FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of cladocerans (Cladocera; Crustacea) in freshwater

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Abstract Cladocera is a primarily-freshwater monophyletic group, an important component of the microcrustacean zooplankton. They inhabit most types of continental fresh and saline water habitats, occurring more abundantly in both temporary and permanent stagnant waters. Cladocera is an ancient group of Palaeozoic origin. About 620 species are currently known, but we estimate that the real number of species is 2–4 times higher. A number of currently-recognised widespread species can be expected to harbour extensive cryptic diversity.

Keywords Cladocera · Species richness · Global assessment · Biogeography · Endemicity

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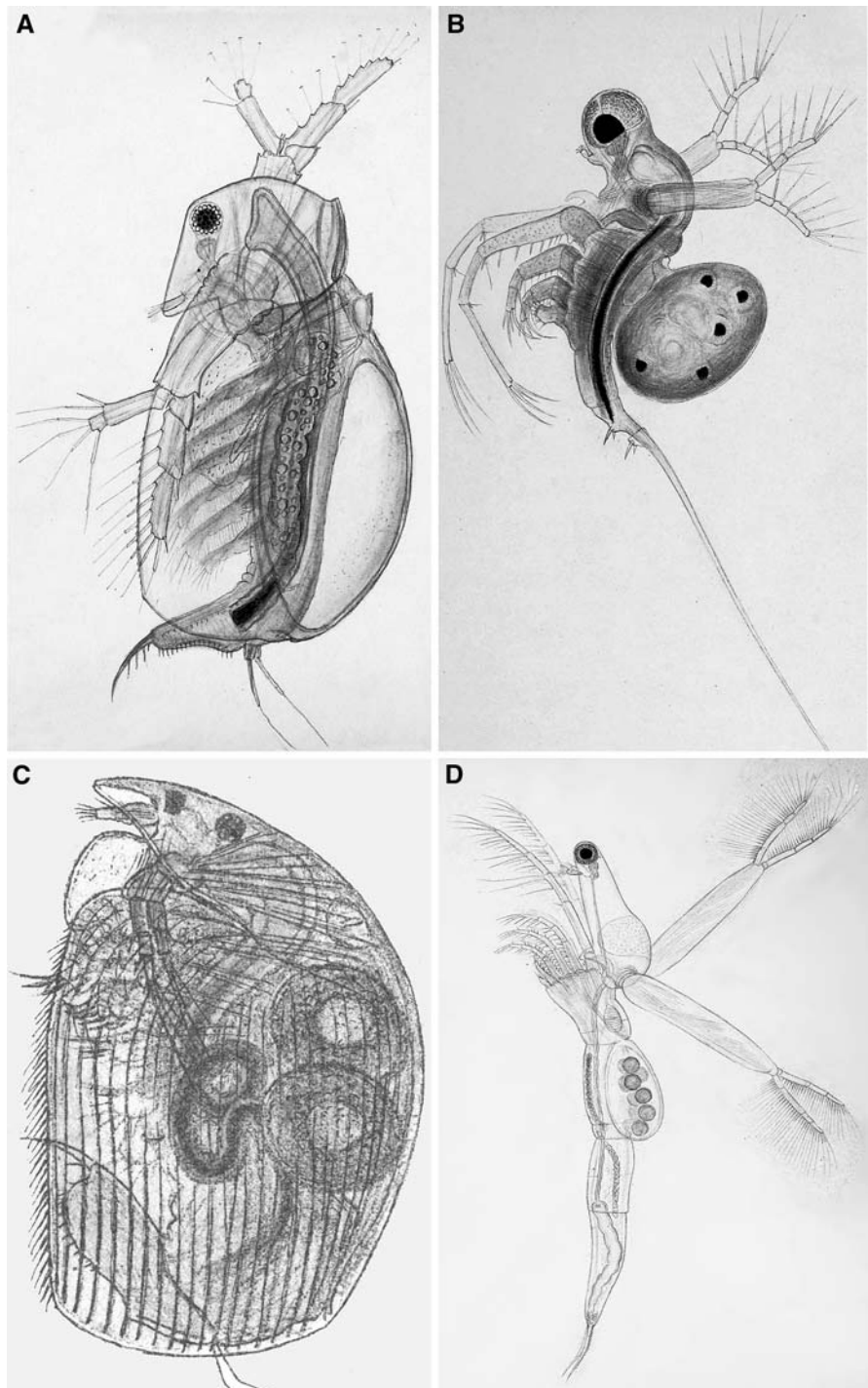Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 12844 Prague 2, Czechia

Introduction

Cladocerans ("water fleas") are primarily-freshwater small-sized (0.2–6 mm, and up to 18 mm in single case of *Leptodora kindtii*) branchiopod crustaceans, inhabiting pelagic, littoral, and benthic zones. Four cladoceran orders are recognised (Fryer, 1987): Anomopoda, Ctenopoda, Onychopoda, and the monotypic Haplopoda (see Fig. 1 A–D for representatives of each order). Most species occur in continental fresh or saline waters, although two ctenopods and several onychopods from the family Podonidae are truly marine, and a few more ctenopod, anomopod and onychopod species occur in brackish waters. Seven known species may be regarded as true inhabitants of subterranean environment, and a few others (of the family Chydoridae) live in semi-terrestrial conditions.

The trunk and appendages of most cladocerans (Anomopoda and Ctenopoda) are enclosed in a bivalved carapace. Tagmosis of the body is obscure (except in *Leptodora kindtii*, the single representative of Haplopoda), and a single eye and ocellus are usually present. Antennules are uniramous, while antennae are biramous (except in females of *Holopedium*), natatory, with 2–4 segments per branch. Four to six pairs of trunk limbs are either mostly similar in shape (Ctenopoda, Onychopoda, Haplopoda) or modified individually for various functions (Anomopoda).

Water fleas are important components of the fauna of fresh waters; they are particularly

Fig. 1 A—*Sida crystallina*
B—*Bythotrephes*
longimanus
C—*Alona* sp.
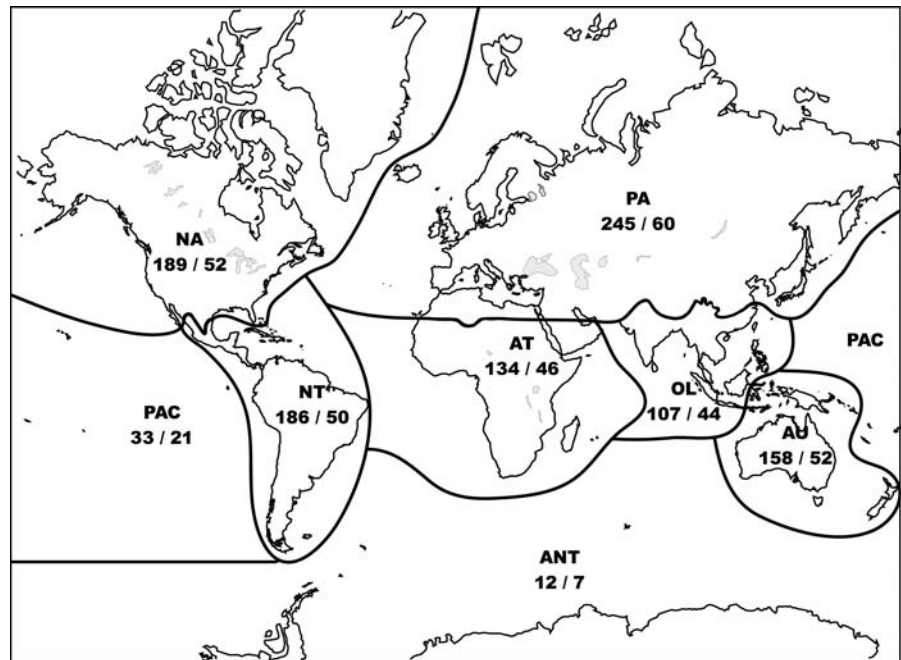D—*Leptodora kindti*
(original drawings by G O
Sars)

significant in the food web of stagnant waters. Most species are filter-feeders; onychopods and haplopods are predatory. They usually reproduce by cyclical parthenogenesis (but asexual lineages are known as

well), and populations are mostly dominated by females. Sexual dimorphism is normally rather distinct. Sexually produced diapausing eggs are resistant to desiccation and other unfavourable

Fig. 2 Global Distribution of species and genus diversity by zoogeographic region (Species Number/Genus Number). PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical ; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands; ANT—Antarctic

conditions, and may even survive passage through the digestive track of birds (Figuerola & Green, 2002); thus, they are important propagules for passive dispersal.

The first information on Cladocera date from the 17th century; the history of research has been divided into three to seven major phases (for a detailed discussion see Korovchinsky, 1997; Dumont & Negrea, 2002). An important change of paradigm, characterised by the rejection of the prevailing assumption of cosmopolitanism of cladoceran species, occurred around the 1950–1980s with a new approach to the taxonomy and phylogeny of Chydoridae (Frey, 1959, 1982, 1987). Subsequently, the concept of non-cosmopolitanism has been supported by numerous morphological, as well as molecular, studies. The increasing use of molecular tools in recent years has and will continue to have a strong impact on our understanding of cladoceran diversity, phylogeny and biogeography (e.g., Adamowicz et al., 2004; Cox & Hebert, 2001; Schwenk et al., 2000; Taylor et al., 2002).

Species diversity

The currently accepted number of cladoceran species based on existing descriptions is around 620. The tables summarize the currently known number of species and genera within orders and families of the group (Tables 1, 2, Fig. 2), based on recent major publications (Smirnov, 1992a, 1996; Korovchinsky, 1996, 2004; Orlova-Bienkowskaja, 2001; Dumont & Negrea, 2002; Benzie, 2005; Kotov & Stifter, 2006) and additional published or as yet unpublished sources. The described taxonomic diversity of Cladocera, however, underestimates the reality, and even higher-ranked taxa are still being discovered, e.g., a new family, Dumontiidae (Santos-Flores & Dodson, 2003).

Only about 45–50% of the species may be considered to be more or less well described and valid, while the status of other species is vague, and many of them likely represent cryptic complexes (Korovchinsky, 1996). The families Chydoridae, Daphniidae, Ilyocryptidae, and Sididae have been studied comparatively better. The largest number of valid species is known from Europe, North America, Australia, and South America, and the smallest number from Africa and Southern Asia. This, however, at least partly reflects the intensity of research rather than real patterns of diversity.

Adamowicz & Purvis (2005) estimated three correction factors to extrapolate global branchiopod diversity from the diversity of described species, and

Table 1 Number of Cladocera species currently known in the main biogeographic areas. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic. (numbers in parentheses indicate endemic species)

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Order Anomopoda	195 (83)	169 (66)	170 (89)	125 (24)	89 (20)	149 (78)	29 (0)	12 (6)	537
Family Daphniidae*	58 (21)	58 (25)	32 (13)	25 (1)	17 (1)	26 (13)	6 (0)	3 (2)	121
Family Moinidae*	13 (6)	7 (2)	10 (5)	10 (1)	3 (0)	7 (3)	4 (0)	0	29
Family Dumontiidae	0	1 (1)	0	0	0	0	0	0	1
Family Ilyocryptidae	11 (3)	10 (2)	9 (4)	8 (3)	5 (3)	5 (3)	1 (0)	1 (0)	28
Family Bosminidae	4 (0)	8 (3)	7 (3)	3 (0)	4 (1)	3 (0)	1 (0)	0	14
Family Acantholeberidae	1 (0)	1 (0)	0	0	0	0	0	0	1
Family Ophryoxidae	3 (1)	3 (1)	0	0	0	0	0	0	3
Family Macrothricidae	16 (10)	10 (5)	21 (12)	12 (2)	12 (4)	20 (9)	2 (0)	3 (1)	60
Family Neothricidae	0	0	0	0	0	3 (3)	0	0	3
Family Eurycercidae	4 (2)	5 (3)	2 (1)	1 (0)	1 (0)	0	0	0	8
Family Chydoridae	85 (40)	66 (24)	89 (51)	66 (17)	48 (11)	85 (47)	15 (0)	5 (3)	269
Order Ctenopoda	17 (5)	18 (7)	16 (9)	9 (0)	15 (4)	9 (5)	4 (1)	0	50
Family Holopediidae	1 (0)	2 (1)	1 (1)	0	0	0	0	0	3
Family Sididae	16 (5)	16 (6)	15 (8)	9 (0)	15 (4)	9 (5)	4 (1)	0	47
Order Haplopoda	1 (0)	1 (0)	0	0	1 (0)	0	0	0	1
Family Leptodoridae	1 (0)	1 (0)	0	0	0	0	0	0	1
Order Onychopoda	32 (31)	1 (0)	0	0	1 (0)	0	0	0	32
Family Polyphemidae	2 (1)	1 (0)	0	0	1 (0)	0	0	0	2
Family Podonidae	17 (17)	0	0	0	0	0	0	0	17
Family Cercopagidae*	13 (13)	0	0	0	0	0	0	0	13
Total	245 (119)	189 (73)	186 (98)	134 (24)	107 (24)	158 (83)	33 (1)	12 (6)	620

* Invasive species not considered

predicted that there are about 2.1 times more branchiopod species in nature than currently known. The overall cladoceran species richness is probably up to 4 times higher than currently known. This is supported by the results of molecular studies. Detailed studies, combining morphological analyses and molecular tools, are especially promising for delineating species boundaries in groups with relatively uniform morphology, fewer qualitative characters, and widespread phenotypic plasticity. Although most molecular analyses have so far focused on a single model genus, *Daphnia*, within a relatively short time this led to the discovery of an unprecedented number of cryptic lineages. According to Hebert & Taylor (1997), the global total for the genus *Daphnia* (including *Daphniopsis*) is likely closer to 200 species instead of 75 included in the last monograph on the genus (Benzie, 2005). Similar patterns of widespread cryptic diversity and high numbers of undescribed lineages can be seen

in other groups, e.g., in *Moina* (Petrusek et al., 2004 and unpublished data), *Ilyocryptus* (Kotov & Štifter, 2006) and several genera of the Chydoridae.

Phylogeny and historical processes

Cladocerans probably derived from large bodied branchiopod ancestors. Recent molecular analyzes have suggested two alternative phylogenetic relationships among cladoceran orders. The monophyly of Gymnomera (Haplopoda and Onychopoda) is supported in both cases but one hypothesis suggests a sister relationship between Anomopoda and the remaining three orders (Swain & Taylor, 2003), while the other clusters Anomopoda and Ctenopoda together (De Waard et al., 2006). Other authors (see review in Negrea et al., 1999) have recently proposed alternative hypotheses on ordinal-level relationships

Table 2 Number of Cladocera genera currently known in the main biogeographic areas. PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Afrotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic. (numbers in parentheses indicate endemic genera)

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Order Anomopoda	44 (4)	43 (3)	44 (3)	42 (1)	36 (1)	48 (11)	19 (0)	7 (0)	76
Family Daphniidae	5 (0)	5 (0)	4 (0)	5 (0)	4 (0)	4 (0)	4 (0)	2 (0)	5
Family Moinidae	1 (0)	2 (0)	2 (0)	2 (0)	2 (0)	2 (0)	1 (0)	0	2
Family Dumontiidae	0	1 (1)	0	0	0	0	0	0	1
Family Ilyocryptidae	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1
Family Bosminidae	2 (0)	2 (0)	2 (0)	2 (0)	2 (0)	2 (0)	1 (0)	0	2
Family Acantholeberidae	1 (0)	1 (0)	0	0	0	0	0	0	1
Family Ophryoxidae	1 (0)	2 (1)	0	0	0	0	0	0	2
Family Macrothricidae	6 (0)	6 (0)	7 (2)	5 (0)	4 (0)	5 (0)	1 (0)	1 (0)	11
Family Neothricidae	0	0	0	0	0	1 (1)	0	0	1
Family Eurycercidae	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	0	0	0	1
Family Chydoridae	26 (4)	22 (1)	27 (1)	26 (1)	22 (1)	33 (10)	11 (0)	3 (0)	49
Order Ctenopoda	7 (1)	7 (0)	6 (0)	4 (0)	6 (0)	4 (0)	2 (0)	0	8
Family Holopediidae	1 (0)	1 (0)	1 (0)	0	0	0	0	0	1
Family Sididae	6 (1)	6 (0)	5 (0)	4 (0)	6 (0)	4 (0)	2 (0)	0	7
Order Haplopoda	1 (0)	1 (0)	0	0	1 (0)	0	0	0	1
Family Leptodoridae	1 (0)	1 (0)	0	0	0	0	0	0	1
Order Onychopoda	8 (5)	1 (0)	0	0	1 (0)	0	0	0	10
Family Polyphemidae	1 (0)	1 (0)	0	0	1 (0)	0	0	0	1
Family Podonidae	5 (3)	0	0	0	0	0	0	0	**7**
Family Cercopagidae	2 (2)	0	0	0	0	0	0	0	2
Total	60 (10)	52 (3)	50 (3)	46 (1)	44 (1)	52 (11)	21 (0)	7 (0)	95

for the Cladocera; these were, however, based only on classical (Fryer, 1987) or cladistic analyses of morphological traits.

Cladocera is an ancient group of Palaeozoic origin (Dumont & Negrea, 2002), but their unambiguous fossil remains are known only from the Mesozoic (Smirnov, 1971, 1992b; Kotov & Korovchinsky, 2006). Recently, Anderson et al. (2004) described crustaceans similar to the Cladocera from the Early Devonian. Molecular phylogenetic data have revealed that the subfamilies of Chydoridae (Anomopoda) were separated in the Middle Palaeozoic (about 400 Myr ago; Sacherová & Hebert, 2003) and representatives of the genus *Daphnia* differentiated at least 200 Myr ago (Colbourne & Hebert, 1996). Any Mesozoic scenarios, such as 'Gondwana-Laurasia' (e.g., Benzie, 2005), are only moderately applicable to cladoceran groups, especially at a generic and subgeneric level. In spite of the general antiquity of Cladocera, radiation within some groups is only recent or even contemporary, e.g., in some Holarctic *Daphnia* and *Bosmina* (Colbourne & Hebert, 1996; Taylor et al., 2002).

Present distribution and main areas of endemicity

The distribution and patterns of endemicity of higher-level taxonomic groups are relatively well-known. The known species diversity, as well as the number of endemic taxa, is nevertheless bound to increase with further faunistic research, especially from non-northern temperate regions, and with the application of detailed morphological and molecular tools to resolve cryptic species complexes. Some endemic species have narrow distributions, and it is therefore likely that many remain overlooked.

The Holarctic cladoceran inland fauna is rich and composed of all four orders. Two orders (Haplopoda and Onychopoda), three families, 13 genera

(including those of the Caspian Sea and Lake Baikal), and about 250 known species are endemic for the region. Many taxa are presumably old and phylogenetically divergent, monotypic, or composed of a few species. The Palaearctic taxa are more diverse than those of the Nearctic due to, first of all, the presence of numerous Caspian and Baikalian endemics. Among other zoogeographical regions, Australasia is rich in endemics, represented by one family, one subfamily, one tribe, 11 genera, and 83+ species, while known endemics in Oriental and Neotropical regions are of a lower rank or fewer (one tribe, one genus and 21+ species, and three genera and 98+ species, respectively). The Afrotropical region, though poorly studied, seems to be especially deprived of known higher-level endemic cladoceran taxa, being represented by a single endemic genus and 24+ endemic species.

Cladoceran species richness does not change evenly with latitude but concentrates in the warm temperate to subtropical zone of both hemispheres (∼25–50°, including mountain areas within the true tropics) (Korovchinsky, 2006). In the belt from the Mediterranean through Central Asia including the Pontocaspian region, northern India to East Asia (Amur region and China), five genera and over 100 known endemic species occur, while those in the North Palaearctic do not exceed 55–60. In North America, the area embracing the United States, Mexican plateau, and southern Canada, is inhabited by many endemics, including one family (Dumontiidae), two genera, and over 70 species. Southern Australia, Tasmania, and New Zealand are rich in endemics of high taxonomic rank: one subfamily (Sayciinae), one tribe (Australospilini), 8 genera, and about 80 currently known species compose altogether most of the known Australasian endemics. Only five of them are shared between Australia and New Zealand, which itself has seven endemic species/subspecies. As the African cladoceran fauna has been relatively poorly studied, there are only a few described endemics (one genus and about 10 species), but e.g., endemic *Daphnia* fauna of the Ethiopian biogeographic region is certainly significantly more numerous (Mergeay et al., unpublished). Cladocerans of subtropical and temperate South America include two endemic genera and 17+ endemic species. In total, the species richness of the southern temperate—subtropical zone amounts to more than 100 endemic

species. The intermediate tropical zone, from which altogether 163 species are known, is characterized by fewer endemic taxa of comparatively lower taxonomic rank: one tribe (Indialonini) and nine genera (Korovchinsky, 2006).

A bipolar (antitropical) disjunct distribution of faunal complexes and taxa (*Daphnia, Pleuroxus, Tretocephala* etc.), the wide ranges of some species (though some of these likely form species complexes) and the narrow restriction of others, the presence of isolated populations, and concentration of endemics in the warm temperate—subtropical zone of both hemispheres, are typical traits of cladoceran zoogeography.

Such patterns stimulated the analysis of cladoceran faunal formation by the modern version of the concept of 'ejected relicts' instead of vicariance. This hypothesis consider the extant Cladocera as a relict group (Korovchinsky, 2006), whose taxa were widely distributed in the past. Tertiary climatic changes, primarily within the present tropical and boreal latitudes, resulted in mass extinction of their biotas, while the warm temperate—subtropical regions remained comparatively unchanged. Additional factors (e.g., the radiation of freshwater planktivorous fish) could have operated in conjunction with climate changes as well.

While this scenario might be likely for most of cladocerans, molecular data suggest that vicariance processes and allopatric speciation at both the intercontinental level and in regional refugia within continents plays a significant role in shaping species diversity in at least some genera (e.g., *Daphnia*). Sweepstake intercontinental dispersals, followed by a local radiation, seems to have been important factors in augmenting the diversity in the different biogeographic regions. Founder effects coupled with habitat shifts, such as pond-lake transitions (Lynch, 1985) or, possibly, shifts among substrates in littoral groups, are also regarded as potentially important drivers of speciation. Finally, interspecific hybridization and hybrid speciation plays an important role in dynamic young species complexes in *Daphnia*, though reports of other hybridizing cladocerans are scarce (Schwenk & Spaak, 1995).

Human related issues

Cladocerans (especially *Daphnia*) are important model organisms in both basic and applied research, due to

their easy culturing, short generation time, and clonal reproduction. Species of *Daphnia* have been widely used in ecological and evolutionary studies (e.g., on trophic interactions, diel vertical migration, interspecific hybridisation, polyploidy and asexuality, host-parasite interactions etc.), and the soon to be available sequence of the whole *Daphnia pulex* s.l. genome will open further research possibilities in genomics and other fields. Cladocerans have also gained certain economic importance as they are also widely used in aquaculture, and large filter-feeding planktonic species have an indirect economic impact as important fish food or phytoplankton-controlling group. These animals as intermediate hosts of some parasites may potentially pose a threat to human health.

A high diversity of cladocerans can be found in the littoral zone of stagnant waters, as well as in temporary water bodies. These habitats are often negatively influenced by human activities, and especially the loss of temporary waters may lead to a decrease of diversity or even local extinction of some species.

Some cladocerans have recently invaded successfully other continents through human-mediated dispersal, and it is likely that this trend will increase. For example, non-indigenous species of *Daphnia* are widespread in Europe, North America or Africa (e.g., Havel et al., 1995; Mergeay et al., 2005), though mostly without a strong ecological impact. The invasion of predatory onychopods (especially *Bythotrephes*) from the Palaearctic into the Laurentian Great Lakes and those of the Canadian Shield, however, have influenced the native fauna significantly (Yan et al., 2002).

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