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ROTIFERA MONOGONONTA

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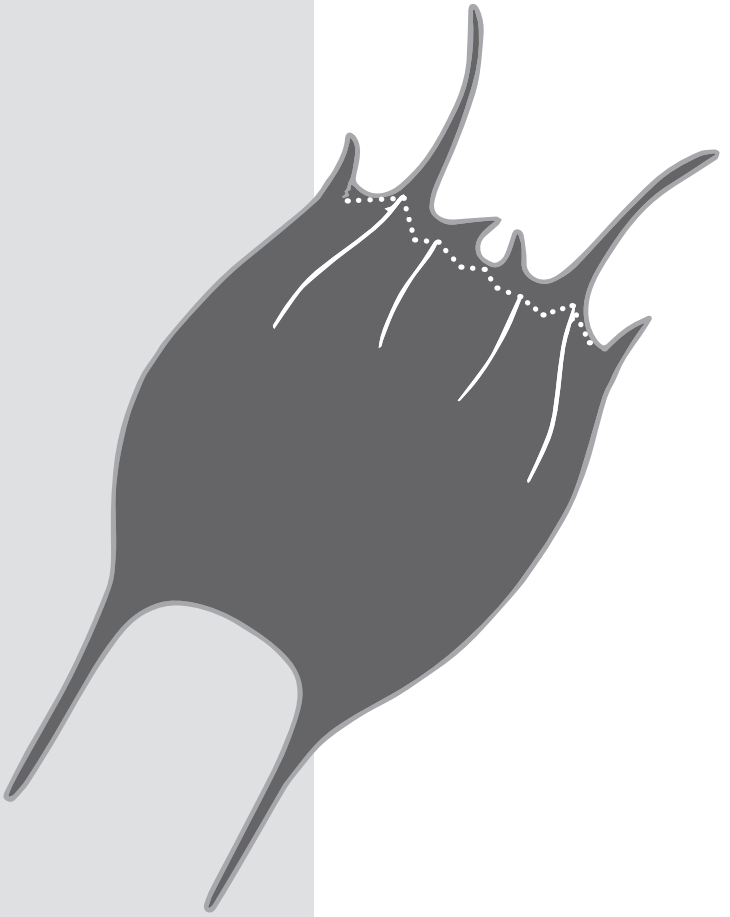

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I. INTRODUCTION

Rotifers (Rotifera) are animals which occur in every type of aquatic environment, both marine and freshwater; they dwell also in moist soil. They owe their wide distribution to rapid reproduction. Due to their high abundances, they play an important role in freshwater ecosystems. The world's fauna includes about 2000 rotifer species, 1350 of them being reported from Europe (Bērziņš 1978). So far, about 480 species belonging to the Monogononta have been recorded in Poland, a further 156 of them being supposed to occur in the country (Bielańska-Grajner and Radwan 1997, Ejsmont-Karabin et al. 2004). As evidenced by the research reported hitherto, the order Bdelloidea is represented by 117 species (Bielańska-Grajner et al. 2013).

This publication is a tribute to the eminent Polish researchers of rotifers who have contributed considerably to the knowledge of rotifer taxonomy, biology, and ecology. While paying homage to those scientists, particularly to Antoni Wierzejski, Antoni Jakubski, Jerzy Wiszniewski, and Leszek K. Pawłowski, we wish to emphasise that the book draws substantially upon their work and, at the same time, provides an overview of 100 years of Polish studies on rotifers.

A particularly important place in the history of Polish rotifer research belongs to Jerzy Wiszniewski who discovered and described the rich and extremely interesting world of psammic rotifers which inhabit interstitial spaces of lacustrine beach sands. His last work, entitled "Fauna wrotków Polski i rejonów przyległych" ["The Rotifer Fauna of Poland and Adjacent Regions"], published posthumously in 1953, contains his message, his last will, addressed to subsequent generations of Polish researchers. The message focuses on the importance of comprehensive research on the biology and ecology of rotifers inhabiting diverse and specific ecosystems and habitats. He wrote: "The future studies should aim, on the one hand, at obtaining a more detailed knowledge of the faunas of habitats that show a considerable potential (small water bodies, subterranean waters, acid and brackish waters, muds, mosses, moist leaves and forest litter, and periphyton as well as putative hosts of various parasitic and commensal rotifers, etc.); on the other hand, the research should address relationships between the rotifer fauna and ecological characteristics of its habitats, intensification of rotifer research being an overall goal" [translation: Teresa Radziejewska]. It is the hope of the present authors that this publication will make it easier for future generations of Polish researchers to live up to what Jerzy Wiszniewski expected of them.

We subscribe to the opinion that species-specific characters of rotifers are poorly differentiated and, in many instances, difficult to describe. It would be then virtually impossible to develop a dichotomous key to all the species present in Poland. Moreover, such a key would be useful only for those biologists who specialise in rotifer taxonomy, and they use numerous original foreign source papers anyway (see References). Because this publication has torovide non-specialists with a relatively simple and user-friendly tool, we decided that the best solution would be to put together descriptions and figures of individual species and to highlight their distinguishing characteristics. The species are arranged alphabetically by their scientific names. For a correct identification, it is necessary to use both keys to families and genera and species descriptions.

Those readers willing to probe deeper into this unusual and so poorly known animal taxon and, perhaps, to discover rotifer species new to Poland, are encouraged to peruse information contained in Chapter VI. It deals with species which, although known from the neighbouring countries, have not been reported from Poland so far.

Those readers who need more detailed data on individual species or who are willing to get acquainted also with the rotifers that do not occur in Poland are advised to consult keys to rotifer families published within the series "Guides to the Identification of the Microinvertebrates of the Continental Waters of the World" (the volumes published so far are listed in References). Individual volumes of the series, edited – since 1992 – by H. J. Dumont of Ghent University (Belgium), were written by the most prominent specialists in rotifer taxonomy and ecology, and are at present the most complete and authoritative source of information on the Rotifera. We wish to add that both the taxonomic position of each species and the nomenclature used conform to our current opinions. If other species and genus names are encountered, it is advisable to consult the list of synonyms (Chapter IX).

THE AUTHORS

II. HISTORY OF RESEARCH ON POLISH ROTIFERS AND THE PRESENT STATE OF THEIR KNOWLEDGE

Initial information on the presence of rotifers in Poland dates back to the late 18th century when, in 1775, these animals were observed and described by Eichhorn, a Lutheran church minister from Gdańsk. A few rotifer species were mentioned briefly by the Rev. K. Kluk in his 1795 book "Zwierząt domowych i dzikich osobliwie krajowych, historyi naturalney początki i gospodarstwo" ["A primer on natural history and management of domesticated and wild animals, particularly those of this country"]. However, the credit for the beginnings of a more in-depth research on the taxonomy and ecology of rotifers is due to Antoni Wierzejski (1843–1916), a professor of the Jagiellonian University.

Wierzejski's most important work is the monograph "Wrotki Galicji" ["The Rotifers of Galicia"] (Wierzejski 1893). The monograph contains a long list of species; some of them are annotated with detailed descriptions of morphology and anatomy and with information on reproduction modes. Wierzejski also provided methodological guidelines with respect to collection and processing of research materials. In addition, he demonstrated the ubiquity of rotifers and described numerous new species, e.g., *Atrochus tentaculatus, Brachionus forficula*, *Synchaeta stylata*, *Polyarthra euryptera*, *Collotheca (Floscularia) atrochoides* and *Trichocerca similis* as well as the genus *Bipalpus* and the species *Trichocerca capucina,* both described jointly with Zacharias.

Somewhat later, the area of the former Galicia became the focus of activity of Antoni Jakubski (1885–1962), a professor of universities in Lvov and Poznań, known for his interesting and diverse research. His major study concerned primarily planktonic rotifers in the environs of Sokal where he identified 257 taxa (Jakubski 1914/15). His other publications contain data on moss-dwelling rotifers (Jakubski 1918) and also on those living in the tropics (Jakubski 1912).

Jerzy Wiszniewski (1908–1944) was, doubtless, the most prolific researcher of the Polish rotifer fauna. During his short life he managed to publish 24 scientific papers (5 were left as manuscripts), 4 popular-science articles, 4 short communications, and 3 essays. His doctoral dissertation, written under the supervision of Professor Janicki, dealt with rotifers inhabiting the environs of Warsaw. In a fragment of the dissertation, published in 1929, Wiszniewski described one rotifer genus and two species new to science. In 1930 Wiszniewski was working as an assistant at the Hydrobiological Station on Lake Wigry. His

most important achievements at that time included papers on psammic rotifers; these contain not only an ecological characterisation of a sandy beach (euarenal), but describe distinct ecological differentiation of rotifers dwelling in that habitat (Wiszniewski 1934a, b, 1937, 1947). Basing his work on physical and chemical analyses, he was able to demonstrate that, although the beach sand is a highly thermally astatic habitat, less oxygenated than the water of the neighbouring lake, it is home for rich and diverse life forms. They include numerous species of algae, protozoans, nematodes, gastrotrichs, tardigrades, oligochaetes, turbellarians, and – primarily – very numerous rotifers. Those studies were importantly complemented by other papers devoted to the psammon (Wiszniewski 1935a, b, 1936a, b) as well as a ground-breaking paper on psammic rotifer males (Wiszniewski 1934a). His largest publication, "Les Rotifères psammiques", contains descriptions of 82 rotifer species, including 14 species and three genera (*Wierzejskiella, Wigrella,* and *Myersinella*) new to science (Wiszniewski 1934a). Wiszniewski's simultaneous studies on rotifers living in the branchial chamber of freshwater crustaceans (Wiszniewski 1953b) attest to the unusual breadth of his knowledge and interests.

A detailed account of the state of knowledge of the rotifer fauna of various areas of Poland is contained in "Fauna wrotków Polski i rejonów przyległych" ["The Rotifer Fauna of Poland and Adjacent Areas"] (Wiszniewski 1953a). As shown by the list of rotifer literature contained in the paper, the period of 1777–1939 spawned about 120 papers dealing with those invertebrates. Considering the major focus of those papers, Wiszniewski divided them into the following six groups:

1) taxonomic and faunistic,
2) biological and anatomical,
3) planktonological,
4) dealing with water pollution,
5) popular science and conference communications,
6) miscellaneous.

The regions of Wielkopolska and Kujawy, Lake Wigry, the region of Podlasie, and the environs of Warsaw, Cracow, Gdańsk, and Łódź are areas within the present boundaries of Poland regarded by Wiszniewski as the best known in terms of their rotifer fauna. Gieysztor (1963) and Brzęk (1988) provide a full description of Wiszniewski's scientific legacy.

Research on rotifers in Poland benefited greatly from the contribution of Professor Leszek Pawłowski (1902–1980), a prominent faunist and taxonomist, the most eminent Polish authority on bdelloid rotifers (Bdelloidea). He left detailed descriptions of the parasitic rotifers *Drilophaga bucephalus* (Pawłowski 1934) and *D. delagei* (Pawłowski 1935) and studied moss-dwelling rotifers (Pawłowski 1938). However, his most important work involves research on the rotifer fauna

of River Grabia and its catchment (Pawłowski 1958, 1960, 1968, 1970, 1973). Pawłowski described numerous species new for the Polish fauna and one species new to science (*Cephalodella bryophila*) (Pawłowski 1954). His last work, "Fauna wrotków pleustonowych w zespole *Wolffietum arrihize*" ["The Pleustonic Rotifer Fauna in the *Wolffietum arrihize* community"] (Pawłowski 1980) contains references to 140 rotifer species occurring in two macrophytic communities of fish ponds, the *Wolffietum* and the *Lemnetum*.

In the post-World War II period, studies on rotifer biology and ecology have been conducted in several Polish research centres. Since 1950, more than 320 papers on rotifers have been published, each year bringing a further 10–15 (Hillbricht-Ilkowska 1995).

Lakes are the best-known habitats for rotifers in Poland, lacustrine rotifer research being dominated by faunistic and ecological studies. Numerous authors have focused on rotifers inhabiting lakes which differ in morphometry and trophic status, are clean or polluted (Bittel 1964, 1965, 1974; Brzęk et al. 1975; Ejsmont-Karabin and Węgleńska 1985; Hillbricht-Ilkowska et al. 1975; Hillbricht-Ilkowska et al. 1977; Karabin 1983, 1985a, b; Karabin and Ejsmont-Karabin 1991, 1993; Pijanowska 1980; Radwan 1966, 1967, 1968, 1969, 1973, 1974, 1980, 1984; Radwan et al. 1984, 1987, 1996; Radwan and Popiołek 1977, 1989; Sterzyński 1979; Tunowski 1992; Widuto 1977, 1979, 1988, 1989; Węgleńska et al. 1983; Zawiślak 1979).

Studies on rotifer productivity and contribution to energy flux in lacustrine ecosystems, based on rotifer abundance, caloric and carbon content, and biomass, were published by Grygierek (1979), Hillbricht-Ilkowska (1977), Hillbricht-Ilkowska et al. (1975, 1977, 1988), and Żurek (1974).

Effects of fertiliser and lime addition as well as influences of fish stock density and quality on rotifer development were studied in the pond-type Lake Warniak (Bownik-Dylińska et al. 1980; Hillbricht-Ilkowska 1977; Hillbricht-Ilkowska and Węgleńska 1973; Ejsmont-Karabin et al. 1975).

A few papers dealt with rotifers occurring in heated waters (Bielańska-Grajner and Pilarczyk 1996; Hillbricht-Ilkowska et al. 1988).

A number of studies tackled responses of zooplankton, including rotifers, to various methods of lake restoration (Bielańska-Grajner and Pilarczyk 2000; Widuto 1977, 1979, 1988, 1989).

Intensive research has been carried out on zooplankton in fish ponds. The problems studied included effects of fish stock density, fertilisation and pollution on rotifer assemblages in ponds and on the zooplankton (rotifer) production important for the production of fish (Fereńska 1966; Fereńska and Lewkowicz 1966; Klimczyk 1956, 1958, 1964; Lewkowicz 1972, 1974; Krzeczkowska-Wołoszyn 1966, 1967, 1972; Bucka and Kyselowa 1967; Kyselowa 1966, 1973; Siemińska and Siemińska 1967; Żurek 1974).

The development of rotifer assemblages in dam reservoirs in relation to the reservoir age and water exchange as well as reservoir effects on the riverine fauna downstream of the dam are fairly well known (Czapik 1958a; Bielańska-Grajner 1978, 1983/1984a, b, 1987, 1990; Krzanowski 1965, 1971, 1986, 1987; Mleczko 1965, 1968; Żurek and Dumnicka 1989).

In contrast, there have been but a few studies on rotifers occurring in small ponds and lakes of the Tatra Mountains. Wierzejski (1882) was the first to describe them; he was followed by Minkiewicz (1914) and, in the post-World War II period, by Gliwicz (1969), Woźniczka (1965), and Woźniczka-Starzykowa (1966a, b).

Moss-dwelling rotifers have not been attracting much attention so far, either. They were studied in Tatra mountain streams (Madaliński 1961) and Pawłowski (1938) investigated moss-dwelling rotifers in the Masurian Lake District, the Tatra Mountains and around Pabianice. Moss-inhabiting rotifers were studied in different peatlands of the Poleski National Park and in the Tatra national Park (Bielańska-Grajner et al. 2011a; Bielańska-Grajner et al. 2011b; Bielańska-Grajner et al. 2011c).

The study of psammic rotifers in Poland was pioneered by Wiszniewski whose contribution to the field is described above. At present, psammic rotifers are attracting much attention again: both their distribution in various zones of sandy beaches and the respective contributions of different ecological groups of psammic rotifers (psammobionts, psammophiles, psamoxenes) to the rotifer fauna are explored in lacustrine habitats (Bielańska-Grajner 2001; Ejsmont-Karabin 1998b, 2003, 2008a, 2008b; Radwan and Bielańska-Grajner 2001; Radwan et al. 2003).

Rotifers of astatic and littoral habitats were studied by Klimowicz (1964, 1967, 1970, 1972). The influence of macrophytes on the structure of littoral communities of Rotifera has been studied by Kuczyńska-Kippen (2005) and Kuczyńska-Kippen and Nagengast (2006).

Rotifers inhabiting brackish waters, the Baltic Sea gulfs and lagoons were fairly thoroughly investigated, both from the faunistic and ecological points of view (Różańska 1962, 1963, 1967; Adamkiewicz-Chojnacka 1978, 1983; Adamkiewicz-Chojnacka and Różańska 1990; Adamkiewicz-Chojnacka et al. 1986; Wiktor 1957, 1958, 1972, 1989; Wiktor et al. 1982; Wiktor and Żmijewska 1985; Radwan and Adamkiewicz-Chojnacka 1989; Gutkowska et al. 2013).

Compared to the intensity of rotifer studies in lakes and ponds, lotic habitats – with the exception of the classic papers by Pawłowski (1958, 1968, 1970, 1973) on River Grabia – have been investigated to a much smaller extent. Generally, the lotic water studies can be divided into those conducted in the major Polish rivers (and their tributaries) and in rivers discharging into lakes.

The Vistula and its tributaries have received most attention in riverine rotifer research. The upper reaches of the Vistula were the area of studies conducted by Bednarz and Żurek (1988) and Żurek (2000, 2002). Krzeczkowska-Wołoszyn

(1985) and Żurek (1985) studied effects of anthropogenic pressure on coloniser organisms in River Brynica. Żurek (2000) provided a qualitative and quantitative analysis of the Rotifera in Vistula tributaries (the Raba, Rudawa, Prądnik, Dłubnia, and Szreniawa) in the environs of Cracow.

Seston, including rotifers, of the middle part of the Vistula was studied by Cabejszek et al. (1959), Klimowicz (1977, 1981), Kowalczewski et al. (1985), Papińska (1990), and Praszkiewicz et al. (1983). Rotifers inhabiting tributaries of the mid- and downstream Vistula reaches were dealt with by Cabejszek et al. (1959), Ejsmont-Karabin and Węgleńska (1990), Klimowicz (1981), and Rozum (1981).

Still fewer are rotifer studies in tributaries of River Odra. Rotifers of the upper reaches of the Stoła and Mała Panew were treated Żurek (1985), those found in the Nacyna and Ruda by Bielańska-Grajner (1990), while Niesler (2001) worked in the Ślepiotka. Rotifers collected from River Cybina, a mid- and downstream tributary of River Warta, itself an Odra tributary, were studied by Romanowicz (1992) and Gołdyn (2000), while Szlauer (1983/84) worked on rotifers of River Płonia and Czerniawski and Domagała (2010) on rotifers of River Drawa and its tributaries. Rotifers of the lower reaches of the Odra were surveyed by Gólcz (1981) and Klimowicz (1979).

A separate group is formed by studies on rotifers inhabiting rivers discharging to lakes of the Masurian Lake District (Węgleńska et al. 1983; Radwan et al. 1996; Ejsmont-Karabin and Kruk 1998).

The faunistic rotifer literature contains papers describing species that are rare in or new to the fauna of Poland; such descriptions were published by Bielańska-Grajner (1980), Czapik (1958b), Ejsmont-Karabin (1999), Lewkowicz (1972), Pawłowski (1954, 1960), Radwan (1971), Siemińska and Siemińska (1967), and Woźniczka-Starzykowa (1966a, b).

Very rare in the Polish rotifer bibliography are studies focusing on embryology and genetics of rotifers (Plasota and Plasota 1980a, b). The authors mentioned followed the embryonic development of *Habrotrocha rosa* up to the formation of intestine and reproductive cells. They found the species to be characterised by spiral cleavage and epiboly gastrulation mode, and isolated 14 chromosomes from the oocytes.

The knowledge of aquatic habitats and their rotifer assemblages is far from uniform. Planktonic rotifers of ponds, lakes, and man-made reservoirs are very well known. In contrast, information on rotifers inhabiting certain special aquatic and moist habitats (e.g., bog-springs and springs, densely vegetated streams and moist soil) is much scantier. Rotifers forming an epizoic fauna on bivalves were studied by Bołtruszko (2010) and Bołtruszko and Ejsmont-Karabin (2013). Rotifer communities from activated sludge were described by Klimowicz (1983) and the role of *Lecane inermis* in the biocoenosis by Kocerba-Soroka et al. (2012) and Klimek et al. (2013).

III. GENERAL PART

1. General characteristics of rotifers

Rotifers are very small animals that possess numerous unusual characteristics, a very diverse morphology, and a complex anatomy. As they occur in so many forms and shapes, it is justifiable to call them "Nature's gems" and to compare them to butterflies and birds (Donner 1973). Pourriot and Francez (1986) claim that rotifers are beautiful, occasionally whimsical, and always fascinating. They most often range in size from 0.1 to 0.6 mm, growing occasionally to 3.00 mm. Their body is not segmented; it is bilateral and has the pseudocoel, i.e., the body cavity lacking its own epithelium and corresponding to the schizocoel. Rotifer growth involves the growth of individual cells or dorsal separation of cells; it is allometric (non-uniform); and rotifers grow very fast, occasionally doubling in size during the initial 24 h of their life (Ejsmont-Karabin et al. 1993). The diversity of rotifer shapes and forms is still more outstanding when one realises that, like in nematodes, the number of rotifer cells is low and constant (eutely) throughout the life span.

Although a relatively small group of animals, their very high production renders them extremely important players in inland water environments. Thanks to their adaptive abilities, rotifers have colonised almost all aquatic habitats: they are present in coastal waters of the seas (with up to 50 species); in lakes, ponds, and episodic pools; among wet plants (e.g., mosses), and in moist soil; they may also parasitise various invertebrates. Rotifers may occur at enormous abundances. Polluted ponds and lakes may support up to 20,000 individuals/dm^3 water (Bielańska-Grajner and Majewska 1994), an Upper Silesian bell pit supporting >> 25,000 individuals/dm^3 (Bielańska-Grajner and Niesler 2002). The highest rotifer abundances (in excess of 100,000 individuals/dm^3) have been so far reported from African lakes (Nogrady 1983), while commercial cultures in Israel produce abundances from 50,000 to 500,000 individuals/dm^3 (Lubzens 1987; Lubzens et al. 1989).

2. The origin of rotifers

All early theories concerning the origin of Rotifera, found in textbooks written before the introduction of modern phylogeny based on the cladistic system of Hennig (1953, 1965), are of historical significance. According to the cladistic

theory, the reconstruction of phylogenetic trees should be based on apomorphies and should only take monophyletic groups into account, i.e. those that have a common ancestor.

Rotifers were included in the obsolete phylum Aschelminthes until the 1990s, but now they are classified as an independent phylum. Traditionally the Rotifera comprise three classes: the Seisonidea (bisexual ectoparasites), Monogononta (cyclical parthenogenesis and sexual reproduction, with haploid males) and Bdelloidea (only asexual reproduction, parthenogenetic). Originally the Bdelloidea and Monogononta were linked together in one group: Eurotatoria (Melone et al. 1998).

With the development of techniques based on DNA analysis, views on the position of rotifers in the phylogenetic animal tree were changing. Originally, based on morphological characteristics (sperm, intracytoplasmic lamina), the Rotifera and Acanthocephala were put together in the clade Syndermata (Ahlrichs 1995a, b; Melone et al. 1998; Wallace et al., 2006). Other studies indicated homology between the jaws of rotifers and gnathostomulids (Ax 1963 and Reisinger 1961). Yet other researchers linked the Rotifera, Gnathostomulida, Micrognathozoa and Acanthocephala together in one clade: the Gnathifera (Ahlrichs 1995a, b, 1997; Haszprunar 1996a; Melone et al. 1998; Kristensen and Funch 2000; Sørensen 2000; Zrzavý 2003).

The phylogenetic position of Gnathifera in the Metazoa was still uncertain and new studies questioned the monophyly of Gnathifera (Giribet et al. 2004; Funch et al. 2005). Analyses based partly or completely on molecular data established that the Gnathifera could be a polyphyletic group (Littlewood et al. 1998) or paraphyletic with reference to Cycliophora, Gastrotricha or Myzostomida, for example (Zrzavý et al. 2001; Giribet 2002). Many researchers consider that, based on morphological structure as well as molecular studies, the Acanthocephala should be seen as advanced rotifers (Garey et al. 1996; Ahlrichs 1997; Garey et al. 1998; Mark Welch 2000; Herlyn et al. 2003), and it has also been suggested that the Micrognathozoa (Kristensen and Funch 2000) are a sister group to the Monogononta (De Smet 2002).

Studies of the genome sequence (18S rRNA) provided molecular evidence that the Acanthocephala and Bdelloidea are sister groups (Garey et al. 1996). Broader genetic studies confirmed these results (Garcia-Varela and Nadler 2006; Witek et al. 2008).

Currently, based on phylogenetic studies, rotifers are placed in the phylogenetic animal tree in the clade Platyzoa together with the Platyhelminthes, Gastrotricha, Gnathostomulida, Micrognathozoa and Acanthocephala. The Platyzoa is one of the Spiralia clades in the Metazoa, Ecdysozoa, Protostomia (Hejnol et al. 2009; for Fontaneto 2014). Detailed considerations on the phylogenetic position of Rotifera can be found in the works of Fussman (2011) and Fontaneto (2014).

In recent years, many cryptic taxa have been discovered among both the Monogononta and the Bdelloidea. Cryptic taxa were earlier considered as one species but mtDNA studies have revealed their diversification into many species (Gomez and Snell 1996; Gomez et al. 2002; Derry et al. 2003; Gomez 2005; Fontaneto et al. 2008; Fontaneto et al. 2011). The results of these studies indicate that the diversity of Rotifera is significantly greater than has been accepted so far (Fontaneto 2014).

3. Taxonomy and systematics

As in many other invertebrate groups, rotifer taxonomy, systematics and classification present a host of extremely difficult problems, which are reflected by continuous modifications of the rotifer system. Due to the incompletely explained origins of rotifer, their unparalleled morphological and anatomical variations, a high intraspecific variability, and a particularly complex internal structure, taxonomic and systematic divisions of rotifers have often produced doubts and ambiguities. The progress in genetic studies on rotifer populations casts a new light on rotifer origins and fundamentals of their taxonomic classification (Koste and Shiel, 1989; Hillis and Moritz, 1990) and has led to still new modifications of the rotifer taxonomic systems which were based primarily on classic morphological characteristics. Thus, the history of rotifer studies, more than one hundred years old, abounds in taxonomic systems, but only few of them have proven to be of a key importance for the development of contemporary animal systematics.

The oldest system of rotifer taxonomy is that developed by Ehrenberg (1838) who divided the class Rotifera into 2 large groups, the Monotrocha and the Sorotrocha, each containing 4 families differing in the structure of their wheel apparatus. In addition, Ehrenberg described the anatomy of numerous rotifer organs. In Ehrenberg's system, some closely related species are very frequently located far apart.

Subsequently, Wesenberg-Lund (1899) proposed to use morphological and anatomical criteria to divide the class into the following two groups: the Digononta (with paired gonads) and the Monogononta (with unpaired gonads). The Digononta were subdivided into 2 orders: the Bdelloidea (with 2 gonads and the vitellarium) and the Seisonacea (with 2 gonads, without the vitellarium), while the Monogononta were subdivided into three orders: the Ploima, Flosculariacea, and Collothecacea.

De Beauchamp (1965) worked out a rotifer system based on differences in the wheel apparatus. He subdivided the Monogononta into two orders: the Pseudotrocha and the Gnesiotrocha, the latter being further divided into two sub-orders: the Monimotrocha and the Paedotrocha. The sub-orders differ markedly in

the structure of their wheel apparatus: the trochus and the cingulum in the Pseudotrocha are fused at the base, no trochus-cingulum fusion being evident in the Gnesiotrocha. In De Beauchamp's system, lower taxa occupy positions similar to those in the system proposed by KUTIKOVA (1970). She based the rotifer taxonomy on function and morphology of the wheel apparatus, an organ that simultaneously serves two important functions: locomotion and feeding; it is also a qualitatively important link in the evolution of the microinvertebrates discussed. She used the wheel apparatus function-morphology as the criterion of the following systematic division of rotifers (down to, and inclusive of, the family level).

Class: Rotatoria
- Subclass: Eurotatoria
  - Superorder: Pseudotrocha
    - Order: Ploimida
      - Family: Notommatidae
        - Trichocercidae
        - Gastropodidae
        - Synchaetidae
        - Lindiidae
        - Dicranophoridae
        - Asplanchnidae
        - Microcodidae
        - Lecanidae
        - Proalidae
        - Epiphanidae
        - Trichotridae
        - Mytilinidae
        - Colurellidae
        - Euchlanidae
        - Brachionidae
  - Superorder: Gnesiotrocha
    - Order: Monimotrocha
      - Family: Flosculariidae
        - Conochilidae
        - Testudinellidae
        - Filinidae
        - Hexarthridae
        - Trochosphaeridae
    - Order: Paedotrochida
      - Family: Collothecidae
        - Atrochidae