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A checklist of epibiotic ciliates (Peritrichia and Suctoria) on the cladoceran crustaceans

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Abstract: Despite the growing awareness of the ecological importance of epibiont-host associations, detailed inventories for planktonic hosts are rare. Here, we provide an updated checklist of the peritrich and suctorian epibiont ciliates (Ciliophora) on the cladocerans (Crustacea: Cladocera). Thirty-nine species of peritrich ciliates (of which 34 are assigned to species) and three species of suctorian ciliates are found to be epibionts on the Cladocera. Fifty-eight cladoceran taxa are known to be hosts of the ciliate epibionts, 33 of these hosts (57%) are planktonic. Seven taxa were determined to the level of genus. Complete species designations were geographically biased (38 of 51 species) towards European sites, suggesting poor taxonomic knowledge beyond Europe. Also, the recently discovered continental endemism of cladoceran hosts could indicate that associated ciliates are more diverse than previously appreciated.

Key words: epibionts; Cladocera; Ciliata; freshwater

Introduction

Although epibionts of Cladocera were discovered in the 18th century (O.F. Muller 1785), the taxonomy and diversity of such associations remain poorly studied. Epibionts (algae, protozoans, and rotifers) typically have negative fitness consequences for their hosts. For example, epibionts increase visibility to planktivore predators (Wiley et al. 1993). Also, epibionts increase the energetic requirements of the host by adding weight and increasing the sinking rates (Markevich & Rivier 1975; Barea-Arco et al. 2001). Epibionts can even compete for food with the host (Kankaala & Eloranta 1987).

Normally, an epibiont behaves as a commensal in a food-rich environment, but it has the potential to increase the mortality rate of its host when food is limited (Xu & Burns 1991). Barea-Arco et al. (2001) demonstrated that attached algal epibionts have a negative effect on *Daphnia* by increasing the weight and sinking rates of infected animals. At the same stage, the epibiont dispersal stages are actively grazed by *Daphnia*, which implies a fitness benefit for the host. Manca et al. (2007) concluded that in case of *Daphnia* infested by gymnostomatid infusorians, the egg predation by the epibiont could be an important mechanism regulating population dynamics of the host. Therefore the relationship of the cladoceran and its epibionts is complex and species-dependent (Threlkeld & Willey 1993; Dumont & Negrea 2002).

Future studies need to be supported by accurate inventories of epibionts and their hosts. Several global inventories exist (Green 1974; Fernández-Leborans & Tato-Porto 2000a, b). In this communication we address two groups of epibionts: peritrich and suctorian ciliates (Ciliophora). These epibionts are common on freshwater (Matthes & Gulh 1973; Evans et al. 1979; Bickel et al. 2012) and marine (Fernández-Leborans et al. 1996; Fernández-Leborans 2003; Zhadan & Mikrjukov 1996) crustaceans.

The aim of this paper is to produce a checklist of all records of peritrich and suctorian cilates on freshwater cladocera (Crustacea: Branchiopoda). In the past, there were some reviews for specific groups of ciliate epibionts living on crustaceans in general, but there was not a special review dedicated to the cladocerans. Also previous inventories containing information about the infusorians on cladocerans were published more than a decade ago (Fernández-Leborans & Tato-Porto 2000a, b). We update the epibiont-host associations in the light of recent changes in cladoceran taxonomy.

Material and methods

The checklist is based on exclusively the records from previous literature.

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Results

A checklist of peritrich and suctorian epibiont ciliates on Cladocera

Subclass PERITRICHIA Stein, 1859
Order SESSILIDA Kahl, 1933
Family Epistylididae Kahl, 1935

Genus *Rhabdostyla* Kent, 1880

***Rhabdostyla bosminae* Levander, 1907**
Bosmina sp. – Lappland, Finland (Levander 1907; Bendt 1988).

***Rhabdostyla conipes* Kahl, 1935**
Daphnia sp. – Germany (Kahl 1935);
Daphnia magna, *D. longispina* and *Scapholeberis mucronata* – United Kingdom; *D. longispina* – Tvärminne archipelago, Finland (Green 1957, 1974; Bendt 1988).

***Rhabdostyla cylindrica* Stiller, 1935**
Leptodora kindti – Lake Balaton, Hungary (Stiller 1935);
L. kindti – Frederiksborg Slotso, Denmark (Green 1974; Bendt 1988).

***Rhabdostyla hungarica* Stiller, 1931**
Leptodora kindti – Lake Balaton, Hungary (Stiller 1931; Bendt 1988).

***Rhabdostyla globularis* Stokes, 1890**
Bosmina longirostris, Diaphanosoma brachyurum – a water body near Erlangen in Germany (Nenninger 1948).

***Rhabdostyla pyriformis* Perty 1852**
Daphnia longispina, *D. hyalina, D. pulex* and *Ceriodaphnia reticulata* – Germany (Kahl 1935, Nenninger 1948, Sommer 1950, Hamman 1952) (as *R. ovum)*;
Daphnia magna, D. pulex, D. cucullata, Simocephalus vetulus, Ceriodaphnia reticulata and *Leptodora kindti* – Denmark (Green 1953) (as *R. ovum*);
Daphnia magna – a tank at Hampton, UK (Green 1955);
Daphnia magna and *D. longispina* – Finland (Green 1957);
Daphnia atkinsoni, D. curvirostris D. hyalina, D. longispina, D. pulex, D. obtusa, Ceriodaphnia laticaudata, C. pulchella, Simocephalus vetulus, Alona rectangula and *Leydigia acanthocercoides* – UK; *Ceriodaphnia pulchella* and *C. megalops* – Denmark; *Scapholeberis mucronata, S.vetulus* – Greenland;*Daphnia magna* and *Ceriodaphnia reticulata* – Gull Lake, Michigan, USA; *Moina micrura* – Cameroon (Green 1974);
Daphnia longispina, D. hyalina, D. pulex, D. magna, D. cucullata, D. atkinsoni, Ceriodaphnia sp., *Simocephalus vetulus, Scapholeberis mucronata, Moina micrura, Alona rectangula, Leydigia acanthocercoides* and *Leptodora kindtii* – Europe (Bendt 1988).

***Rhabdostyla* sp.**
Different cladocerans – Czechoslovakia (Šrámek-Hušek et al. 1962);
Different cladocerans – Donghu Lake, China (Ji et al. 1999);
Bosminopsis deitersi and *Moina minuta* – Monjolinho Reservoir, Brazil (Regali-Seleghim & Godinho 2004).

Genus *Epistylis* Ehrenberg, 1830

***Epistylis anastatica* L., 1767**
Daphnia pulex – Hampton, England, United Kingdom (Green 1974; Bendt 1988).

***Epistylis breviramosa* Stiller, 1931**
Bosmina longirostris and *Alona affinis* – Regents Park Lake and Hampton, England, UK;
Daphnia magna – Lake Balaton, Hungary (cf. Green 1974; Bendt 1988).

***Epistylis daphniae* Fauré-Fremiet, 1905**
Daphnia magna – Germany (Nenninger 1948);
Sida crystallina – Germany (Nenninger 1948) (as *Epistylis daphnia* Fauré-Fremiet var. *infundibulate*);
Daphnia obtusa, D. pulex, D. longispina, D. curvirostris, Simocephalus vetulus, S. serrulatus, Ceriodaphnia laticaudata, C. pulchella, C. reticulata, Chydorus sphaericus, Moina macrocopa, M. micrura, Diaphanosoma leuchtenbergianum – Europe (Bendt 1988);
Moina macrocopa – Weijin River, Tianjin, China (Xu Z. 1992, 1993);
Different cladocerans – Donghu Lake, Wuhan, China (Ji et al. 1999).

***Epistylis fungitans* Kellicot, 1887**
Sida crystallina – North America (Kellicot 1887).

***Epistylis halophila* Stiller, 1942**
Daphnia longispina and *D. pulex* – Lake Cserepeser, Hungary (Stiller 1942; Bendt 1988).

***Epistylis helenae* Green, 1957**
Daphnia pulex – Denmark (as *E. daphniae* Faure Fremiet) (Green 1953);
Daphnia magna, Ceriodaphnia reticulata and *Simocephalus vetulus* – Germany (Nenninger 1948; Matthes 1950) (as *E. daphniae* Kahl);
Daphnia obtusa, D. magna D. pulex, D. curvirostris D. longispina, Simocephalus vetulus and *Ceriodaphnia pulchella* – England; *Ceriodaphnia reticulata, Diaphanosoma leuchtenbergianum* – Denmark; *Daphnia magna, D. pulex, D. longispina* and *Chydorus sphaericus* – Finland; *Moina macrocopa* – Czechoslovakia; *Simocephalus vetulus* – Italy and Greenland; *Simocephalus vetulus, S. serrulatus, Ceriodaphnia laticaudata, Moina macrocopa* – USA; *Moina micrura* – Cameroon (Green 1974).

***Epistylis niagarae* Kellicott, 1883**
Daphnia pulex, *D. rosea, Ceriodaphnia reticulata*, and *Scapholeberis mucronata* – Colorado, U.S.A. (Willey & Threlkeld 1993).

***Epistylis nympharum* Engelman, 1862**
Unidentified cladocerans – Germany (Nenninger 1948);
Daphnia hyalina – Germany (Sommer 1950; Bendt 1988);
Ilyocriptus sordidus – Hampton Court, England, UK (Green 1974).

Epistylis ovum **(Kent 1881)**
Daphnia sp. – Hungary (Stiller 1931);
Leptorora kindti – Lake Balaton, Hungary (Stiller 1942);
Bosmina sp. – Germany (Hammann 1952);
Daphnia pulex – Godhavn, Greenland (Green 1974);
Daphnia sp., *D. pulex, Bosmina* sp., *Leptodora kindtii* – Europe (Bendt 1988).

Epistylis pygmaeum **(Ehrenberg, 1838)**
Bosmina longirostris, *Ceriodaphnia reticulata*, *Daphnia galeata mendotae*, *D. pulex*, *Diaphanosoma brachyurum*, *Scapholeberis kingi* – a temporary pond in Patagonia, Argentina (Gilbert & Schroder 2003).

Epistylis zschokkei **(Keiser, 1921)**
Acantholeberis curvirostris – Erlangen, Germany (Nenninger 1948; Bendt 1988).

Epistylis **sp.**
Unidentifiied cladocerans – Czechoslovakia (Šrámek-Hušek et al. 1962);
Diaphanosoma brachyurum, Daphnia cucullata – Germany (Bickel et al. 2012);
Bosmina tubicen, *Ceriodaphnia cornuta*, *Diaphanosoma* sp. – Tulé Reservoir, Venezuela (López et al. 1998);
Moina micrura, Ceriodaphnia quadrangula, Simocephalus vetulus, Ilyocryptus sordidus, Macrothrix groenlandica and *Chydorus sphaericus* – Asi River, Turkey (Bozkurt & Genc 2009);
Different cladocerans from Donghu Lake, Wuhan, China (Ji et al. 1999).

Family Lagenophryidae Bütschli, 1889

Genus *Lagenophrys* Stein, 1852

Lagenophrys bipartita **Stokes, 1890**
Daphnia sp. – U.S.A. (Stokes 1890).

Family Operculariidae Fauré-Fremiet, 1979 emend. Corliss, 1979

Genus *Opercularia* Stein, 1854

Opercularia nutans **(Ehrenberg, 1831)** emend. Stein, 1854
Alona affinis – Germany (Matthes 1950).

Family Scyphidiidae Kahl, 1933

Genus *Scyphidia* Dujardin, 1841

Scyphidia **sp.**
Scapholeberis kingi, *Alona costata* and *Picrileuroxus denticulatus* (as *Pleuroxus*) – Ashmore Lake, Illinois, U.S.A. (Henebry & Ridgeway 1979);
Bosminopsis deitersi and *Moina minuta* – Monjolinho Reservoir, Brazil (Regali-Seleghim & Godinho 2004).

Family Vorticellidae Ehrenberg, 1838

Genus *Vorticella* L., 1767

Vorticella abbreviata **Kieser, 1921**
Daphnia pulex – Cserepeser Lake, Hungary (Stiller 1942)

Vorticella bosminae **Srámek-Husek, 1948**
Bosmina longirostris – fresh waters in the former Czechoslovakia (Bendt 1988).

Vorticella campanula **Ehrenberg, 1831**
Daphnia magna, *D. obtusa*, *Sida crystallina*, *Polyphemus pediculus*, and *Simocephalus vetulus* – England, UK(Green 1974; Bendt 1988);
Sida crystallina and *Simocephalus vetulus* – Switzerland (Green 1974);
Ceriodaphnia reticulata, *Daphnia pulex*, *D. rosea*, and *Scapholeberis mucronata* – an artificial pond in Colorado, U.S.A. (Willey & Threlkeld 1993).

Vorticella chydoricola **Srámek-Hušek, 1946**
(According to Warren 1986, this is an epibiont variety of *V. microstoma*)
Disparolana rostrata (as *Rhynchotalona rostrata*) and *Macrothrix laticornis* – Czechoslovakia (Srámek-Hušek 1946).

Vorticella convallaria **Linnaeus, 1767**
Sida crystallina and *Scapholeberis mucronata* – Germany (Nenninger 1948).

Vorticella inconstans **Green, 1974**
Macrothrix hirsuticornis and *D. pulex* – Greenland (Green 1974; Bendt 1988).

Vorticella kahli **Stiller, 1931**
Daphnia hyalina, *Leptodora kindtii*, and *Sida crystallina* – Lake Balaton, Hungary (Stiller 1931; Bendt 1988).

Vorticella microstoma **Ehrenberg, 1830**
Eurycercus lamellatus – Germany (Nenninger 1948);
Eurycercus lamellatus – European Russia (Smirnov 1971);
Scapholeberis kingi – Ashmore Lake, Illinois, U.S.A. (Henebry & Ridgeway 1979);
Scapholeberis kingi – Great Lakes region, U.S.A.-Canada (Evans et al. 1981);
Different cladocerans from Donghu Lake, Wuhan, China (Ji et al. 1999).

Vorticella octava **Stokes, 1885**
(Taxonomic status of this species has been questioned; it is a freshwater variety of *V. striata* according to Noland & Finley 1931 and Warren 1986).
Scapholeberis mucronata – Germany (Nenninger 1948);
Daphnia magna, D. pulex, *D. longispina, Scapholeberis mucronata* and *Chydorus sphaericus* – Finland (Green 1957);
Daphnia magna, D. longispina, D. obtusa, Polyphemus pediculus, Eurycercus lamellatus and *Chydorus sphaericus* – England, UK; *Scapholeberis mucronata* – Denmark; *Daphnia magna, D. pulex, D. longispina, Scapholeberis mucronata, Chydorus sphaericus* and *Diaphanosoma brachyurum* – Czechoslovakia; *Scapholeberis mucronata* – Italy; *Scapholeberis mucronata* and *Daphnia pulex* – Greenland; *Macrothrix laticornis, Simocephalus vetulus, S. serrulatus Ceriodaphnia quadrangula, Scapholeberis kingi* and *Chydorus sphaericus* – Michigan, USA (Green 1974).

***Vorticella platysoma* Stokes, 1887**

Scapholeberis mucronata – Germany (Nenninger 1948).

***Vorticella solitaria* Stiller, 1932**

Unidentified cladocerans – Lake Balaton, Hungary (Stiller 1932).

***Vorticella* sp.**

Diaphanosoma celebensis – Sulawesi, Indonesia (Stingelin 1900);
Macrothrix montana – Susie Lake, Lake Michigan and Lake of Rock, Ontario, Canada (Birge 1904);
unidentified cladocerans – Czechoslovakia (Šrámek-Hušek et al. 1962);
Daphnia pulex s.str., *D. pulex* s.lat., *Chydorus sphaericus* – tunrda ponds of Subarctic in European Russia (Vekhov 1987);
Daphnia longispina – Lake Mekkojärvi, Finland (Kankaala & Eloranta 1987);
all species of *Ilyocryptus* – European Russia (Chirkova 1974);
Holopedium gibberum – lakes in New York State, U.S.A. (Montvillo et al. 1987);
Daphnia magna – ponds in Belgium (Decaestacker et al. 2004, 2005);
Diaphanosoma celebensis – tropics of Old World (Korovchinsky 2004);
Different cladocerans – Donghu Lake, Wuhan, China (Ji et al. 1999).

Genus *Carchesium* Ehrenberg, 1831

***Carchesium brevistylum* Stiller, 1931**

Leptodora kindtii – Lake Balaton, Hungary (Stiller 1931).

***Carchesium polypinum* Linnaeus, 1758**

Bosmina sp. – Germany (Hammann 1952);
Daphnia magna – Hampton Water Woks, England, UK (Green 1974).

***Carchesium*sp.**

Daphnia magna – a tank at Hampton, England, UK (Green 1955);
Daphnia pulex and *D. rosea* – beaver ponds in Colorado, U.S.A. (Threlkeld & Willey 1993).

Genus *Intranstylum* Fauré-Fremiet, 1904

***Intranstylum invaginatum* Stokes, 1886**

Daphnia sp., *Bosmina* sp. and *Chydorus sphaericus* – Germany (Kahl 1935, Matthes 1950);
Daphnia magna, *D. atkinsoni* from Bedford College, England, UK (Green 1974);
Daphnia pulex and *Chydorus spahericus* – Foulden Common, Norfolk, England, UK (Green 1974);
Daphnia magna, D. longispina and *Chydorus sphaericus* – Tvärminne archipelago, Finland (Green 1957);
Scapholeberis mucronata – Lago di Ghirla, Italy (Green 1974).

Genus *Pseudocarchesium* Sommer, 1951

***Pseudocarchesium erlangensis* Nenninger, 1948**

Ilyocryptus sordidus – Germany; *Daphnia* and *Simocephalus* – Czechoslovakia (Nenninger 1948).

Class Suctoria Claparède & Lachmann, 1858
Order EXOGENIDA Collin, 1912
Family Urnulidae Fraipont, 1878

Genus *Paracineta* Collin, 1911

***Paracineta elegans* Collin, 1912**

Bythotrephes longimanus – Lakes of Zurich, Zug, Greifensee, Lucerna, Katzensee and Agerisee, Switzerland (Collin 1912)

Order ENDOGENIDA Collin, 1912
Family Acinetidae Stein, 1859

Genus *Acineta* Ehrenberg, 1833

***Acineta compressa* Claparède & Lachmann, 1859**

Daphnia sp. – Europe (Claparède & Lachmann 1859).

Family Tokophryidae Jankowski, 1978

Genus *Tokophrya* Bütschli, 1889

***Tokophrya tripharetrata* (Entz, 1902)**

Daphnia pulex – Lakes of Patagonia, Argentina (Matthes et al. 1988).

Brief analysis of the cladoceran taxa carrying epibionts

Thirty-nine species of peritrich ciliates (of which 34 determined upto species level) and three species of suctorian ciliates are found to be epibiont on the Cladocera. Fifty eight taxa of the cladocerans are known to be hosts of the ciliate epibionts to date (Table 1), among them, 33 species (57%) are "planktonic" (= not associated with a substratum, although it is difficult to distinguish between a planktonic and a non-planktonic mode of life in shallow temporary pools). Seven cladoceran taxa were determined only up to generic level, among 51 species determined to species level, 38 species (75%) were initially described from Europe. It means that only European plankton is studied relatively well.

Discussion

Epibiotic species of ciliates are relatively more poorly known than free-living species. Many species of epibiotic ciliates that have a high degree of host-specificity, live on rarely occurring hosts, or inhabit restricted or sharply defined geographical areas (e.g., islands, polar habitats) may be awaiting discovery by science. Some papers on cladocerans contain records of undetermined peritrich ciliates as epibionts (e.g., *Macrothrix*, *Pleuroxus*, *Leydigia* and *Monospilus* from Lake Balaton, Hungary in Sebestyén 1947 or *Macrothrix tripectinata* from the Pamir Mountains, Tajikistan in Kotov 1999). It is probably correct to assume that epibiotic ciliates are relatively common on cladocerans, but usually do not receive consideration from hydrobiologists, undoubtedly because of the difficulty of identifying the

Table 1. List of the cladocerans for which the presence of epibiont ciliates is recorded.

No.	Taxon	Described from Europe?	Continents, where the species was found	Planktonic?
	Family Sididae Baird, 1850			
1.	*Sida crystallina* (O.F. Müller, 1776)	+	EU, NA	
2.	*Diaphanosoma brachyurum* (Liévin, 1848)	+	EU, SA	+
3.	*Diaphanosoma celebensis* Stingelin, 1900		AS	+
4.	*Diaphanosoma leuchtenbergianum* Fischer, 1850	+	EU	+
5	*Diaphanosoma* sp.		SA	+
	Familu Holopediidae Sars, 1865			
6.	*Holopedium gibberum* Zaddach, 1855	+	NA	+
	Family Daphniidae Straus, 1820			
7.	*Daphnia atkinsoni* Baird, 1859	+	EU	+
8.	*D. cucullata* Sars, 1862	+	EU	+
9.	*D. curvirostris* Eylmann, 1887	+	EU	+
10.	*D. galeata mendotae* Birge, 1918		SA	+
11.	*D. hyalina* Leydig, 1860	+	EU	+
12.	*D. longispina* (O. F. Müller, 1776)	+	EU	+
13.	*Daphnia magna* Straus, 1820	+	EU, NA	+
14.	*D. obtusa* Kurz, 1874 emend. Scourfield, 1942	+	EU	+
15.	*D. pulex* (De Geer, 1778)	+	EU, NA, SA	+
16.	*D. rosea* Sars, 1862	+	NA	+
17.	*Daphnia* sp.		EU, NA	+
18.	*Ceriodaphnia cornuta* Sars, 1885		SA	+
19.	*C. laticaudata* P.E. Müller, 1867	+	EU	+
20.	*C. megalops* Sars, 1890	+	EU	+
21.	*C. pulchella* Sars, 1862	+	EU	+
22.	*C. quadrangula* (O.F.Müller, 1785)	+	AS	+
23.	*C. reticulata* (Jurine, 1820)	+	EU, NA, SA	+
24.	*Ceriodaphnia* sp.		EU	+
25.	*Simocephalus serrulatus* (Koch, 1841)	+	EU, NA	
26.	*Simocephalus vetulus* (O.F. Müller, 1776)	+	EU, AS, NA	
27.	*Scapholeberis kingi* Sars 1888		NA, SA	
28.	*Scapholeberis mucronata* (O.F. Müller 1776)	+	EU, NA	
	Family Moinidae Goulden,1968			
29.	*Moina macrocopa* (Straus, 1820)	+	EU, AS, NA	+
30.	*Moina micrura* Kurz, 1875	+	EU, AS, AF	+
31.	*Moina minuta* Hansen, 1899		SA	+
	Family Ilyocryptidae Smirnov, 1976 emend. Smirnov, 1992			
32.	*Ilyocriptus sordidus* (Liévin, 1848)	+	EU, AS	
33.	*Ilyocryptus* sp.		EU	
	Family Acantholeberidae Smirnov, 1976 sensu Dumont & Silva-Briano, 1998			
34.	*Acantholeberis curvirostris* (O.F. Müller, 1776)	+	EU	
	Family Macrothricidae Norman & Brady, 1867			
35.	*Macrothrix groenlandica* Lilljeborg, 1901		AS	
36.	*Macrothrix hirsuticornis* Norman & Brady, 1867	+	NA	
37.	*Macrothrix laticornis* (Jurine, 1820)	+	EU, NA	
38.	*Macrothrix montana* Birge, 1904		NA	
39.	*Macrothrix tripectinata* Weisig, 1934		AS	
40.	*Macrothrix* sp.		EU	
	Family Bosminidae Baird, 1845 sensu Sars, 1865			
41.	*Bosmina longirostris* (O.F. Müller, 1776)	+	EU, SA	+
42.	*Bosmina tubicen* Brehm, 1953		SA	+
43.	*Bosmina* sp.		EU	+
44.	*Bosminopsis deitersi* Richard, 1895		SA	+
	Family Eurycercidae Kurz, 1875 sensu Dumont & Silva-Briano, 1998			
45.	*Eurycercus lamellatus* (O.F. Müller, 1776)	+	EU	
	Family Chydoridae Dybowski & Grochowski, 1894			
46.	*Alona affinis* (Leydig, 1860)	+	EU	
47.	*Alona costata* Sars, 1862	+	NA	
48.	*Chydorus sphaericus* (O.F. Müller, 1776)	+	EU, AS, NA	
49.	*Coronatella rectangula* (Sars, 1862)	+	EU	
50.	*Disparolana rostrata* (Koch, 1841)	+	EU	
51.	*Leydigia acanthocercoides* (Fischer, 1854)	+	EU	
52.	*Leydigia* sp.		EU	
53.	*Monospilus* sp.		EU	
54.	*Picripleuroxus denticulatus* (Birge, 1879)		NA	
55.	*Pleuroxus* sp.		EU	

Table 1. (continued)

No.	Taxon	Described from Europe?	Continents, where the species was found	Planktonic?
	Family Cercopagidae Mordukhai-Boltovskoi, 1968			
56.	*Bythotrephes longimanus* Leydig, 1860	+	EU	+
	Family Polyphemidae			
57.	*Polyphemus pediculus* (L., 1761)	+	EU	+
	Family Leptodoridae			
58.	*Leptodora kindti* (Focke, 1844)	+	EU	+

Continents: AF – Africa; AS – Asia; EU – Europe; NA – North America (including Greenland); SA – South America.

ciliates to the level of species. In addition, the majority of papers on cladocerans deal with plankton species even though littoral and benthic cladocerans are significantly more diverse. It is precisely that the littoral species of cladocerans, however, have more potential to harbour epibiotic ciliates than planktonic ones, owing to a combination of characteristics: (1) incomplete moulting in some taxa, which results in retention of exuvia from previous instars with epibionts still covering them; (2) presence of special sculpturing on the carapace, which contributes to retention of mineral and detritus particles that can provide a substratum for different epibionts; and (3) presence of strong marginal setae that provide an attractive support for attachment of microscopic epibionts (Kotov 2006; Kotov & Elías-Gutiérrez 2009). Therefore, it can be concluded that, despite the relatively great amount of information on epibionts of planktonic species of cladocerans, the majority of epibiotic taxa are still unknown owing to a poor knowledge of benthic cladocerans.

Data on host preferences of epibionts are somewhat contradictory. Gibert & Schroder (2003) found some instances of host specificity, but Thiéry & Cazaubon (1992) and Regali-Seleghim & Godinho (2004) concluded that the epibiotic relationships are influenced more by the habitat and swimming habits of the crustacean hosts than preference for a specific host taxon. To complicate matters, Vekhov (1987) demonstrated that vulnerability to infestation by epibionts does not depend on the swimming speed or size of the host.

Defining characteristics of epibiosis in tropical bodies of water are difficult to determine. López et al. (1998) studied epibiotic ciliates on the Cladocera inhabiting a large reservoir in Venezuela. In majority cases, they found that only one species of ciliate was present on a single cladoceran species. Only in few cases did females of *Diaphanosoma* sp., which was the host most infested by epibionts, carry two different species of epibiotic ciliates. A higher prevalence of epibionts was found during the early part of the dry season. The authors concluded that smaller-bodied zooplankton would support fewer epibiotic taxa than larger-bodied zooplankton and that the levels epibiotic populations on tropical hosts are generally lower than on temperate ones owing to shorter intermolt periods in the cladocerans living in warmer water.

The authors of a majority of the published reports of epibiotic ciliates on cladocerans cite identifications of the same species of hosts and associated epibionts from bodies of water in different regions of the Paleaearctic and even from different continents. In these cases, identifications of the Cladocera are contrary to the “non-cosmopolitan” paradigm (Frey 1982, 1987; Forró et al. 2008), also called “continental emdemism” (Xu S. et al. 2009), that has been recognized in cladoceran taxonomy and biogeography. Recent research has demonstrated that, even in the Holarctic, taxa such as *Daphnia pulex*, *Ilyocryptus sordidus*, *Chydorus sphaericus*, *Holopedium gibberum*, *Polyphemus pediculus*, *Leptodora kindti* probably represent species complexes (Štifter 1991; Rowe et al. 2007; Belyaeva & Taylor 2009; Adamowicz et al. 2009; Xu S. et al. 2009; Xu L. et al. 2010; Millette et al. 2011). Earlier determinations of species in the *Daphnia longispina* complex even in Europe and *Alona* s.lat. in any localities outside Europe also are problematic owing to the unstable taxonomy of these groups (Petrusek et al. 2008; Van Damme et al. 2010). Discrimination between species of *Simocephalus* and *Eurycercus* also was very imperfect before recent revisions (Orlova-Bienkowskaja 2001; Bekker et al. 2012). In reality, the true identities of the host species on which epibiont ciliates were found in many of the cases recorded above are very dubious.

Biogeography of epibiotic ciliates is a complex subject. The distribution of these organisms depends not only on environmental conditions but on characteristics of the hosts, including their own geographic distribution. Colonization of the host’s surface depends on a number of factors such as surface characteristics that influence choice of substrate (e.g., microtexture, humidity, electrostatic characteristics, and pH) as well as the presence of chemical inducers, bacterial exudates, and diatoms. Physical factors such as light, gravity, colour, pressure, or turbulence have less influence (Wahl 1989). On the other hand, the cryptobiotic life stages typical of protists allow species to disperse by means of water, wind, or avian transport (Weisse 2008); consequently, the geographical distribution of epibionts may be very wide (Batisse 1994).

Keeping in mind recent, large-scale changes in cladoceran taxonomy, it can be stated that any previous discussions of host preferences by ciliate epibionts are vulnerable to criticism. Our checklist is only a first step in moving toward adequate knowledge of the host preferences of epibionts and their real geographic distribution. In general, it appears that the distribution of epibiotic ciliates follows that of their hosts and, thus, conforms more closely to the main paradigm for biogeography of freshwater crustaceans (i.e., continental endemicity) rather than the paradigms proposed for free-living protists ("everything is everywhere" and "moderate endemicity," see review by Weisse 2008). In reality, protistan biogeography is probably more complicated than was thought in the past, and it is better to conclude that the dispersal and survival rates of protists are, in reality, still unknown and could differ significantly among taxa (Weisse 2008). For example, Guo et al. (2012) recently found a very high genetic diversity of epibionts on marine copepods. Currently, it might still be expected that the same freshwater epibiont species will associate with a relatively restricted group of host species spread over different continents, which could be quite wrong. We believe that our work will stimulate investigators to make accurate revisions of the taxa of epibiotic ciliates from different geographic areas following revision of their hosts.

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