the postdoctoral dissertation are part of these activities.

In conclusion, the main results from my research on the endemic fauna of Lake Ohrid are:

- endemic taxa of the genera *Gammarus* and *Proasellus* form species flocks created as a result of intralacustrine radiation;
- the endemic fauna of the lake is probably derived from the western Balkan system of the Neogene lake system and is most associated with the endemic fauna of the lake area;
- the dating of major evolutionary events taking place in Lake Ohrid is a part of the scenario presented by other researchers;
- the shown phylogenetic relationships within the species flocks are not fully reflected at the phenotype level, probably due to incomplete lineage sorting and/or hybridization processes;
- at the same time, there is the presence of new endemic taxa, including cryptic species;
- verification of taxonomy based on diagnostic morphological features can be carried out by means of molecular methods of species delimitation;
- describing new species, not only cryptic, can be carried out using diagnostic molecular features.

I consider my contribution to expanding knowledge about evolutionary processes as the main achievement of my research, which has led to the emergence of extremely high biodiversity and the level of endemism in ancient lakes.

The resulting publications falling within the scope of scientific achievement include the results of research, the implementation of which was financed by the research grant MNiSW No. 3 P04F 076 23 and the project of the Faculty of Biology of University of Gdańsk No. 1030-5-0227-4 [publications: **1, 2**] and own research grant NCN No. N N303 581 839 [publications: **3, 4, 5**]. I presented the results together with co-authors at 11 international conferences [oral presentations (3); posters (7)] and 3 national conferences [oral presentations (1), posters (2)].

## 5. Discussion of other scientific and research (artistic) achievements.

The publications marked in bold, cited below, are other scientific and research achievements of the author

Since my studies I have been fascinated by the biodiversity of the world, especially the genetic basis of its manifestations within various groups of animals, especially invertebrates. At the beginning of my research work, inspired by my promoter's suggestions, prof. dr hab. Tadeusz Sywula, in my Master Thesis I focused on the analysis of the genetic diversity of the freshwater ostracod species,

*Candona neglecta* G.O. Sars, 1887. Its occurrence is noted in extremely different environments: in permanent/periodically drying small water reservoirs, in the profundal of postglacial lakes, or unexpectedly, in the deep parts of the Gulf of Gdansk. Analysis of the allozymatic variability showed the genetic similarity of deep-sea populations from the Gulf of Gdansk and lakes, simultaneously indicating the genetic differences of isolated populations from small water reservoirs, probably resulting from the founder effect. It seems that the observed pattern of genetic diversity may be a consequence of the participation of water birds in the dispersion of *C. neglecta*. The results of the Master Thesis were published in the JCR journal (Wysocka et al., 2000).

During preparation of the Master Thesis, for the first time I got to know field research, while collecting the material. From now on almost every research project in which I participated involved this type of activity. In my opinion, field research is one of the most important elements of the researcher's workshop, and the proper selection of sampling location and methods of collecting material determine the credibility of the obtained results.

The field trips aimed at collecting the samples for my Master Thesis allow also collecting the profundal sediments of lakes from the north-eastern part of Poland for the assessment of the subfossil ostracod species composition. Three ostracod assemblages were identified, and their species composition correlated with trophic conditions in the analyzed water reservoirs (Namiotko et al., 2012). The project was realized in cooperation with prof. dr. hab. Tadeusz Namiotko (Department of Genetics and Cytology, University of Gdansk).

After completing my Master's degree I became a student of the Environmental Doctoral Study at the Faculty of Biology, Geography and Oceanology, University of Gdansk. The Phd thesis "Genomic DNA hybridization as a method of verification of ostracod taxonomy" was carried out under the supervision of prof. dr. hab. Tadeusz Sywula. The research was concentrated on representatives of old lineages, probably separated in the Miocene and represented three superfamilies in the order of Podocopida Sars, 1866: Darwinuloidea Brady & Norman, 1889, Cytheroidea Baird, 1850 and Cypridoidea Baird, 1845. This project was a great challenge for me, not only because of the laboratory skills. At this time there were no reports of using DNA for analyses of this particular group of organisms (and they are relatively poor until today). The genomic DNA hybridization method was an alternative to the sequence analysis of selected genome fragments. With very good results it was used as a taxonomic tool in several groups of vertebrates and invertebrates. However, due to the limited availability of genetic material in ostracods compared to the previously studied organisms, it was necessary to significantly modify the method and design a number, verified in terms of suitability, of experiments; from the elaboration of DNA isolation procedure, through the column separation to obtain the unique DNA fractions and radio/non-radioactive labeling molecular probes, to determining the hybridization conditions. The courtesy of prof. dr. hab. Grzegorz Węgrzyn and dr Grażyna Konopa, the part of the laboratory research was carried out at the Department of Molecular Biology of the

University of Gdansk. The final method used was the "slot-blot" DNA hybridization with a non-radiolabeled probe of the unique DNA fraction, which indicated both the congruence with the morphological taxonomy of this group (e.g. within the Cyprididae Baird, 1845), and incongruence (e.g. within the Candonidae Kaufmann family, 1900) requiring verification by independent methods (**Wysocka et al., 2006**). I have now returned to this project and in the light of my cox 1 and 28S rRNA sequence data of Candoninae Kaufmann subfamily, 1900 a number of inconsistencies within its taxonomy were confirmed (A. Wysocka, unpublished data, a partial funding from grant **UG Nr L155-5-0100-9**; principal investigator). The research carried out as a part of the doctoral thesis was financed from the supervisory grant **KBN Nr 6P04C 057 17**, and awarded by the Council of the Faculty of Biology of the University of Gdansk.

In the years 2000-2001 I was associated with the Laboratory of Molecular Biology and Marine Biotechnology, Center for Marine Biology in Gdynia (PAN). Working in a new team was an invaluable experience for me. Performing the current researches of the Institute, I have been extending my laboratory skills, also in relation to prokaryotes.

After my employment as a full-time tutor in the Department of Genetics and Cytology of the University of Gdansk and a break related to maternity leave, at the end of 2002 I became involved in the project concentrated on studying the fauna diversity and evolutionary processes in Lake Ohrid. In this way, I have started the international cooperation with the Institute of Hydrobiology in Ohrid (Macedonia), and at the same time an inspiring scientific adventure. Unfortunately, at the beginning of this way, in 2004, during my first field trip to the lake, my mentor and supervisor, prof. dr hab. Tadeusz Sywula, died tragically, in Macedonia. This event had a serious impact on my academic career and made me manage it myself.

In the first years I conducted research on endemic isopod fauna (**UG Nr 1030-05-0227-4**; head), of which preliminary conclusions were presented in **Wysocka & Kilikowska (2004)** i **Kilikowska et al., (2006)**. The summary of these studies is a part of the scientific achievements presented here [**1, 2**]. At the same time, I was a participant in a project concerning the phylogenetic relationships between endemic Tricladida species from Lake Ohrid. In order to expand my laboratory skills, in 2004 I did a short-term scientific stage in the laboratory of prof. Marta Riutort from Departamento de Genètica (Universitat de Barcelona), dealing with the phylogeny of freshwater planarians for many years. The stage was funded by the EU research program, Center of Biosafety Research and Molecular Biomedicine (**UG Nr 1030-5-03-94**). Analysis of the allozymatic variability showed i.e. that the Ohridian population of *Dendrocoelum lacteum* (Müller, 1774) is genetically closer to the endemic species, *D. adenodactylosum* Ørsted, 1844 from the lake rather than its conspecific populations from Central Europe, suggested the necessity of systematic revision of the Ohridian population (**Sywula et al., 2006**).

Since 2008, I have been interested in another group of Ohridian endemics, amphipods of the genus *Gammarus*. In the same year I did a short-term scientific stage at the Institute of Hydrobiology in Ohrid, during which, in collaboration with Dr. Lyubomir Kendrov (Department of General and Applied Hydrobiology, University of Sofia), I learned the morphological identification of endemic species of *Gammarus* from Lake Ohrid; as it turned out, difficult groups due to the close relationship of some taxa and the reported cryptic diversity [3, 4, 5]. The turning point of this work was started in 2009, and lasting to these days, the fruitful cooperation with dr hab. Michał Grabowski, prof. University of Lodz, Department of Invertebrate Zoology and Hydrobiology. Based on the preliminary results of my pilot research on the endemic gammarids, I obtained financing for the project in 2010 (NCN Nr N N303 581 839, head). The results obtained during its implementation are part of the scientific achievements presented here [3, 4, 5].

In the years 2004-2015, I took part in six scientific expeditions to the Lake Ohrid area and the Balkan Peninsula. For two of them I was the organizer and manager. I also maintain close contacts with the Institute of Hydrobiology in Ohrid, thanks to which my adventure with the unique fauna of the lake has continued. I am currently continuing research on endemic amphipods of the genera *Synurella* Wrześniowski, 1877 and *Niphargus* Schiødte, 1847. Huge biological material of this group was obtained during the collection of Ohridian gammarids. At the beginning, using the DNA barcoding approach, I focused on verification of the taxonomic status of representatives of both genera (unpublished data).

In the years of preparing my habilitation thesis, the studies of the Lake Ohrid endemic fauna were not the only research projects I was working on. In cooperation with dr hab. Iwona Głazewska (Department of Plant Taxonomy and Nature Conservation, UG) I studied the Polish Arabian horse populations, one of the oldest and most important Arabian populations in the world. The main aim of study was to verify the origin of the founders of Polish Arabian dam lines using the D-loop region of mtDNA. The obtained results indicated a significant genetic similarity between some lines founded by Polish mares of unknown origin and lines established by desert-bred mares. The conclusions from these studies have been published in a prestigious international journal (**Głazewska et al., 2007**).

The cooperation with dr. Lech Krzysztofiak from the Wigry National Park in 2007-2008 was aimed at assessing the genetic diversity of Polish sibling populations of ant species, *Lasius niger* (Linnaeus, 1758) and *L. platythorax* Seifert, 1991 and in the case of the latter, confirmation of the taxonomic status with the rank of the species. I conducted the studies based on the sequence analysis of two mtDNA regions (cox 1, 16S rRNA) and analysis of the variability of four gene loci encoding enzymes (*Pgi*, *Pgm*, <sup>10</sup>*Idh*, *Mdh*<sup>11</sup>). The project was funded by University of Gdansk (Nr 1410-5-0114-7, head) and ended with publication in an international journal (**Wysocka et al., 2011**).

---

<sup>10</sup> isocitrate dehydrogenase

<sup>11</sup> malate dehydrogenase

In 2008-2009, in cooperation with dr Lech Buchholz (Świętokrzyski National Park), I worked on a project that aimed to determine the taxonomic status of individuals showing intermediate morphological characteristics between typical representatives of two click beetle species: *Athous vittatus* (Fabricius, 1792) and *A haemorrhoidalis* (Fabricius, 1801) based on the sequence analysis of mtDNA, cox 1 and 16S rRNA, nuclear ITS1/ITS2 region and analysis of the variability of nuclear genes encoding enzymes (*Idh*, *Pgi*, *Mdh*, *Pgd*<sup>12</sup>, *Pgm*<sup>13</sup> oraz *Me*<sup>14</sup>). In the paper, **Wysocka et al., (2011)** it was shown i.e. that in the case of individuals with intermediate traits, we are dealing with phenotypic plasticity which is a response to environmental conditions, thus undermining the hypothesis of the existence of a group of individuals that are interspecific hybrids. The project was financed from by University of Gdansk (Nr 1410-5-0394-8, head).

In cooperation with prof. dr hab. Tadeusz Namiotko (Department of Genetics, University of Gdansk), I examined the congruence between morphological variability and molecular divergence within the stygobiont ostracod species group, *Pseudocandona eremita* s.l. (Vejdovský) (Candoninae) from subterranean waters in Romania. The results show that for the most studied populations of *P. eremita* s.l. subtle morphological differences are accompanied by weak molecular divergence, suggesting that *P. eremita* is a morphologically diverse taxon. On the other hand, the occasional occurrence within the analysed group of highly different forms, both morphologically and genetically, does not exclude that the traditionally defined species group *P. eremita* s.l. is in fact a complex of (partly sympatric) species. The project was founded by University of Gdansk (No. L155-5-0100-9, principal investigator) and publication is currently being prepared.

The next step of cooperation with prof. dr hab. Namiotko has become a verification morphological taxonomy of the subfamily Candoninae Kaufmann, 1900 using mtDNA (cox 1 and 16S rRNA) and nuclear (28S rDNA) markers. The current project includes representatives of 9 out of 13 orders of this subfamily. The preliminary results indicating the lack of monophyly in a part of the orders types, and thus showing the requirement of taxonomic revision of Candoninae, is currently being prepared for printing.

Since 2010, I have been interested in the widespread in Europe, freshwater crustacean, water louse, *Asellus aquaticus* (Linnaeus, 1758). Initially, the research assumed the analysis of intraspecific genetic variability of Polish populations of this species (UG L155-5-0423-0, head). The first results, presented in the Master Thesis prepared by Ms. Lidia Sworobowicz, showed a surprisingly high, like a limited range, level of genetic diversity and became an inspiration to broaden the research to a further European populations also in terms of phylogeography. The obtained results, published in a prestigious international journal (**Sworobowicz et al., 2015**), indicated that *A. aquaticus* is a complex

---

<sup>12</sup> phosphogluconate dehydrogenase

<sup>13</sup> phosphogluconate dehydrogenase

<sup>14</sup> malate dehydrogenase (decarboxylating, NADP+)

of genetically distant lineages, one of which is the most widely represented in the postglacial region of Europe and corresponds to the nominative subspecies of *A. aquaticus aquaticus*, and the others, with narrow ranges in southern Europe, are probably of pre-Pleistocene origin. The results do not exclude the existence of potentially cryptic species within *A. aquaticus*. This publication will be part of the doctoral dissertation of Mrs Lidia Sworobowicz "Phylogeography of water louse *Asellus aquaticus* Linnaeus, 1758 (Crustacea, Isopoda) in Europe", of which I am the auxiliary supervisor. Currently, another publication is being finalized, indicating that the colonization of postglacial Europe by water louse took place from the proglacial system of lakes constituting the network of (micro) refugia, in which, surprisingly, this organism survived the Last Glacial Maximum. The publication will be submitted for review in the near future.

The discovery of hidden diversity in relation to a keystone in rivers in Europe and widespread amphipod species, *Gammarus fossarum* (Koch, 1836) has been a part of international cooperation. In this project I analyzed molecularly populations of that species from alpine lakes. Our current database includes nearly 500 locations in Europe and nearly 5,000 *cox1* sequences. Results will be presented in the near future as a publication.

In 2010-2015 I was the investigator of a project carried out on the population genetic structure of thick shelled river mussel, *Unio crassus* Philipsson, 1788 in the aspect of protective strategy for this endangered species (MNiSW Nr N N304 363 638, head dr hab. Jerzy Sell, prof UG). The first of the series of publications of which I am co-author regarding the correlation between the genetic variation of *U. crassus* and its geographical distribution associated with occurrence in a particular river basin is in preparation for printing.

Since 2015, I have been the main investigator and coordinator of the task in a project "Neogene and Quaternary sea level changes and origins of epigeal freshwater malacostracan fauna of the Periadriatic Region", led by dr hab. Michał Grabowski, prof. UŁ (Department of Invertebrate Zoology and Hydrobiology, University of Lodz) and implemented within the framework of international scientific cooperation. In the project I concentrated on molecular analyses of isopods from this region, including *A. aquaticus* and amphipods, including *G. roeseli*. One of the first papers to be co-authored is the chapter in the book on the fauna of a unique water reservoir, Lake Skadar (Montenegro) (**Grabowski et al. 2018**).

I was a participant in two scientific expeditions organized to collect material from Serbia, Macedonia, Greece (2015) and Italy and Austria (2016).

Another area of my interests is the aspect of inheritance of developmental dyslexia and its coexistence with hyperkinetic syndrome. The result of cooperation with dr hab. Małgorzata Lipowska (Institute of Psychology, Faculty of Social Sciences, University of Gdansk) are two review papers (**Wysocka et al., 2010, Wysocka & Lipowska, 2010**) and one original work (**Lipowska et al., 2011**).

**Summary of current achievements and scientific and teaching activities** (detailed information is presented in Appendix 3b)

All the research was conducted within 9 national scientific grants. The results were presented in 20 scientific papers, out of which 13 were published in significant journals listed in Journal Citation Report, e.g. *Journal of Biogeography*, *Freshwater Biology*, *Zoological Journal of the Linnean Society*, *Fundamental and Applied Limnology*, *Genetics Selection Evolution*, *Insectes Sociaux*, *Central European Journal of Biology*. Overall *impact factor* reported for these publications is 19,73 according to the year of publication and 24,96 according to the 5-year index. The publications were cited 92 times by other authors, and my Hirsh index is 6 according to Web of Science. The total number of points based on the list of Ministry of Science and Higher Education for the papers published in the JCR journals is 410.

I was author or co-author of 24 presentations during international and 19 during national scientific conferences. I reviewed 4 scientific papers including 3 indexed in the JCR.

I participated in 7 scientific expeditions to the Balkan Peninsula, Apennine Peninsula, and numerous national field studies.

My teaching experience included supervising of 27 Master and 5 Bachelor theses. I was a co-supervisor of 2 Master, 6 Bachelor theses. Since January 2015 I have been an auxiliary supervisor of one PhD thesis. During my employment at the Department of Genetics and Biosystematics, University of Gdansk I was teaching 12 different classes for students of biology, medical biology, biotechnology, neurobiopsychology and psychology. I actively participated in a number of campaigns promoting science within the framework of, e.g. Baltic Festival of Science, Discover the work of a biologist, Invite a scientist to school, the Universal Science Zone, Night of biologists. Since 2004, I have been conducting classes for primary and secondary school students.

#### References:

- Albrecht C, Vogel H, Hauffe T, Wilke T (2010) Sediment core fossils in ancient Lake Ohrid: testing for faunal change since the Last Interglacial. *Biogeosciences* 7: 3435-3446.
- Albrecht C, Trajanovski S, Kuhn K, Streit B, Wilke T (2006) Rapid evolution of an ancient lake species flock: freshwater limpets (Gastropoda: Ancyliidae) in the Balkan Lake Ohrid. *Organisms Diversity and Evolution* 6: 294-307.
- Albrecht C, Wilke T (2008) Ancient Lake Ohrid: biodiversity and evolution. *Hydrobiologia* 615: 103-140.
- Albrecht C, Wolff C, Glöer P, Wilke T (2008) Concurrent evolution of ancient sister lakes and sister species: the freshwater gastropod genus *Radix* in lakes Ohrid and Prespa. *Hydrobiologia* 615: 157-167.
- Belmecheri S, Namiotko T, Robert C, von Grafenstein U, Danielopol DL (2009) Climate controlled ostracod preservation in Lake Ohrid (Albania, Macedonia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 277: 236-245.
- Brooks JL (1950) Speciation in ancient lakes. *The Quarterly Review of Biology* 25: 131-176.
- Cohen A, Johnston MR (1987) Speciation in brooding and poorly dispersing lacustrine organisms. *PALAIOS* 2: 426-435.
- Cohen AS, Soreghan MJ, Scholz CA (1993) Estimating the age formation of lakes: an example from Lake Tanganyika, East African Rift system. *Geology* 21: 511-514.
- Cohen AS, Stone JR, Beuning KRM, Park LE, Reinthal PN, Dettman D, Scholz CA, Johnson TC, King JW, Talbot MR, Brown ET, Ivory SJ (2007) Ecological Consequences of Early Late-Pleistocene Megadroughts in Tropical Africa. *Proceedings of the National Academy of Sciences USA* 104: 16422-16427.

- Coulter GW (1991) Lake Tanganyika and its life. British Museum (Natural History), London & Oxford University Press, Oxford & New York.
- Cristescu ME, Adamowicz SJ, Vaillant JJ, Haffner DG (2010) Ancient lakes revisited: from the ecology to the genetics of speciation. *Molecular Ecology* 19: 4837–4851.
- Elmer KR, Reggio C, Wirth T, Verheyen E, Salzburger W, Meyer A (2009) Pleistocene desiccation in East Africa bottlenecked but did not extirpate the adaptive radiation of Lake Victoria haplochromine cichlid fishes. *Proceedings of the National Academy of Sciences USA* 106: 13404–13409.
- Eme D, Malard F, Konecny-Dupre L, Lefébure T, Douady C J (2013) Bayesian phylogeographic inferences reveal contrasting colonization dynamics among European groundwater isopods. *Molecular Ecology* 22: 5685–5699.
- Föllner K, Stelbrink B, Hauffe T, Albrecht C, Wilke T (2015) Constant diversification rates of endemic gastropods in ancient Lake Ohrid: ecosystem resilience likely buffers environmental fluctuations. *Biogeosciences* 12: 7209–7222.
- Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34: 397–423.
- Głazewska I, Wysocka A, Gralak B, Prus R, Sell J (2007) A new view on dam lines in Polish Arabian horses based on mtDNA analysis. *Genetics Selection Evolution* 39: 609–619.
- Gorthner A (1994) What is an ancient lake? In: Martens K, Coulter G, Goddeeris B, eds. *Speciation in ancient lakes*. Stuttgart: E. Schweizerbart'sche
- Greenwood PH (1984) What is a species flock? In: Echelle AA, Kornfield I, eds. *Evolution of fish species flocks*. Orono: University of Maine at Orono, 13–19.
- Hauffe T, Albrecht C, Wilke T (2015) Gastropod diversification and community structuring processes in ancient Lake Ohrid: a metacommunity speciation perspective. *Biogeosciences Discussion*: 16081–16103.
- Hauswald, A-K, C Albrecht, T Wilke (2008) Testing two contrasting evolutionary patterns in ancient lakes: Species flock vs. species scatter in valvate gastropods of Lake Ohrid. *Hydrobiologia* 615: 169–179.
- Hebert PD, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences* 270: 313–321.
- Jörger K, Schrödl M. 2013. How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology* 10: 1–27.
- Jovanovska E, Cvetkoska A, Hauffe T, Levkov Z, Wagner B, Sulpizio R, Francke A, Albrecht C, Wilke T (2015) Differential resilience of ancient sister lakes Ohrid and Prespa to environmental disturbances during the Late Pleistocene. *Biogeosciences Discussions*, 12: 16049–16079.
- Karaman SL (1929) Beitrag zur Kenntnis der Amphipoden Jugoslaviens II. *Glasnik Zemaljskog muzeja u Bosni i Hercegovini* 41: 83–100.
- Karaman SL (1931) Beitrag zur Kenntnis der Amphipoden Jugoslaviens, sowie einiger Arten aus Griechenland. *Prirodoslovne Razprave, Prirodoslovna sekcija Muzejskega društva za Slovenijo* 1: 31–66.
- Karaman SL (1953) Die Aselliden des Ohridsees. – *Periodicum Biologorum Societas Scientiarum Naturalium Croatica Ser. II/B* 4–6: 46–76.
- Karaman GS (1977) Contribution to the knowledge of the Amphipoda 77. *Gammarus ochridensis* Schaf. species complex of Ohrid Lake. *Glasnik Odjeljenja Prirodnih Nauka, Crnogorska Akademija Nauka i Umjetnosti* 2: 49–89.
- Karaman GS (1989) New species of the family Gammaridae from Ohrid Lake basin, *Gammarus sketi*, n. sp., with emphasis on the subterranean members of genus *Gammarus* Fabr. (Contribution to the knowledge of the Amphipoda 191). *Glasnik Odjeljenja prirodnih nauka, Crnogorska akademijanauka i umjetnosti* 7: 53–71.
- Karaman G, Pinkster S (1977a) Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea–Amphipoda). Part I. *Gammarus pulex* group and related species. *Bijdragen tot de Dierkunde* 47: 1–97.
- Karaman G, Pinkster S (1977b) Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea–Amphipoda). Part II. *Gammarus roeseli* group and related species. *Bijdragen tot de Dierkunde* 47: 165–196.
- Karaman G, Pinkster S (1987) Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea–Amphipoda). Part III. *Gammarus balcanicus*-group and related species. *Bijdragen tot de Dierkunde* 57: 207–260.
- Kaygorodova IA, Sherbakov D, Martin PJ (2007) Molecular phylogeny of Baikalian Lumbriculidae (Oligochaeta): Evidence for recent explosive speciation. *Comparative Cytogenetics* 1(1): 71–84.
- Kilikowska A, Wysocka A, Sell J, Ziętara M, Sywula T (2006) Notes on genetic differentiation within the endemic *Proasellus* species group from Lake Ohrid (Balkan Peninsula). *Biological Letters* 43: 21–32.
- Kobl Müller S, Sefc KM, Sturmbauer C (2008) The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. *Hydrobiologia* 615: 5–20.



- Kroll O, Hershler R, Albrecht C, Terrazas EM, Apaza R, Fuentealba C, Wolff C, Wilke T (2012) The endemic gastropod fauna of Lake Titicaca: correlation between molecular evolution and hydrographic history. *Ecology and Evolution*, 2: 1517–1530.
- Lavenu A (1992) Formation and geological evolution. In: *Lake Titicaca: A Synthesis of Limnological Knowledge*. Dejoux C, Iltis A, eds. Dordrecht: Kluwer.
- Lindhorst K, Krastel S, Reicherter K, Stipp M, Wagner B, Schwenk T (2015) Sedimentary and tectonic evolution of Lake Ohrid (Macedonia/Albania). *Basin Research*, 27: 84–101.
- Lindhorst K, Vogel H, Krastel S, Wagner B, Hilgers A, Zander A, Schwenk T, Wessels M, Daut G (2010) Stratigraphic analysis of lake level fluctuations in Lake Ohrid: an integration of high resolution hydro-acoustic data and sediment cores. *Biogeosciences* 7: 3531–3548.
- Lipowska M, Czaplewska E, Wysocka A (2011) Visuospatial deficits of dyslexic children. *Medical Science Monitor* 17: 216–221.
- Macdonald III KS, Yampolsky L, Duffy JE (2005) Molecular and morphological evolution of the amphipod radiation of Lake Baikal. *Molecular Phylogenetics and Evolution* 35: 323–343.
- Mamos T, Wattier R, Burzński A, Grabowski M (2016) The legacy of a vanished sea: a high level of diversification within a European freshwater amphipod species complex driven by 15 My of Paratethys regression. *Molecular Ecology* 3: 795–810.
- Marijnissen SAE, Michel EE, Daniels SR, Erpenbeck D, Menken SBJ, Schram FR (2006) Molecular evidence for recent divergence of Lake Tanganyika endemic crabs (Decapoda: Platythelphusidae). *Molecular Phylogenetics and Evolution* 40: 628–634.
- Martens K (1997) Speciation in ancient lakes (review). *Trends in Ecology and Evolution* 12: 177–182.
- Matzinger A, Jordanoski M, Veljanoska-Sarafiloska E, Sturm M, Muller B, Wüest A (2006) Is Lake Prespa jeopardizing the ecosystem of ancient Lake Ohrid? *Hydrobiologia* 553: 89–109.
- Mitic V, Kostoski G., Guseska D., Patceva S. (2002) *Limnological investigations of Lake Ohrid*. Hydrobiological Institute, Vol.1&2, Ohrid.
- Morvan C, Malard F, Paradis E, Lefébure T, Konecny-Dupré L, Douady C (2013) Timetree of aselloidea reveals species diversification dynamics in groundwater. *Systematic Biology* 62: 512–522.
- Nagl S, Tichy H, Mayer WE, Takezaki N, Takahata N, Klein J (2000) The origin and age of haplochromine fishes in Lake Victoria, East Africa. *Proceedings of the Royal Society London, Series B* 267: 1059–1061.
- Namietko T, Namietko L, Wysocka A (2012) Distribution of subfossil ostracod assemblages (Crustacea: Ostracoda) in lacustrine profundal sediments of North-eastern Poland. *Revue de Micropaleontologie* 54: 17–27.
- Pešić V (2015) A new species of the water mite genus *Hygrobatas* Koch, 1837 (Acari: Hydrachnidia: Hygrobatidae) from the ancient Lake Ohrid. *Zootaxa* 3926: 287–295.
- Rossiter A (1995) The cichlid fish assemblages of Lake Tanganyika: ecology, behaviour and evolution of its species flock. *Advances in Ecological Research* 26: 187–252.
- Rossiter A, Kawanabe H, eds. (2000) *Ancient Lakes: Biodiversity, Ecology and Evolution*. *Advances in Ecological Research*, Vol. 31. San Diego: Academic Press.
- Rüber L, Verheyen E, Sturmbauer C, Meyer A (1998) Lake level fluctuations and speciation in rock-dwelling cichlid fish in Lake Tanganyika, East Africa. In: Grant, P (ed.), *Evolution on Islands*. Oxford University Press, Oxford.
- Salemaa H, Kamal'tynov RM (1994) The chromosome numbers of endemic Amphipoda and Isopoda – an evolutionary paradox in the ancient lakes Ohrid and Baikal. *Archiv für Hydrobiologie Ergebnisse der Limnologie, Beiheft* 44: 247–256.
- Salemaa, H (1985) Karyological studies in *Gammarus* and *Asellus* species from Lake Ohrid. Hydrobiological Station Ohrid, Edition jubilaire 1, 245–254.
- Scholz CA, Johnson TC, Cohen AS, King JW, Peck JA, Overpeck JT, Talbot MR, Brown ET, Kalindekafe L, Amoako PYO, Lyons RP, Shanahan TM, Castaneda IS, Heil CW, Forman SL, McHargue LR, Beuning KR, Gomez J, Pierson J (2007) East African megadroughts between 135 and 75 thousand years ago and bearing on early-modern human origins. *Proceedings of the National Academy of Sciences USA* 104: 16416–21.
- Schön I, Martens K. 2004. Adaptive, pre-adaptive and nonadaptive components of radiations in ancient lakes: a review. *Organisms Diversity and Evolution* 4: 137–156.
- Schreiber K, Hauffe T, Albrecht C, Wilke T (2012) The role of barriers and gradients in differentiation processes of pyrgulinid microgastropods of Lake Ohrid. *Hydrobiologia* 682: 61–73.
- Schultheiß R, Albrecht C, Bößneck U, Wilke T (2008) The neglected side of speciation in ancient lakes: phylogeography of an inconspicuous mollusc taxon in lakes Ohrid and Prespa. *Hydrobiologia* 615: 141–156.
- Schultheiß R, Wilke T, Jørgensen A, Albrecht C (2011) The birth of an endemic species flock: demographic history of the *Bellamyia* group (Gastropoda, Viviparidae) in Lake Malawi. *Biological Journal of the Linnean Society* 102: 130–143.

- Seehausen O. 2006. African cichlid fish: A model system in adaptive radiation research. *Proceedings of the Royal Society B: Biological Sciences* 273: 1987–98.
- Sell J, Spirkovski Z (2004) Mitochondrial DNA differentiation between two forms of trout *Salmo letnica*, endemic to the Balkan Lake Ohrid, reflects their reproductive isolation. *Molecular Ecology*, 13: 3633-3644.
- Sherbakov DY (1999). Molecular phylogenetic studies on the origin of biodiversity in Lake Baikal. *Trends in Ecology and Evolution* 14: 92–95.
- Stankovič S (1960) The Balkan Lake Ohrid and its living world. *Monographiae Biologicae*, Vol. 9. Den Haag: Uitgeverij Dr.W. Junk.
- Stocchino GA, Sluys R, Deri P, Manconi R (2013) Integrative taxonomy of a new species of planarian from the Lake Ohrid basin, including an analysis of biogeographical patterns in freshwater triclads from the Ohrid region (Platyhelminthes, Tricladida, Dugesiidae), *Zookeys* 313: 25–43.
- Stager JC, Johnson TC (2008) The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. *Hydrobiologia* 596: 5-16.
- Stelbrink B., Shirokaya AA, Föller K, Wilke T, Albrecht C (2016) Origin and diversification of Lake Ohrid's endemic acroloxid limpets: the role of geography and ecology. *BMC Evolutionary Biology*. doi 10.1186/s12862-016-0826-6
- Sturmbauer C, Baric S, Salzburg W, Rüber L, Verheyen E (2001) Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Molecular Biology and Evolution* 18: 144–154.
- Sturmbauer C, Meyer A (1992) Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature* 358: 578-581.
- Sturmbauer C, Verheyen E, Rüber L, Meyer A (1997) Phylogeographic patterns in populations of cichlid fishes from rock habitats in Lake Tanganyika. In: *Molecular Phylogeny of Fishes*. Kocher TD & Stepien C, eds. San Diego: Academic Press.
- Sušnik S, Knizhin I, Snoj A, Weiss S (2006) Genetic and morphological characterization of a Lake Ohrid endemic, *Salmo (Acantholingua) ohridanus* with a comparison to sympatric *Salmo trutta*. *Journal of Fish Biology* 68 (Suppl. A): 2–23.
- Sworobowicz L, Grabowski M, Mamos T, Burzyński A, Kilikowska A, Sell J, Wysocka A (2015) Revisiting COI phylogeography of *Asellus aquaticus* in Europe: insight into cryptic diversity and spatiotemporal diversification. *Freshwater Biology* 60: 1824–1840.
- Sywula T, Krstanovski Z, Biala A, Wysocka A, Kilikowska A, Sell J (2006) Phylogenetic position of *Dendrocoelum lacteum* (Tricladida) from the Balkan Lake Ohrid evidenced by allozyme data. *Biochemical Systematics and Ecology*, 34: 212-218.
- Sywula T, Krstanovski Z, Tasevska O, Sell J, Kretowicz T (2003) Genetic differences among several species of Tricladida from the relict Lake Ohrid as revealed by enzyme electrophoresis. *Folia Biologica (Kraków)*, 51: 105-109.
- Trajanovski S, Albrecht C, Schreiber K, Schultheiß R, Stadler T, Benke M, Wilke T (2010) 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.
- Väinölä R, Kamal'tynov RM (1999) Species diversity and speciation in the endemic amphipods of Lake Baikal: molecular evidence. *Crustaceana* 72: 945–956.
- Van Bocxlaer B, Schultheiß R, Plisnier P-D, Albrecht C (2012) Does the decline of gastropods in deep water herald ecosystem change in Lakes Malawi and Tanganyika? *Freshwater Biology* 57: 1733–1744.
- Wagner B, Wilke T, Francke A, Albrecht C, Baumgarten H, Bertini A, Combourieu-Nebout N, Cvetkoska A, D'Addabbo M, Donders TH, Föller K, Giaccio B, Grazhdani A, T Hauffe, J Holtvoeth, S Joannin, E Jovanovska, J Just, K Kouli, A Koutsodendris, S Krastel, JH Lacey, N Leicher, MJ Leng, Z Levkov, K Lindhorst, A Masi, AM Mercuri, SNomade, N Nowaczyk, K Panagiotopoulos, O Peyron, JM Reed, E Regattieri, L Sadori, L Sagnotti, B Stelbrink, R Sulpizio., S Tofilovska, P Torri, H Vogel, T Wagner, F Wagner-Cremer, GA Wolff, T Wonik, G Zanchetta, XS Zhang (2017) The environmental and evolutionary history of Lake Ohrid (FYROM/Albania): interim results from the SCOPSCO deep drilling project. *Biogeosciences* 14: 2033–2054.
- Wagner B, Wilke T, Krastel S, Zanchetta G, Sulpizio R, Reicherter K, Leng MJ, Grazhdani A, Trajanovski S, Francke A, Lindhorst K, Levkov Z, Cvetkoska A, Reed JM, Zhang X, Lacey JH, Wonik T, Baumgarten H, Vogel H (2014) The SCOPSCO drilling project recovers more than 1.2 million years of history from Lake Ohrid, *Scientific Drilling* 17: 19–29.
- Watzin MC, Puka V, Naumoski TB, eds. (2002) Lake Ohrid and its watershed, state of the environment report. Lake Ohrid Conservation Project. Tirana, Albania and Ohrid, Macedonia.
- Wilke T, Albrecht C, Anistratenko VV, Sahin SK, Yildirim MZ (2007) Testing biogeographical hypotheses in space and time: faunal relationships of the putative ancient Lake Egirdir in Asia Minor. *Journal of Biogeography* 34: 1807–1821.

- Wilke T, Schultheiß R, Albrecht C (2009) As time goes by: A simple fool's guide to molecular clock approaches in invertebrates. *American Malacological Bulletin* 27: 25-45.
- Wilson AB, Glaubrecht M, Meyer A (2004) Ancient lakes as evolutionary reservoirs: Evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society B, Biological Sciences* 271: 529-536.
- Wysocka A, Kilikowska A (2004) Dywergencja molekularna ośliczek (Isopoda, Asselidae) z Jeziora Ochrydzkiego (Macedonia). W: Namiotko T., Sywula T. *Bioróżnorodność środowisk dna zbiorników wodnych*. BEL Studio, Gdańsk – Warszawa: 98-100
- Wysocka A, Konopa G, Węgrzyn G, Wróbel B (2006) Genomic DNA hybridization as an attempt to evaluate phylogenetic relationships of Ostracoda. *Crustaceana* 11: 1309-1322.
- Wysocka A, Krzysztofiak L, Krzysztofiak A, Żołnierkiewicz O, Ojdowska E, Sell J (2011) Low genetic diversity in Polish populations of sibling ant species: *Lasius niger* (L.) and *Lasius platythorax* Seifert (Hymenoptera, Formicidae). *Insectes Sociaux* 58: 191-195.
- Wysocka A, Kaczmarczyk A, Buchholz L, Sell J (2011) Morphologically intermediate form between *Athous haemorrhoidalis* and *A. vittatus* (Coleoptera: Elateridae): a case of hybridization? *Annales Zoologici (Warszawa)* 61(4): 629-635.
- Wysocka A, Lipowska M (2010) Genetyczne podłoże współwystępowania ADHD i dysleksji rozwojowej. *Psychiatria i Psychologia Kliniczna* 10: 189-194.
- Wysocka A, Lipowska M, Kilikowska A (2010) Genetics in solving dyslexia puzzles: the overview. *Acta Neuropsychologica* 8: 315-331.
- Wysocka A, Sell J., Sywula T. 2000. Genetic variability in natural populations of eurytopic ostracod *Candona neglecta* Sars. *Zoological Science*, 17(1): 55-59.

Anna Wysocka