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On the Global Distribution of Microscopic Animals: New Worldwide Data on Bdelloid Rotifers

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Diego Fontaneto, Elisabeth A. Herniou, Timothy G. Barraclough, and Claudia Ricci (2007) On the global distribution of microscopic animals: new worldwide data on bdelloid rotifers. *Zoological Studies* **46**(3): 336-346. The faunistic knowledge of the distribution of certain groups of microscopic animals is so small that it borders on total ignorance. The biogeographical patterns of protists and microscopic animals seem to differ from those of larger animals, with most species widely distributed. Nevertheless, few data are available for many groups of microscopic eukaryotes within otherwise well-studied areas such as Europe, let alone from remote areas. In this respect, bdelloid rotifers are one of the groups that is particularly understudied. This is mostly due to intrinsic taxonomic difficulties and ambiguities in the identification of these ancient asexual animals. Herein, we report 302 records of 61 species collected around the world, covering poorly known areas such as Mexico, Tanzania, and Australia, but also reporting new records for European countries. Some species have a cosmopolitan distribution, while others seem to be geographically limited to certain areas. We discuss the morphological, ecological, and biogeographical coherence of bdelloid species.
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Key words: Faunistic survey, Rotifera, Bdelloidea, Cosmopolitism, Endemism.

Most energy flux occurs through microscopic organisms (Stead et al. 2005, Woodward et al. 2005). Therefore, small and microscopic animals play key roles in the environment even if they are largely ignored and mostly insignificant in terms of individual biomass. However, our knowledge of the biology and taxonomy of small organisms is rather poor, their geographical distributions are mostly unknown, and the few data available reflect the distribution of the taxonomists rather than those of the organisms themselves (Dumont 1983).

Bdelloid rotifers represent 1 such group that suffers from a lack of extensive faunistic studies. They are free-living micro-invertebrates found in fresh water and ephemeral aquatic habitats throughout the world. Bdelloid rotifers have 2 particular features that have attracted the attention of a number of scientists. 1). They can dwell in any aquatic habitat, even if it is ephemeral, because they are able to survive desiccation through a form of dormancy called anhydrobiosis (Ricci 2001a, Ricci and Caprioli 2005). 2). The entire Bdelloidea group appears to have evolved without sexual reproduction, being the largest, oldest, and most-diverse multicellular taxon for which there is morphological, cytological, and molecular evidence of long-term 'asexual' evolution (Mark Welch and Meselson 2000, Mark Welch et al. 2004). When dormant, any bdelloid represents an easily dispersible propagule, which can colonize any new suitable habitat. Any propagule can be the founder of a new population, as there is no need for sexual mates. Thus, in theory, a given species could be encountered in any suitable habitat anywhere in the world. In fact, bdelloid species

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are usually assumed to be cosmopolitan (Fontaneto et al. 2006). However, determining exactly what a bdelloid species is has now come to the forefront, as no current biological definition of species (sensu Mayr) appropriately fits bdelloids because of their uniparental reproduction. The reality of species as common lineages has been suggested on a theoretical background (Barraclough and Herniou 2003), and recently confirmed by phylogenetic and morphological analyses (Fontaneto et al. 2007a, 2007b), but whether morphotypes from distant areas actually form unique phylogenetic lineages remains to be assessed. Before answering this question through a molecular approach, more data on the geographical distributions of several morphological species are required, as information collected worldwide has been rather scarce to date.

One of the major reasons for the poor knowledge of the distributions of bdelloid species rests with the difficulty of identification. The facts that bdelloids possess a soft body and the vast majority are not identifiable when fixed prevent their faunistic study from field samples which are usually preserved with fixatives. The consequence of this situation can better be appreciated from examining lists of rotifer species; together with a detailed list of monogonont rotifers, identified to species rank, a single entry may report "undetermined bdelloids", or no bdelloids are reported at all (e.g., Savatenalinton and Segers 2005, De Smet 2006). A specific effort therefore has to be made to collect live bdelloid rotifers. The easiest way is to desiccate fresh samples and study the bdelloids after rehydrating the dried samples. Almost all species are able to survive desiccation; however, a few might possibly be lost through the use of this process. If possible, wet samples should be brought back to the laboratory for examination as soon as possible.

Significantly, most bdelloid taxonomists worked in Europe until the middle part of the last century (e.g., Bartoš 1951, Donner 1965), and as a consequence, of the ~380 species described worldwide, over 300 are known from Europe. However, our biogeographical knowledge of European bdelloids is still incomplete as recent reports from the Ukraine and northern Italy have added several unreported species to known lists (e.g., Yakovenko 2000a b, Fontaneto and Melone 2003a), and reports from Europe often deal with unrecognizable, possibly new, species (e.g., Schmid-Araya 1998, Yakovenko 2000b, Fontaneto et al. 2005). A database of bdelloid species from all European countries is currently available on the web (Ricci and Fontaneto 2004). New studies are being published from poorly known areas like eastern Asia (Song and Kim 2000), Australia (Ricci et al. 2003), and Antarctica (Sohlenius and Bostrom 2005), and illustrate that European species have been found on distant continents, suggesting their worldwide distribution. Nevertheless, endemism can occur in bdelloids, as some species appear to be restricted to specific areas (e.g., Schmid-Araya 1995, Fontaneto and Melone 2003b), and undescribed taxa are being uncovered from remote unexplored sites (e.g., Örstan 1995, Koste 1996, Ricci et al. 2001 2003).

The number of species is expected to increase worldwide, including Europe, as modern taxonomic revisions are likely to reveal the existence of numerous previously undistinguished species (e.g., Ricci 2001b, Fontaneto et al. 2004b). Furthermore, bdelloids can occupy remarkable habitats which have never been studied in detail, such as pitcher plants or the gill chambers of crustaceans (Petersen et al. 1997, Fontaneto et al. 2004a).

The aim of the present paper was to document the occurrence of bdelloid species collected during recent field surveys all over the world, in order to build a database relating taxon distribution and geography, to test the presumed cosmopolitan nature of bdelloids and to assess to what extent similar morphotypes occur in similar or different ecological habitats.

MATERIALS AND METHODS

Sampling localities cover almost every continent : Africa, Asia, Australia, Europe, and North America (Table 1). Europe has already been extensively explored, while other areas, such as Africa and Mexico have mostly been ignored. We separated Alaska from the continental US in the analysis.

Bdelloid rotifers were sampled in any habitat in which they could survive; we sampled aquatic and terrestrial mosses, liverworts, and lichens found on rocks, soil, and bark. In addition, water and sediments of streams, rivers, ponds, and lakes, as well as soils were collected and processed. Dry and wet samples were collected and kept in envelopes or plastic bottles for the duration of the field trip. We focused mostly on species assemblages in moss and lichen samples that can be desiccated, as the time lapse between fieldtrips and laboratory analyses can be long, and dry anhydrobiotic bdelloids may survive better than living animals in water samples.

The samples were examined back at the laboratory. After rehydration of the samples, active animals were sorted out in Petri dishes under a dissection microscope, and determined to species under a compound microscope at 400-1000x magnification (Donner 1965).

RESULTS

Of the 302 populations isolated from the 185 samples of this study (Table 1), we identified 61 species of bdelloids, distributed in 4 different families: 6 of the Adinetidae, 2 of the Philodinavidae, 47 of the Philodinidae, and 6 of the Habrotrochidae (Table 2). Other bdelloids recorded in the samples were not identified to species level.

National checklists were appended with the following new records: 1 previously unrecorded species was added to Alaska and Thailand; 2 species were added to Norway, Sweden, and Taiwan; 3 species to Australia, Mexico, and Russia; 4 to Italy; 5 to Tanzania and the UK; 6 to Spain; 7 to France; and 8 to Finland.

Remarks on some species

Henoceros falcatus (Milne) and *Philodinavus paradoxus* (Murray)

Considered rare species (Schmid-Araya 1995, Ricci and Melone 1998), these were readily found in our samples when their typical habitat, submerged mosses in clean running water, was investigated.

Didymodactylos carnosus Milne

This was originally described from South Africa in 1916 and has only rarely been reported: in Australia, New Zealand (Ricci et al. 2003), Austria, Italy, Hungary, and the Canary I. (Fontaneto and Melone 2003a, Ricci and

Table 1. Sample identification (ID) in alphabetical order, sampling dates, collectors, localities, habitats, and approximate coordinates

ID	Date	Collector*	Locality	Habitat	Approx. coordinates
A204	July 03	DF	Val d'Ossola, Piedmont, Italy	lichen on rock	46°27'N, 8°25'E
A204bis	July 03	MO	Breithorn, Cervinia, Valle d'Aosta, Italy	lichen on rock	45°58'N, 7°40'E
A205	July 03	DF	Val d'Ossola, Piedmont, Italy	moss on rock	46°28'N, 8°27'E
A239	Sept. 03	SF	Corno Grosso, Alagna, Piedmont, Italy	moss on rock	45°48'N, 7°51'E
A300	Apr. 04	DF	Edolo, Lombardy, Italy	moss in running water	46°11'N, 10°20'E
A302	Feb. 04	DF	Fontaneto d'Agogna, Piedmont, Italy	moss on alder	45°38'N, 8°27'E
A305	Oct. 03	DF	Argnaccia Lake, Campertogno, Piedmont, Italy	water sample	45°48'N, 8°01'E
A308	Feb. 04	DF	San Martino Spring, Fontaneto d'Agogna, Piedmont, Italy	water sample	45°39'N, 8°29'E
A309	Nov. 03	DF	Fontanone Spring, Fontaneto d'Agogna, Piedmont, Italy	water sample	45°38'N, 8°27'E
A313	Nov. 03	CR	Gorgonzola, Lombardy, Italy	water sample in a small pond	45°32'N, 9°25'E
A316	Apr. 04	DF	Castellon, Spain	lichen on Holm oak	40°20'N, 0°16'E
A321	May 04	DF	Alpe Vucce, Postua, Piedmont, Italy	submerged moss in spring	45°44'N, 8°10'E
A324	May 04	DF	Tracciora, Rossa, Piedmont, Italy	water sample in a small pond	45°51'N, 8°05'E
A325	May 04	DF	Tracciora, Rossa, Piedmont, Italy	moss on common ash	45°51'N, 8°05'E
A326	May 04	DF	Malonno, Lombardy, Italy	sphagnum	46°06'N, 10°18'E
A327	Feb. 04	DF	Fontanone Spring, Fontaneto d'Agogna, Piedmont, Italy	water sample	45°38'N, 8°27'E
A328	Feb. 04	DF	Cavaglio d'Agogna, Piedmont, Italy	water sample in a small pond	45°37'N, 8°27'E
A330	June 04	DF	Campertogno, Piedmont, Italy	epibiont on caddis fly larvae	45°48'N, 7°52'E
A332	June 04	DF	Monchezzola Stream, Serravalle Sesia, Piedmont, Italy	moss in running water	45°40'N, 8°17'E
A333	May 04	AF	Mont Blanc, France	lichen on rock	45°53'N, 6°55'E
A334	June 04	DF	Poiala, Piedmont, Italy	sphagnum	46°19'N, 8°15'E
A335	May 04	DF	Tracciora, Rossa, Piedmont, Italy	moss on beech	45°51'N, 8°05'E
A336	June 04	DF	Lamaccia Lake, Rassa, Piedmont, Italy	sphagnum	45°43'N, 7°57'E
A337	June 04	DF	Cavo Ferri, Fontaneto d'Agogna, Piedmont, Italy	epibiont on *Asellus aquaticus*	43°38'N, 8°29'E
A338	June 04	DF	Fontaneto d'Agogna, Piedmont, Italy	moss on rock	43°38'N, 8°29'E
A340	July 04	DF	Alagna, Piedmont, Italy	moss in running water	45°54'N, 7°53'E
A341	July 04	DF	Alagna, Piedmont, Italy	wet moss	45°53'N, 7°54'E

Table 1. (Cont.)

ID	Date	Collector*	Locality	Habitat	Approx. coordinates
A342	July 04	MO	Zermatt, Valais, Switzerland	lichen on rock	46°03'N, 7°41'E
A344	July 04	DF	Fontanone Spring, Fontaneto d'Agogna, Piedmont, Italy	epibiont on *Asellus aquaticus*	45°38'N, 8°27'E
A346	July 04	DF	Lamaccia Lake, Rassa, Piedmont, Italy	wet sediment	45°43'N, 7°57'E
A347	July 04	DF	Alagna, Piedmont, Italy	moss on rock	45°53'N, 7°54'E
A348	Aug. 04	DF	Piode, Piedmont, Italy	water sample	45°46'N, 8°02'E
A360	Dec. 04	DF	Monchezzola Stream, Serravalle Sesia, Piedmont, Italy	moss in running water	45°40'N, 8°18'E
A361	Dec. 04	DF	Sostegno, Piedmont, Italy	lichen on rock	45°39'N, 8°15'E
A364	Dec. 04	DF	Rovasenella Stream, Sostegno, Piedmont, Italy	moss in running water	45°38'N, 8°15'E
A366	Jan. 05	DF	Cesara, Piedmont, Italy	moss in running water	45°50'N, 8°21'E
A369	Feb. 05	DF	Varallo Sesia, Piedmont, Italy	moss in running water	45°47'N, 8°14'E
A371	Mar. 05	DF	Romagnano Sesia, Piedmont, Italy	water sample in a small pond	45°38'N, 8°21'E
A389	July 05	DF	Novara, Piedmont, Italy	water sample in a rice field	45°29'N, 8°35'E
ALK3	Mar. 05	EAH	Chena Hot Spring Resort, Alaska, USA	wet moss in hot spring outlet	64°53'N 147°35'W
ALK7	Mar. 05	EAH	Chena Hot Spring Resort, Alaska, USA	sphagnum and moss	64°53'N 147°35'W
ARG1	Oct. 04	DF	Argnaccia Lake, Campertogno, Piedmont, Italy	water sample	45°48'N, 8°01'E
B13	Aug. 03	EAH	Brem sur Mer, Vendée, France	moss near pine tree dunes	46°35'N, 1°50'W
B4	Mar. 03	EAH	Little Bookham, Bookham, Surrey, UK	moss on barks	51°17'N, 0°24'W
BE1	June 04	TGB	Bergen, Norway	sphagnum	60°23'N, 5°20'E
BL2	Nov. 03	EAH	Bruges, Belgium	water and leaves in small canal	51°10'N, 3°11'E
BO1	Nov. 04	DF	Jamaica Plain, Boston, MA, USA	pond	42°19'N, 71°07'W
BO2	Nov. 04	DF	Jamaica Plain, Boston, MA, USA	pond	42°19'N, 71°07'W
BO3	Nov. 04	DF	Jamaica Plain, Boston, MA, USA	stream	42°19'N, 71°06'W
C1	Jan. 03	EAH	Chateauneuf sur Loire, France	moss in the back lawn	47°53'N, 2°08'E
CAT6	Apr. 04	EAH	Catalonia, Spain	moss	41°43'N, 2°04'E
CEB23	Oct. 03	EB	Chobham Common, Chobham, Surrey, UK	water sample in a small pond	51°21'N, 0°34'E
CEB34	Oct. 03	EB	Chobham Common, Chobham, Surrey, UK	water sample	51°21'N, 0°34'E
CH7	Jan. 04	EAH	Chateauneuf sur Loire, France	lichen on *Prunus*	47°53'N, 2°08'E
CH9	Jan. 04	EAH	Sully sur Loire, France	water from castle ditch	47°46'N 2°22'E
CH10	Jan. 04	EAH	Foret d'Orleans, France	moss from forest floor	47°52'N 2°16'E
G2	Apr. 03	EAH	Guilly Loiret, France	water sample from river	47°47'N, 2°16'E
G3	Apr. 03	EAH	Guilly Loiret, France	moss on poplar	47°47'N, 2°16'E
GSEB10	Dec. 03	EB	Gibson spout, Bootle, Cumbria, UK	moss on rotting log	54°17'N, 3°23'W
Gseb8	Dec. 03	EB	Gibson spout Bootle, Cumbria, UK	moss on rotting log	54°17'N, 3°23'W
IL3	June 03	EAH	Illmitz, Austria	mud from dry part of lake	47°44'N, 16°48'E
IT2	Oct. 04	CF	Verbania, Piedmont, Italy	water sample from river	45°56'N, 8°30'E
IT3	Oct. 04	CF	Maggiore Lake, Verbania, Piedmont, Italy	water sample	45°56'N, 8°31'E
K4	May 03	LKS	Kestor, Devon, UK	moss	50°44'N, 3°59'W
KS5	Apr. 05	CLV	Koh Tan Island, Thailand	pond water	9°22'N 99°57'E
L1	Apr. 03	EAH	Languedoc - Roussillon, France	water sample from a lake	43°49'N, 4°11'E
LL1	Apr. 04	EAH	Catalonia, Spain	Llogaret source	41°34'N, 1°57'E
LL2	Apr. 04	EAH	Catalonia, Spain	Llogaret source	41°34'N, 1°57'E
LL3	Apr. 04	EAH	Catalonia, Spain	Llogaret source	41°34'N, 1°57'E
LL5	Apr. 04	EAH	Catalonia, Spain	Llogaret source	41°34'N, 1°57'E
M1	Nov. 02	EAH	Silwood Park, Ascot, Berkshire, UK	rotten wood in Japanese garden	51°24'N, 0°38'W
MX26	Nov. 03	EAH	Matias Romero, Oaxaca, Mexico	lichen on acacia	17°04'N, 95°53'W
MX5	Nov. 03	EAH	Alverado, Veracruz, Mexico	water sample from a river	31°29'N, 107°23'W
MX55	Nov. 03	EAH	Valsequillo, Puebla, Mexico	lichen on rock	25°25'N, 101°19'W
Mx74	Nov. 03	EAH	La malinche, Tlaxala, Mexico	moss	19°34'N, 99°26'W
MX76	Nov. 03	EAH	La malinche, Tlaxala, Mexico	moss	19°34'N, 99°26'W
NF1	Feb. 03	EAH	New Forest, Hampshire, UK	moss near stream	50°48'N, 1°35'W
NF11	Oct. 04	DF	New Forest, Hampshire, UK	sphagnum	50°48'N, 1°35'W
NF12	Oct. 04	DF	New Forest, Hampshire, UK	sphagnum	50°48'N, 1°35'W
NF13	Oct. 04	DF	New Forest, Hampshire, UK	sphagnum	50°48'N, 1°35'W
NF14	Oct. 04	DF	New Forest, Hampshire, UK	sphagnum	50°48'N, 1°35'W

Table 1. (Cont.)

ID	Date	Collector*	Locality	Habitat	Approx. coordinates
NF15	Oct. 04	DF	New Forest, Hampshire, UK	moss	50°48'N, 1°35'W
NF18	Oct. 04	DF	New Forest, Hampshire, UK	lichen	50°48'N, 1°35'W
NF19	Oct. 04	DF	New Forest, Hampshire, UK	lichen	50°48'N, 1°35'W
NF2	Feb. 03	EAH	New Forest, Hampshire, UK	water sample in a small pond	50°48'N, 1°35'W
NF20	Oct. 04	DF	New Forest, Hampshire, UK	lichen	50°48'N, 1°35'W
NF4	Oct. 04	DF	New Forest, Hampshire, UK	water sample in a small pond	50°48'N, 1°35'W
NF5	Oct. 04	DF	New Forest, Hampshire, UK	water sample in a small pond	50°48'N, 1°35'W
NF7	Oct. 04	DF	New Forest, Hampshire, UK	water sample in a small pond	50°48'N, 1°35'W
NF8	Oct. 04	DF	New Forest, Hampshire, UK	stream	50°48'N, 1°35'W
NF9	Oct. 04	DF	New Forest, Hampshire, UK	water sample in a small pond	50°48'N, 1°35'W
NUP1	Aug. 04	EAH	Nuuksio National Park, Finland	slow stream vegetation	60°15'N, 24°37'E
NUP2	Aug. 04	EAH	Nuuksio National Park, Finland	lake side vegetation	60°15'N, 24°37'E
NUP4	Aug. 04	EAH	Nuuksio National Park, Finland	wet moss in a pond	60°15'N, 24°37'E
NUP7	Aug. 04	EAH	Nuuksio National Park, Finland	sphagnum	60°15'N, 24°37'E
NUP9	Aug. 04	EAH	Nuuksio National Park, Finland	lichen	60°15'N, 24°37'E
NZ1	Jan. 04	JC	Coatisville, New Zealand	moss	36°48'S, 174°42'E
OZ1	Aug. 04	EAH	Australia Lamington NP, Australia	moss on stone	28°16'S, 153°02'E
OZ18	Aug. 04	EAH	Australia Eungella NP, Australia	moss	28°21'S, 153°19'E
OZ19	Aug. 04	EAH	Australia Eungella NP, Australia	moss	28°21'S, 153°19'E
OZ2	Aug. 04	EAH	Australia Lamington NP, Australia	moss on fallen twigs	28°16'S, 153°02'E
OZ20	Aug. 04	EAH	Australia Eungella NP, Australia	moss	28°21'S, 153°19'E
OZ26	Aug. 04	EAH	Australia Eungella NP, Australia	lichen	28°21'S, 153°19'E
OZ28	Aug. 04	EAH	Australia Eungella NP, Australia	moss	28°21'S, 153°19'E
OZ35	Aug. 04	EAH	Australia Hinchinbrook I., Australia	moss on stone	18°22'S, 146°14'E
OZ4	Aug. 04	EAH	Australia Lamington, Australia	moss and lichen on stone	28°16'S, 153°02'E
OZ41	Aug. 04	EAH	Australia Tully Gorge, Australia	lichen on stone	17°45'S, 145°37'E
OZ42	Aug. 04	EAH	Australia Tully Gorge, Australia	moss on stone	17°45'S, 145°37'E
OZ43	Aug. 04	EAH	Australia Tully Gorge, Australia	moss on rooting tree	17°45'S, 145°37'E
OZ53	Aug. 04	EAH	Australia Lake Barrine, Australia	water sample with sediments	17°15'S, 145°38'E
OZ7	Aug. 04	EAH	Australia Lamington NP, Australia	moss	28°16'S, 153°02'E
OZ85	Aug. 04	EAH	Australia Litchfield NP, Australia	moss from monsoon forest	13°11'S, 130°48'E
OZ9	Aug. 04	EAH	Australia Lamington NP, Australia	moss from stone in spring path	28°16'S, 153°02'E
P10	Aug. 03	EAH	les Sables d'Olonnes, Pays de Loire, France	moss on *Populus*	46°29'N, 1°48'W
QF1	Aug. 03	EAH	Lac des Francais, Quebec, Canada	moss on wall	46°07'N, 73°38'W
QL8	Aug. 03	EAH	Lac Leon, Quebec, Canada	moss on rock in lake	46°22'N, 74°16'W
QL9	Aug. 03	EAH	Lac Leon, Quebec, Canada	wet moss and rotting bark	46°22'N, 74°16'W
QN1	July 03	EAH	St Norbert, Quebec, Canada	semi-aquatic plant and soggy soil	46°10'N, 73°18'W
R1	Aug. 05	EAH	Peterhof Castle, St. Petersburg, Russia	pond water	59°53'N 29°53'E
R4	Aug. 05	EAH	Peterhof Castle, St. Petersburg, Russia	moss	59°53'N 29°53'E
S25	Aug. 03	EB	Silwood Park Campus, Ascot, Berkshire, UK	moss on lawn	51°24'N, 0°38'W
S3	Dec. 02	EAH	Silwood Park Campus, Ascot, Berkshire, UK	rotten wood	51°24'N, 0°38'W
S35	Mar. 04	EAH	Silwood Park Campus, Ascot, Berkshire, UK	sphagnum	51°24'N, 0°38'W
S36	Mar. 04	EB	Silwood Park Campus, Ascot, Berkshire, UK	moss from stump	51°24'N, 0°38'W
S40	Apr. 04	YB	Silwood Park Campus, Ascot, Berkshire, UK	moss in grass	51°24'N, 0°38'W
S45	Apr. 04	YB	Silwood Park Campus, Ascot, Berkshire, UK	wet moss	51°24'N, 0°38'W
S82	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	beech tree hole	51°24'N, 0°38'W
S83	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss	51°24'N, 0°38'W
S85	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	water sample from a small pond	51°24'N, 0°38'W
S87	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	liverwort	51°24'N, 0°38'W
S88	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	epibiont on *Asellus aquaticus*	51°24'N, 0°38'W
S91	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss on trunk	51°24'N, 0°38'W
S92	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss	51°24'N, 0°38'W
S93	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss	51°24'N, 0°38'W
S94	Sept. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	lichen on concrete	51°24'N, 0°38'W

Table 1. (Cont.)

ID	Date	Collector*	Locality	Habitat	Approx. coordinates
SH1	May 03	LKS	Shobrooke Park, Crediton, Devon, UK	moss	50°47'N, 3°38'W
SIL	Oct. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss	51°24'N, 0°38'W
SILD2	Oct. 04	DF	Silwood Park Campus, Ascot, Berkshire, UK	moss	51°24'N, 0°38'W
SMV12	Apr. 03	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	moss	44°24'N, 4°17'E
SMV13	Feb. 04	MLF	St Martin de Valgagues, Languedoc - Roussillon, France	moss	44°24'N, 4°17'E
SMV14	Feb. 04	MLF	St Martin de Valgagues, Languedoc - Roussillon, France	moss	44°24'N, 4°17'E
SMV15	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	Bambouseraie water	44°24'N, 4°17'E
SMV17	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	water sample from spring	44°24'N, 4°17'E
SMV18	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	water sample from spring	44°24'N, 4°17'E
SMV19	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	water sample from a river	44°24'N, 4°17'E
SMV21	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	spring near school	44°24'N, 4°17'E
SMV26	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	lichen on *Populus*	44°24'N, 4°17'E
SMV27	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	wet moss at fountain	44°24'N, 4°17'E
SMV28	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	moss from side of stream	44°24'N, 4°17'E
SMV30	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	lichen on oak	44°24'N, 4°17'E
SMV31	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	moss on oak	44°24'N, 4°17'E
SMV32	Sept. 04	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	moss	44°24'N, 4°17'E
SMV7	Apr. 03	EAH	St Martin de Valgagues, Languedoc - Roussillon, France	moss in river, les carabioles	44°24'N, 4°17'E
SP14	Mar. 04	CLV	Fontesanta, Galicia, Spain	moss on oak	42°54'N, 8°09'W
SP15	Mar. 04	CLV	Fontesanta, Galicia, Spain	moss on oak	42°54'N, 8°09'W
SP18	Mar. 04	CLV	Rio Iso, Galicia, Spain	moss on oak	42°54'N, 8°09'W
SP19	Mar. 04	CLV	Rio Iso, Galicia, Spain	moss on oak	42°54'N, 8°09'W
SP21	Mar. 04	CLV	Aguia, Vigo, Galicia, Spain	moss on rocks	43°32'N, 6°37'W
SP23	Mar. 04	CLV	Branza, Galicia, Spain	moss and lichen on oak wood	42°51'N, 8°13'W
SP24	Mar. 04	CLV	Encoro Portodemouros, Galicia, Spain	moss in eucalyptus plantation	42°49'N, 8°10'W
SP26	May 04	CLV	Xures, Ourense, Galicia, Spain	wet moss	42°19'N, 7°52'W
SP27	May 04	CLV	Xures, Ourense, Galicia, Spain	moss	42°19'N, 7°52'W
SP30	May 04	CLV	Barra beach, Pontevedra, Galicia, Spain	moss on *Populus*	42°26'N, 8°38'W
SP32	May 04	CLV	Courel, Galicia, Spain	wet moss	43°13'N, 7°14'W
SP33	May 04	CLV	Courel, Galicia, Spain	moss	43°13'N, 7°14'W
ST1	Oct. 04	RM	Stockholm, Sweden	moss	59°21'N, 18°02'E
ST3	Oct. 04	RM	Stockholm, Sweden	moss	59°21'N, 18°02'E
SW8	Sept. 03	CLV	Neuchatel, Switzerland	water sample with sediment	47°00'N, 6°57'E
TB4	May 03	LKS	Twobridges, Dartmoor, Devon, UK	moss	50°54'N, 3°52'W
TB5	May 03	LKS	Twobridges, Dartmoor, Devon, UK	moss attached to rock	50°54'N, 3°52'W
TB7	May 03	LKS	Twobridges, Dartmoor, Devon, UK	moss attached to rock	50°54'N, 3°52'W
TW1	Aug. 05	DQ	Dasyueshan Forest, Taiwan	moss	24°01'N, 120°52'E
TZ13	Sept. 03	CdM	East Usambara, Tanzania	moss on bark	5°00'S, 38°58'E
TZ15	Sept. 03	CdM	East Usambara, Tanzania	moss with soil	5°00'S, 38°58'E
TZ16	Sept. 03	CdM	East Usambara, Tanzania	moss with soil	5°00'S, 38°58'E
TZ18	Sept. 03	CdM	East Usambara, Tanzania	moss	5°00'S, 38°58'E
TZ2	Sept. 03	CdM	East Usambara, Tanzania	wet moss	5°00'S, 38°58'E
V2	Sept. 03	EAH	Vendee River, Pays de Loire, France	river water	46°29'N, 0°43'W
W2	Mar. 03	EAH	Wisley, Surrey, UK	moss and lichen	51°19'N, 0°28'W
W3	Mar. 3	EAH	Wisley, Surrey, UK	moss	51°19'N, 0°28'W
W4	Mar. 03	EAH	Wisley, Surrey, UK	sphagnum	51°19'N, 0°28'W
WE11	Apr. 04	YB	Trefening, Ceredigion, Wales, UK	moss in heather	52°14'N, 4°15'W
WE14	Apr. 04	YB	Ceredigion, Wales, UK	moss in heather	52°14'N, 4°15'W
WE16	Apr. 04	YB	Ceredigion, Wales, UK	water	52°14'N, 4°15'W
WE6	Apr. 04	YB	Ystwyth Valley, Ceredigion, Wales, UK	moss	52°19'N, 3°51'W

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Fontaneto 2004). Of the 4 records obtained during this study, 3 are new records for Finland, Sweden, and the UK. The species might not be as uncommon as previously considered.

Dissotrocha aculeata crystallina (Murray)

This is known from Sweden and the UK (Ricci and Fontaneto 2004), and the record from Finland reinforces the idea that this taxon has a Northern-European distribution.

Philodina nitida Milne

This was described from South Africa, and then found in New Zealand (Haigh 1965). It has never been found in samples from the northern hemisphere. Its presence in our Australian samples, together with an its almost certain absence from Europe, suggests a Gondwanaland distribution of the species, although more detailed faunistic knowledge is needed to confirm this hypothesis.

Pleuretra costata Bartoš

This was known only from former Czechoslovakia and European part of the Soviet Union (Bartoš 1951). The Swedish record supports a distribution in northeastern Europe.

Pleuretra hystrix Bartoš

This is only known from Switzerland and Italy as a supposed Alpine endemic (Fontaneto and Melone 2003b), and its occurrence in Alpine streams in Italy confirms its west Alpine distribution.

DISCUSSION

Microscopic organisms are known to have almost no biogeographical patterning: taxonomists working on microscopic organisms hoped to find interesting new species during scientific expeditions in remote areas in the last century, but most of the organisms they found could be ascribed to already known morphologies. The saying, "everything is everywhere", which Fenchel and Finlay (2004) used to characterize the distribution of protists could also be true for bdelloids. The extensive sampling of bdelloids confirms that some "morphospecies" can be found in distant areas on different continents.

Nevertheless, some biogeographical patterns are beginning to emerge. Some species, such as *Philodina nitida*, seem to be localized to areas of Gondwanaland origin. Other taxa seem to be restricted to smaller regions, such as *Dissotrocha aculeata crystallina* in Northern Europe, *Pleuretra hystrix* in the Alps, and *Pleuretra costata* in northeastern Europe. Other species that have recently been described seem to be specific to the locality where they were first found, e.g., *Abrochtha carnivora* in Barbados, *Adineta ricciae* and *Philodinavus aussiensis* in Australia, and *Macrotrachela sonorensis* in the Sonora desert (Örstan 1995, Ricci et al. 2001 2003, Segers and Shiel 2005). Of course, we do not yet have sufficient faunistic data to confirm their supposed endemism or restricted distributions, but the fact that some species are encountered only outside of Europe may be significant, because Europe is the area where most bdelloid scholars have worked and sampled.

The biogeography of small organisms such as bdelloid rotifers cannot rely on a large adequate dataset as none is available like those for large animals or plants, and no clear conclusions can yet be obtained. A generalized cosmopolitanism was postulated for such microscopic organisms in the past, but recent large-scale analyses of distribution patterns in other microscopic animals, such as monogonont rotifers and crustaceans, are revealing latitudinal gradients as well as examples of geographical endemism (e.g., Pejler 1977, Frey 1986 1987, Segers 1996 2003).

Most of the bdelloid species we recorded appear to truly be cosmopolitan, but some exceptions were highlighted. The potential for dispersal by bdelloids due to their dormant propagules makes the assumption of cosmopolitan distributions more plausible. Furthermore, it has to be stressed that the habitats we predominately investigated (mosses and lichens) are by definition exposed to desiccation, as are the bdelloids living in them. Therefore, our investigation may have been biased towards species capable of desiccation, and would likely to have mostly yielded cosmopolitan species. The findings of localized distributions even for species capable of desiccation confirm the existence of some geographic localization.

However, we still do not know whether the morphological approach used for bdelloid identification is always capable of discriminating evolutionary lineages (Fontaneto et al. 2007a, 2007b). Actually, the presence of sibling species in bdelloids is likely to be underestimated (e.g., Ricci 2001b, Ricci et al. 2003, Fontaneto et al. 2004b), and this might affect the cosmopolitan patterns of bdelloid distribution.

One confirmation of the validity of the morphological approach in species identification and the plausibility of their cosmopolitan distribution can rest on the ecological consistency within each morphospecies: most taxa, either in close or distant areas, are found in similar habitats. This holds true for *Henoceros falcatus* and *Philodinavus paradoxus* in clean running water, *Philodina citrina* and *Rotaria macrura* among submerged plants in lentic waters, and *Macrotrachela habita* and

Table 2. New and interesting data regarding bdelloid species collected from worldwide sampling. Sampling localities are in alphabetical order; see table 1 for details on samples. New national records are marked by an asterisk after the name of the state

Family	Species	Sampling locality
Adinetidae		
	Adineta barbata Janson, 1893	Australia (OZ35), Tanzania* (TZ16)
	Adineta gracilis Janson, 1893	Finland* (NUP7), Norway* (BE1), Spain* (SP14, SP23, SP24, SP26, SP27), UK (K4, NF5, NF11, NF12)
	Adineta steineri Bartos, 1951	Alaska*,a (ALK7), Australia (OZ53), Finland* (NUP9), France (CH10), Norway* (BE1), Russia* (R4), UK* (GSEB10, NF11, S92, WE14)
	Adineta tuberculosa Janson, 1893	France* (SMV30, SMV31)
	Adineta vaga (Davis, 1873)	Alaska (ALK7), Australia (OZ9, OZ20, OZ28, OZ35, OZ42, OZ43), Finland* (NUP7), France (CH7, G3, L1, SMV7, SMV13, SMV14, SMV32), Mexico* (MX74, MX76), New Zealand (NZ1), Spain (Cat6, LL2, LL3, LL5, SP19, SP21, SP24, SP30, SP32, SP33), UK (B4, Gseb8, S25, S35, S83, S91, SILD2, TB4, TB7, W4), Taiwan* (TW1), Tanzania* (TZ13, TZ15, TZ18)
	Bradyscela clauda (Bryce, 1893)	Australia* (OZ1, OZ26, OZ41), UK (S87)
Philodinavidae		
	Henoceros falcatus (Milne, 1916)	Italy (A332, A360, A364, A369)
	Philodinavus paradoxus (Murray, 1905)	Italy (A300, A340, A360, A364, A366)
Philodinidae		
	Didymodactylos carnosus Milne, 1916	Finland* (NUP9), Italy (A361), Sweden* (ST1), UK* (NF18)
	Dissotrocha aculeata (Ehrenberg, 1832)	Italy (A341), Russia* (R1)
	Dissotrocha aculeata crystallina (Murray, 1908)	Finland* (NUP1)
	Dissotrocha aculeata medioaculeata (Janson, 1893)	Belgium (BL2)
	Dissotrocha macrostyla (Ehrenberg, 1838)	Finland (NUP2), Italy (A346), UK (NF13, NF5, NF7), USA (BO1)
	Dissotrocha macrostyla tuberculata (Gosse, 1886)	Italy (A341, ARG1), UK (NF2, NF5)
	Embata commensalis (Western, 1893)	Italy* (A300)
	Embata parasitica (Giglioli, 1863)	Italy (A330)
	Macrotrachela bullata (Murray, 1906)	Tanzania* (TZ16, TZ18)
	Macrotrachela habita (Bryce, 1894)	Canada (QF1), Italy (A302), Spain (A316, SP30), Sweden (ST3), UK (NF18)
	Macrotrachela multispinosa Thompson, 1892	Australia (OZ4), France (B13), Italy (A326)
	Macrotrachela multispinosa crassispinosa (Murray, 1907)	Australia (OZ19, OZ1, OZ26), France* (SMV32)
	Macrotrachela musculosa (Milne, 1886)	Canada (QN1)
	Macrotrachela papillosa (Thompson, 1892)	Australia (OZ19), Finland* (NUP7), Italy (A334), Sweden (ST1, ST3), UK (NF12)
	Macrotrachela plicata (Bryce, 1892)	Spain* (SP23, SP24, SP27, SP33), UK (NF12, S40), USA (BO1)
	Macrotrachela plicata hirundinella (Murray, 1905)	Italy (A335, A347), Spain* (SP15)

Table 2. (Cont.)

Family	Species	Sampling locality
	Macrotrachela punctata (Murray, 1911)	Italy* (A239)
	Macrotrachela quadricornifera Milne, 1886	Australia (OZ1), Canada (QL8, QN1), Finland* (NUP9), France (C1), Italy (A336), Norway (BE1), Spain (SP14, SP18), UK (NF15, NF20, S35, S87, S93, TB5, TB7, WE6, WE11)
	Macrotrachela vesicularis (Murray, 1906)	France* (SMV32)
	Mniobia circinata (Murray, 1908)	Italy (A204bis)
	Mniobia obtusicornis Murray, 1911	UK* (NF19)
	Mniobia russeola (Zelinka, 1891)	Australia (OZ85), France* (A333, B13), Italy (A204, A325), Switzerland (A342)
	Mniobia scarlatina (Ehrenberg, 1853)	Italy* (A205)
	Philodina acuticornis Murray, 1902	Austria (IL3) UK (S45), France (SMV12, SMV15, SMV19, SMV27), Switzerland (SW8)
	Philodina citrina Ehrenberg, 1832	France (SMV28), Italy (A305, A309, ARG1), UK (NF4, NF8)
	Philodina flaviceps Bryce, 1906	France* (SMV27), Spain (LL1, LL5), USA (BO3)
	Philodina megalotrocha Ehrenberg, 1832	Italy (IT2, IT3)
	Philodina nitida Milne, 1916	Australia* (OZ26)
	Philodina proterva Milne, 1916	Spain (LL5)
	Philodina roseola Ehrenberg, 1832	France (SMV12, SMV28), UK (WE16)
	Philodina rugosa Bryce, 1903	France* (SMV26, SMV30, SMV31), Italy (A335), Spain* (SP30), UK (S83, S91, SIL)
	Philodina vorax (Janson, 1893)	Australia (OZ1, OZ18, OZ28), France* (SMV14, SMV27), UK (S94, SIL)
	Pleuretra africana Murray, 1911	Mexico* (MX26S5D5)
	Pleuretra brycei (Weber, 1898)	Australia (OZ26), Italy (A332, A360)
	Pleuretra costata Bartos, 1898	Sweden* (ST1)
	Pleuretra humerosa (Murray, 1905)	Spain* (SP21)
	Pleuretra hystrix Bartos, 1850	Italy (A321, A341)
	Pleuretra lineata Donner, 1962	Australia* (OZ2), Italy (A335)
	Rotaria citrina (Ehrenberg, 1838)	Italy (A389)
	Rotaria macroceros (Gosse, 1851)	UK (NF8), USA (BO1)
	Rotaria macrura (Schrank, 1803)	Italy (A327, A328, A371), UK (NF8)
	Rotaria magnacalcarata (Parsons, 1892)	Italy (A308, A337, A344), UK (S88)
	Rotaria neptunia (Ehrenberg, 1832)	France (G2), Italy (A313), UK* (NF2)
	Rotaria rotatoria (Pallas, 1766)	Alaska (ALK3), Belgium (BL2), France (CH9, SMV17, SMV18, SMV21, V2), Italy (A305, A313, A324, A336, IT2, IT3), Mexico* (MX5), Russia* (R1), Tanzania* (TZ2), Thailand* (KS5), UK (NF1, NF2, NF4, NF5, NF7, NF8, NF9, NF13, NF14, S85), USA (BO1, BO2)
	Rotaria socialis (Kellicott, 1888)	Italy (A337, A344), UK (S88)
	Rotaria sordida (Western 1893)	Australia (OZ1, OZ4, OZ7, OZ9, OZ26), France (P10, SMV12, SMV13, SMV32), Italy (A325, A334, A338), Spain (SP19), Sweden (ST1, ST3), Taiwan* (TW1), Tanzania* (TZ16), UK (NF15, S83, SH1, W2)
	Rotaria tardigrada (Ehrenberg, 1832)	Finland (NUP2), Italy (A313, A324, A348, ARG1), USA (BO1)
Habrotrochidae		
	Habrotrocha bidens (Gosse, 1851)	UK (CEB34)
	Habrotrocha constricta (Dujardin, 1841)	Spain (SP18), UK (S3, TB7, W3)
	Habrotrocha lata (Bryce, 1892)	Canada (QL9), Finland* (NUP4), Spain* (SP26), UK (CEB23, CEB34, S82)
	Habrotrocha pulchra (Murray, 1905)	UK (S35, S36, WE6)
	Otostephanos donneri Bartos, 1959	Italy (A324, A346), UK* (NF4, NF8, NF13)
	Otostephanos torquatus (Bryce, 1913)	Italy* (A334)

[a]Alaska is listed separately from the continental US in this table.

Pleuretra lineata in arid mosses. Of course, there are exceptions, as some species can be found in quite-different habitats, like *Philodina rugosa* in both submerged and dry terrestrial mosses, or *Adineta vaga* that dwells in almost any habitat. The use of molecular barcoding for species identification as proposed by Hebert et al. (2003) would be invaluable in uncovering the true identities of these euryoecious morphospecies, and, as a consequence, the distributions of bdelloid species.

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