



A biogeographical analysis of rotifers of the genus *Trichocerca* Lamarck, 1801 (Trichocercidae, Monogononta, Rotifera), with notes on taxonomy

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Abstract

An analysis of distribution patterns reveals a unique group of Nearctic endemics in *Trichocerca* Lamarck, 1801. This group, comprising 13.4% of all taxa analysed in the genus, is of diverse origin. A glacial origin is postulated for one species. The observed biogeographic pattern of eight others, and possibly two New World taxa, suggests a pre-Pleistocene origin followed by differential extinctions during glaciations in the Nearctic and Palaearctic. In general, endemism in *Trichocerca* is strongly biased towards the Northern hemisphere, with no endemism in tropical regions. This suggests a Laurasian origin of the genus. The analysis further reveals a majority (65.7%) of widely distributed taxa, with strict cosmopolitanism in more than a third of the species analysed. Latitudinal variation is evident in 26.9% of *Trichocerca*, and a warm-water preference appears to be indicated for a majority of these. Although the results should be interpreted with caution due to confused taxonomy, a Southern hemisphere, warm-water and Northern hemisphere, cold water component appear to be present. Comments on the taxonomy and distribution of several species are provided, along with illustrations of poorly known species. Suggestions include elevating *T. maior* (Hauer, 1936) to species rank, and several new cases of synonymy.

Introduction

The study of rotifer chorology, typical of the biogeography of passively dispersing freshwater organisms, has revived during past decades. After a century in which a generalized cosmopolitanism was postulated for such organisms (Jennings, 1900; Rousselet, 1909; Ruttner-Kolisko in Dumont, 1980), it is increasingly becoming clear that this hypothesis does not hold for many taxa. The first well-documented cases of rotifer endemism were reported as early as 1940 (Ahlstrom, 1940, 1943). Large-scale analysis of distribution patterns in rotifers revealed latitudinal gradients as well as geographical endemism (e.g., Green, 1972; Pejler, 1977a, b; De Ridder, 1981; Dumont, 1983; Segers, 1996), but it also became clear that much of the apparent cosmopolitanism followed from inadequate taxonomic and faunistic knowledge (Pejler, 1977a; Dumont, 1980, 1983; Koste & Shiel, 1989; Nogrady

et al., 1993). These insights largely concur with the results of similar studies in other groups of organisms with passive dispersal strategy (e.g., Anomopoda: Frey, 1986, 1987).

One of the peculiarities of rotifer chorology is, that there are few taxonomic groups in which endemism is focussed in a specific region. The most notable and well-illustrated exception to this trend is the endemic *Notholca* species flock of the Lake Baikal region (Kutikova, 1980; Dumont, 1983). Here, I present a chorological analysis of the genus *Trichocerca* Lamarck, 1801, which appears to exhibit a similarly unique distributional pattern. The genus *Trichocerca* is special amongst Rotifera, as it is ecologically diverse, including freshwater and marine, pelagic, littoral and psammobiotic species. Also, it is the only species-rich genus of Rotifera in which both trophi as well as lorica morphology are taxonomically significant. Surprisingly, there appears to

be little concordance in similarity in trophi and lorica morphology. Illustrative of this are several cases of different species having similar external, but different trophi morphology, and *vice-versa*. The fact that both lorica and trophi morphology are varied, and taxonomically significant, makes *Trichocerca* one of the few rotifer genera in which a relatively large number of features is available for analysis (see Ruttner-Kolisko, 1989). On the other hand, it is unfortunate that trophi morphology has not been consistently included in taxonomic treatments, although the significance of this feature in *Trichocerca* had long been realized. In addition, the lorica of *Trichocerca* is asymmetric and easily deformed, leading to the description of poorly contracted or contorted specimens as taxonomic novelties. Study of *Trichocerca* is further hampered by the absence of an early taxonomic revision such as those by H.K. Harring and F.J. Myers, which constitute milestones for the study of taxonomy in many other rotifer groups. As for most Rotifera (e.g., Dumont, 1983; Koste & Shiel, 1989), confused taxonomy impacts on our knowledge on distribution of *Trichocerca*, so published records need to be interpreted with caution. In an attempt to rectify this I provide brief discussions on taxonomy and distribution regarding a number of taxa. Nevertheless, several controversies remain unresolved.

Materials and methods

The material used for the present study is largely based on a revision in progress of the Trichocercidae for the series "Guides to the Identification of the Microinvertebrates of the Continental Waters of the World", edited by H.J. Dumont. The taxonomy follows Koste (1978), with additions and changes as proposed in the recent literature, and including results of original taxonomic research on material from various regions of the world, and from various collections (the Academy of Natural Sciences of Philadelphia, PA, U.S.A.: ANSP; Ghent University, Belgium; the Royal Belgian Institute of Natural Sciences, Brussels, Belgium). Comments on taxonomy, and on a number of species included in the bibliography by De Ridder & Segers (1997) are included. Distributional records are based in part on De Ridder (1986, 1991, 1994) and De Ridder & Segers (1997). For the biogeographical analysis, the conventions of Segers (1996) are followed.

Results and discussion

Taxonomy

A checklist of the taxa considered is presented in Table 1. Two frequently recorded *Trichocerca* species were excluded from the biogeographical analysis because of their confused taxonomy. These are *T. gracilis* (Tessin, 1890) and *T. lophoessa* (Gosse, 1886). The true identity of *T. gracilis* is unclear. A complete and detailed description of this species does not exist, and it appears that several similar taxa have been lumped under this name. Exemplary of the confusion is Myers' (1942) account of the species. Segers & Dumont (1995) depict a specimen with an external morphology matching literature descriptions of *T. gracilis*, but with unique trophi. The case of *T. lophoessa* is similar (e.g., compare the reports on this species by Stemberger, 1979 and Jersabek & Schabetsberger, 1992). These cases illustrate the well-known fact that present-day taxonomy remains an imperfect tool for the study of rotifer biology.

As mentioned above, the present study is largely based on the taxonomic revision by Koste (1978). Some poorly described taxa included in that work are listed as *species inquirendae* in Table 1. In most of these, no account is provided of trophi morphology, and/or the material on which their description is based was in poor condition. Although some may be valid taxa, they are not included in the biogeographical analysis. In the following section, I present arguments for being at variance with the views expressed in Koste's (1978) book.

- ***Trichocerca bicristata*** (Gosse, 1887) and ***Trichocerca mucosa*** (Stokes, 1896): Small specimens of *T. bicristata* have frequently been referred to as *T. bicristata* var./f. or subspecies *mucosa*. All verifiable records of *T. bicristata* var./f. *mucosa* concern such specimens. However, *T. mucosa* (Stokes, 1896) is a different, unrelated taxon (Stemberger, 1979; Segers, 1997).
- ***Trichocerca braziliensis*** (Murray, 1913) and ***Trichocerca rattus*** (Müller, 1776): It is likely that *T. braziliensis* (= *T. elongata braziliensis* (Murray, 1913) after Koste, 1978; subspecies status rejected by Shiel & Koste, 1992) and *T. rattus* have frequently been confused, as both their trophi and lorica morphology are similar (Segers & De Meester, 1994). I have never found *T. rattus* in collections from regions with a (sub)tropical climate, hence I suspect that many tropical records

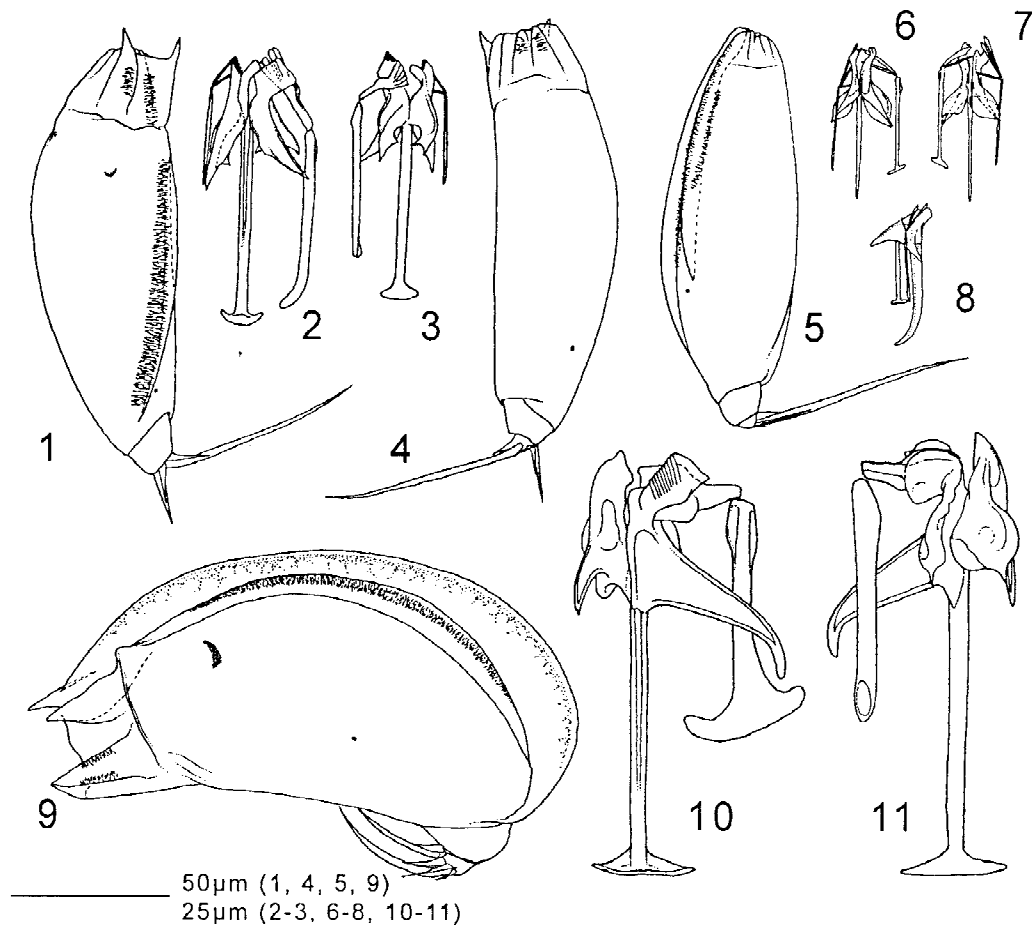
Table 1. Checklist of *Trichocerca* species

<i>Trichocerca abilioi</i> Segers, 1993	<i>Trichocerca mus</i> Hauer, 1937/38
<i>Trichocerca agnatha</i> Wulfert, 1939	<i>Trichocerca musculus</i> (Hauer, 1936)
<i>Trichocerca bicristata</i> (Gosse, 1887)	<i>Trichocerca myersi</i> (Hauer, 1931)
<i>Trichocerca bicuspes</i> (Pell, 1890)	<i>Trichocerca obtusidens</i> (Olofsson, 1918)
<i>Trichocerca bidens</i> (Lucks, 1912)	<i>Trichocerca orca</i> (Murray, 1913)
<i>Trichocerca brachyura</i> (Gosse, 1851)	<i>Trichocerca ornata</i> Myers, 1934
<i>Trichocerca braziliensis</i> (Murray, 1913)	<i>Trichocerca pediculus</i> Remane, 1949
<i>Trichocerca capucina</i> (Wierzejski & Zacharias, 1893)	<i>Trichocerca plaka</i> Myers, 1938
<i>Trichocerca cavia</i> (Gosse, 1886)	<i>Trichocerca platessa</i> Myers, 1934
<i>Trichocerca chattoni</i> (de Beauchamp, 1907)	<i>Trichocerca porcellus</i> (Gosse, 1851)
<i>Trichocerca collaris</i> (Rousselet, 1896)	<i>Trichocerca pusilla</i> (Jennings, 1903)
<i>Trichocerca cylindrica</i> (Imhof, 1891)	<i>Trichocerca pygocera</i> (Wiszniewski, 1932)
<i>Trichocerca dixonnutalli</i> (Jennings, 1903)	<i>Trichocerca rattus</i> (Müller, 1776)
<i>Trichocerca edmondsoni</i> (Myers, 1936)	<i>Trichocerca rosea</i> (Stenroos, 189)
<i>Trichocerca elongata</i> (Gosse, 1886)	<i>Trichocerca rotundata</i> Myers, 1937
<i>Trichocerca flagellata</i> Hauer, 1937	<i>Trichocerca rousseleti</i> (Voigt, 1902)
<i>Trichocerca gracilis</i> (Tessin, 1890)	<i>Trichocerca rutneri</i> Donner, 1953
<i>Trichocerca harveyensis</i> Myers, 1941	<i>Trichocerca scipio</i> (Gosse, 1886)
<i>Trichocerca hollaerti</i> De Smet, 1990	<i>Trichocerca siamensis</i> Segers & Pholpunthin, 1997
<i>Trichocerca iernis</i> (Gosse, 1887)	<i>Trichocerca similis</i> (Wierzejski, 1893)
<i>Trichocerca insignis</i> (Herrick, 1885)	<i>Trichocerca similis</i> f. <i>grandis</i> Hauer, 1965
<i>Trichocerca insolens</i> (Myers, 1936)	<i>Trichocerca simoneae</i> De Smet, 1990
<i>Trichocerca insulana</i> (Hauer, 1937/38)	<i>Trichocerca stylata</i> (Gosse, 1851)
<i>Trichocerca intermedia</i> (Stenroos, 1898)	<i>Trichocerca sulcata</i> (Jennings, 1894)
<i>Trichocerca kostei</i> Segers, 1993	<i>Trichocerca taurocephala</i> (Hauer, 1931)
<i>Trichocerca lata</i> (Jennings, 1894)	<i>Trichocerca tenuior</i> (Gosse, 1886)
<i>Trichocerca longiseta</i> (Schrank, 1802)	<i>Trichocerca tigris</i> (Müller, 1786)
<i>Trichocerca longistyla</i> (Olofsson, 1918)	<i>Trichocerca uncinata</i> (Voigt, 1902)
<i>Trichocerca lophoessa</i> (Gosse, 1886)	<i>Trichocerca vargai</i> Wulfert, 1961
<i>Trichocerca macera</i> (Gosse, 1886)	<i>Trichocerca vassilijevae</i> Kutikova & Arov, 1985
<i>Trichocerca maior</i> Hauer, 1936	<i>Trichocerca vernalis</i> (Hauer, 1936)
<i>Trichocerca marina</i> (Daday, 1890)	<i>Trichocerca voluta</i> (Murray, 1913)
<i>Trichocerca mollis</i> Edmondson, 1936	<i>Trichocerca wanarra</i> Segers & Shiel, 2003
<i>Trichocerca mucosa</i> (Stokes, 1896)	<i>Trichocerca weberi</i> (Jennings, 1903)
<i>Trichocerca multicrinis</i> (Kellcott, 1897)	

*List of *species inquirenda*.

- Trichocerca taurocephala* after Koste & Zhuge, 1996: endemic, Hainan, China (Segers, 1998)
- Trichocerca antilopaea* (Petr, 1891): unrecognisable; possible synonym of *T. collaris* after Koste (1978).
- Trichocerca artmanni* (Zelinka, 1927): unrecognisable.
- Trichocerca barsica* (Varga & Dudich, 1938): unrecognisable.
- Trichocerca bicurvirostris* (Mola, 1913): unrecognisable.
- Trichocerca caspica* (Tschugunoff, 1921)(= *T. marina caspica* (Tschugunoff) after Koste, 1978): no account of trophi. Unrecognisable. "Anscheinend mit f. typ. identisch": Koste (1978).
- Trichocerca cryptodus* (Hauer, 1937): no account of trophi; a relative of *T. cavia* or *T. parvula*?
- Trichocerca euodonta* (Hauer, 1937): no account of trophi. Unrecognisable.
- Trichocerca flava* (Voronkov, 1907): not contracted, no account of trophi; unrecognisable.
- Trichocerca gillardi* Koste, 1978: no account of trophi.
- Trichocerca heterodactyla* (Tschugunoff, 1921): no account of trophi available; compare with *T. dixonnutalli*.
- Trichocerca inermis* (Linder, 1904): no account of trophi; compare with *T. dixonnutalli*.
- Trichocerca marina longicauda* (Tschugunoff, 1921) (= *Rattulus caspicus* var. *longicaudis* Tschugunoff, 1921): no account of trophi. Unrecognisable.
- Trichocerca mucripes* Ahlstrom, 1938: no account of trophi. North Carolina, U.S.A. Not seen since discovery.
- Trichocerca nitida* Haring, 1914: no account of trophi.
- Trichocerca parva* (Manfredi, 1927): unrecognisable.
- Trichocerca rectangularis* Evens, 1947: close to *T. gracilis* according to Koste (1978). Insufficiently described.
- Trichocerca ripli* Berzins, 1972: insufficiently described. New Zealand, endemic. Not seen since discovery.
- Trichocerca tenuidens* (Hauer, 1931): Insufficiently described; compare with *T. tenuior*. Europe, North America.
- Trichocerca stenroosi* Wulfert after Haberman, 1978: nomen nudum.
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* Species considered valid



Figures 1–4. *Trichocerca edmondsoni* (Myers). 1: habitus, right; 2: trophi, ventral; 3: trophi, dorsal; 4: habitus, left (1, 3, 4: Pocono Lake, Pennsylvania, U.S.A. 1940: ANSP 602, 2: Id., 1939: ANSP 157, sub. *T. rossae* Edmondson). Figures 5–8. *Trichocerca mollis* Edmondson. 5: habitus, right; 6–8: trophi; 6: ventral, 7: dorsal, 8: right (Minas Gerais, Brazil 1992). Figures 9–11. *Trichocerca maior* Hauer. 9: habitus, left; 10–11: trophi (short, rod-shaped right manubrium not drawn); 10: ventral (left manubrium tilted), 11: dorsal (Pocono Lake, Pennsylvania, U.S.A. 1939. ANSP 689).

of this species concern a different taxon, probably *T. braziliensis*. Of the latter, there are only a few records from temperate regions (e.g., Tasmania: see Shiel & Koste, 1992). *T. rattus* is a variable species, and is here considered to include several variants without taxonomic or geographic significance (e.g., *Trichocerca rattus carinata* (Ehrenberg, 1830), *Trichocerca rattus f. globosa* Dartnall & Hollowday, 1985; *Trichocerca rattus minor* Fadeew, 1925).

- ***Trichocerca capucina*** (Wierzejski & Zacharias, 1893) and ***Trichocerca multicornis*** (Kellicott, 1897): Confusion in literature between *T. capucina* and *T. multicornis* (*T. capucina multicornis* after Koste, 1978) is suspected, on account of the sim-

ilar morphology of the two. Whereas *T. multicornis* has an egg-shaped body, *T. capucina* is slender. Single, unverifiable records of *T. multicornis* from Siberia (see Koste, 1978), India (Kashmir) and Uganda are not considered here.

- ***Trichocerca chattoni*** (de Beauchamp, 1907) and ***Trichocerca cylindrica*** (Imhof, 1891): Tropical records of *T. cylindrica* may refer to the related *T. chattoni* (= *T. cylindrica* var. *chattoni* De Beauchamp; *T. cylindrica chattoni* (De Beauchamp)(sic!) after Koste (1978); subspecies status rejected by Shiel & Koste, 1992). Ecological differences between the two are reported by Shiel & Koste (1992). I have never found *T. cylindrica*

in collections from (sub)tropical regions, nor is *T. chattoni* known to occur in temperate regions.

- **Trichocerca edmondsoni** (Myers, 1936) (**new synonyms**: *T. rossae* Edmondson, 1936, ?*T. compressa* Edmondson, 1937)(Figs 1–4): a comparison of the description and drawings of *T. edmondsoni* (Myers, 1936) and *T. rossae* Edmondson, 1936, and study of specimens identified as *T. rossae* by F.J. Myers (ANSP 157, 602), reveals that both are probably synonyms. In particular, they share an exceptionally stout right toe claw, held at an angle with the longest, left toe claw. Other distinctive features are, the almost symmetrical rami alulae, double frontal mucro, and elongate dorsal keel. Another nominal species with similar morphological features is *T. compressa* Edmondson, 1938, which may also be synonymous. As the name *T. edmondsoni* was included in a publication dated March 20, 1936 (Myers, 1936), and the description of *T. rossae* followed in April 1936 (Edmondson, 1936), the former name is the senior synonym and the valid name for the taxon. The animal is recorded in literature from North America only, however, it also occurs in South America (Brazil: São Paulo, Itirapira; Minas Gerais, Uberaba-Coletto, coll. M. Beatriz Gomes, S. Dabés: H. Segers, unpublished). Edmondson (1938) records his *T. compressa* also from Kashmir, India. This record, the only one from outside the Americas of this species, needs to be confirmed, as the variability of this and related species has long remained unclear (e.g., Myers, 1942), and as similar, and easily confused species exist (e.g., *T. myersi*, *T. plaka*).
- **Trichocerca elongata** (Gosse, 1886) (**new synonym**: *T. tschadiensis* Pourriot, 1968) (= *T. elongata tschadiensis* (Pourriot, 1968)(sic!) after Koste, 1978), is here interpreted as (a) specimen(s) with particularly strongly contracted head aperture, hence a junior synonym of *T. elongata*.
- **Trichocerca hollaerti** De Smet, 1990 and **Trichocerca lophoessa** (Gosse, 1886): The body of these two species is morphologically very similar. Whereas *T. hollaerti* can only be diagnosed by its trophi, reports on the trophi of *T. lophoessa* are contradictory. Older records of *T. lophoessa* should therefore be interpreted with care. Accordingly, the area of *T. lophoessa* has to be considered insufficiently known, and the identity of *T. lophoessa* f. *carinata* Koste, 1978 cannot be ascertained.
- **Trichocerca insignis** (Herrick, 1885) and **Trichocerca myersi** (Hauer, 1931): *T. insignis* and *T. myersi* are two easily confused, close relatives. The trophi features in the differential diagnosis of the two by Hauer (1931; see Koste, 1978) are not reliable. Both taxa appear to be cosmopolitan, notwithstanding the confusion.
- **Trichocerca insolens** (Myers, 1936) and **T. pygocera** (Wiszniewski, 1932): A synonymy between these two as suggested by Koste (1978) was rejected by Segers (1998). The separation between the rare *T. pygocera* and *T. taurocephala* has been questioned and requires confirmation.
- **Trichocerca insulana** (Hauer, 1937) (**new synonym**: *T. montana* Hauer, 1956): A comparison of the original descriptions of *T. insulana* and *T. montana*, in addition to the study of material from various regions of the world indicates that these two are synonyms. The only reported difference, the straight (*T. insulana*) versus terminally curved (*T. montana*) left manubrium may result from an erroneous observation in the original description of *T. insulana*: it is very easy to overlook the terminal curve in the manubrium in a frontal view as depicted in Hauer's (1937) trophi figure (e.g., compare Figs 10 and 11). The Canadian record of *T. insulana* by Chengalath & Mulamoottil (1975) probably is a misidentification, on account of the different claw length in the specimen depicted.
- **Trichocerca longiseta** (Schrank, 1802) (**new synonym**: *Trichocerca falx* Edmondson, 1936): The specimen depicted by Edmondson (1936) as *T. falx* clearly is a newly hatched individual of *T. longiseta*, in which the spines and toe claws are not yet straightened.
- **Trichocerca longistyla** (Olofsson, 1918): The identity of this species follows its redescription by De Smet (1993). A comparison with *Trichocerca parvula* Carlin, 1939 (nom. nov. for *Diurella parva* Rodewald, 1935 non Manfredi, 1927) reveals a synonymy between the two. A synonymy between *T. longistyla* and *T. rotundata* (sub. *T. parvula*) as suggested by Segers & Sarma (1993) must be ruled out, considering the different trophi of the two taxa. The Brazilian record of *T. longistyla* (sub. *T. rotundata*) by Segers & Sarma (1993) requires confirmation. The single specimen, although clearly related, is much smaller and has trophi that differ slightly from those of North American specimens. Published records of *T. longistyla* (as *T. parvula*) and *T. musculus*

should be interpreted with care, as these two are superficially similar (Koste, 1978).

- **Trichocerca mollis** Edmondson, 1936: Literature records of *T. mollis* are from North America only; unverifiable records from Europe (see De Ridder & Segers, 1997) are not considered here. The animal also occurs in South America (Brazil: Minas Gerais, Uberaba-Coletto, coll. M. Beatriz Gomes, S. Dabés: H. Segers, unpublished). As no account is available on the trophi of the species, some relevant drawings are provided (Figs 5–8).
- **Trichocerca mus** Hauer, 1938: This species had to be considered insufficiently described until the re-description by Nogrady (1983) and Koste (1988). The distribution of this taxon is poorly known, but records appear to indicate that the species is thermophilic.
- **Trichocerca obtusidens** (Olofsson, 1918): This taxon is frequently reported under one of the following names:
 - T. minuta* (Olofsson, 1918): (junior homonym of *T. minuta* (Gosse, 1886)(ex. *Coelopus*)), and its replacement name *T. arctica* Voigt, 1957). Synonymy suggested by Koste (1978) and De Smet (1988);
 - T. relictata* (Donner, 1950): synonymy suggested by De Smet (1988), who erroneously gave priority to the junior name *T. relictata*.
- **Trichocerca porcellus** (Gosse, 1851) and *Trichocerca maior* Hauer, 1936 (**new status**) (Figs 9–11): Differences in trophi morphology between *T. porcellus* and *T. porcellus* f. *maior*, as reported by Carlin (1939) are confirmed by personal observations, and appear taxonomically significant. This, in addition to the differences in lorica shape and area of *T. porcellus* and *T. maior*, argue for attributing species rank to *T. maior*.
- **Trichocerca siamensis** Segers & Pholpunthin, 1997 and **Trichocerca uncinata** (Voigt, 1902): *T. siamensis* may have been confused with *T. uncinata*, considering the almost identical external morphology of the two. It is likely that tropical records of the distinctly cold-water *T. uncinata* may refer to *T. siamensis*. There are no verifiable records of *T. uncinata* outside of the Holarctic region.
- **Trichocerca scipio** (Gosse, 1851) (synonym: *T. jenningsi* Voigt, 1957): I here follow Shiel & Koste (1992) rather than Koste (1978) in considering these two taxa synonyms.
- **Trichocerca similis** (Wierzejski, 1893) and **Trichocerca similis** f. **grandis** Hauer, 1965: Although there appear to be no morphological differences between the two forms apart from a difference in body size, they have different areas: whereas *T. similis* is cosmopolitan, *T. similis* f. *grandis* is tropical. The identity of *T. birostris* Minkiewisz, 1900 is unclear. Although *T. birostris* and *T. similis* are reported ecologically different (Carlin, 1943), the absence of a reliable diagnosis (see Koste, 1978) has led to its synonymy with *T. similis* (see Shiel & Koste, 1992), and prevents its inclusion in the present analysis.
- **Trichocerca tenuior** (Gosse, 1886) (**new synonym**: *T. neeli* Edmondson, 1948): The original description of *T. neeli* by Edmondson (1948) depicts a specimen with heavily contracted head region. All relevant features are strikingly similar to *T. tenuior*, in particular foot and toe spine shape, body, head sheath with single spine, and trophi. *T. tenuior* also frequently inhabits the psammon, similar to what is recorded for *T. neeli*.
- **Trichocerca voluta** (Murray, 1913) (**new synonym**: *T. tropis* Hauer, 1937): A comparison of the original descriptions of *T. voluta* and *T. tropis*, and study of material of the taxon from South America, Africa, and Southeast Asia could not discriminate between the two. They are therefore considered synonyms.
- **Trichocerca taurocephala** after Koste & Zhuge, 1996: The taxon depicted has characteristic trophi which show a striking resemblance to those of *T. mucosa*. The material may represent an unnamed taxon endemic to Hainan, China (Segers, 1998).

Biogeography

A total of 67 taxa (plus *T. taurocephala* after Koste & Zhuge, 1996) are considered in the biogeographical analysis. Of these, one (*T. similis* f. *grandis*) is of infrasubspecific rank, but this position is conditional pending taxonomic revision. The majority of *Trichocerca* (44 or 65.7%, Table 2) have to be considered widely distributed taxa, occurring in both the Eastern and Western hemisphere, without being restricted to the Holarctic region. Of these, true cosmopolitan species are predominant: no latitudinal preference can be distinguished for 26 taxa (38.8%). Due to the difficulty in interpreting records in the group, it is hard to reliably distinguish between different latitudinal groups, however, a cold-water preference can

Table 2. Widely distributed taxa (44–65.7%)

Cosmopolitan taxa (26–38.8%)	
<i>T. bicristata</i> (Gosse, 1887)	<i>T. musculus</i> (Hauer, 1936)
<i>T. bidens</i> (Lucks, 1912)	<i>T. myersi</i> (Hauer, 1931)
<i>T. brachyura</i> (Gosse, 1851)	<i>T. porcellus</i> (Gosse, 1851)
<i>T. capucina</i> (Wierzejski & Zacharias, 1893)	<i>T. pusilla</i> (Jennings, 1903)
<i>T. cavia</i> (Gosse, 1886)	<i>T. rosea</i> (Stenroos, 1898)
<i>T. collaris</i> (Rousselet, 1896)	<i>T. scipio</i> (Gosse, 1886)
<i>T. dixonnutalli</i> (Jennings, 1903)	<i>T. similis</i> (Wierzejski, 1893)
<i>T. elongata</i> (Gosse, 1886)	<i>T. stylata</i> (Gosse, 1851)
<i>T. iernis</i> (Gosse, 1887)	<i>T. sulcata</i> (Jennings, 1894)
<i>T. insignis</i> (Herrick, 1885)	<i>T. tenuior</i> (Gosse, 1886)
<i>T. intermedia</i> (Stenroos, 1898)	<i>T. tigris</i> (Müller, 1786)
<i>T. longiseta</i> (Schrank, 1802)	<i>T. vernalis</i> (Hauer, 1936)
<i>T. marina</i> (Daday, 1890)	<i>T. weberi</i> (Jennings, 1903)
Cold-water taxa (5–7.5%)	
<i>T. cylindrica</i> (Imhof, 1891)	<i>T. rattus</i> (Müller, 1776)
<i>T. macera</i> (Gosse, 1886)	<i>T. rousseleti</i> (Voigt, 1902)
<i>T. obtusidens</i> (Olofsson, 1918)	
Warm-water taxa (6–9.0%)	
<i>T. braziliensis</i> (Murray, 1913)	<i>T. flagellata</i> Hauer, 1937
<i>T. chattoni</i> (de Beauchamp, 1907)	<i>T. rutneri</i> Donner, 1953
<i>T. insulana</i> (Hauer, 1937)	? <i>T. siamensis</i> Segers & Pholpunthin, 1997
Pan(sub)tropical taxa (7–10.4%)	
<i>T. abilioi</i> Segers & Sarma, 1993	<i>T. simoneae</i> De Smet, 1990
<i>T. hollaerti</i> De Smet, 1990	<i>T. similis</i> f. <i>grandis</i> Hauer, 1965
<i>T. kostei</i> Segers, 1993	<i>T. voluta</i> (Murray, 1913)
<i>T. mus</i> Hauer, 1938	

be suspected for five taxa, six taxa appear confined to warmer waters. Seven taxa, including *T. similis* f. *grandis*, are Pan(sub)tropical. Patterns of latitudinal distributions were amongst the first biogeographical patterns to be distinguished in Rotifera (Green, 1972), hence it is not surprising to see these revealed in *Trichocerca* as well. The figures appear to indicate a prevalence of warm water preferences for the genus, similar to what is found in *Brachionus* (see Pejler, 1977b; Dumont, 1983) and *Lecane* (Segers, 1996). However, the four Holarctic, and probably also some of the Palaearctic and Nearctic taxa (Table 3) should be considered in this argument, taking into account the preliminary nature of our knowledge on the distribution of *Trichocerca*. For example, *T. obtusidens* is restricted to the Northern hemisphere, and is rather

common in cold-water environments, but cannot be considered Holarctic because of records of the species from the Galápagos archipelago (De Smet, 1989). So, a northern-hemisphere component exists in the genus *Trichocerca*, which concurs with *Notholca* and *Keratella*. In contrast to these (e.g., Pejler, 1977b; Dumont, 1983; Battistoni, 1992; De Smet, 2001), no southern-hemisphere cold-water taxa are as yet known in *Trichocerca*. The presence of a warm-water component in *Trichocerca* is at variance with *Notholca*, which is exclusively cold-water.

Endemism (Table 3) appears to be rare in *Trichocerca*, and is centred on the Northern hemisphere (Palaearctic, Nearctic, Holarctic taxa). Tropical endemic *Trichocerca* are surprisingly rare. There are no Neotropical, Ethiopian or tropical Australian endem-

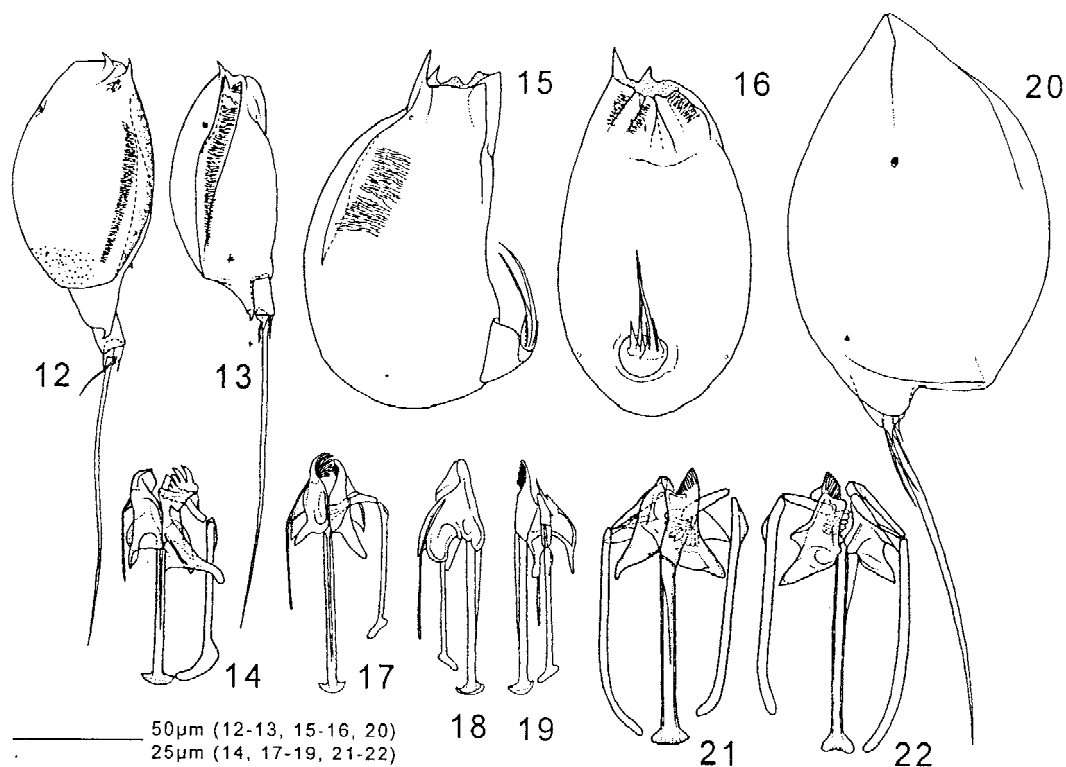
Table 3. Endemic taxa: (23–34.3%)

	Holarctic taxa (4–6.0%)	
<i>T. harveyensis</i> Myers, 1941		<i>T. taurocephala</i> (Hauer, 1931)
<i>T. maior</i> Hauer, 1936		<i>T. uncinata</i> (Voigt, 1902)
	Nearctic taxa (9–13.4%)	
<i>T. bicuspes</i> (Pell, 1890)		<i>T. ornata</i> Myers, 1934
<i>T. insolens</i> (Myers, 1936)		<i>T. plaka</i> Myers, 1938
<i>T. lata</i> (Jennings, 1894)		<i>T. platessa</i> Myers, 1934
<i>T. mucosa</i> (Stokes, 1896)		<i>T. rotundata</i> Myers, 1937
<i>T. multicrinis</i> (Kellicott, 1897)		
	New World taxa (2–3.0%)	
<i>T. edmondsoni</i> (Myers, 1936)		<i>T. mollis</i> Edmondson, 1936
	Palaeartic (5–7.5%)	
<i>T. longistyla</i> (Olofsson, 1918)		<i>T. vargai</i> Wulfert, 1961
<i>T. pediculus</i> Remane, 1949		<i>T. vassilijevae</i> Kutikova & Arov, 1985 (endemic to Lake Baikal)
<i>T. pygocera</i> (Wiszniewski, 1932)		
	Old World (2–3.0%)	
<i>T. agnatha</i> Wulfert, 1939		<i>T. orca</i> (Murray, 1913)
	Oriental	
<i>(T. taurocephala</i> after Koste & Zhuge, 1996)		
	Australia (1–1.5%)	
<i>T. wanarra</i> Segers & Shiel, 2003		

ics; only the enigmatic *T. taurocephala* after Koste & Zhuge (1996) could be an Oriental endemic. This contrasts with results for other groups of rotifer like *Anuraeopsis*, *Brachionus*, and *Lecane*. Only *Notholca*, a notorious cold-water genus equally lacks tropical endemic representatives (Pejler, 1977b; Dumont, 1983). Basing on the preponderance of endemics in the Northern hemisphere, and notwithstanding the presence of a warm-water, tropical component, a Laurasian origin can be surmised for *Trichocerca*. This concurs with hypothesis on the origin of *Notholca* and, possibly, *Synchaeta* (Dumont, 1983). It should be cautioned, again, that taxonomic tangles and lack of data on distribution weigh heavily on these interpretations. The southwest Australian endemic *T. wanarra* has only recently been diagnosed as separate species in the difficult *T. myersi*-group (Segers & Shiel, 2003), exemplifying that detailed taxonomic studies are a prerequisite to sound biogeographical analysis. The recent record from Thailand of the easily recognized

T. orca, which had not been seen since its description from New Zealand (see Sanoamuang & Savatnalinton, 2001), shows how little is still known about the distribution of rare species. The case of *T. siamensis*, described only in 1997 but soon after recorded from Brazil and northeast North America (Segers, 1997) is equally revealing.

The North American endemic *Trichocerca* are remarkable. This group contains nine species (13.4% of *Trichocerca*; Table 3), all of which have been found on several occasions. Of these, only one is psammobiotic, thus inhabits a habitat that has only sporadically been investigated worldwide. This stands out against the Palaeartic endemic *Trichocerca*, of which three are psammobiotic (*T. pediculus* – marine, *T. pygocera*, *T. vassilijevae*). Admittedly, some of the species have been mentioned from localities outside North America, but these concern isolated records, none of which is verifiable by published illustrations or voucher specimens (*T. lata* – Figs 20–22: single records from



. Figures 12–14. *Trichocerca ornata* Myers. 12–13: habitus; 12: left-dorsal; 13: right; 14: trophi, ventral (Atlantic County, New Jersey, U.S.A. 1936: ANSP 283). Figures 15–19. *T. rotundata* Myers. 15–16: habitus; 15: right; 16: ventral; 17–19: trophi; 17: ventral, 18: right; 19: left (Goose Pond, New Jersey, U.S.A. 1996). Figures 20–22. *Trichocerca lata* Myers. 20: habitus, left; 21–22: trophi; 21: ventral; 22: dorsal (Goose Pond, New Jersey, U.S.A. 1996).

Europe (marine!) and New Zealand; *T. ornata* – Figs 12–14: one record from Northeast Asia; *T. plaka*: Europe, New Zealand, but is easily confused with *T. myersi*; *T. rotundata* – Figs 15–19: single record from Afghanistan). These records must therefore be discarded as unreliable. Wang's (1961) Chinese record of *T. bicuspes* is accompanied by a figure, but it is unclear if this is an original drawing. If confirmed, the species would be a rare example of a rotifer with a disjunct Northeast Asia–Northeast North America distribution, similar to *Lecane satyrus* Harring & Myers, 1926 (see Segers, 1995). All nine North American *Trichocerca* occur in the Northeast of North America, only *T. multirinis* is found as far south as Panama, three reach Florida (*T. bicuspes*, *T. lata*, *T. mucosa*: see Ahlstrom, 1934), and one (*T. lata*) is found in Northwest Canada (Chengalath & Koste, 1987). Hence, the North American *Trichocerca* are largely confined to the regions of the Great Lakes and the Northeast. Here, several endemics occur in well-studied groups like *Keratella*, *Lecane*, and *Notholca* (Stemberger, 1976, 1990a, b;

Dumont, 1983; Segers, 1996). That a large number of rotifers belonging to several families are restricted to the Northeast of North America has long been realised. However, this was suspected to be an artefact, considering that the monumental taxonomic works by H.K. Harring and F.J. Myers (e.g., Harring & Myers, 1922, 1924, 1926, 1928; Myers, 1936, 1942; to cite a few) constitute a disproportionate research effort to the rotifers of this region (Segers, 1996). The recent record from Australia of *Dorria*, a monotypic genus long considered endemic to northeast North America, was interpreted in the same way (Shiel, pers. comm.). As H.K. Harring and F.J. Myers did not treat *Trichocerca*, this suspicion can be ruled out and the Nearctic *Trichocerca* may represent the first trustworthy indication that the region really is a centre of endemism for rotifers.

The northeast North American endemics in the genera *Keratella* and *Notholca* are morphologically very similar to other, more widespread species (Stemberger, 1976, 1990a, b), hence it was hypothesized

that they represent recently diverged taxa, probably of glacial origin. On the other hand, a phylogenetic analysis of the endemic *Notholca* of Lake Baikal (Kutikova, 1980) reveals that this group is morphologically distinct, and is even considered consistent with genus rank by Dumont (1983). The origin of the North American *Trichocerca* is less clear, and more diverse. There is no doubt that *T. multicornis* is a close relative of *T. capucina*, and a glacial origin of this species, similar to the above-mentioned Brachionidae, can be surmised. In contrast to the endemic *Keratella* and *Notholca* species, however, its range encompasses North and Central America. The restricted distribution of the northeast North American *Keratella* and *Notholca* was attributed to habitat characteristics, and/or the inability to produce resting eggs as propagules (Dumont, 1983; Stemberger, 1990; Segers, 1996). This may hold for a number of *Trichocerca*, but not for *T. multicornis*, considering the vast range of this pelagic species.

In contrast to *T. multicornis*, the relations of the other species are less obvious. *T. bicuspes* probably belongs to the *T. rattus*-group, by its similar trophi (see Nogrady, 1989), *T. plaka* is close to *T. myersi* (see Segers & Shiel, 2003), *T. mucosa* has trophi similar only to *T. taurocephala* after Koste & Zhuge (1996). The relations of the other species in the group, and those of the two New World endemics (*T. mollis* and *T. edmondsoni*), cannot be ascertained at the moment. However, regardless of their precise phylogenetic relations, it is clear that they represent independent evolutionary lineages. Also, the large morphological dissimilarity with their closest relatives indicates that they must be the product of relatively ancient, probably pre-Pleistocene, radiations. As such, they may be relicts of an endemic Nearctic fauna. The *Trichocerca* species now restricted to the northeast of North America may have survived the glaciations in local refugia, those which occur as far south as Florida (or to South America in the case of *T. mollis* and *T. edmondsoni*) may have done so by migrating along with the shifting climate. The second option is much less likely in the Palaearctic, due to the major mountain ranges having an East–West orientation, hence becoming effective barriers against North–South migration of organisms during glaciations. So, that relatively fewer Palaearctic than Nearctic taxa survived the Pleistocene glaciations is consistent with contemporary theories on the impact of glacial extinctions (see, for example, Brown & Lomolino, 1998). It is unfortunate that so little is known about the *Trichocerca* of Beringia, as a particularly

interesting fauna can be expected there, based on the present interpretations.

Conclusions

Analysing distribution patterns in 67 taxa of *Trichocerca* reveals a majority (65.7%) of widely distributed species, with strict cosmopolitanism in more than a third of the taxa. Latitudinal variation is evident in 26.9% of *Trichocerca*, and a preference for warm waters appears to be indicated. Endemism, on the other hand, is strongly biased towards the Northern hemisphere, with no endemism in the Neotropical, Ethiopian, and (?)Oriental regions, and tropical Australia. Moreover, a distinct Southern-hemisphere temperate *Trichocerca* fauna cannot be identified. These results appear to indicate a Laurasian origin of the genus, although both a Southern hemisphere, warm water and Northern hemisphere, cold-water component can at present be distinguished in the genus.

It should be cautioned that the preponderance of widely distributed taxa and the low degree of endemism might at least partly result from the inability of present-day taxonomy to distinguish between closely related species. However, and notwithstanding the confused taxonomy, a group of Nearctic endemics stands out in *Trichocerca*. The origin of the taxa in this group is diverse: *T. multicornis* is a close relative of *T. capucina* and may be of glacial origin, the others and two New World taxa are morphologically distinct, to the extent that they probably belong to independent lineages or, at least, are the result of more ancient radiations. A pre-Pleistocene radiation of a Northern hemisphere fauna, followed by differential extinction during the glaciations in the Nearctic and Palaearctic is postulated to account for the relatively high degree of endemism of *Trichocerca* in the Nearctic.

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