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Cosmopolitanism and endemism in free-living nematodes

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SUMMARY

Most free-living nematodes should have a global distribution if they would follow general tendencies of microbial organisms. Information on free-living nematodes presented in this review demonstrates that this cosmopolitanism is less common than assumed by theory. While very large distribution ranges are observed in a number of nematode species, various examples of endemism are described for isolated units like islands, extreme environments and ancient pre-Quaternary lakes. Endemism is generally rare among microorganisms, but a typical observation for larger organisms. The biogeography of nematodes thus reflects their intermediate position between macro- and microorganisms and future studies on this interesting group may help identifying why the positive relationship between body size and range size observed in large animals shifts to a negative relationship in microbial organisms.

INTRODUCTION

Traditionally, zoogeography is based on the geographic distribution of macro-organisms, mainly mammals and birds. Little knowledge is available on the distribution of small terrestrial species (e.g. insects, mites, worms) as those are often difficult to detect and to identify. While many micro- and meio-organisms seem to be almost cosmopolitan, significant geographical pattern may exist undetected. The idea that microbes only depend on ecological factors has been famously summarized by Beijerinck's quote 'Everything is everywhere, but the environment selects' (de Wit and Bouvier 2006). While Beijerinck's principle has triggered considerable research on cosmopolitanism in microorganisms, it has received mixed support (e.g. Fenchel and Finlay 2004, Martiny et al. 2006, Fontaneto 2011).

While the distribution ranges of big organisms tend to be proportional to their size (larger animals having larger range sizes), contrasting biogeographic tendencies have been suggested for very small (microscopic) organisms (Finlay 2002, Jenkins et al. 2011). The range size of small organisms is suggested to be proportional to organism abundance and thus inversely proportional to organism size. Small organisms (microbes) are thus also able to exhibit wide distributions due to unlimited dispersal and very high abundance (Segers and De Smet 2007). A shift between the two contrasting tendencies emerges when body size gets too large for ubiquitous dispersal (Finlay 2002), which is suggested to happen between 1 and 2 mm.

THE BIOGEOGRAPHY OF NEMATODES

Soil and freshwater nematodes usually range between 0.5 and 3 mm in length, mostly around 1 mm (Andrássy 2005) placing them between microbes and macrobes. However, for wormlike animals body length might be a bad size parameter to distinguish macro- from microfauna. Instead, body width or volume is particularly relevant for interstitial soil and sediment dwellers. The body width of soil and freshwater nematodes usually span between 10 and 70 µm, which would suggest that they should follow general biogeographic principles identified for microbes and would thus argue for a tendency for cosmopolitanism.

The phylum Nematoda is ubiquitous with a distribution that spans all kinds of extreme habitats. Many species of freshwater nematodes appear to follow this cosmopolitan distribution with occurrence records in all continents (Antarctica excepted). The most cosmopolitan among freshwater species seem to be *Dorylaimus stagnalis*, *Ethmolaimus pratensis*, *Prismatolaimus intermedius*, *Tripyla glomerans*, and *Mononchus truncatus* (Zullini 2014). Alike, soil nematodes are both numerous (in non-desert soil, averaging 2 million individuals per square meter) and usually more or less cosmopolitan. Many of them can withstand long periods of cryptobiosis and therefore can be transported at great distances by wind (Orr and Newton 1971, Carroll and Viglierchio 1981, Baujard and Martiny 1994, de Rooij-van der Goes et al. 1997, Womersley et al. 1998, Wharton 2004, Nkem et al. 2006), water (Faulkner and Bolander 1966, 1970, Roccuzzo and Ciancio 1991), even tap water (Dózsa-Farkas 1965, Mott and Harrison 1983, Lupi et al. 1994) and animals (Thorne 1968, Kiontke 1996, Gaugler and Bilgrami 2004, Curčic et al. 2004).

It is, however, plausible that many seemingly cosmopolitan taxa are morphologically indistinguishable sister species or misidentified due to limited group-specific taxonomic expertise. Lack of extensive molecular studies on free-living forms might contribute to this situation. In fact, the well-studied genus *Caenorhabditis*, for which comprehensive morphological, molecular, and extensive biological data exists shows considerable geographic differentiation. For instance, two species of this genus that belong to what is known as *elegans*-group, i.e. *Caenorhabditis elegans* and *C. briggsae*, are morphologically almost indistinguishable. Genetically they are well separated, diverging almost 100 million years ago. These and other nematode species differ from one another much more in DNA than in morphology (Hillier et al. 2007). Similar data available for 26 *Caenorhabditis* species reveal considerable biogeographic differences including remarkable cosmopolitanism (*C. briggsae*) as well some very restricted distributions (*C. brenneri*, *C. remanei*) (Kiontke and Sudhaus 2006). Similar provincialism has been shown within the genus *Pristionchus*, for which similar morphological and molecular data are available for 18 species (Mayer et al. 2007). The available data would even allow correlating the distribution of the free-living nematode species with ancient geological and geographical events, as proposed by Ferris et al. (1976, 1981), Procter (1984) and Boag and Yeates (1998).

It seems that nematode genera are often cosmopolitan, while many species have distinct geographic distributions. Genera of the predatory nematode family Mononchidae, a relatively well-known group with 151 species, were able to colonize several continents and show no clear geographic patterns and no relation with past geological events. However, only 3% of the Mononchidae species are really cosmopolitan. An interesting case is *Coomansus*, a cosmopolitan genus, with 8 of its 30 species known only from East Siberia. Alike, *Cobbonchus* has 11 of its 27 species found exclusively in Africa, whereas the other 16 species inhabit exclusively other Gondwanian territories.

ENDEMISM IN NEMATODES

Strict endemism – the occurrence of a focal taxon in a restricted area – is the opposite of cosmopolitanism. The identification of endemic distribution patterns is difficult for nematodes because many species were only recently described, or described several decades ago and never found again (not even in their locus typicus). A relatively large species, *Heterodorus nepalensis* (2.3 mm long), was found only once, in 1961, in soil samples from a mountain valley between 4500 and 5200 m and never found again (Zullini 1973). For *Eumonhystera*, a very common soil and freshwater genus, half of its 38 species are known for single restricted geographic areas, but it is unlikely that all of these species are local endemics. On the other hand, *Thornia thermophila* (0.6 mm long) was described by Meyl (1953) for isolated thermal springs on Ischia island. It was found again only once, 40 years later, on the same island and in the same water temperature (36°C) (Zullini, unpublished data). A genus accumulation curve for the free-living nematodes of a particularly well-studied area seems to start leveling of in recent years (Fig. 1a). Presumably, the potential to find new genera in continued global worldwide sampling is thus limited. In contrast, the accumulation curve for species in the same area indicates that the discovery of new species will continue in about a constant rate for the foreseeable future (Fig 1b). As a result, our current conclusions regarding endemism and biogeography will most probably hold true for the genus level, while new information and discovery is expected for the species level. Unexplored habitats my reveal yet many undiscovered endemic species.

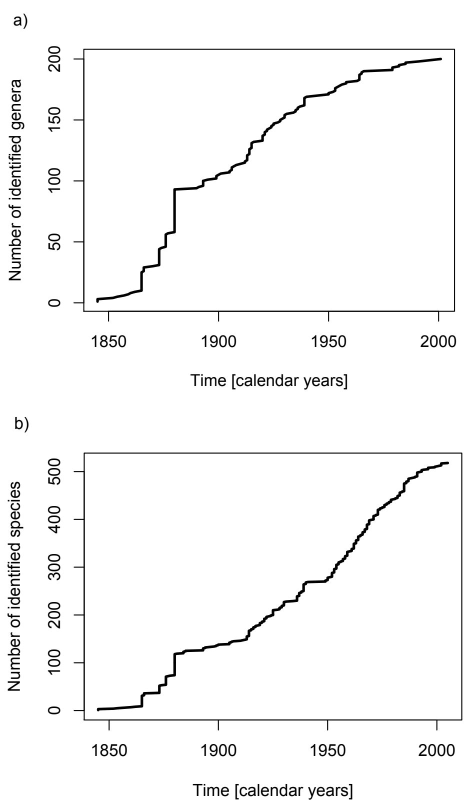

Figure 1. a) Genus accumulation curve with time for all currently known free-living nematodes in Hungary (200 genera). Data are not based on the legal status of genera (time of first official description), but on the real discovery of a new (even not yet recognized) genus. b) Species accumulation curve for Hungary, the area with currently most reliable knowledge on free-living nematodes: 518 extensively described species are considered (Andrássy's Pedozoologica Hungarica 2005, 2007, 2009).

Sites for which one would expect to find endemic species are isolated units like islands, extreme environments and ancient pre-Quaternary lakes. A very peculiar isolated situation is the freshwater environment inside an oceanic island. Such a case was studied by Eyualem-Abebe and Coomans (1995) and Muschiol and Traunspurger (2009): they found in the islands Floreana, San Cristobal and Isabela (Galápagos) a total of 25 freshwater nematode species, but only three of them (12%) were presumably endemic. The other species were cosmopolitan or already known to the Southern hemisphere. This is in contrast with the other animals of this archipelago where 30-80% are endemic (depending on the species group). The authors summarized the problematic of defining endemism in nematodes highlighting that "the South American nematode fauna is insufficiently known" and that "the existence of cryptic species […] can be difficult to detect solely on morphological characters" (Muschiol and Traunspurger 2009).

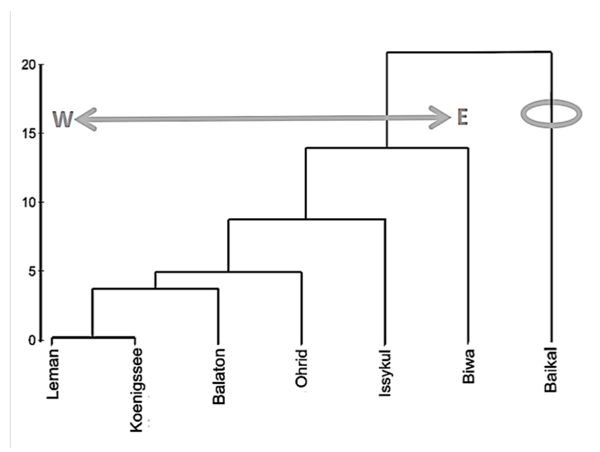

Figure 2. Cluster analyses of nematode communities in major lakes based on Jaccard similarity. A W-E gradient is revealed. The unique community composition of lake Baikal reveals its high share of endemic species. These lakes are located, respectively, in Switzerland, Germany, Hungary, Macedonia, Kyrgyzstan, Japan, Siberia (modified from Zullini 2014).

Other instances of lacustrine environments where one would expect to find endemic species are still existing ancient (Tertiary) lakes with Lake Baikal being the most ancient (30 million years old for the cuvette, and 6 million years old for the hypolimnion) and deepest (1642 m). Resulting from its age and biological isolation, especially in its deep portion, this lake hosts many (> 80%) endemic animals. In fact, 70% of all known nematodes from Lake Baikal are endemic and their endemic status is largely accepted (Tsalolikhin 1980). Typical Baikal nematodes are Tobrilidae, believed to be the most ancient inhabitants; subsequent settlers probably are Monhysteridae and Chromadoridae (some of them deriving from marine ancestors); Dorylaimidae and Mononchidae are likely the last arriving taxa and of terrestrial origin (Tsalolikhin 1980). Lake Tanganyika (maximum depth 1470 m), another very old lake, has one third of its nematode species assigned as being endemic. Typical nematodes of this lake are Actinolamidae (Martens 1997). Lake Ohrid, the only European Tertiary lake also hosts a number of nematodes that are very likely endemic (Gerlach and Meyl 1957). The lac Geneva or Léman, the largest Alpine lake, is not so old, but still hosts at a depth of 60 m some endemic Desmoscolecidae (only 0.2 mm long), nematodes common in sea but very rare in fresh water. Extreme environments are isolated by their differing environmental setting and thus often host unique species assemblages (Hodda et al. 2006). For Antarctica, being very different from all other continents, 94% of all nematodes are considered to be endemic for this continent (Andrássy 1998, 2008).

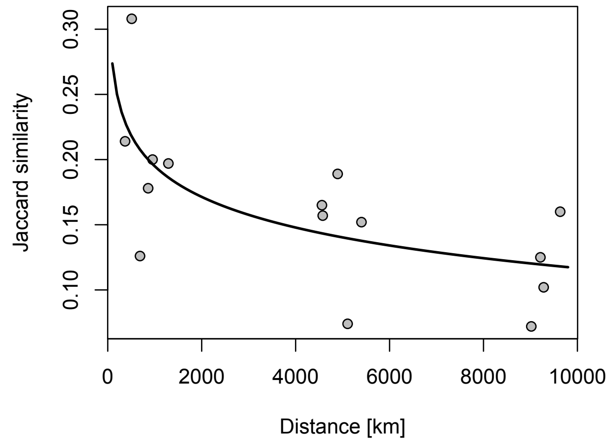

Figure 3. Distance-decay in similarity of nematode lake communities. Nematode community composition of each lake was compared with each other (Jaccard index) and related to their distance (in km). Distant lakes are less similar inter se, corroborating data of fig. 2 (see fig. 2 for names of lakes; Baikal was excluded owing to its peculiar nematocoenosis). The decline in similarity with distance is visualised using linear regression of Jaccard similarity with log-transformed distance values. A mantel test (R package ecodist version 2.0.1) revealed a significant ($p < 0.05$) decline in similarity with distance ($r = -0.64$).

Table 1. Jaccard similarity indices for freshwater nematodes of the seven temperate lakes mentioned in fig. 2. Lake Baikal presents the lowest values, indicating its biological isolation.

	Léman	Königssee	Balaton	Ohrid	Issykul	Baikal
Königssee	0.31					
Balaton	0.18	0.21				
Ohrid	0.20	0.20	0.13			
Issykul	0.15	0.19	0.16	0.17		
Baikal	0.03	0.03	0.03	0.06	0.03	
Biwa	0.16	0.13	0.07	0.10	0.07	0.04

SPATIAL PATTERNS IN NEMATODE COMMUNITIES

Most knowledge on the biogeography of the continental free-living nematodes is based on simple quantitative data (Eyualem-Abebe et al. 2008). Only few studies analyse detailed macroecological patterns, such as on the effect of geographic distance on similarity in nematode community composition. Zullini (2014) calculated the nematode similarity among the communities of seven temperate lakes from West (Léman) to East (lake Biwa) for a total of 312 species to assess the effect of distance in these island-like habitats. Comparisons were made using the Jaccard's index (Jaccard 1901). A cladogram (stress 0.03) was obtained using the program PRIMER (Clarke and Warwick 1997). A clear West-East gradient could be visualized, except for the lake Baikal owing to its exceptional antiquity (Oligocene) and its rich endemic species content (Fig. 2, Tab.1). Not considering this lake, due to its peculiar history and biotic community, similarity in species composition is negatively correlated with the distances of the six lakes to their neighbours ($r = -0.64$, mantel $p < 0.05$, Fig. 3). A higher negative correlation is obtained if distances are computed as absolute values between Königssee and the other five lakes ($r = -0.79$).

CONCLUSION

In conclusion, nematodes lack the clear biogeographic patterns usually observed in vertebrates and insects. This may result from scarcity of data on the group but could also reflect the biology and ecology of these meio-organisms. The biogeography of these animals may reflect their intermediate position between macro- and microorganisms. Studies on nematodes may thus be particularly helpful in identifying why the positive relationship between body size and range size observed in large animals shifts to a negative relationship in microbial organisms. Future studies should focus on the specific biogeographic and geologic factors that are relevant to their dispersal and distribution.

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REFERENCES

Andrássy, I. (1998) Nematodes in the Sixth Continent. Journal of Nematode Morphology and Systematics, 1, 107–186.

Andrássy, I. (2005) Free-living nematodes of Hungary, vol. I, Hungarian National History Museum and Systematic Zoology Research Group of the Hungarian Academy of Sciences. Budapest, 518 pp.

Andrássy, I. (2007) Free-living nematodes of Hungary, vol. II, Hungarian National History Museum and Systematic Zoology Research Group of the Hungarian Academy of Sciences. Budapest, 496 pp.

Andrássy, I. (2008) *Eudorylaimus* species (Nematoda: Dorylaimida) of continental Antarctica. Journal of Nematode Morphology and Systematics, 11, 49–66.

Andrássy, I. (2009) Free-living nematodes of Hungary, vol. III, Hungarian National History Museum and Systematic Zoology Research Group of the Hungarian Academy of Sciences. Budapest, 608 pp.

Baujard, P. & Martiny, B. (1994) Transport of nematodes by wind in the peanut cropping area of Senegal, West Africa. Fundamental and Applied Nematology, 17, 543–550.

Boag, B. & Yeates, G.W. (1998) Soil nematode biodiversity in terrestrial ecosystems. Biodiversity and Conservation, 7, 617–630. DOI: 10.1023/A:1008852301349

Carroll, J.J. & Viglierchio, D.R. (1981) On the transport of nematodes by the wind. Journal of Nematology, 13, 476–482.

Clarke, K.R. & Warwick, R.M. (1997) PRIMER. Plymouth, UK, Plymouth Marine Laboratory.

Curčic, B.P.M., Sudhaus, W. & Dimitrijevic, R.N. (2004) Phoresy of *Rhabditophanes schneideri* (Bütschli) (Rhabditida: Alloionematidae) on pseudoscorpiones (Arachnida: Pseudoscorpiones). Nematology, 6: 313–317. DOI: 10.1163/1568541042360500

de Rooij-van der Goes, P.C.E.M., van Dijk, C., van der Putten, W.H. & Jungerius, P.D. (1997) Effects of sand movement by wind on nematodes and soil-borne fungi in coastal foredunes. Journal of Coastal Conservation, 3, 133–142. DOI: 10.1007/BF02908189

de Wit, R. & Bouvier, T. (2006) 'Everything is everywhere, but the environment selects'; what did Baas Becking and Beijering really say? Environmental Microbiology, 8, 755–758. DOI: 10.1111/j.1462-2920.2006.01017.x

Dózsa-Farkas, K. (1965) Untersuhungen über die Fauna des Budapester Leitungswassers, mit besonderer Berücksichtigung der Nematoden. Opuscola Zoologica, Budapest, 5, 173–181.

Euyalem-Abebe & Coomans, A. (1995) Freshwater nematodes of the Galápagos. Hydrobiologia, 299, 1–51. DOI: 10.1007/BF00016885

Eyualem-Abebe, Decraemer, W. & De Ley, P. (2008) Global diversity of nematodes (Nematoda) in freshwater. Hydrobiologia, 595, 67–78. DOI: 10.1007/978-1-4020-8259-7_8

Faulkner, L.R. & Bolander, W.J. (1966) Occurrence of large nematode populations in irrigation canals in South Central Washington. Nematologica, 12, 591–600. DOI: 10.1163/187529266X00446

Faulkner, L.R. & Bolander, W.J. (1970) Agriculturally-polluted irrigation water as a source of plant-parasitic nematode infestation. Journal of Nematology, 2, 368–374.

Fenchel, T. & Finlay, B.J. (2004) The ubiquity of small species: patterns of local and global diversity. BioScience, 54, 777–784. DOI: 10.1641/0006-3568(2004)054[0777:TUOSSP]2.0.CO;2

Ferris, V.R., Goseco, C.G. & Ferris, J.M. (1976) Biogeography of free-living soil nematodes from the perspective of plate tectonics. Science, 193, 508–510. DOI: 10.1126/science.193.4252.508

Ferris, V.R., Ferris, J.M. & Goseco, C.G. (1981) Phylogenetic and biogeographic hypotheses in Leptonchidae (Nematoda: Dorylaimidae) and a new classification. Proceedings of the Helminthological Society of Washington, 48, 163–171.

Finlay, B.G. (2002) Global dispersal of free-living microbial eukaryote species. Science, 296, 1061–1063. DOI: 10.1126/science.1070710

Fontaneto, D. (ed.) (2011) Biogeography of microscopic organisms. The Systematics Association, Special Vol. 79. Cambridge, UK, Cambridge University Press, 365 pp.

Gaugler, R. & Bilgrami, A.L. (2004) Nematode Behaviour. Wallingford, CABI Publishing.

Gerlach, S.A. & Meyl, A.H. (1957) Freilebende Nematoden aus dem Ohrid-See. Beaufortia, 5, 157–169.

Hillier, L. W., Miller, R.D., Baird, S.E., Chinwalla, A., Fulton, L.A., Kobolt, D.C. & Waterston, R.H. (2007) Comparison of *C. elegans* and *C. briggsae* genome sequences reveals extensive conservation of chromosome organization and synteny. PLoS Biology, 5, e167: 1603–1616. DOI: 10.1371/journal.pbio.0050167

Hodda, M., Ocaña, A. & Traunspurger, W. (2006) Nematodes from extreme freshwater habitats. In: Euryalem-Abebe, Traunspurger, W., Andrássy, I. (eds.) Freshwater nematodes: ecology and taxonomy. CABI Publ., 179–210.

Jaccard, P. (1901) Etude comparative de la distribution florale dans une portion des Alpes et du Jura. Bulletin de la Société Vaudoise des Sciences Naturelles, 37, 547–579.

Jenkins, D.G., Medley, K.A. & Franklin, R.B. (2011) Microbes as a test of biogeographic principles. In: Fontaneto, D. (ed.): Biogeography of microscopic organisms. The Systematics Association, Special Vol. 79. Cambridge, UK, Cambridge University Press, 309–323.

Kiontke, K. (1996) The phoretic association of *Diplogaster coprophila* Sudhaus & Rehfeld, 1990 (Diplogastridae) from cow dung with its carriers, in particular flies of the family Sepsidae. Nematologica, 42, 354–366. DOI: 10.1163/004425996X00083

Kiontke, K. & Sudhaus W. (2006) Ecology of *Caenorhabditis* species. (January 09, 2006), WormBook, ed. The *C. elegans* Research Community, WormBook. DOI: 10.1895/wormbook.1.37.1

Lupi, E., Ricci, V. & Burrini, D. (1994) Occurrence of nematodes in surface water used in a drinking water plant. Journal Water SRT-Aqua, 43, 107–112.

Martens, K. (1997) Speciation in ancient lakes. Trends in Ecology and Evolution, 12, 177–182. DOI: 10.1016/S0169-5347(97)01039-2

Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreas, L., Reysenbach, A.L., Smith, V.H., Staley & J.T. (2006) Microbial biogeography: putting microorganisms on the map. Nature Reviews Microbiology, 4, 102–112. DOI: 10.1038/nrmicro1341

Mayer, W.E., Herrmann, M. & Sommer, R.J. (2007) Phylogeny of the nematode grenus *Pristionchus* and implications for biodiversity, biogeography and the evolution of hermaphroditism. BMC Evolutionary Biology, 7, 104. DOI: 10.1186/1471-2148-7-104

Meyl, A.H. (1953) Die in Thermalgewässern der Insel Ischia vorkommenden Nematoden. Zeitschrift für Morphologie und Ökologie der Tiere, 42, 159–208.

Mott J.B. & Harrison A.D. (1983) Nematodes from river drift and surface drinking water supplies in southern Ontario. Hydrobiologia, 102: 27–38. DOI: 10.1007/BF00006045

Muschiol, D. & Traunspurger, W. (2009) Life at the extreme: meiofauna from three unexplored lakes in the caldera of the Cerro Azul volcano, Galápagos Islands, Ecuador. Aquatic Ecology, 43, 235–248. DOI: 10.1007/s10452-008-9202-y

Nkem, J.N., Wall, D.H., Virginia, R.A., Barrett, J.E, Broos, E.J., Porazinska, D.L. & Adams, B.J. (2006) Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. Polar Biology, 29, 346–352. DOI: 10.1007/s00300-005-0061-x

Orr, C.C. & Newton, O.H. (1971) Distribution of nematodes by wind. Plant Disease, 55, 61–63.

Procter, D.L.C. (1984) Towards a biogeography of free-living soil nematodes. Changing species richness, diversity and densities with changing latitude. Journal of Biogeography, 11, 103–117. DOI: 1 0.2307/2844684

Roccuzzo, G. & Ciancio, A. (1991) Notes on nematodes found in irrigation water in southern Italy. Nematologia Mediterranea, 19, 105–108.

Segers, H. & De Smet, W.H. (2007) Diversity and endemism in Rotifera: a review, and *Keratella* Bory de St Vincent. Biodiversity and Conservation, 2, 303–316. DOI: 10.1007/s10531-007-9262-7

Thorne, G. (1968) Nematodes of the Northern Great Plains. I. Tylenchida (Nemata, Secernentea). Brookings, SD: Agricultural Experiment Station, South Dakota State University, 1–111.

Tsalolikhin, S.J. (1980) Free-living nematodes of Baikal. Nauka, Novosibirsk, 118 pp. (in Russian).

Wharton, D.A. (2004) Survival strategies. In Gaugler, R., Bilgrami, A.L. (eds.) Nematode Behaviour. Wallingford, CABI Publishing, 371–399.
Womersley, C.Z., Wharton, D. & Higa, L.M. (1998) Survival biology. In Perry, R.N., Wright, D.J. (eds.) The Physiology and Biochemistry of Free-living and Plantparasitic Nematodes. Wallingford, CABI Publishing, 271–302.
Zullini, A. (1973) Su alcuni nematodi di alta quota del Nepal. Khumbu Himal, 4, 401–412.
Zullini, A. (2014) Is a biogeography of freshwater nematodes possible? Nematology, 16, 1–8. DOI: 10.1163/15685411-00002779

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