# Global diversity of rotifers (Rotifera) in freshwater

Hendrik Segers

**Abstract**  Rotifera is a Phylum of primary freshwater Metazoa containing two major groups: the heterogonic Monogononta and the exclusively parthenogenetic Bdelloidea. Monogononta contains 1,570 species-level taxa, of which a majority (1,488) are free-living fresh or inland water taxa. Bdelloidea contains 461 "species," only one of which is marine, but with many limnoterrestrial representatives or animals of unknown ecology. Actual numbers may be much higher, considering the occurrence of cryptic speciation in Monogononta and the unsatisfactory nature of taxonomic knowledge. Rotifers, mostly monogononts, occur in all types of water bodies, worldwide. They are particularly diverse in the littoral zone of stagnant waterbodies with soft, slightly acidic water and under oligo- to mesotrophic conditions. The rotifer record is highest in the Northern hemisphere, which may be due to the concentration of studies in those regions. Diversity is highest in the (sub)tropics; hotspots are northeast North America, tropical South America, Southeast Asia, Australia, and Lake Baikal, endemicity is low in Africa (including Madagascar), Europe, the Indian subcontinent, and Antarctica. Although the lack of fossil evidence and of molecular phylogenetic studies are major hindrances, contrasting hypotheses on the origin and evolutionary history of *Brachionus*, *Macrochaetus*, and *Trichocerca* are presented.

**Keywords**  Monogononta · Bdelloidea · Freshwater · Biodiversity · Zoogeography · Review

H. Segers (✉)
Belgian Biodiversity Platform, Freshwater Laboratory,
Royal Belgian Institute of Natural Sciences, Vautierstraat
29, 1000 Brussels, Belgium
e-mail: Hendrik.Segers@naturalsciences.be

## Introduction

Rotifera (see Wallace et al., 2006 for a recent, comprehensive introduction to the taxon) is a group of primary freshwater invertebrates. Rotifers play a pivotal role in many freshwater ecosystems. They are ubiquitous, occurring in almost all types of freshwater habitat, from large permanent lakes to small temporary puddles, and interstitial and capillary water; from acidic mining lakes to natron lakes and the open ocean, from hyperoligotropic Alpine lakes to sewage ponds. They commonly occur in densities up to 1,000 individuals per liter, and are important filter-feeders on algae and bacteria. Their ubiquity and abundance explain their standing as one of the three main groups of freshwater zooplankton in limnological studies, together with the 'Cladocera' (Anomopoda) and Copepoda, and as organisms used in mass aquaculture. They are permanently and obligatorily connected to aquatic habitats in all active stages, only their resting stages are drought-resistant.

Classically, three groups are recognized within the Phylum Rotifera. The species-poorest is Seisonacea, with only three species living epizootically on marine crustaceans of the genus *Nebalia*. Most well-known and diverse are the predominantly freshwater Bdelloidea and Monogononta. Molecular studies have indicated that a fourth group, Acanthocephala, previously considered a separate Phylum of exclusively endoparasitic organisms, actually belongs to Rotifera (Mark Welch, 2000; Giribet et al., 2000). Little is actually known about the phylogeny of rotifers, due to a lack of modern comprehensive studies (but see Sørensen & Giribet, 2006), and the lack of a robust fossil record.

Rotifers are minute metazoans (50–2,000 µm), characterized by the presence of an anterior ciliated corona, a stiff body wall named lorica bearing variable appendages, and a specialized pharyngeal organ, the mastax, containing hard elements, termed trophi (Fig. 1). Especially, the rotifer's small size, capability of phenotic plasticity and highly adaptable masticatory apparatus are important elements explaining the success of the group. Their propagules consist of single, hard-shelled, and durable encapsulated cysts (monogononts) or anhydrobiotic individuals (bdelloids). These propagules being small and drought-resistant, makes rotifers perfectly adapted to passive, aerial or phoretic dispersal. Monogononts and bdelloids reproduce parthenogenetically. In monogononts, periods of parthenogenetic reproduction are interspersed with sexual phases (heterogony), but bdelloids are unique in being the most diverse group of metazoans in which reproduction is by diploid, mitotic parthenogenesis only. The combination of their high dispersal capacity and their parthenogenetic reproduction, enabling them to establish or renew a population starting off from a single resting stage, and to reach high effective population sizes relatively quickly, makes them theoretically superbly apt (re)colonizers.

The ability of many bdelloids to shift from active to anhydrobiotic stage enables them to live in particularly ephemeral, even predominantly dry conditions such as



**Fig 1** (**a**) Schematic representation of a *Brachionus* rotifer; (**b**) Incudate trophi (*Asplanchna*); (**c**) Malleoramate trophi (*Sinantherina*). Scale bars: 10 µm
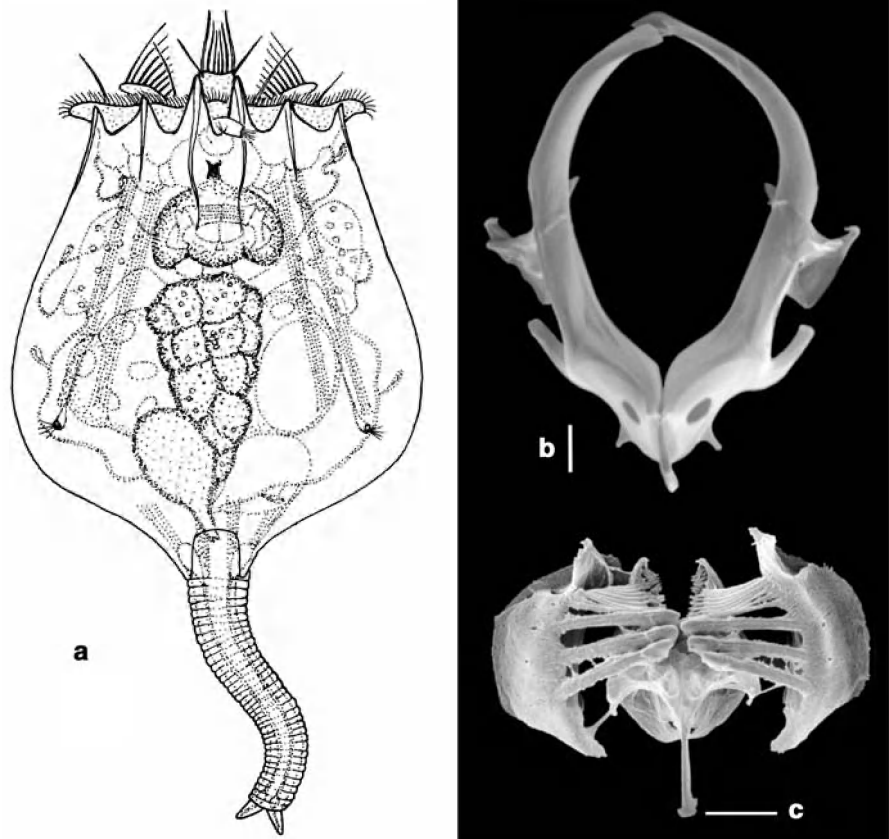
lichens or terrestrial mosses. As such, they should probably be considered limnoterrestrial rather then limnetic. Bdelloid rotifers, however, can at present only be identified while alive and need to be examined during feeding and creeping. Their study is, consequently, tedious and very little if any information is available on the ecology of the majority of them. So, notwithstanding that the present project focuses on limnetic representatives of these animals, I include counts of the diversity and distribution of all freshwater bdelloid taxa, as it is not possible to distinguish reliably between the two ecological groups.

## Biodiversity of Rotifera

### Data collection

Data on which the present analysis is based are restricted to those rotifer taxa that are freshwater or brackishwater and marine. Exclusively marine species have not been included but are listed in the electronic appendix (http://fada.biodiversity.be; see Fontaneto et al., 2006 for a recent review). The taxonomy follows recent taxonomic views as expressed in recent revisions of selected rotifer families (Nogrady et al., 1995; Segers, 1995a, 2003; De Smet, 1996; De Smet & Pourriot, 1997; Nogrady & Segers, 2002), and numerous taxonomic publications. When alternative taxonomies exist, a splitting rather than lumping approach was followed. Species that are insufficiently described and therefore have to be considered *species inquirenda* are not counted. A more complete account on the taxonomic approach is provided in Segers (2007).

Distributional data are based on the literature review of De Ridder (1986, 1991, 1994), De Ridder & Segers (1997), Segers (1995b, 2003) and recent articles (e.g., Jersabek, 2003; Ricci et al., 2003). Rare regional records of species otherwise common in other regions were critically assessed and eventually included only after verifications of published illustrations or material. The data are presented in Segers (2007) and in the electronic appendix (http://fada.biodiversity.be).

### Rotifer taxonomy and zoogeography: state of the art

Before analyzing rotifer diversity and distribution, it is necessary to give an account on the limitations of the data. The usual *caveat*, that new species are still to be discovered, applies, but there is more. Rotifer taxonomy is almost exemplary of the taxonomic impediment, as recognized by governments through the Convention on Biological Diversity (see http://www.biodiv.org/programmes/cross-cutting/taxonomy/default.shtml). Serious knowledge gaps exist in the taxonomic system of rotifers and trained taxonomists and curators are (very) few. These deficiencies have a significant impact on our ability to understand the diversity and chorology of these animals. Rotifer taxonomy is all but adequate, an observation that was already made some 25 years ago (Dumont, 1980) but which still holds. Basic, detailed morphological revisions still contribute significantly to our understanding (e.g., Giri & José de Paggi, 2006). Molecular studies with an impact on taxonomy are still scarce. However, the work by Gómez et al. (2002) on the economically important and particularly well-studied *B. plicatilis* O.F. Müller has shown that the taxon, which was long treated as a single but variable species, contains no less then nine different, phylogenetically distinct lineages. Only few of these are morphologically diagnosable (see Ciros-Pérez et al., 2001). Such cryptic speciation is probably common in rotifers, as hinted at by the reproductive isolation of geographically separated, yet morphologically identical strains of *Asplanchna brightwellii* Gosse (see Snell, 1989). These problems are further convoluted in bdelloid rotifers. Here, the difficulties are not only the classic ones hampering rotifer taxonomy (small size of the animals, scarcity of useful morphologic features, high variability: see Ruttner-Kolisko, 1989), but also the practical problem that, to date, only living and actively moving animals can be identified or serve as a basis for taxonomic study. In addition, the animal's unique exclusively parthenogenetic reproduction implies that most species concepts are inapplicable as theoretical framework for their study. Clearly, the counts of rotifer diversity as presented here are tentative and should be interpreted with great caution.

Due to the *caveat* mentioned above, and because identification of rotifers is difficult, rotifer literature is littered with dubious records. Our knowledge on the diversity and distribution of rotifers is moreover biased by the uneven research intensity in different regions (Dumont, 1983). There are only a few rotifer families for which a large number of fairly reliable

data is available. These are loricate taxa, which can mostly be identified using external morphology of contracted, fixed material, notably Brachionidae: Pejler (1977) and Dumont (1983), Lecanidae: Segers (1996), and Trichocercidae: Segers (2003).

Genus- and species-level diversity

A total of 1,570 Monogononta and 461 Bdelloidea valid species are presently recognized worldwide (Table 1). Of these, the vast majority (1488 monogononts, 460 bdelloids) are either exclusively freshwater or brackishwater and marine; only 70 described species are exclusively marine (Table 2). The most diverse taxa are Notommatidae, with *Cephalodella* as most speciose genus, the monogeneric Lecanidae, and Dicranophoridae. All of these contain almost exclusively benthic-littoral or psammon-inhabiting species, with a majority inhabiting oligo- to mesotrophic, slightly acidic, soft waters. The same holds for Lepadellidae; *Brachionus* is a notable exception, as most of these prefer alkaline and eutrophic conditions. These preferences are well known and have been commented upon as early as Harring & Myers (1928).

Beres et al. (2005) found that the distribution of genera over families in rotifers is a hollow curve distribution which fits a model given by Hubbell's unified neutral theory of biodiversity (Hubbell, 2001). Basically, this distribution infers that there are relatively numerous taxa containing only one or a few subordinate taxa; that the relative frequency of taxa decreases sharply with increasing number of included subordinate taxa, whereas there are only a few highly diverse taxa (e.g., *Lecane:* 200 species, *Cephalodella*: 159 species). The same seems to hold for the relation between genera and species in Monogononta (Fig. 2), however, it is as yet unclear what this may signify in respect to evolution or biodiversity.

Rotifers, especially monogononts, form a relatively diverse constituent of the fauna of stagnant freshwater ecosystems. Dumont & Segers (1996) calculated that a non-polluted lake with developed weedy littoral would harbour about 150 species in temperate, and up to 250 species in tropical regions. This implies that 7.5–12.5% of all species globally, and ca. one fifth of the regional fauna can be found in a single locality. Myers' (1942) intensive studies on

some lakes and ponds in and near the North-American Pocono region (Pennsylvania) yielded 457 Monogononta and 32 Bdelloidea, which constitute more than half of the known Nearctic rotifer fauna in a relatively small region. This remarkably high species diversity, which actually concerns littoral and benthic rotifers, which are mostly present in relatively low numbers, can be ascribed to fine niche partitioning amongst rotifer species in combination with high micro- and macroscale habitat heterogeneity, especially in littoral and benthic environments. On the other hand, local diversity can represent a sizable fraction of regional diversity. This is probably a result of the high (re)colonization and dispersal capacity of rotifers: available niches, even if these are only temporarily present, are relatively quickly filled by recruitment from resting stages that may or may not already be present in the habitat. This situation may be different from that in pelagic habitats, where the presence of a large resting propagule bank produced by locally adapted populations consisting of large numbers of individuals, presents an effective barrier against newly invading genotypes (the Monopolization Hypothesis: De Meester et al., 2002). Alternatively, the observation may be due to a lack of taxonomic resolution in littoral rotifers.

**Present distribution and main areas of endemicity**

The most diverse and, not coincidently, best-studied region is the Palaearctic, closely followed by the Nearctic region (Map 1). A substantial research effort resulting in a relatively high species record has been devoted to the Neotropical region and, more recently, the Oriental region. There are a fair number of contributions on the Australian and Afrotropical (Ethiopian) regions, but far less on Oceanic islands (see Wallace et al., (2006) for a literature review). That research intensity is largely responsible for this ranking is best illustrated by the regional diversity of taxonomically difficult illoricate taxa such as Dicranophoridae and Notommatidae: the diversity of these in the best studied Palaearctic and Nearctic regions, where most rotifer taxonomists live(d), is almost 7- to 8-fold that of the least studied African region; this is much less so for the relatively easier loricate taxa such as Brachionidae and Lecanidae.

**Table 1** Number of genera per family, per region

| Number of genera | Palearctic | Afrotropical | Australian | Oriental | Nearctic | Neotropical | Antarctic | Pacific | **Total**[*] |
|---|---|---|---|---|---|---|---|---|---|
| *Monogononta* | | | | | | | | | |
| Asciaporrectidae | 1 | | | | 1 | | | | 1 |
| Asplanchnidae | 3 | 2 | 2 | 3 | 3 | 3 | | 1 | 3 |
| Atrochidae | 3 | 1 | 2 | 3 | 2 | 1 | | | 3 |
| Birgeidae | | | | | 1 | | | | 1 |
| Brachionidae | 7 | 7 | 6 | 7 | 7 | 7 | 3 | 1 | 7 |
| Collothecidae | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 2 |
| Conochilidae | 1 | 1 | 2 | 1 | 2 | 1 | | | 2 |
| Dicranophoridae | 14 | 5 | 8 | 5 | 12 | 6 | 2 | 5 | 19 |
| Epiphanidae | 5 | 4 | 5 | 5 | 5 | 3 | 2 | 4 | 5 |
| Euchlanidae | 4 | 4 | 4 | 5 | 4 | 4 | 1 | 2 | 5 |
| Flosculariidae | 7 | 6 | 7 | 6 | 7 | 7 | 1 | 4 | 7 |
| Gastropodidae | 2 | 2 | 2 | 2 | 2 | 2 | | | 2 |
| Hexarthridae | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 1 |
| Ituridae | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 |
| Lecanidae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Lepadellidae | 3 | 3 | 3 | 4 | 4 | 4 | 2 | 3 | 4 |
| Lindiidae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Microcodidae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 |
| Mytilinidae | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 |
| Notommatidae | 15 | 9 | 11 | 9 | 15 | 10 | 3 | 5 | 18 |
| Proalidae | 4 | 3 | 3 | 2 | 4 | 3 | | 3 | 4 |
| Scaridiidae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Synchaetidae | 3 | 3 | 3 | 3 | 4 | 3 | | 2 | 4 |
| Testudinellidae | 2 | 2 | 2 | 3 | 2 | 2 | | 1 | 3 |
| Tetrasiphonidae | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 |
| Trichocercidae | 3 | 2 | 3 | 3 | 3 | 2 | 1 | 2 | 3 |
| Trichotriidae | 3 | 3 | 3 | 3 | 3 | 3 | | 1 | 3 |
| Trochosphaeridae | 3 | 3 | 3 | 3 | 2 | 3 | 1 | | 3 |
| Subtotal: | 94 | 70 | 80 | 78 | 94 | 76 | 23 | 40 | 108 |
| *Bdelloidea* | | | | | | | | | |
| Adinetidae | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| Habrotrochidae | 3 | 3 | 3 | 1 | 3 | 2 | 1 | 2 | 3 |
| Philodinavidae | 3 | 1 | 2 | 1 | 2 | 2 | | | 3 |
| Philodinidae | 11 | 10 | 10 | 6 | 9 | 9 | 4 | 4 | 12 |
| Subtotal: | 19 | 15 | 16 | 9 | 15 | 15 | 6 | 7 | 20 |
| Total: | 113 | 85 | 96 | 87 | 109 | 91 | 29 | 47 | 128 |

[*] Total number of species includes exclusively marine taxa, not included are Clariaidae (1 species, *Claria segmentata* Kutikova, Markevich & Spiridonov, 1990), and 3 Seisonacea.

Antarctica is a special case; there are quite a few studies but here rotifer diversity is markedly and effectively lower then in other regions (Fig. 3).

Endemicity at higher taxonomic levels is rare in rotifers. There is a single endemic free-living rotifer family, the Nearctic (northeast North American)

**Table 2** Number of species-level taxa per family, per biogegraphic region

| | PA | NA | NT | AT | OL | AU | PAC | ANT | End. | Cosmo. | World | Mar. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Monogononta*[a] | | | | | | | | | | | | |
| Asciaporrectidae | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | |
| Asplanchnidae | 11 | 11 | 10 | 9 | 12 | 9 | 2 | 0 | 2 | 8 | 15 | |
| Atrochidae | 4 | 2 | 1 | 1 | 3 | 2 | 0 | 0 | 0 | 1 | 4 | |
| Birgeidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | |
| Brachionidae | 94 | 66 | 71 | 51 | 57 | 58 | 4 | 16 | 94 | 36 | 169 | 1 |
| *Brachionus* | 32 | 23 | 32 | 26 | 33 | 34 | 3 | 5 | 29 | 20 | 63 | |
| *Keratella* | 21 | 22 | 18 | 15 | 12 | 15 | 0 | 5 | 26 | 7 | 48 | |
| *Notholca* | 31 | 13 | 8 | 3 | 2 | 2 | 0 | 6 | 27 | 2 | 40 | 1 |
| Collothecidae | 42 | 18 | 15 | 14 | 8 | 12 | 2 | 2 | 24 | 10 | 47 | |
| Conochilidae | 5 | 7 | 5 | 5 | 5 | 6 | 0 | 0 | 1 | 5 | 7 | |
| Dicranophoridae[b] | 137 | 93 | 21 | 19 | 15 | 24 | 5 | 6 | 98 | 9 | 181 | 39 |
| *Dicranophorus* | 36 | 38 | 10 | 12 | 8 | 8 | 1 | 0 | 21 | 7 | 52 | 1 |
| *Encentrum* | 64 | 28 | 3 | 2 | 4 | 6 | 1 | 5 | 54 | 1 | 78 | 31 |
| Epiphanidae | 16 | 10 | 10 | 9 | 9 | 8 | 4 | 2 | 4 | 9 | 16 | |
| Euchlanidae | 19 | 18 | 14 | 15 | 15 | 18 | 3 | 2 | 8 | 11 | 27 | |
| Flosculariidae | 35 | 38 | 37 | 22 | 23 | 30 | 5 | 2 | 7 | 19 | 50 | |
| Gastropodidae | 10 | 7 | 8 | 8 | 6 | 7 | 0 | 0 | 2 | 6 | 12 | |
| Hexarthridae | 11 | 11 | 7 | 8 | 4 | 6 | 3 | 0 | 7 | 4 | 18 | |
| Ituridae | 4 | 4 | 4 | 2 | 3 | 5 | 0 | 0 | 0 | 2 | 6 | |
| Lecanidae | 93 | 108 | 94 | 82 | 99 | 61 | 30 | 2 | 81 | 49 | 200 | |
| Lepadellidae | 95 | 67 | 70 | 54 | 59 | 55 | 18 | 11 | 81 | 37 | 160 | 3 |
| *Lepadella* | 66 | 42 | 52 | 39 | 42 | 41 | 11 | 7 | 70 | 25 | 122 | 2 |
| Lindiidae | 7 | 11 | 4 | 2 | 3 | 7 | 2 | 1 | 4 | 3 | 13 | 3 |
| Microcodidae | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 0 | 1 | 1 | |
| Mytilinidae | 21 | 10 | 14 | 12 | 12 | 12 | 1 | 2 | 13 | 8 | 29 | |
| Notommatidae | 201 | 165 | 70 | 29 | 48 | 72 | 11 | 11 | 149 | 45 | 277 | |
| *Cephalodella* | 118 | 79 | 37 | 6 | 26 | 31 | 14 | 8 | 93 | 16 | 159 | |
| *Notommata* | 29 | 36 | 12 | 10 | 8 | 14 | 6 | 1 | 25 | 10 | 47 | |
| Proalidae | 34 | 34 | 7 | 10 | 7 | 14 | 5 | 0 | 20 | 6 | 47 | 9 |
| Scaridiidae | 3 | 3 | 4 | 4 | 4 | 3 | 1 | 1 | 3 | 2 | 7 | |
| Synchaetidae | 38 | 26 | 18 | 13 | 15 | 17 | 3 | 0 | 16 | 12 | 45 | 12 |
| Testudinellidae | 19 | 19 | 19 | 18 | 15 | 17 | 1 | 0 | 19 | 9 | 40 | 1 |
| Tetrasiphonidae | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | |
| Trichocercidae | 50 | 53 | 45 | 39 | 41 | 43 | 18 | 4 | 13 | 34 | 70 | 2 |
| Trichotriidae | 13 | 11 | 15 | 12 | 11 | 10 | 1 | 0 | 10 | 9 | 23 | |
| Trochosphaeridae | 13 | 8 | 1 | 13 | 10 | 13 | 0 | 0 | 5 | 9 | 19 | |
| Subtotal | 980 | 805 | 566 | 453 | 486 | 511 | 119 | 63 | 663 | 345 | 1488 | 70 |
| *Bdelloidea* | | | | | | | | | | | | |
| Adinetidae | 17 | 8 | 6 | 7 | 5 | 12 | 1 | 6 | 7 | 5 | 20 | |
| Habrotrochidae | 130 | 25 | 37 | 45 | 18 | 53 | 7 | 7 | 75 | 14 | 152 | |
| *Habrotrocha* | 108 | 22 | 33 | 39 | 18 | 44 | 6 | 7 | 64 | *13* | 128 | |
| Philodinavidae | 3 | 2 | 2 | 1 | 2 | 2 | 0 | 0 | 3 | 0 | 6 | |
| Philodinidae | 220 | 77 | 71 | 85 | 33 | 109 | 6 | 15 | 152 | 41 | 282 | 1 |

**Table 2** continued

|  | PA | NA | NT | AT | OL | AU | PAC | ANT | End. | Cosmo. | World | Mar. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Macrotrachela* | 75 | 19 | 22 | 31 | 11 | 41 | 3 | 7 | 50 | *14* | 95 | |
| *Mniobia* | 41 | 11 | 10 | 5 | 0 | 21 | | 2 | 29 | *2* | 49 | |
| *Philodina* | 35 | 17 | 14 | 24 | 6 | 18 | 1 | 5 | 28 | *10* | 50 | |
| Subtotal | 370 | 112 | 116 | 138 | 58 | 176 | 14 | 28 | 237 | 60 | 460 | 1 |
| Total | 1,350 | 917 | 682 | 591 | 544 | 687 | 133 | 91 | 900 | 405 | 1948 | 71 |

PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic. End. = Endemics, Cosmo. = Cosmopolites, Mar. = Marine

[a] Excluding Clariaidae, a monospecific family of exclusively parasitic animals living in terrestrial Oligochaeta

[b] Excluding *Albertia* (4 species) and *Balatro* (7species), exclusively endoparasitic in Oligochaeta (both) and gastropods (*Albertia*);

Endemics: present in one region only

Cosmopolites: present in 5 or more regions

Marine: exclusively marine species
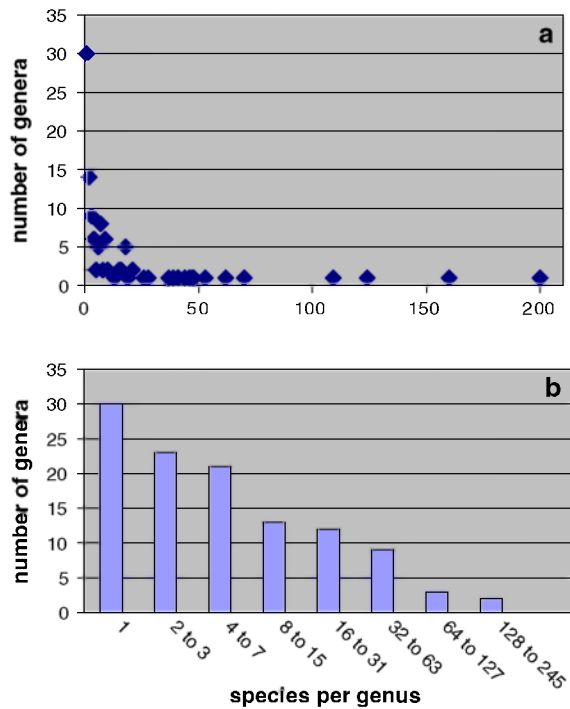


**Fig 2** Distribution of rotifer species diversity over different genera. (**a**) normal representation, (**b**) number of species (x-axis) sorted out in octaves

Birgeidae. A number of endemic genera exist: In the Palaearctic these are *Pseudoharringia*, the psammobiotic *Wigrella*, the European Alpine *Glaciera* and the Baikalian *Inflatana*; in the Nearctic (northeast North American) *Rousseletia* and the littoral *Streptognatha*, and, probably, *Pseudoploesoma* (the appurtenance of *P. greeni* Koste to this genus is doubtful: De Smet & Segers, unpublished); in the Oriental region *Pseudoeuchlanis* and *Anchitestudinella;* and the Subantarctic (Kerguelen Island) *Pourriotia*. The biogeographical relevance of these is, however, low: all but *Wigrella* are monospecific, many (*Glaciera, Inflatana, Pseudoeuchlanis, Anchitestudinella* and *Pourriotia*) have only been found once. The fate of *Dorria* is revealing: this monospecific genus was long considered a rare northeast North American endemic taxon, until it was found in southern Australia and on Hawaii (Jersabek, 2003). More reliable, also taxonomically, are Birgeidae, *Streptognatha* and *Pseudoploesoma*; all three of these are northeast North American. This concurs with the main center of endemicity of Trichocercidae (Segers, 2003).

Endemic species occur in all regions and in all but the species-poorest rotifer genera and families. The count of endemics in Table 2, however, underrepresents endemicity and complexity of the distributions of rotifers: quite a few species technically occur in more than one biogeographical region as accepted for this study, yet are clearly restricted to a circumscribed area (e.g., *Keratella kostei* Paggi occurs in Patagonia, the Falkland Islands and South Georgia Island hence both in the Neotropical and Antarctic region) or have far more restricted ranges (e.g., the numerous Baikalian endemics, mostly of *Notholca*). Lecanidae is a

**Fig 3** Rotifer diversity in the major biogeographic regions. Number of species/ number of genera. Upper: Monogononta, Lower: Bdelloidea.
PA—Palaearctic;
NA—Nearctic;
NT—Neotropical;
AT—Afrotropical ;
OL—Oriental;
AU—Australasia;
PAC—Pacific Oceanic Islands; ANT—Antarctic
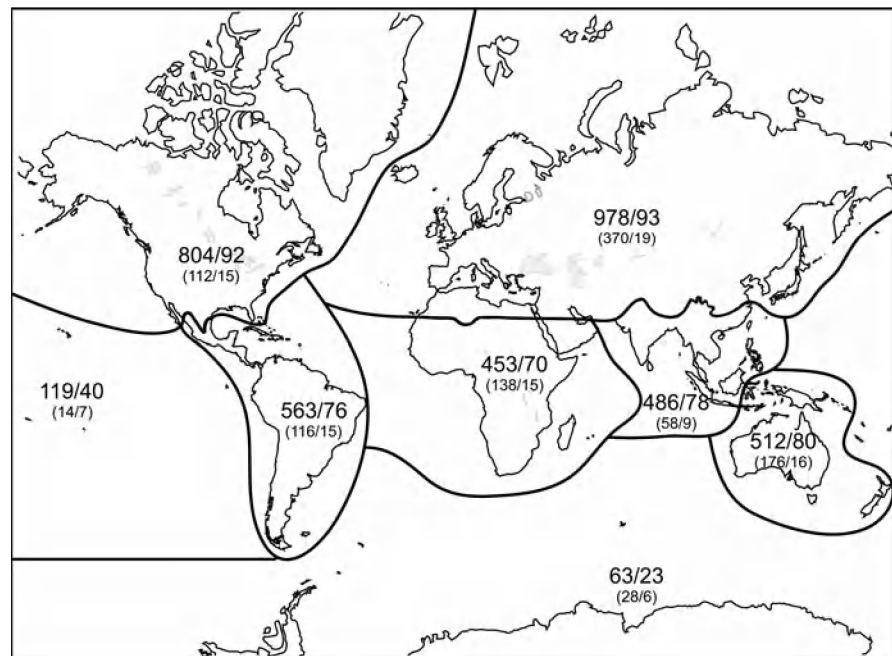


good illustration of the diversity of distribution patterns (Segers, 1996). Since this 1996 paper, over 30 *Lecane* have been added as valid, either as a result of the application of a less inclusive taxonomic concept or by the description of new species. In general, ranges of *Lecane* have been refined and counts of regional endemicity increased, notwithstanding that some range extensions have been reported. Lecanidae species are predominantly (sub)tropical or warm-water, with numerous regional and local endemics, and some Holarctic, Palaeotropical, Australasian, New World, and Old World taxa illustrating more complex patterns.

Also Brachionidae contains taxa with well-documented ranges (see Pejler, 1977; Dumont, 1983). An update on the distribution of some Brachionidae is as follows:

Anuraeopsis

Of the eight species considered valid here, four are regional endemics. Whereas *A. cristata* Bērziņš, *A. miracleae* Koste and *A. urawensis* Sudzuki are rare, taxonomically difficult and may have been overlooked, the two Neotropical taxa (*A. quadriantennata* (Koste) and *A. sioli* Koste are meaningful, as they are unmistakable and have been recorded repeatedly. As all *Anuraeopsis* species are warm-

water animals, and as the only reliable endemics are Neotropical, it can be hypothesized that the taxon may be of Neotropical origin.

Brachionus

This species-rich and predominantly warm-water genus contains 29 endemic (sub)species, most of which are Neotropical (9) or Australian (7). There are only three Oriental, and one Afrotropical endemics. Three taxa are American but probably of Neotropical origin (*B. havanaensis* Rousselet, *B. satanicus* Rousselet and *B. zahniseri* Ahlstrom). *Brachionus dichotomus reductus* Koste & Shiel is Australasian and most likely of Australian origin, by its relation with the Australian *B. dichotomus dichotomus* Shephard. Most of the Neotropical and Australian endemics are phylogenetically and taxonomically distinct. This is much less clear for the Palaearctic and Nearctic endemics, most of which are clear relatives of the *B. plicatilis* complex (*B. asplanchnoides*, *B. ibericus*, *B. spatiosus*). The emerging pattern is one of centered endemicity in South America and Australia, with hardly any endemicity in Africa and the Northern hemisphere. Such a pattern may hint at a late Cretaceous South American-Antarctic-Australian (see Hay et al., 1999), rather than a Gondwanan (Dumont, 1983) origin of the taxon.

Keratella

Within Brachionidae, *Keratella* is the genus with the highest degree of endemicity (52%), and this may even be an underestimate considering the confused taxonomy of a number of species complexes like *Keratella cochlearis*. Endemicity is high in the Eastern Palearctic (*K. mongoliana* Segers & Rong, *K. sinensis* Segers & Wang, *K. trapezoida* Zhuge & Huang, *K. wangi* Zhuge & Huang and *K. zhugeae* Segers & Rong) and Northern Nearctic (*K. armadura* Stemberger, *K. canadensis* Bērziņš, *K. crassa* Ahlstrom, *K. taurocephala* Myers). Here, a Southern hemisphere cold-water faunal component is represented by *K. kostei* Paggi, *K. sancta* Russell (New Zealand, Kerguelen, Macquarie Island) and *K. reducta* (Huber-Pestalozzi) (Cape region, South Africa), amongst others. Considering the relatively small area of southern hemisphere temperate regions, these taxa balance the northern hemisphere temperate *Keratella* fauna. In addition, there are some reliable Australian (e.g., *K. australis* Bērziņš), Oriental (*K. edmondsoni* Ahlstrom), and warm-water Neotropical (*K. nhamundaiensis* Koste) endemics, as well as Palaeotropical (*K. javana* Hauer) and Holarctic (*K. hiemalis* Carlin) taxa. In contrast to *Brachionus*, no clear general pattern emerges in *Keratella*.

Another remarkable genus is *Macrochaetus*. It contains 6 endemics out of 13 species, 4 of which are Neotropical. Three of these are clearly distinct and quite primitive in lacking the elongate dorsal spines typical of the genus. Hence, also *Macrochaetus* could be Neotropical in origin. The surmised origin of *Brachionus* and *Macrochaetus* contrasts with *Trichocerca*, in which a northern hemisphere pre-Pleistocene origin, followed by glacial extinctions in the (west) Palearctic, was postulated to account for an observed lack of endemics in the tropics versus high endemicity in northeast North America (Segers, 2003).

Clearly, and notwithstanding the unsatisfactory nature of our knowledge of their taxonomy, rotifers do exhibit complex and fascinating patterns of diversity and distribution as illustrated in a number of contributions (Green, 1972; Pejler, 1977; De Ridder, 1981; Dumont, 1983; Segers, 1996, 2003). In summary, many species are cosmopolitan, either or not exhibiting latitudinal variation as a result of temperature preferences. Regional differences may result from environmental conditions such as water chemistry. Endemism is real and occurs at diverse geographical scales; more complex patterns exist. Rotifer diversity is highest in the tropics, with endemicity centered in tropical South America and Australia; tropical Africa including Madagascar and the Indian subcontinent are notable for their relatively poor rotifer fauna including few endemics. Hotspots occur in northeast North America, Australia (probably west Australia) and, in contrast to the low endemicity on the Indian subcontinent, Southeast Asia. On a more local scale, Lake Baikal is most noteworthy by its high endemicity; much less is known of other ancient lakes. (Harring & Myers, 1928; Green, 1972; Pejler, 1977, Dumont, 1983; Segers, 1996, 2001, 2003). The remarkable rotifer diversity in northeast North America, in contrast to the low endemicity in European waters is attributed to the presence of glacial refugia in the region during the Pleistocene, at least for *Trichocerca* (Segers, 2003).

Fenchel & Finlay (2004) postulated that small-sized organisms (<1 mm) tend to have a cosmopolitan distribution as a consequence of huge absolute population sizes. At the local scale, their diversity exceeds that of larger organisms yet at the global scale this relation is reversed because endemism is largely responsible for the species richness of large-sized taxa. A latitudinal diversity gradient is absent or weak. Monogonont rotifers appear to comply with this pattern: their local diversity is relatively high compared to the total species diversity of the group, and cosmopolitanism is important. On the other hand, a latitudinal diversity gradient is clearly evident in rotifers (e.g., Green, 1972). Two factors may account for this apparent contradiction: first, the statement that all rotifer resting stages are eminently suited for dispersal may not be correct. Such a generalization is contradicted by the abundance of well-documented cases of locally endemic rotifers. Second, the monopolizing effect of large resting propagule banks may counteract successful colonization.

**Human-related issues**

Rotifer distribution and diversity is largely influenced in two ways. The most important is that of the decline of the water quality in freshwater ecosystems. As

mentioned above, the most diverse rotifer assemblages can be found in soft, slightly acidic, oligo- to mesotrophic waters. These are particularly vulnerable to eutrophication and salinization. Regarding water pollution by pesticides, there are numerous laboratory studies on rotifer ecotoxicology, even using rotifers as test organisms for ecotoxicological assessments. The effects of pollutants on rotifer diversity in nature also has been studied. Rotifers are often less sensitive to insecticides than cladocerans and their sensitivity to specific compounds varies widely. They also exhibit indirect effects from exposure to toxicants, e.g., through reduction of competition from more sensitive organisms or cascading food web effects (see Wallace et al., 2006).

Due to the large dispersal and colonization capacities of many species, rotifers are easily transported to new habitats by man. An illustrative case is that of *Filinia camasecla* Myers, 1938, which was described from the Panama Canal zone; however, the species has subsequently never been found back in the Americas, but has been shown to be a relatively common Oriental species. Several additional instances are known of rotifers being introduced to regions where they did not naturally occur before (e.g., Dartnall, 2005; see Wallace et al., 2006). This phenomenon may have been going on for a long time (see Pejler, 1977) and may be responsible for isolated records of regionally common species outside their natural range. It may, however, have passed unnoticed because of the small size of rotifers and dearth of comprehensive studies. The same reasons explain why rotifers have hardly been used in biodiversity assessments and conservation, notwithstanding their economic relevance in aquaculture.

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