

## Diversity and endemism in Rotifera: a review, and *Keratella* Bory de St Vincent

Hendrik Segers · Willem H. De Smet

Received: 1 October 2007 / Accepted in revised form: 10 October 2007 / Published online: 3 November 2007  
© Springer Science+Business Media B.V. 2007

**Abstract** We confront patterns in the chorology and diversity of freshwater and limnoterrestrial Rotifera with predictions following from the recently revived ubiquity theorem on the distribution of microscopic organisms. Notwithstanding a strong taxonomic impediment and lack of data, both bdelloid and monogonont rotifers appear to conform to the hypothesis' predictions that local diversity is relatively high compared to global diversity and that cosmopolitanism is important. To the contrary, however, a latitudinal diversity gradient is obvious, and endemism is present, and exhibits diverse patterns. This is illustrated by the case of *Keratella* rotifers, in which we identify purported relict endemism hotspots in the east Palaearctic (China) and in temperate and cold regions of the southern hemisphere, and a recent radiation in North America. The apparent paradox may result from an antagonism between rotifer's high population sizes and presence of potentially highly efficient propagules, versus pre-emption of habitats and local adaptation by resident populations, specific dispersal ability, and ecological and geographical factors. We conclude that distribution patterns of microscopic organisms, as represented by rotifers, most likely span the whole range of alternatives, from full cosmopolitanism to local endemism, and suggest that studying this diversity is more productive to come to an understanding of their chorology and diversity.

**Keywords** Micro-organisms · Ubiquity theorem · Cosmopolitanism · Freshwater · Limnoterrestrial · Marine

---

Special Issue: Protist diversity and geographic distribution. Guest editor: W. Foissner.

---

H. Segers (✉)

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

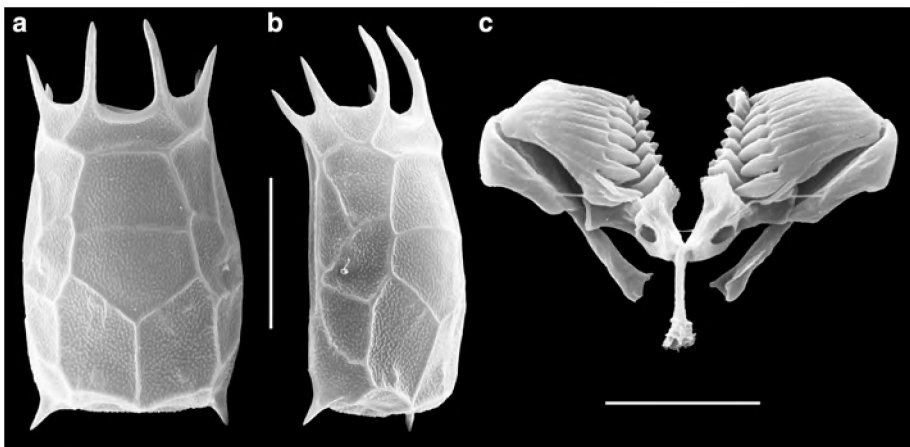
W. H. De Smet

Department of Biology, Section Polar Ecology, Limnology and Palaeobiology, University of Antwerp,  
Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium  
e-mail: willem.desmet@ua.ac.be

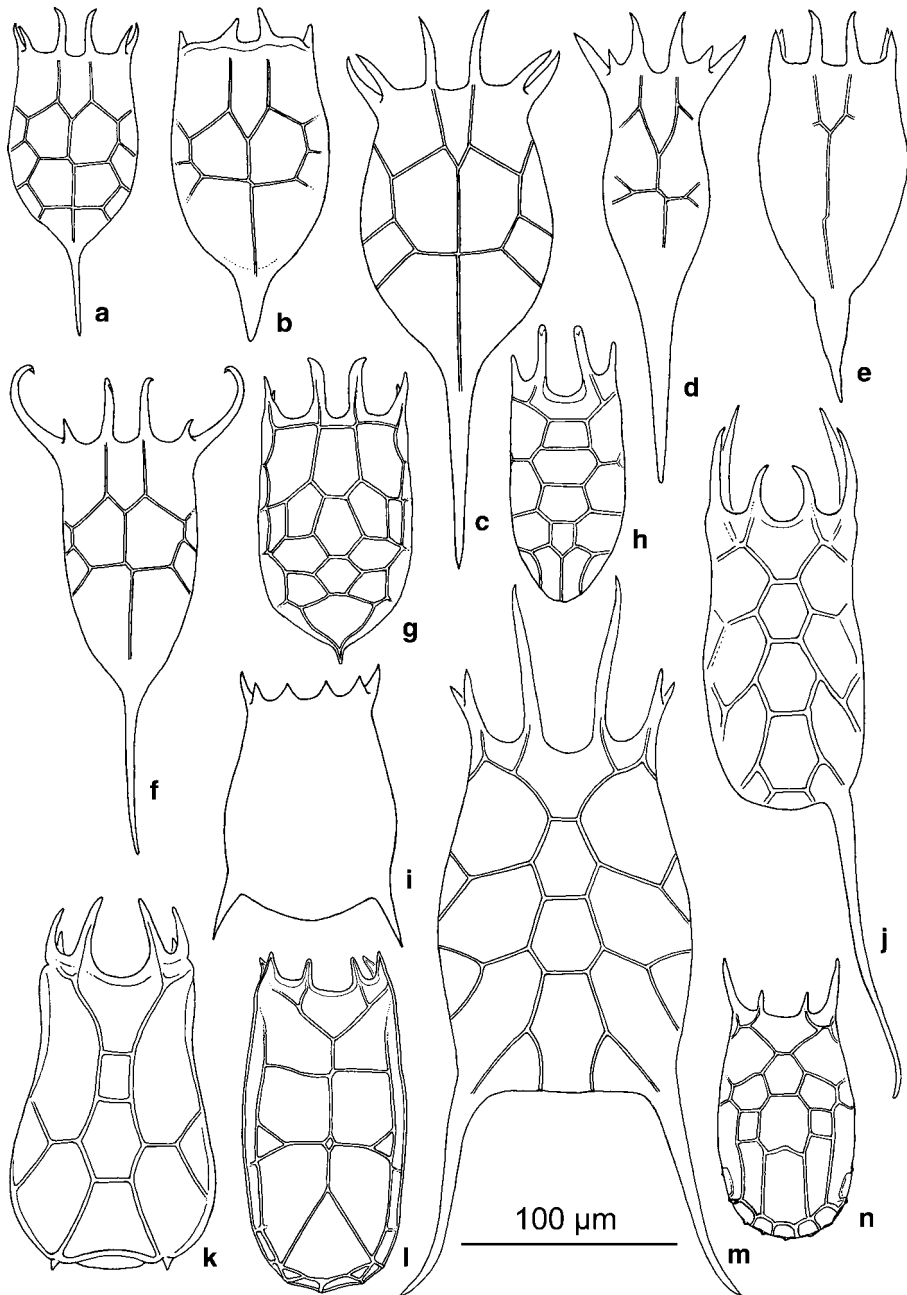
## Introduction

Recently, the debate on the biogeography, or lack thereof, of microscopic organisms has regained interest. Indeed, some recent molecular studies on the diversity and distribution of small-sized taxa, with body lengths of less than 1 mm, seem to corroborate the ancient adagio (e.g. Jennings 1900; Rousselet 1909) that such organisms are potentially cosmopolitan, and that it is the environment that determines the diversity and composition of local communities (Baas-Becking 1934; Finlay 2002; Fenchel and Finlay 2004). The underlying idea is that high rates of dispersal and low rates of local extinction, both related to the huge population sizes of microscopic organisms, lead to a situation in which “everything is everywhere”, and that the species found in a given habitat are a function only of habitat properties and not of historical factors. Consequences of this ubiquity theorem are that a latitudinal diversity gradient would be absent or weak, that local diversity would be relatively high compared to the global diversity of the group, and that cosmopolitanism would be important (Fenchel and Finlay 2004).

Rotifera, with an adult size range of 50–2,000  $\mu\text{m}$  (and far smaller propagules; for an introduction see Wallace et al. 2006), are perfectly suited to test this hypothesis, which, in fact, has already raised substantial criticism (Foissner 1999, 2006; Whitaker et al. 2003; Lachance 2004; Jenkins et al. 2007). The debate on cosmopolitanism has a long history in rotiferology (review in Segers 1996) and is still being fed by new data derived from diverse research approaches. Here, we present an overview of the knowledge on diversity and endemism of rotifers in the light of the ubiquity theorem and illustrate the issue by a case study, namely that of the common and ubiquitous genus *Keratella* Bory de St. Vincent (Figs. 1, 2). *Keratella* rotifers are found on all continents and several species are amongst the most common pelagic rotifers. The genus as a whole is eurytopic and cosmopolitan, yet attempts to analyse its chorology have, while demonstrating some intriguing features, so far not been able to elucidate a general pattern (Pejler 1977; De Ridder 1981; Dumont 1983).



**Fig. 1** *Keratella sancta*, known from the Kerguelen Islands, Macquarie I, and New Zealand. (a) Surface ornamentation of lorica, dorsal view; (b) *ibidem*, lateral view; (c) masticatory apparatus or trophi, ventral view



**Fig. 2** *Keratella* spp. (a) *K. cochlearis*, cosmopolitan; (b) *K. cochlearis polaris*, Canadian high arctic; (c) *K. cochlearis* var. *faluta*, northern USA, Canada; (d) *K. armadura*, Michigan, USA; (e) *K. cochlearis pachyacantha*, tropical Africa, South America; (f) *K. taurocephala*, northeast North America; (g) *K. yamana*, Tierra del Fuego, Argentina; (h) *K. taksinensis*, southern Thailand; (i) *K. kostei*, Patagonia, Falkland Island, South Georgia; (j) *K. tropica* f. *taurocephala*, the Caspian; (k) *K. shieli*, Victoria, southern Australia; (l) *K. mongoliana*, inner Mongolia, PR China; (m) *K. quadrata* var. *adnata*, Lake Christine, Alberta, Lake Lilian, BC, Canada; (n) *K. reducta*, Cape region, South Africa

## The taxonomic impediment

One of the issues raised in most of the relevant communications is that any analysis has to be interpreted in the context of present taxonomic knowledge, which is far from perfect in most microscopic organism groups (Fenchel and Finlay 2004; Lachance 2004). Also rotifer students have lamented the state of knowledge in taxonomy (e.g. Koste in Dumont 1980), and no treatise on rotifer chorology or diversity can circumvent the problem. The causes of confusion are well known (Koste and Shiel 1989; Ruttner-Kolisko 1989; Segers 1998) and break down to (purportedly) high morphological variability or cyclomorphosis including the rotifer's ability to phenotypic plasticity, their parthenogenetic reproduction, and, regretfully, poor quality of taxonomic work. The *Keratella cochlearis* complex is illustrative: here, caudal spine length and degree of development of lorica pustulation, amongst other features, were demonstrated as being variable relatively early (Lauterborn 1898, 1900; Ahlstrom 1943). A less desirable consequence of this discovery was that morphologically similar entities were generally lumped in encompassing species concepts, resulting in a complicated and inaccessible nomenclature including subspecies, infrasub-specific variants, and frequent shifts in rank (Koste 1978). For bdelloids, the situation is similar: their exclusive parthenogenetic reproduction, in combination with an apparently high morphological variability and a lack of students, account for the confused bdelloid taxonomy. That diversity has been underestimated is supported by recent studies that demonstrated high genetic taxonomic diversification concealed by, occasionally superficial, morphological stasis both in monogononts (e.g. *Brachionus plicatilis* group: Gomez et al. 2002; Suatoni et al. 2006) and bdelloids (Fontaneto et al. 2007). It is highly likely that such cryptic diversity is far more common than thought in rotifers.

Furthermore confounding is the obvious lack in precision of many rotifer identifications and that a multitude of records are produced during routine surveys or limnological studies. These studies are concentrated in a few regions and habitat types and focus on taxa that are sometimes mistakenly considered "easy", like *Keratella* (e.g. Bērziņš 1955). For example, De Ridder and Segers (1997) contains four full pages of records of the pelagic *K. cochlearis* from the Palaearctic region (mostly Europe), versus a quarter of a page each from the Australian and Oriental regions. The notoriously difficult genus *Enicentrum* (100+ species), living in littoral or interstitial habitats, takes up seven pages in the same work. All this impedes the derivation of the area of rotifers from historical records and exhorts a critical approach to the use of literature data in the study of the distribution and diversity of rotifers.

## General patterns in diversity and endemism in Rotifera

In a recent review of the global diversity and distribution of the rotifers (Segers 2007a), building on the works of Green (1972), Pejler (1977), De Ridder (1981), Dumont (1983), and Segers (1996, 2003), the following patterns could be discerned:

### Diversity

- Rotifera totals 1,571 valid species of Monogononta, 461 of Bdelloidea and 3 Seisonacea, which is an underestimate of extant diversity. Only 69 monogononts, 1 bdelloid and the 3 Seisonacea are exclusively marine, all others are freshwater or brackish water and marine.

- Local species diversity of monogonont rotifers reaches about 150 species per lake in temperate, and up to 250 species in tropical regions. Consequently, 7.5–12.5% of all global species diversity can be found in a single locality. In contrast, Fontaneto et al. (2006b) found a low local species richness with strong habitat selection in both limnoterrestrial and freshwater bdelloid communities inhabiting cushions of dry mosses, and flocks of submerged mosses in running waters and lakes, but reported fairly high local diversity accounting for about 20% of all known bdelloids worldwide. Differences in scale may account for the apparent disparity.
- The relatively low global versus high local diversity is consistent with the hypothesis that small-sized organisms tend to have cosmopolitan distributions (Fenchel and Finlay 2004). On the other hand, many rotifer taxa exhibit complex patterns of distribution and endemism.
- There is a strong discrepancy between diversity and distribution patterns in pelagic habitats, typically with low species diversity and high abundances, and littoral habitats where the opposite is the case.
- Latitudinal variation in the distribution of rotifers is clear in a number of important taxa (*Lecane*, *Brachionus*), which reach their highest diversity in (sub)tropical or, at least, warm waters whereas only a few, less diverse taxa (*Synchaeta*, *Notholca*) are predominantly cold water; as a result, rotifer diversity in general declines from the equator to the poles. The most diverse taxa (100+ species: *Lecane*, *Cephalodella*, *Lepadella*) contain almost exclusively benthic-littoral or psammon-inhabiting species, with a majority inhabiting oligo- to mesotrophic, slightly acidic, soft waters; *Brachionus* is an exception, generally preferring alkaline and eutrophic conditions; local species diversity is especially high in littoral-benthic habitats; in contrast, pelagic diversity is much lower.
- Diversity hotspots are hard to discern, as research intensity appears to be the major factor determining available data on regional diversity and comparable data are scarce.

### Endemicity

- About 22% of non-marine monogononts are regional endemics, whereas a surprising 50% of bdelloid species are purportedly endemic. Many of these, however, are only known from their type locality and have not been recorded since their description, for instance, ca. 25% of the about 300 European bdelloids (Fontaneto and Melone 2003). Endemics occur in all geographic regions and may be among the most frequently observed and abundant species, e.g. *Philodina gregaria* on the Antarctic continent and isles. Some 60 species are cosmopolitan.
- Reliable examples of endemics at higher taxonomic levels are particularly rare in rotifers; species-level endemicity occurs at diverse scales in all regions and regards all but the species-poorest genera and families.
- Endemicity hotspots appear to exist in tropical South America (especially in the genera *Anuraeopsis*, *Brachionus*, *Macrochaetus*), Australia (*Brachionus*, *Keratella*), northeast North America (endemic Birgeidae, *Streptognatha*, *Pseudoploesoma*; species of *Trichocerca*, *Lecane*), and Lake Baikal (*Notholca*); endemicity is relatively low in Africa (including Madagascar) and the Indian subcontinent; in contrast to Lake Baikal, records of endemics from other ancient lakes are scarce.

## A case study: diversity and endemism in the genus *Keratella*

### Approach

For the analysis of diversity and endemism in *Keratella*, we started off with the taxonomy as in Koste (1978), Koste and Shiel (1987) and Segers (2007b). Here, however, we include a number of taxa that are presently considered of infrasubspecific rank, but are either being characterized by morphological features that have been confirmed as taxonomically relevant in the diagnosis of species-level taxa in the genus (e.g. foundation pattern and anterior spine morphology) and/or that have reliably and repeatedly been reported from circumscribed areas. This approach is in line with preliminary results of molecular analysis (Derry et al. 2003) indicating cryptic speciation in *K. cochlearis*. As taxonomy is not the scope of this paper, we merely list them as they occur most commonly in the literature. Distributional data are based on the literature reviews of De Ridder (1986, 1991, 1993), and De Ridder and Segers (1997). Isolated regional records of species otherwise common in other regions were critically assessed and included only after verification of published illustrations or material.

### Biogeography of *Keratella*

A list of the *Keratella* included in the analysis and their distribution is as in Table 1. We recognize 53 relevant taxa, rather than the 48 recorded by Segers (2007a, b). This is a significant increase since the analyses by Peljer (1977; 25 taxa) and Dumont (1983; 37 taxa). A minority only (eight or 15%) can be called cosmopolitan, and even within this group some are restricted to warmer (*K. lenzi*, *K. procurva procurva*, *K. tropica*) or colder (*K. quadrata*) climates. Even if some widespread taxa (e.g. *K. serrulata*) are added to this category, the proportion of true cosmopolites remains surprisingly low.

The northern hemisphere is endowed with a number of Holarctic (5: 9.5%, also *K. testudo*?), Palearctic (6: 11.3%) and Nearctic (8: 15%) endemics. In addition, all marine taxa (5: 9.5%) known to date are restricted to the northern hemisphere. However, knowledge on marine rotifers is sketchy at best, and the isolated marine records of freshwater *Keratella* from the southern hemisphere may require re-examination (De Ridder and Segers 1997). Endemism in other regions varies greatly, from two (Africa) to eight (Neotropical region). Remarkably, most endemism in the southern hemisphere is concentrated in temperate and cold regions. This holds for the single reliable African, as well as for all but one (*K. australis*) Australian/New Zealand and six out of eight Neotropical species. Many of the taxa concerned (*K. kostei*, *K. ona*, *K. yamana*, *K. reducta*, *K. sancta*, *K. shieli*) are phylogenetically isolated; they may represent a true Gondwanan faunal element, being represented in the temperate and cold regions of South America, South Africa, South Australia and New Zealand. This contrasts with the late Cretaceous South American-Antarctic-Australian origin purported for the tropic-centred *Brachionus* by Segers (2007a).

In addition to the, for Rotifera, unique southern hemisphere temperate fauna, two more assemblages stand out. First, endemism in the Palearctic region is centred in the southeast (China), whereas most Nearctic endemics occur in the northern boreal and northeast temperate part. This pattern reminds of a postglacial relict distribution. However, the Chinese endemics are of diverse affiliation and may indeed be ancient relics, whereas most of the northern North American taxa are close relatives of *K. cochlearis*, by sharing this

**Table 1** List of *Keratella* spp with their distribution

## Cosmopolitan species

*Keratella cochlearis* (Gosse, 1851)*Keratella lenzi* Hauer, 1953 (tropicopolitan)*Keratella procurva procurva* (Thorpe, 1891) (tropicopolitan)*Keratella quadrata* (Müller, 1786) (cold water)*Keratella tecta* (Gosse, 1851)*Keratella testudo* (Ehrenberg, 1832) (common in Nearctic and Palearctic regions; two African records (Mauretania, Congo); one Venezuelan record)*Keratella tropica* (Apstein, 1907) (warm-water; several atypical cold-water records exist)*Keratella valga* (Ehrenberg, 1834)

## Holarctic species

*Keratella hiemalis* Carlin, 1943 (incl. Himalaya region)*Keratella irregularis* (Lauterborn, 1898) (northern North America; Palearctic, incl. Nepal)*Keratella mixta* (Oparina-Charitonova, 1924) (single illustrated Thai record)*Keratella paludosa* (Lucks, 1912) (single doubtful, pre-1930 Congo record)*Keratella ticinensis* (Callerio, 1921) (incl. Himalaya; doubtful pre-1940 African records)

## Widespread species

*Keratella cochlearis pachyacantha* Thomasson, 1980 (tropical Africa, South America)*Keratella javana* Hauer, 1937 (tropical Old World; New Zealand, Tasmania)*Keratella serrulata* (Ehrenberg, 1838) (not in Australia)

## Regional and local endemics

## Afrotropical

*Keratella maliensis* Koste & Tobias, 1987: AFR (Mali) (doubtful taxon)*Keratella reducta* (Huber-Pestalozzi, 1929) (Cape region, South Africa)

## Australia

*Keratella ahlstromi* Russell, 1951 (South Island, New Zealand)*Keratella australis* Bērziņš, 1963 (Australia incl. Tasmania)*Keratella procurva robusta* Koste & Shiel, 1980 (temperate Australia incl. Tasmania)*Keratella sancta* Russell, 1944 (Kerguelen, Macquarie Isl., New Zealand)*Keratella shieli* Koste, 1979 (Victoria, South Australia)*Keratella slacki* Bērziņš, 1963 (temperate Australia, incl. Tasmania)

## Palearctic

*Keratella cochlearis nordica* Kutikova, 1978 (Siberian tundra)*Keratella mongoliana* Segers & Rong, 1998 (inner Mongolia, PR China)*Keratella sinensis* Segers & Wang, 1997 (Lake Yaoquan, Wudalianchi; Shanghai, PR China; South Korea)*Keratella trapezoida* Zhuge & Huang, 1998 (Dongting Lake, Hunan province, PR China)*Keratella wangi* Zhuge & Huang, 1997 (Yangtze river near Dongting Lake, Hunan province, PR China)*Keratella zhugeae* Segers & Rong, 1998 (Indian Tibet; Inner Mongolia, PR China)

## Nearctic

*Keratella armadura* Stemberger, 1990 (Michigan, USA)*Keratella canadensis* Bērziņš, 1954 (boreal region of North America)*Keratella cochlearis polaris* De Smet & Bafort, 1990 (Canadian high arctic)

**Table 1** continued

---

*Keratella cochlearis* var. *faluta* Ahlstrom, 1943 (northern USA, Canada)

*Keratella crassa* Ahlstrom, 1943

*Keratella quadrata* var. *adnata* Ahlstrom, 1943 (= *Keratella quadrata neali* Bērziņš, 1961; Christine Lake, Alberta; and Lilian Lake, BC, Canada)

*Keratella taurocephala* Myers, 1938 (northeast North America)

*Keratella earlinae* Ahlstrom, 1943 (northeast North America; single record from Grand Bahamas)

#### Neotropical

*Keratella mexicana* Kutikova & Silva-Briano, 1995 (Mexico, northern Brazil)

*Keratella nhamundaiensis* Koste, 1982 (central Amazonia, northern Argentina)

*Keratella ona* Boltovskoy & Urrejola, 1977 (Tierra del Fuego, Argentina)

*Keratella kostei* Paggi, 1981 (Patagonia, the Falkland Islands, and South Georgia Island)

*Keratella thomassoni* Hauer, 1958 (Tepuhuico Lake, southern Chile)

*Keratella morenoi* Modenutti, Diéguez & Segers, 1998 (Argentina, Patagonian plateau)

*Keratella valdiviensis* Thomasson, 1957 (Valdivian Lakes, Chilean Patagonia)

*Keratella yamana* Boltovskoy & Urrejola, 1977 (Tierra del Fuego, Argentina)

#### Oriental

*Keratella edmondsoni* Ahlstrom, 1943 (India, Thailand)

*Keratella taksinensis* Chittapun, Pholpunthin & Segers, 2002 (southern Thailand)

#### Marine taxa

*Keratella cochlearis* var. *recurvispina* (Jägerskiöld, 1894)

*Keratella cruciformis* (Thompson, 1892) (Atlantic: Europe, Canada; Laptev Sea)

*Keratella eichwaldi* (Levander, 1894) (Holarctic)

*Keratella quadrata* var. *platei* (Jägerskiöld, 1894) (Black Sea, East Sea, Baltic Sea, Northern North Sea)

*Keratella tropica* f. *taurocephala* Koste, 1978 (southern part of Caspian Sea)

---

taxon's typical, and probably apomorphic, foundation pattern of lorica ornamentation. This clade, which is in dire need of revision, further contains *K. tecta*, *K. cochlearis pachyacantha*, *K. valdiviensis* and *K. cochlearis nordica* in the present analysis, and a suite of named infrasubspecific variants. The taxa in this group are undoubtedly closely affiliated and may result from a relatively recent radiation, when compared to the origin of the Chinese group.

There are few widespread tropical species, and true tropical endemics occur only in the Oriental (*K. edmondsoni*, *K. taksinensis*) and Neotropical region (*K. mexicana*, *K. nhamundaiensis*). *K. javana* can hardly be considered tropical as it occurs as far south as New Zealand and Tasmania, where it overlaps with Australia's share of southern hemisphere temperate and cold-water taxa. By this peculiar distribution and its isolated phylogenetic position, we hypothesize that it belongs to south Australia's Gondwanan *Keratella* group, but has expanded secondarily into the Australian and later Old World tropics. Another peculiar case is that of *K. americana*, which is exceedingly common in the Americas and of which isolated records exist from the eastern hemisphere; it is likely that the latter records concern introductions (Segers 2001). Peljer (1977) formulated similar comments on the presence of *K. irregularis* in North America: also this taxon is fairly

common in the Palearctic, whereas records from the Nearctic are rare and recent only. The presence of *K. cochlearis pachyacantha* in Africa, where it appears to be far less common in suitable habitats than in South America, could be explained in a similar way.

When compared to other rotifer taxa for which sufficient reliable data are available (*Brachionus*: see Pejler 1977, Dumont 1983, Segers 2007a; *Lecane*: Segers 1996, *Trichocerca*: Segers 2003), *Keratella* turns out to contain the smallest fraction of cosmopolitan (*sensu lato*) species. We could identify two diverse, possibly ancient groups of endemics: one in the southeast Palearctic (China) and another, probably a Gondwanan relict, in the southern hemisphere temperate and cold regions. In addition to these, there is a possibly recent radiation in the *K. cochlearis* group in North America. Whereas the two former have no counterpart in other groups, the latter is complemented, in the northeast Nearctic, by endemics in *Lecane* and *Trichocerca* (Segers 1996, 2003). Only the Nearctic group of endemics had been discerned in *Keratella* before (Bērziņš 1954; Pejler 1977).

### Processes of dispersal and colonization

The main processes underpinning the extant patterns in the diversity and endemism of rotifers are, obviously, their mode of dispersal and reproduction.

#### Propagules

Rotifer propagules consist of dormant mictic or resting eggs, i.e. hard-shelled, encysted embryos in monogononts or equally dormant anhydrobiotic animals and parthenogenetically produced eggs in bdelloids. Both resting eggs and anhydrobiotic stages of bdelloids have a capacity for extended periods of dormancy (from days to years depending the species), are minute (most smaller than 100  $\mu\text{m}$ ), and are the main stages of dispersal (Gilbert 1974; Pourriot and Snell 1983; Schröder 2005).

Resting eggs are characterized by a thick shell, which often is ornamented with bristles, spines, knobs, bubbles, etc. The function of eggshell ornamentation is not well known, but it may enhance buoyancy and/or aid in dispersal. Resting eggs are resistant to drought, heat, cold, or other adverse chemical or physical conditions of the habitat for long periods, thus aiding in the dispersal of the species (Wallace et al. 2006). The thickness of the shell and its reduced porosity may also protect against digestive enzymes following ingestion, and hence resting eggs could survive gut passage of predators.

The great majority of bdelloid species are capable of anhydrobiosis (Ricci 1998; Ricci and Caprioli 2005), a form of quiescence in response to unpredictable and fast changes of water availability in unstable habitats. When subjected to drying, bdelloids withdraw their head and foot into the trunk and contract into a compact 'barrel'. Desiccation during tun formation reduces volume and density, which results in very small and light propagules suitable for aerial transport. Survival of desiccated bdelloid eggs has been rarely studied and demonstrated in a few species only (Dobers 1915; Örstan 1995; Ricci et al. 1987). Egg desiccation survival times of 2 days to 14 months have been reported, indicating that bdelloid eggs may form airborne propagules as well.

Clearly, the nature of rotifer propagules is a strong argument supporting the validity of the ubiquity theorem in these microscopic organisms. However, viability of propagules can be reduced by environmental factors, like extended exposure or physical and chemical unsuitability of the substratum or habitat (Chittapun et al. 2005). Likewise, the implicit

generalization that propagules of all rotifers species are efficient is unlikely correct, which could account for the local or regional, “ancient” endemics mentioned above. For one, the “classic” sampling methodology for bdelloids, viz. examination of rehydrated, dry moss samples may preclude discovery of possible local taxa that have inefficient anhydrobiotic capacities.

## Dispersal

Rotifers achieve dispersal in space and time through passive transport by water currents, wind or animal vectors (Örstan 1998; Wallace et al. 2006). It is commonly assumed that transport by wind is most likely the major way of long-distance dispersal of the desiccation-resistant propagules, as has been demonstrated for algae and Protozoa (Gislén 1948; Schlichting 1961, 1964). Direct evidence was provided by Jenkins and Underwood (1998) who looked for rotifers in samples collected by windsocks and in rain samplers, and by Janiec (1996) who used traps filled with 4% formalin solution. Their results show that, contrary to the commonly accepted premise, rotifers may not disperse that readily by wind or rain. Indirect evidence of a potential of primary dispersal by wind and rain was provided by several dispersal-colonization experiments with artificial bodies of water (Maguire 1963; McCormick and Cairns 1990; Holland and Jenkins 1998; Cáceres and Soluk 2002).

In running waters active animals and propagules, originating from the catchment area or from the bottom of the riverbed, are transported by downstream drift (Sandlund 1982). The formation of temporary connections between stagnant waters during heavy rain-fall and flooding (Jenkins and Boulton 2003), or e.g. occasional breaching of Antarctic ponds and consequent formation of streams (Suren 1990) also aids in dispersal over 100s of metres to 1,000s of kilometres. Oceanic currents may be responsible for the cosmopolitanism of many marine species (Fontaneto et al. 2006a), and rotifers living in multi-year sea ice are transported by the ‘Transpolar Drift’ from the Eurasian shelf regions over the central Arctic Basin to the Greenland Sea (Friedrich and De Smet 2000).

Animal-mediated passive transport of rotifers (“zoochory”), both internal and external, has hardly been studied. Insects, amphibians and birds were found carrying propagules and/or active rotifers externally on their body (Maguire 1959, 1963; Schlichting 1960; Schlichting and Milliger 1969; Sides 1973). Internal transport in the gut of animal vectors, followed by defecation of viable stages surviving digestion, has yet not been demonstrated in rotifers; Wallace et al. (2006) erroneously state that Euliss et al. (1991) reported endozoochory in waterfowl. However, active bdelloids and developing eggs have been observed in the rectum or midgut of dipterid larvae belonging to *Culex*, *Chironomus* (Marchoux 1898) and *Simulium* (Nelder and McCreddie 2003), suggesting that internal transport, at least in insects, may occur.

Dispersal of rotifers can also be achieved through human activities, e.g. intentional stocking programs for fisheries (Pejler 1998), release from aquaria (Padilla and Williams 2004), release with bait fish (Havel and Stelzleni-Schwent 2000), release of ballast water (Bailey et al. 2003), etc. Studying potential survival after ballast exchange, Gray et al. (2005) demonstrated that the viability of freshwater rotifer resting eggs was not affected after exposure to open-ocean water (32‰), despite the low salinity tolerance of the adult stages of most species.

## Colonization and adaptation

As rotifer propagules consist of resistant, dormant stages, they remain viable after dispersal, even when the target habitat is unsuitable at the moment of arrival. Moreover, due to their parthenogenetic reproduction a single specimen is able of establishing a new population. Consequently, the colonization capability of rotifers is potentially very high. Indeed, experiments studying colonization of artificial ponds (Jenkins 1995) or mesocosms (Langley et al. 2001; Cáceres and Soluk 2002) found rapid colonization by rotifers, amongst other zooplankton.

On the other hand, different factors thwart successful colonization. Competition by occupant species or populations appears to play a major role, as indicated by experiments by Shurin (2000). Similarly, the presence of a large propagule bank of locally adapted genotypes may present an effective barrier against newly arriving genotypes (De Meester et al. 2002).

Phylogenetic analysis of mitochondrial *cox1* genes by Birky et al. (2005) showed a significant correlation between geographical distance and sequence difference, but with indication of rapid dispersal. Using the rate of dispersal they found that bdelloid species could have dispersed around the world many times since their divergence, and suggested that continued independent evolution, in absence of isolation by distance, can be most easily explained by adaptation to different niches. Mills et al. (in press) found strong phylogenetic structure in the saline water monogonont *B. plicatilis* (sensu stricto), in addition to a strong correlation between genetic and geographic distance. They conclude that this is likely to have been produced through the colonization process, and that even potentially dispersive microscopic organisms can achieve substantial geographic subdivision which can lead to reproductive incompatibility. These intriguing results appear compatible with the patterns outlined above. Whereas a substantial body of data is becoming available on species-level chorology, however, hiatuses regarding cryptic taxa and phylogeography hamper our understanding of diversity and distribution of these microscopic metazoans. The debate on the ubiquity theorem will possibly continue to rage on for some time to come. However, it is clear that the diversity of distribution patterns in rotifers varies widely. Both local endemism and broad cosmopolitanism as well as intermediates occur, and either of the alternatives may be common, depending on the taxon. If chorology of rotifers is representative of that of other microscopic organisms, then it may be more productive to examine the relative importance and diversity of distribution patterns, and the factors determining these, at different taxonomic levels, in order to come to an understanding of their chorology and biodiversity. Basically, the rotifer data match the moderate endemism model of Foissner (2006) and Chao et al. (2006) better than the ubiquity model of Finlay (2002) and Fenchel and Finlay (2004).

### A special case: Seisonacea and other marine rotifers

The above treatments of dispersal and propagules hold for bdelloid and monogonont rotifers; Seisonacea are exclusively marine and composed of two genera: *Seison* with two species (*S. africanus*, *S. nebaliae*) and the monospecific *Paraseison annulatus* (Ricci et al. 1993; Sørensen et al. 2005). *Paraseison annulatus* and *S. nebaliae* both are exclusively epibiotic on species of the leptostracan crustacean *Nebalia* and show a similar distribution: Mediterranean, North Sea, European part of northern Atlantic and the Amiva Bay, Sakhalin Island, Sea of Okhotsk. *Seison africanus* was described from Gazi Bay, Indian

Ocean, Kenya; it was not attached to a host, and *Nebalia* was absent. Unidentified specimens have been found on *Nebalia* at Morro Bay, Pacific Ocean, California; McMurdo Sound, Ross Sea, Antarctica; and Magellanic Chile. *Seisonacea* are bisexual and no resting stages are present. Hardly anything is known about the life cycle and dispersal of *Seisonacea*, but their obligatory relation with *Nebalia*, sexual reproduction and absence of known resting stages or specialized propagules appear key to their distribution. Considering the evolutionary age and ubiquity of *Nebalia*, and the paucity of studies on *Seisonacea*, it is highly likely that diversity of the taxon is greatly underestimated. In general, it is presently hardly possible to derive patterns on the diversity and distribution of marine rotifers due to lack of data.

## References

- Ahlstrom EH (1943) A revision of the Rotatorian genus *Keratella* with descriptions of three new species and five new varieties. Bull Am Mus Nat Hist 80:411–457
- Baas-Becking LGM (1934) Geobiologie of Inleiding tot de Milieukunde. Van Stockum en Zoon, The Hague, The Netherlands
- Bailey SA, Duggan IC, van Overdijk et al (2003) Viability of invertebrate diapausing eggs collected from residual sediment. Limnol Oceanogr 48:1701–1710
- Bērziņš B (1954) A new rotifer, *Keratella canadensis*. J Quekett Microsc Club 4:113–115
- Bērziņš B (1955) Taxonomie und Verbreitung von *Keratella valga* und verwandten Formen. Ark Zool 8:549–559
- Birky CW, Wolf C, Maughan H et al (2005) Speciation and selection without sex. Hydrobiologia 546:29–45
- Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408
- Chao A, Li P, Agatha S et al (2006) A statistical approach to estimate soil ciliate diversity and distribution based on data from five continents. Oikos 114:479–493
- Chittapun S, Pholpunthin P, Segers H (2005) Restoration of tropical peat swamp rotifer communities after perturbation: an experimental study of recovery of rotifers from the resting egg bank. Hydrobiologia 546:281–289
- De Meester L, Gómez A, Okamura B et al (2002) The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecol 23:121–135
- De Ridder M (1981) Some considerations on the geographical distribution of rotifers. Hydrobiologia 85:209–225
- De Ridder M (1986) Annotated checklist of non-marine rotifers (Rotifera) from African inland waters. Zoologische Documentatie, Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium, 21, 123 pp
- De Ridder M (1991) Additions to the “annotated checklist of non-marine rotifers (Rotifera) from African inland waters”. Rev Hydrobiol Trop 24:25–46
- De Ridder M (1993) Additions II to the “annotated checklist of non-marine rotifers (Rotifera) from African inland waters”. Biol Jb Dodonaea 61:99–153
- De Ridder M, Segers H (1997) Rotifera Monogononta in six zoogeographical regions after publications between 1960–1992. In: Van Goethem J (ed) Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, 481 pp
- Derry AM, Hebert PDN, Prepas EE (2003) Evolution of rotifers in saline and subsaline lakes: a molecular phylogenetic approach. Limnol Oceanogr 48:675–685
- Dobers E (1915) Über die Biologie der Bdelloidea. Int Rev Hydrobiol Hydrograph, Suppl 7:1–128
- Dumont HJ (1980) Workshop on taxonomy and biogeography. In: Dumont HJ, Green J (eds) Rotatoria. Hydrobiologia 73:205–206
- Dumont HJ (1983) Biogeography of rotifers. Hydrobiologia 104:19–30
- Euliss ND, Jarvis RL, Gilmer DS (1991) Feeding ecology of waterfowl wintering on evaporation ponds in California. Condor 93:582–590
- Fenchel T, Finlay JB (2004) The ubiquity of small species: patterns of local and global diversity. Bioscience 54:777–784
- Finlay JB (2002) Global dispersal of free-living microbial eukaryote species. Science 96:1061–1063
- Foissner W (1999) Protist diversity: estimates of the near-imponderable. Protist 150:363–368
- Foissner W (2006) Biogeography and dispersal of micro-organisms: a review emphasizing protists. Acta Protozool 45:111–136

- Fontaneto D, Melone G (2003) Redescription of *Pleuretra hystrix*, an endemic alpine bdelloid rotifer. *Hydrobiologia* 497:153–160
- Fontaneto D, De Smet WH, Ricci C (2006a) Rotifers in saltwater environments, re-evaluation of an inconspicuous taxon. *J Mar Biol Assoc UK* 86:623–656
- Fontaneto D, Ficetola GF, Ambrosini R et al (2006b) Patterns of diversity in microscopic animals: are they comparable to those in protists or in larger animals? *Glob Ecol Biogeogr* 15:153–162
- Fontaneto D, Herniou EA, Boschetti C et al (2007) Independently evolving species in asexual bdelloid rotifers. *PLoS Biol* 5:1–8
- Friedrich C, De Smet WH (2000) The rotifer fauna of arctic sea ice from the Barents Sea, Laptev Sea and Greenland Sea. *Hydrobiologia* 432:73–89
- Gilbert JJ (1974) Dormancy in rotifers. *Trans Am Microsc Soc* 93:490–513
- Gislén T (1948) Aerial plankton and its conditions of life. *Biol Rev* 23:109–126
- Gomez A, Serra M, Carvalho GC et al (2002) Speciation in ancient cryptic species complexes: evidence from the molecular phylogeny of *Brachionus plicatilis* (Rotifera). *Evolution* 56:1431–1444
- Gray DK, Bailey SA, Duggan IC et al (2005) Viability of invertebrate diapausing eggs exposed to saltwater: implications for Great Lakes' ship ballast management. *Biol Invasions* 7:531–539
- Green J (1972) Latitudinal variation in associations of planktonic Rotifera. *J Zool, Lond* 167:31–39
- Havel JE, Stelzleni-Schwent J (2000) Zooplankton community structure: the role of dispersal. *Verh Int Ver Limnol* 27:3264–3268
- Holland LE, Jenkins DG (1998) Comparison of processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* 387/388:207–214
- Janiec K (1996) Short distance wind transport of microfauna in maritime Antarctic (King George Island, South Shetland Islands). *Pol Polar Res* 17:203–211
- Jenkins DG (1995) Dispersal-limited zooplankton distribution and community composition in new ponds. *Hydrobiologia* 313/314:15–20
- Jenkins KM, Boulton AJ (2003) Connectivity in a dryland river: short-term aquatic microinvertebrate recruitment following floodplain inundation. *Ecology* 84:2708–2723
- Jenkins DG, Underwood MO (1998) Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* 387/388:15–21
- Jenkins DG, Brescacin CR, Duxbury CV et al (2007) Does size matter for dispersal distance? *Glob Ecol Biogeogr* 16:415–425
- Jennings HS (1900) Rotatoria of the United States, with especial reference to those of the Great Lakes. *Bull US Fish Comm* 1899:67–104
- Koste W (1978) Rotatoria. Die Rädertiere Mitteleuropas, vol 2. Borntraeger, Berlin
- Koste W, Shiel RJ (1987) Rotifera from Australian inland waters. II. Epiphanidae and Brachionidae (Rotifera: Monogononta). *Invertebr Taxon* 7:949–1021
- Koste W, Shiel RJ (1989) Classical taxonomy and modern methodology. *Hydrobiologia* 186/187:79–284
- Lachance M-A (2004) Here and there or everywhere? *Bioscience* 54:884
- Langley JM, Shiel RJ, Nielsen DL et al (2001) Hatching from sediment egg-bank, or aerial dispersing?-the use of mesocosms in assessing rotifer biodiversity. *Hydrobiologia* 446/447:203–211
- Lauterborn R (1898) Vorläufige mittheilung über den Variationskreis von *Anurea cochlearis* Gosse. *Zool Anz* 21:597–604
- Lauterborn R (1900) Der Formenkreis von *Anurea cochlearis*. Ein Beitrag zur Kenntniss der Variabilität bei Rotatorien. *Verh Nat-Med Ver Heidelberg* 6:412–448
- Maguire BJ (1959) Passive overland transport of small aquatic organisms. *Ecology* 40:312
- Maguire BJ (1963) The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecol Monogr* 33:161–185
- Marchoux E (1898) Note sur un rotifère (*Philodina parasitica* n. sp.) vivant dans le tube digestif de larves aquatiques d'insectes. *Compt rend Séanc Soc Biol Fil, Sér* 10:749–750
- McCormick PV, Cairns J (1990) Microbial colonization dynamics in temporary aquatic systems. *Hydrobiologia* 196:229–253
- Mills S, Lunt DH, Gómez A (in press) Global isolation by distance despite strong regional phylogeography in a small metazoan. *BMC Evol Biol*
- Nelder MP, McCreddie JW (2003) Bdelloid rotifers (Rotifera: Bdelloidea) inhabiting larval black flies (Diptera: Simuliidae) and their effect on trichomycete (Zygomycota) fungal abundance. *Proc Entomol Soc Wash* 105:794–796
- Örstan A (1995) Desiccation survival of the eggs of the rotifer *Adineta vaga* (Davis, 1873). *Hydrobiologia* 313/314:373–375
- Örstan A (1998) Microhabitats and dispersal routes of bdelloid rotifers. *Sci Nat* 1:27–36

- Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Front Ecol Environ* 2:131–138
- Pejler B (1977) On the global distribution of the family Brachionidae (Rotatoria). *Arch Hydrobiol* 53(Suppl):255–306
- Pejler B (1998) History of rotifer research in northern Europe. *Hydrobiologia* 387/388:267–278
- Pourriot R, Snell TW (1983) Resting eggs in rotifers. *Hydrobiologia* 104:213–224
- Ricci C (1998) Anhydrobiotic capabilities of bdelloid rotifers. *Hydrobiologia* 387/388:321–326
- Ricci C, Caprioli M (2005) Anhydrobiosis in bdelloid species, populations and individuals. *Integr Comp Biol* 45:759–763
- Ricci C, Vaghi L, Manzini ML (1987) Desiccation of rotifers (*Macrotrachela quadricornifera*): survival and reproduction. *Ecology* 68:1488–1494
- Ricci C, Melone G, Sotgia C (1993) Old and new data on Seisonidea (Rotifera). *Hydrobiologia* 255/256:495–511
- Roussellet CF (1909) On the geographical distribution of the Rotifera. *J Quekett Microsc Club* 10:465–470
- Ruttner-Kolisko A (1989) Problems in the taxonomy of rotifers, exemplified by the *Filinia longiseta-terminalis* complex. *Hydrobiologia* 186/187:291–298
- Sandlund OT (1982) The drift of zooplankton and microzoobenthos in the river Strandaelva, western Norway. *Hydrobiologia* 94:33–48
- Schlichting HE (1960) The role of waterfowl in the dispersal of algae. *Trans Am Microsc Soc* 79:160–166
- Schlichting HE (1961) Viable species of algae and Protozoa in the atmosphere. *Lloydia* 24:81–88
- Schlichting HE (1964) Meteorological conditions affecting the dispersal of airborne algae and Protozoa. *Lloydia* 27:64–78
- Schlichting HE, Milliger LE (1969) The dispersal of microorganisms by a hemipteran, *Lethocerus uhleri* (Montadon). *Trans Am Microsc Soc* 88:452–454
- Schröder T (2005) Diapause in monogonont rotifers. *Hydrobiologia* 546:291–306
- Segers H (1996) The biogeography of littoral *Lecane* Rotifera. *Hydrobiologia* 323:169–197
- Segers H (1998) An analysis of taxonomic studies on Rotifera: a case study. *Hydrobiologia* 387/388:9–14
- Segers H (2001) Zoogeography of the Southeast Asian Rotifera. *Hydrobiologia* 446/447:233–246
- Segers H (2003) A biogeographical analysis of rotifers of the genus *Trichocerca* Lamarck, 1801 (Trichocercidae, Monogononta, Rotifera), with notes on taxonomy. *Hydrobiologia* 500:103–114
- Segers H (2007a) Global diversity and distribution of the rotifers (Phylum Rotifera). *Hydrobiologia* (in press)
- Segers H (2007b) A global checklist of the rotifers (Phylum Rotifera). *Zootaxa* 1564:1–104
- Shurin JB (2000) Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086
- Sides SL (1973) Internal and external transport of algae and protozoa by sea gulls. *Trans Amer Microsc Soc* 92:307–311
- Sørensen MV, Segers H, Funch P (2005) On a new *Seison* Grube, 1861 from coastal waters of Kenya, with a reappraisal of the classification of the Seisonida (Rotifera). *Zool Stud* 44:34–43
- Suatoni E, Vicario S, Rice S et al (2006) An analysis of species boundaries and biogeographic patterns in a cryptic species complex: the rotifer *Brachionus plicatilis*. *Mol Phylogenet Evol* 18:70–74
- Suren A (1990) Microfauna associated with algal mats in melt ponds of the Ross Ice Shelf. *Polar Biol* 10:329–335
- Wallace RL, Snell TW, Ricci C et al (2006) Rotifera vol 1: biology, Ecology and Systematics. In: Segers H, Dumont HJF (eds) Guides to the identification of the microinvertebrates of the continental waters of the World 23. Kenobi productions, Ghent/Backhuys Acad Publ/The Hague 299p
- Whitaker RJ, Grogan DW, Taylor JW (2003) Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* 301:976–978