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Ubiquity of microscopic animals? Evidence from the morphological approach in species identification

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13.1 Introduction

Zoologists always hope to find unusual and interesting new animals in exotic places. Over the last few centuries, scientific expeditions in remote places outside Europe and North America have indeed discovered new species and even higher taxa of vertebrates, insects and other macroscopic animals, completely different from the ones previously known in the home country. In contrast, scientists working on microscopic animals, looking at samples from remote areas, have often found organisms that could be ascribed to familiar species. Microscopic animals have thus been considered not interesting in biogeography, as their distribution may not be limited by geography.

Are microscopic animals really widely distributed? Is their cosmopolitanism an actual biological property or only a common misconception based on false assumptions and unreliable evidence? Is the scenario more complex than the claimed clear-cut difference between micro- and macroscopic animals? This chapter will review all the faunistic knowledge gathered so far on the global distribution of free-living microscopic animals smaller than 2 mm (gastrotrichs, rotifers, tardigrades, micrognathozoans, cycliophorans, loriciferans, kinorhynchs and gnathostomulids). Moreover, we will deal with microscopic free-living species in other groups of animals such as nematodes and flatworms, which have both micro- and macroscopic species. The focus will be on species identification from traditional taxonomy based on morphology, whereas Chapter 14 will deal with more recent evidence gathered from analyses on molecular phylogeny and phylogeography from the same groups.

13.2 Gastrotrichs

(M. Antonio Todaro and William D. Hummon)

Gastrotrichs are microscopic free-living, acoelomate, aquatic worms of a meiobenthic lifestyle. In marine habitats they are mainly interstitial, whereas in fresh waters they are ubiquitous in the periphyton and epibenthos, and to a limited extent also in the plankton. Their total length ranges between 70 µm for the freshwater *Heterolepidoderma lamellatum* and 3.5 mm for the marine *Megadasys pacificus*. The simultaneous presence of ventral ciliation, adhesive tubes and terminal mouth make the Gastrotricha easily distinguishable from other microscopic biota (Fig 13.1). The body is enwrapped by a two-layered cuticle, which in many species forms protective ornamentations such as plates, scales and spines, whose ample variety of shape and size is extensively used for taxonomic purposes (e.g. taxon/species identification).

The phylum counts about 765 species grouped into two orders: Macrodasyida, with some 310 strap-shaped species (in 32 genera of eight families), all but two of
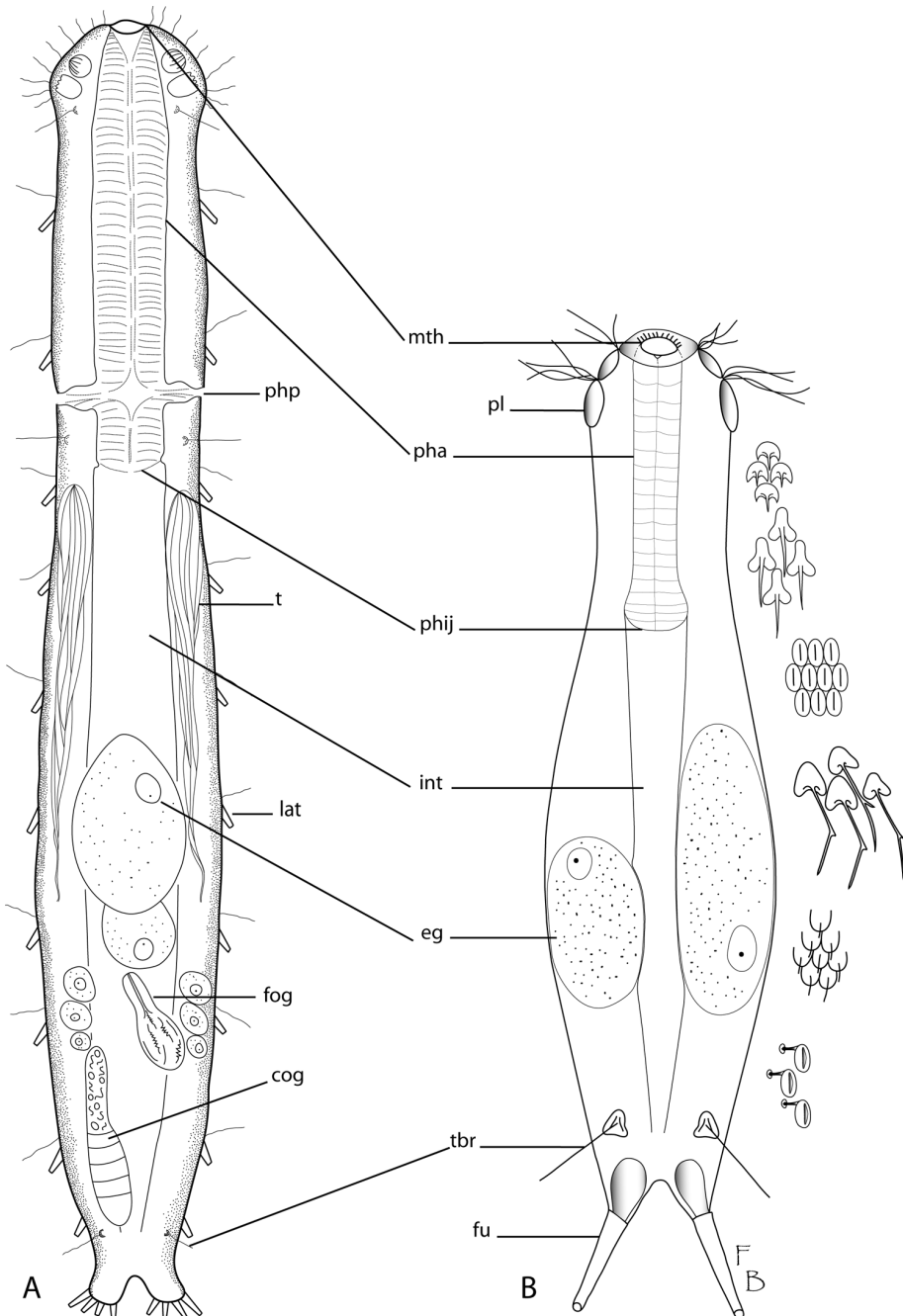
Fig 13.1 Drawing of generalised gastrotrichs, seen from dorsal side: (A) hermaphroditic Macrodasyida, (B) parthenogenetic Chaetonotida (showing on the side different types of cuticular covering), not in scale. cog: caudal organ; eg: egg; fog: frontal organ; fu: furca; int: intestine; lat: lateral adhesive tubes; mth: mouth; pha: pharynx; phij: pharyngeo-intestinal junction; php: pharyngeal pores; pl: pleurae; t: testis; tbr: tactile bristle.

which are marine or estuarine, and Chaetonotida with some 455 tenpin-shaped species (in 31 genera of eight families), 70% of which are freshwater (Balsamo et al., 2009; Hummon and Todaro, 2010). The continuing discovery and description of new species and the many areas of the world still unexplored with regard to the gastrotrich fauna, suggest that these statistics should be considered as very conservative (e.g. Todaro et al., 2005; Hummon, 2008; Kanneby et al., 2009).

Macrodasyidan gastrotrichs are hermaphroditic practising internal, putatively cross-fertilisation; the same appears to be true for members of the marine chaetonotidan families Muselliferidae, Neodasyidae and Xenotrichulidae (six genera and *c*. 30 spp.; Todaro and Hummon, 2008). By contrast, most chaetonotidans, including all the freshwater families and also the marine representatives of the family Chaetonotidae (*c*. 420 spp.), reproduce largely by obligate, apomictic parthenogenesis (Hummon, 1984). In fact, spermatozoa produced after the parthenogenetic phase (Weiss, 2001) have never been proved to be functional and their ultrastructure suggests otherwise (e.g. Balsamo, 1992). Resting eggs are known for several freshwater species, but so far they are unreported for marine taxa. High gastrotrich diversity, found in temporary inland water bodies, suggests that the occurrence of resting eggs is more widespread across the spectrum of freshwater taxa than is currently believed. Among a handful of chaetonotidans cultured in the laboratory, mature gastrotrichs lay 1–10 eggs singly, by rupture of the body wall, eggs being attached to sediment grains, where cleavage usually begins (Balsamo and Todaro, 1988). Development is direct and adulthood is reached within a few days from hatching, with the lifespan extending from 10–20 days to a couple of months. Almost nothing is known about macrodasyidans, but slower growth and longer lifespan (6–12 months) should not come as a surprise for large marine species, such as species of *Dolichodasys*, where the presence of mature specimens only in certain seasons is suggested (Todaro and Hummon, unpublished data).

The phylum Gastrotricha is cosmopolitan in distribution; this is also true of the two orders, almost all families and taxonomically reliable genera. Given the short life cycle, the small number of offspring, the absence of a pelagic larval stage and the comparatively limited swimming ability of the adults, gastrotrich species would be expected to have restricted geographic ranges. Dispersal via long-shore currents over a long geological time combined with oceanic dispersal and continental drift may be invoked to explain biogeographic patterns of Gastrotricha distribution in many marine systems; however, indirect dispersal by phoretic, rafting and ballast may play a relevant role too. Of the 45 species found by Todaro et al. (1995) along the northern Gulf of Mexico the proportion of amphi-Atlantic/cosmopolitan, regional and endemic species found amounted to 60, 22 and 18% respectively, most endemics being macrodasyidans. Of the 56 putative species found by Todaro and Rocha (2004, 2005) from the Brazilian beaches of the State of São Paulo, 31 (55%) could be endemics, again mostly macrodasyidans. A key role of the asexual reproduction in the widespread distribution of chaetonotidian species

in marine habitas is best testified to by the high occurrence among cosmopolitan taxa of the initially parthenogenetic Chaetonotidae and by the widespread geography of three marine species belonging to otherwise hermaphroditic higher taxa, i.e. *Draculiciteria tesselata*, *Heteroxenotrichula pygmaea* and *Urodasys viviparus*. Meanwhile, one of the species found along the Gulf of Mexico has been reclassified as a new species (*Xenotrichula lineata*, redescribed as *X. paralineata*, see Hummon and Todaro, 2007), so that the contrasts between North and South America indicate that a latitudinal gradient may have influenced the biogeographic patterns of marine gastrotrichs. Hermaphroditic species currently thought as cosmopolitan gastrotrichs may be reconsidered as having narrower geographic boundaries as more precise studies are completed, e.g. some species of *Neodasys* and *Musellifer* (see Hochberg, 2005; Leasi and Todaro, 2010). In this framework, a paradigmatic example is provided by the chaetonotidan *Xenotrichula intermedia*. Todaro et al. (1996), using morphometric characters and mitochondrial DNA (CO-I), demonstrated that trans-Atlantic morphologically indistinguishable populations are in fact genetically distinct, bearing different haplotypes with genetic divergence among populations up to 11%. Also, individuals of the Mediterranean Sea and the Arabian Gulf, that appear almost identical when surveyed with conventional microscopy (i.e. DIC and/or SEM), show clearly different arrangements of the muscular system when studied under confocal microscopy (Leasi and Todaro, 2009).

Small size of the adults and resting eggs makes freshwater gastrotrichs good candidates for passive dispersal, aerial and especially phoretic. For instance, single parthenogenetic females hatching from resting eggs and transported over wide areas and even around the world by avian fauna, could initiate a new population. By contrast, many species have been reported as having a wide distribution with a large number of certain cases of cosmopolitanism. Balsamo et al. (2008), in summarising data for freshwater taxa, reported that approximately 33% of European species appear to be cosmopolitan. Detailed faunistic comparisons at several spatial scales were made by Kisielewski (1991, 1999) through extensive studies carried out in Poland, Brazil and Israel. About 34% of the species found in the South American countries were also known in Europe, while in Israel the percentage of European species was higher, 55%, probably due to the closer zoogeographic relationships and shorter distance between the two areas. The high diversity of endemic freshwater genera in the Brazilian fauna, evidenced by Kisielewski (1991), may be due to the scarcity of comparable works carried out in other tropical-equatorial regions of the world. The great faunistic homogeneity of the European freshwater gastrotrich fauna, on the other hand, seems confirmed by preliminary results of the first extensive survey in Sweden, which found several Italian *Ichtydium* species previously unknown outside the Mediterranean peninsula (Kanneby et al., 2009, and own unpublished data).

To summarise, in spite of the unsatisfactory knowledge of their taxonomy, Gastrotricha do exhibit specific patterns of diversity and distribution.

Notwithstanding possible problems and biases in the interpretations of gastrotrich distribution, some blueprints emerge: the percentage of widespread taxa is high, especially among the highly speciose chaetonotids; some species have a more restricted geographic range, but even these species are relatively widespread within one biogeographic region. Future molecular and detailed microscopy investigations will reveal whether morphological identification based on current microscopical techniques alone may be misleading, as the case of *Xenotrichula intermedia* seems to suggest.

13.3 Rotifers

(Diego Fontaneto)

Rotifers (see Wallace et al., 2006 for a recent review of the group) are common microscopic aquatic animals, smaller than 2 mm and usually between 50 μm and 800 μm in length. They can be easily distinguished from other microscopic organisms by the corona of cilia on the head (Fig 13.2) and by the typical hard jaws called trophi; these trophi are so variable that they are widely used as a species-specific taxonomic feature. There are three major groups of rotifers: monogononts, bdelloids and seisonids. Monogonont rotifers may occur in any kind of water and are the richest group, with 1500 species (Wallace et al., 2006; Segers, 2007); they reproduce by cyclical parthenogenesis and the outcome of sexual recombination is usually a dormant embryo called a resting egg, which is considered the dispersal propagule. Bdelloid rotifers only reproduce via obligate parthenogenesis, indeed only females are present (Ricci and Fontaneto, 2009); they occur in any aquatic habitat, from proper water bodies to soil, lichens, mosses and even to deserts; *c.* 450 species have been described. They are able to enter a dormant stage in any period of their life; in their dry dormant stage they can be passively dispersed. Resting eggs in monogononts and dormant stages in bdelloids can remain viable for a long time, surviving desiccation, high temperatures and frost, and thus may act as very effective indirect dispersal propagules. The third group of rotifers, seisonids, is represented by four marine species living only as epibionts on crustaceans of the genus *Nebalia* (Ricci et al., 1993). They do not have resting stages and very few data are available on their distribution; thus, they will not be mentioned here.

The presence of small and drought-resistant dormant stages, perfectly tailored for passive dispersal, aerial or phoretic, make both monogonont and bdelloid rotifers potential candidates for a widespread or even cosmopolitan distribution. Moreover, parthenogenetic females hatch from resting eggs in monogononts and recover from dormancy in bdelloids, so that a single individual can potentially found a new population. These biological properties combined with presumed
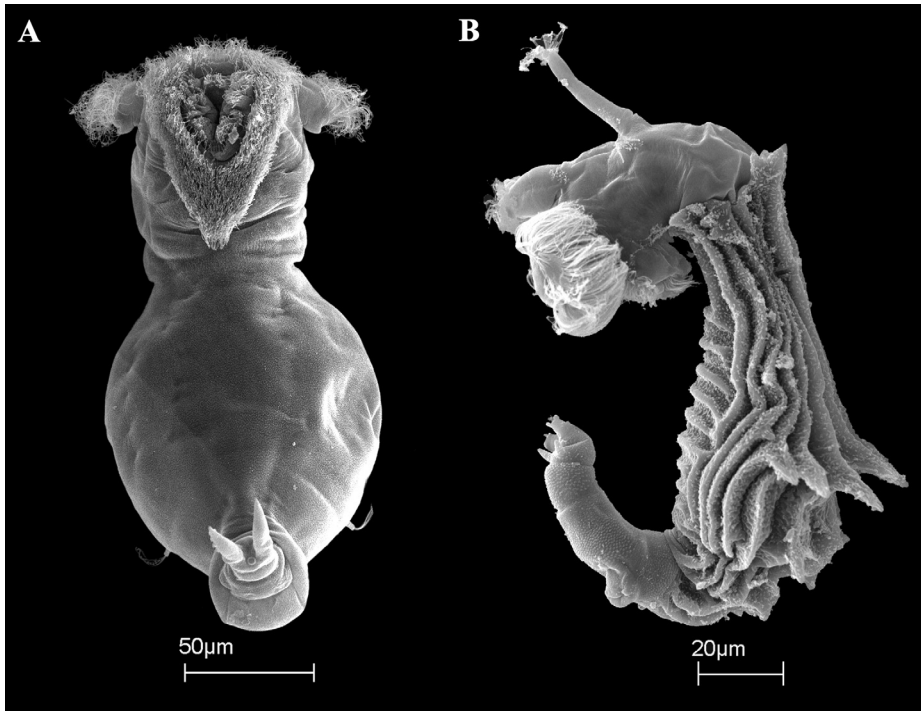
Fig 13.2 Scanning electron microsopy micrographs of (A) a monogonont rotifer, *Notommata collaris*, in ventral view and (B) a bdelloid rotifer, the potential 'flagship' species, *Pleuretra hystrix* in lateral view.

ubiquity, traditionally were believed to render rotifers useless for biogeographic studies (Rousselet, 1909; Hutchinson, 1967; Ball, 1976). Indeed, many species have been reported from different continents, thus supporting their ubiquity (Fontaneto et al., 2007; Segers, 2007).

Other than a large number of cosmopolitan species, another theoretical expectation of rotifer ubiquity is that a locally large representation of the global diversity should be found (Fenchel and Finlay, 2004). This expectation appears to be fulfilled by rotifers: in that any temperate or tropical water body is expected to host between 150 and 250 species respectively, that is 7–12.5% of global diversity (Dumont and Segers, 1996). In a study focused on bdelloids, 20% of all known species were found in a few samples collected in one afternoon in a small valley in Italy (Fontaneto et al., 2006).

According to this evidence, rotifers seem to be potentially and actually ubiquitous. Nevertheless, the fact that some species may be cosmopolitan does not immediately imply that all rotifers are cosmopolitan. Early studies from the 1970s provided increasing evidence of spatial patterns in rotifer biogeography and

restricted distributions, comparable to those commonly found in larger animals. For example, Green (1972) showed a latitudinal zonation in planktonic rotifers; Pejler (1977) confirmed restricted distributions in monogononts of the family Brachionidae, highlighting a striking number of endemic species in Lake Baikal for the genus *Notholca*; and De Ridder (1981) demonstrated limited distribution for almost 50% of periphytic and benthic rotifers. More recently, the suspicion that the apparent cosmopolitanism was due more to inadequate knowledge than to reality arose (Dumont, 1983; Segers, 1996). More detailed studies on specific taxa of monogononts found compelling evidence of endemic species for several genera in all the major biogeographic regions: with 6–22% of all *Lecane* spp. in each region being endemic (Segers, 1996); hotspots of biodiversity and endemism exist for *Trichocerca* in the northern hemisphere, especially north-east Nearctic (Segers, 2003); in the case of *Keratella*, hotspots of relict endemics have been identified in the east Palaearctic and in temperate and cold regions of the southern hemisphere, together with a recent radiation in the Nearctic (Segers and De Smet, 2008).

Recently, Segers (2008) analysed the non-marine fauna (96.5% of all rotifers) and found that in monogononts 44% of the species are endemic to one biogeographic region and only 23% of the species may be considered as truly cosmopolitan (defined as present in five or more of the eight biogeographic regions); the same scenario was also shown for bdelloids, with 51% endemic and only 13% truly cosmopolitan species.

It is of course difficult to ascertain the absence of rotifer species from any specific area, especially with the dearth of available information. Moreover, many species are known only from the locality where they have been described; even in Europe, the most well-known area, *c*. 25% of the *c*. 300 European bdelloids have never been collected since their original description (Fontaneto and Melone, 2003). Thus, the high number of species supposedly endemic for only one biogeographic region may reflect a biased picture, resulting from a lack of knowledge rather than representing the actual distribution pattern. Faunistic data for rotifers are scarce, and it has been suggested that rotifer distribution follows the distribution of rotiferologists studying them and not the actual distribution of rotifers (Wallace et al., 2006). Notwithstanding this problem, some easily recognised 'flagship' species (*sensu* Foissner, 2006), are limited in distribution. For instance, the bdelloid *Pleuretra hystrix*, with a characteristic spiny lorica (Fontaneto and Melone, 2003), is known only from arctic or alpine samples; it has never been found in the Antarctic or sub-Antarctic area, despite the more intensive southern polar faunistic studies for bdelloids (Kaya et al., 2010).

It is interesting to note, however, that even some of the biological assumptions for widespread distribution in rotifers are not verified but originate from potentially unreliable generalisations. For instance, resting eggs are known only for

very few species, and it is only assumed, but not proven, that all monogononts are able to produce them: thus, it is possible that only few species have such potential for passive dispersal. Moreover, resting eggs of some species do not survive desiccation, and hatching from dormant resting eggs is triggered by rather specific environmental cues, so that even if dispersal may be possible, colonisation of distant habitats is prevented.

There are also other caveats when considering rotifer biogeography. For instance, rotifer taxonomy is all but adequate and it is almost exemplary of the taxonomic impediment; many new species are still to be discovered and very few taxonomists are actively working on rotifers (Dumont, 1980; Segers and De Smet, 2008). Moreover, species identification from morphology alone may be misleading, as suggested by the increasing evidence of complexes of cryptic species in all rotifers analysed so far (Gómez et al., 2002; Schroeder and Walsh, 2007; Fontaneto et al., 2009).

These difficulties may have a significantly negative impact on our ability to understand the diversity of rotifers and consequently their distribution. Nevertheless, in spite of the unsatisfactory knowledge of their taxonomy, rotifers do exhibit patterns of diversity and distribution. Notwithstanding possible problems and biases in the interpretations of rotifer distribution, one pattern is clear: the percentage of widespread taxa is high; some species are more restricted geographically, but even the species with more restricted distributions are relatively widespread within one biogeographic region. Moreover, almost all genera and higher taxa are really cosmopolitan, one feature that is completely different from macroscopic organisms, even if the definition of taxa higher than species in different groups may not be directly comparable.

13.4 Tardigrades

(Sandra J. McInnes)

Tardigrades, common name for the phylum Tardigrada, are also known as water bears, moss piglets and bear animalcules (Fig 14.3). They were first recorded in the 1770s (Goeze, 1773; Spallanzani, 1776) and have been subject to several monographs and systematic revisions (Thulin, 1928; Marcus, 1929, 1936; Ramazzotti, 1962, 1972; Ramazzotti and Maucci, 1983). They are 'aquatic' in that they require a coating of water to permit locomotion and respiration. As a common component of the limno-terrestrial meiofauna they are found in a variety of habitats including bryophytes, cushion-forming plants, lichens, algae and soils, to truly aquatic habitats, and from polar to tropical environments. Marine tardigrades range from the tide line to the abyssal depths.

Tardigrades are typically 100–500 µm but range from 50 to 1700 µm. They are cylindrical with four pairs of lobopodal limbs that terminate in 'claws'; they have a nervous system that may include eyespots and sensory structures, a digestive tract with mouth and anus, and a reproductive system (Kinchin, 1994; Nelson, 2002). Two classes are recognised; the Heterotardigrada, incorporating the Arthrotardigrada (marine) and Echiniscoidea (marine and terrestrial); and the Eutardigrada, incorporating the Parachela (mainly terrestrial) and Apochela (terrestrial). A third class (Mesotardigrada) with a single species is considered dubious (e.g. Nelson, 2002; Nelson and McInnes, 2002) as neither the type material nor the type locality have survived. The original description of this species (*Thermozodium esakii*) was limited and modern classification now suggests a potential relationship with Carphaniidae, which is placed in the order Echiniscoidea (Binda and Kristensen, 1986). The palaeontological record for tardigrades is limited to subfossil records from Cretaceous amber (Cooper, 1964; Bertolani and Grimaldi, 2000), Eocene lake sediments (Cromer et al., 2006, 2008), and Pliocene peat cores (Jankovska, 1991; Miller and Heatwole, 2003). A current comprehensive taxonomic summary of all known extant tardigrade taxa can be found in Guidetti and Bertolani (2005) with updates in Degma and Guidetti (2007) and at: http://www.tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf

Reproductive strategies within the Tardigrada include both sexual and parthenogenesis (Nelson, 1982a; Bertolani, 1982, 1987; Rebecchi and Bertolani, 1988, 1994; Bertolani and Rebecchi, 1999), with parthenogenesis conveying an advantage for the invasion of new habitats. Reproduction produces eggs (40–60 µm in diameter), which may be smooth and laid singly or en masse inside an exuvium or are ornamented and laid free. Both individually free eggs and those encased in exuvia have the potential for transportation. As with many of the micrometazoans, changes in environmental conditions can induce the tardigrade to enter a latent state (i.e. cryptobiosis). Cryptobiosis provides resistance to environmental extremes (i.e. cold, heat, drought, chemicals and ionising radiation), which has a significant impact on the ecological role of the organism (see Wright et al., 1992; Kinchin, 1994; Wright, 2001) and offers the potential for relatively long-range dispersal (Kristensen, 1987; Pugh and McInnes, 1998).

The combination of small size, parthenogenesis and potential for cryptobiosis had led to the assumption that limno-terrestrial tardigrades should be cosmopolitan. However, the analysis of the most likely form of transport – wind – has barely been explored. A simple experiment run by Sudzuki (1972) showed that tardigrades and other microinvertebrates were rarely dispersed by wind speeds less than 2 m/s over 2 months. In the Antarctic, Janiec (1996) and Nkem et al. (2006) found that most microinvertebrates are transported with sediment or habitat (moss, lichen) near ground level and over relatively short distances. Kristensen (1987) mentioned that *Echiniscus* sp. were 'common in raindrops or 'air plankton' after Föhn storms in Greenland'.

Tardigrada have a limited suite of morphological characters and are morphologically conserved, factors which make traditional taxonomic classification challenging. For example, in some of the early reports bi-polar tardigrade species were recorded (e.g. Richters, 1905; Murray, 1906), which in part may be a consequence of the then relatively immature state of tardigrade taxonomy, microscopy limitations and observer expectations. Subsequent researchers have used the predominantly northern hemisphere taxonomic literature to create several cosmopolitan species or group-complexes (e.g. *Echiniscus arctomys*, *Pseudechiniscus suillus*, *Macrobiotus harmsworthi*, *Mac. hufelandi*, *Minibiotus intermedius*, *Hypsibius convergens*, *H. dujardini*, *Diphascon* (*Diphascon*) *pingue*, *Milnesium tardigradum*). More recent traditional taxonomic literature has indicated that some of these group-complexes are 'hiding' a number of species that are more restricted in their distribution (e.g. Bertolani and Rebecchi, 1993; Claxton, 1998).

The confusion over group-complexes and potential errors in published taxonomic records would imply that the phylum Tardigrada was not a good subject for biogeographic studies. However, there seems to be a general understanding that while there are cosmopolitan genera, most of these exhibiting parthenogenesis and capable of cryptobiosis (Pilato, 1979), not all genera are cosmopolitan and many of these have a lower capacity for cryptobiosis and/or reproduce sexually (Kristensen, 1987). Of the 64 limno-terrestrial genera only 11 are considered endemic (Europe: *Macroversum* (Murryidae), *Necopinatum* (Necopinatidae), *Carphania* (Carphaniidae), *Pseudohexapodibius* (Macrobiotidae); Africa: *Paradiphascon* (Hypsibiidae); Asia: *Famelobiotus* (Macrobiotidea); Australasia: *Milnesioides*, *Limmenius* (Milnesiidae); North America: *Haplohexapodibius* (Calohypsibiidae), *Proechiniscus* (Echiniscidae); South America: *Minilentus* (Macrobiotidae)). Endemism at the species level is relatively high (between 25–58%) for the major continents (McInnes and Pugh, 2007). Despite the potential identification problems, Tardigrada can be used to explore biogeography (Pilato and Binda, 2001) and the current biogeographic distribution patterns of the non-marine tardigrades show evidence of palaeogeographic events such as the break-up of Pangaea, and the division of east and west Gondwana (McInnes and Pugh, 2007).

13.5 Micrognathozoans, cycliophorans, loriciferans, kinorhynchs and gnathostomulids

(Martin V. Sørensen)

Other microscopic animals exist which may provide further empirical evidence supporting or denying cosmopolitanism for microorganisms.

Micrognathozoa is a recently described animal group with affinities to Rotifera and Gnathostomulida (Sørensen, 2003). Only one species, *Limnognathia maerski*, is currently known, and our extremely scarce knowledge about its biogeography suggests that it has a peculiar bipolar and patchy distribution. The species was described from a spring on Disko Island, Greenland (Kristensen and Funch, 2000), where it occurs in relatively high numbers in the short Arctic summer. Among the thousands of springs on Disko Island, it has only been recorded in one other spring on the island, and only at a single occasion (R. M. Kristensen, personal communication). Outside Disko Island, the species has been recorded once from a spring area in Wales, UK (J. M. Schmid-Araya, personal communication), and from the Subantarctic Crozet Islands (De Smet, 2002). On the latter, the species is quite abundant. The Subantarctic recording of the species, in particular, is puzzling. The great distance between this locality and the Greenlandic type locality suggests that the species possess a great migratory potential, but this is contradicted by the otherwise very few recordings of the species. The most likely explanation would probably be that *L. maerski* is a relatively widespread species throughout the cold and temperate regions of both hemispheres, but that it often occurs in very low numbers, and therefore are rarely encountered. In general, *L. maerski* does not appear to be a species adapted for distribution over great ranges. The adults are short lived, without cryptobiotic capabilities, and apparently intolerant to great abiotic changes in their environment. However, since they can survive the Arctic winter, one would expect that at least the eggs are freeze tolerant, and therefore could be tolerant to dehydration and other stresses that would be lethal for the hatched specimen. One kind of micrognathozoan egg actually resembles sculptured rotifer resting eggs, but hatching from previously frozen eggs has not yet been observed, hence this adaptation is still speculative. However, if the sculptured eggs turn out to be comparable with rotifer resting eggs, they would be more suitable for dispersal than the adults.

Cycliophora is another recently discovered microscopic animal group with only few known species (Funch and Kristensen, 1995). The animals live as commensals on the mouthparts of lobsters, and are characterised by an extremely complex life cycle that involves asexual feeding stages, parthenogenetic Pandora larvae, short-lived females, Prometheus larvae that produce dwarf males, and the sexually produced chordoid larvae (Funch and Kristensen, 1997; Obst and Funch, 2003). Currently two species are described: *Symbion pandora* from the Norwegian lobster, *Nephrops norvegicus* (Funch and Kristensen, 1995), and *Symbion americanus* from the American lobster *Homarus americanus* (Obst et al., 2006). A yet to be described species has been recorded from the European lobster, *Homarus gammarus* in the Mediterranean Sea (Nedved, 2004; Baker and Giribet, 2007; R. M. Kristensen, personal communication). *Symbion pandora* has been recorded on the Norwegian lobster all along the Atlantic European West Coast

from Norway to Portugal and around Faroe Island (Funch and Kristensen, 1997; Neves et al., 2010). The American species, *S. americanus*, is distributed along the North American East Coast, and has been found in lobster populations at several localities between Nova Scotia and Maryland (Obst et al., 2006; Baker et al., 2007). *Symbion americanus* appears to be a complex of cryptic species that may co-occur on the same lobster specimen (Baker et al., 2007). Knowledge on the distribution of these organisms is still scanty, but it seems that each morphologically recognisable species is restricted to specific regions (Northern Europe, east coast of North America and Mediterranean Sea, respectively), and that the cryptic species on *H. americanus* do not show any geographic patterning and their distributions overlap (Baker et al., 2007).

The restricted distribution is clearly tied to the host specificity, cycliophoran species are constrained to the distribution of the host. Furthermore, no stage in the cycliophoran life cycle is adapted for dispersal over greater ranges. The feeding stage is sessile, while the female, the Prometheus larva and the Pandora larva are only capable of moving over very short distances – probably not longer than from one mouthpart bristle to another. Usually the chordoid larva is considered the 'dispersal stage' in the life cycle, as it has the most developed locomotory ciliation (Funch and Kristensen, 1997). However, 'dispersal' in this context means dispersal to another mouth appendage, or eventually, another host in the same population. Nothing indicates that the chordoid larva can disperse over greater distances. Until now species of cycliophorans have been recorded from Europe and northeast America only, and other preliminary reports of potential cycliophorans from other parts of the world have always turned out to be sessile protists after closer examination.

Loricifera (Kristensen, 1983) is another recently described phylum of microscopic marine animal. The loriciferans are among the smallest known metazoans, but they are morphologically complex, and may have an extremely complicated life cycle with various larval and pre-adult stages. They are found in the interstices of sand and shell gravel, but may also be present in more muddy sediments. The first loriciferans were described from coastal areas in West Europe and along the North American East Coast (Kristensen, 1983; Higgins and Kristensen, 1986), but more recent studies have demonstrated a relatively high loriciferan diversity on banks and seamounts (Heiner, 2004, 2008; Gad, 2005a). In addition, the number of recordings and discovery of new species from the deep sea is currently increasing, and there are indications that the deep sea holds a diverse loriciferan fauna (Kristensen and Shirayama, 1988; Gad, 2005b, 2005c).

Loricifera have now been recorded in most parts of the world, and so the group can be considered cosmopolitan (e.g. Todaro and Kristensen, 1998; Gad and Martinez Arbizu, 2005; Heiner et al., 2009). The species, however, all have relatively limited distributions, and usually a species is restricted to a specific

region, such as the West European Coast or North American East Coast. However, the distribution of the animals is extremely patchy, which limits the chances of finding a species outside its type locality, or sometimes even the chances of re-finding it on a locality where it previously has been recorded. The latter is probably best exemplified by one of the first loriciferan specimens ever recorded. The specimen was collected in 1975 in Øresund, Denmark, but was lost during preparation. Knowing that the individual could represent a new animal phylum, the locality was sampled intensively for several years to obtain more specimens; but even today, 35 years later, no further loriciferans have been recorded from Øresund.

It is unclear why loriciferans occur in such a patchy distribution and why they do not, at least in coastal areas, form more continuous populations. One explanation could be very specific requirements to the sediment and abiotic conditions in their habitat, but this is only speculation. What is certain, however, is that no stage in the loriciferan life cycle is specialised for dispersal over great distances. Neither the eggs, the primary larva (Higgins larva, see Fig 13.3A), nor the adult appear to leave the sediment; even still, in the sediment they move very slowly. Species that inhabit seamounts or submarine banks are likewise trapped on these localities. For example, a species that is adapted to inhabit the calcareous shell sediment on Faroe Bank (see Heiner, 2004, 2008) would have difficulties leaving the bank and would therefore need to migrate through the surrounding muddy sediments to reach another bank in the area. Our knowledge on deep sea loriciferans is
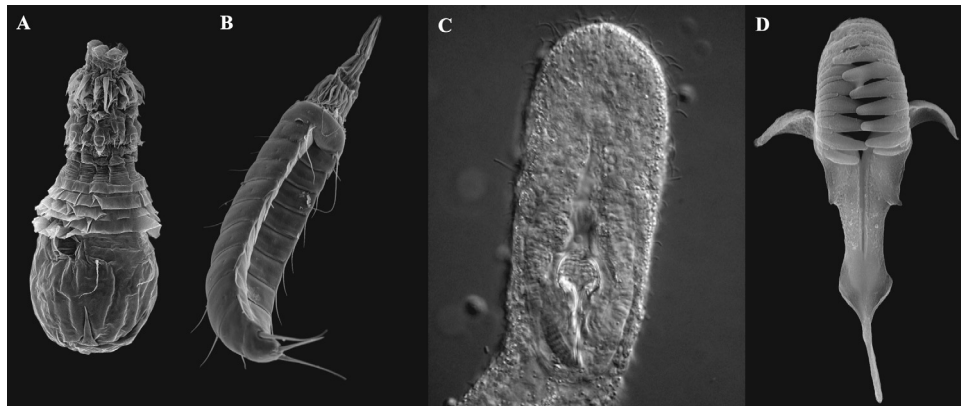
Fig 13.3 Scanning electron microscopy micrographs of (A) Higgins larva of an as yet undescribed species of Loricifera from the Western Pacific and (B) the kinorhynch species *Campyloderes* cf. *macquariae* from the Faroe Island, North Atlantic; this species could be the only known example of a cosmopolitan kinorhynch. Light (C) and scanning electron (D) micrographs of the gnathostomulid *Rastrognathia macrostoma*, showing its head with the prominent pharyngeal hard parts inside (C), and the isolated hard parts (D).

still extremely limited, but it is not unlikely that loriciferans living at great depths would show broader distributional ranges.

The Kinorhyncha represents another phylum of marine, microscopic animals. They are composed of a head with numerous appendages (so-called scalids), a short neck region and a trunk with 11 segments. Kinorhynchs show the highest diversity in muddy sediments, but are also present in sandy sediments (Sørensen and Pardos, 2008). They are known from marine localities throughout the world and have the highest levels of diversity in coastal areas. The latter, however, may be a sampling artefact due to coastal areas being sampled more frequently than less accessible oceanic and deep sea localities, and thus does not reflect the true distribution of the species.

The known kinorhynch distribution in some ways resembles the distributional patterns for loriciferans; their occurrence is patchy (although more consistent than the loriciferans), and the distribution of a species appears to be regional and in restricted areas of a few hundred kilometres squared. Our knowledge on kinorhynch distribution is still scarce. Only a few regions, such as the North American East Coast, the European West Coast and the Mediterranean, can be considered relatively well-investigated in terms of systematic kinorhynch studies, but even within these regions, the discovery of new species is not unusual (e.g. GaOrdóñez et al., 2008). When sampling in previously unstudied regions, discovering new species is much more likely than finding known ones (e.g. Sørensen, 2008; Sørensen and Rho, 2009). There are only a few examples of either cosmopolitan kinorhynch species distribution, or a distribution that spans across several oceans, and whether specimens from distant and separated populations are conspecific is questionable. One of the few kinorhynchs that, according to previous recordings, could be considered cosmopolitan is *Echinoderes dujardinii*. The species is widely distributed through the Mediterranean and along the European West Coast, but it has also been reported from Japan and the North American West Coast. In light of this rather wide distribution, Higgins (1977) revised the species and concluded that the identity of the Japanese specimens should be considered doubtful, and reports of the American specimens, in actuality, were based on a new species that he described as *E. kozloffi*. Consequently, *E. dujardinii* turned out to be a strictly European species, with a restricted and continuous distribution along the European West Coast.

There are only one or two kinorhynch species that are currently candidates as true cosmopolitans, but the taxonomy of these species, or species complexes, is puzzling and currently under investigation. The species *Campyloderes vanhoeffeni* and *C. macquariae* (Fig 13.3B) are both described from localities close to Antarctica (Zelinka, 1913; Johnston, 1938). In the descriptions the two species appear literally identical and they should most certainly be considered as a single species. Interestingly, *C. macquariae/vanhoeffeni* has over the years been

reported from various localities around the world, including New Caledonia, Korea, Galapagos, the Pacific Coast of Central America and the North Atlantic (see complete list in Sørensen and Pardos, 2008). Specimens from additional localities are currently being examined (Neuhaus and Sørensen, work in progress), and the numerous recordings suggest that this could be the only example of a cosmopolitan kinorhynch species. However, specimens from the various populations tend to differ in minor details, and the consistency of this variation still requires further studies to determine if they indicate the presence of several distinct and regionally restricted species, or whether *C. macquariae/vanhoeffeni* is a true cosmopolitan.

In general kinorhynchs do not possess any dispersal mechanisms that would suggest cosmopolitanism or very wide distributional ranges. They have no locomotory cilia, and move very slowly through the sediment, and thus are unable to enter the epibenthic or pelagic zones. In fact, their highly hydrophobic cuticular surface makes even a short stay in the open water rather dangerous, as contact with a small air bubble would mean immediate adhesion and subsequent transport to the surface where they would be trapped. Additionally their eggs are not efficient dispersal stages because only one or a few eggs are laid at a time, and they are immediately coated with detritus and sediment (Kozloff, 2007). This makes it even more unlikely that the eggs could enter the water column and be dispersed by the water currents.

Gnathostomulida is a phylum of microscopic marine worms that inhabit the interstices in sandy sediments. The animals appear in many ways very simple, but are equipped with a rather complex pharyngeal apparatus (Sterrer, 1972; Sørensen and Sterrer, 2002). About 100 valid species are currently known, of which some show very narrow distributional ranges, whereas others must be considered cosmopolites (e.g. Sterrer, 1998). As is the case with many other meiofaunal organisms, Gnathostomulida is an under-sampled group and thus their biodiversity and the distributional ranges of known species are probably greater than we currently know. Nevertheless, we have indications that distributional ranges differ greatly between the species. For example, *Rastrognathia macrostoma* represents a species of the monotypic genus *Rastrognathia* (Kristensen and Nørrevang, 1977); specimens are always found in relatively high numbers at its type locality north of Zealand, Denmark, but this species or any other undescribed *Rastrognathia* species have never been recorded anywhere else. Its pharyngeal hard parts are very prominent (Fig 13.3C), and if specimens had been collected elsewhere, they would not have been confused with anything else; this indicates that *R. macrostoma* most probably has a very limited distribution. Several other gnathostomulid species are only known from single localities, and even some genera, for example *Problognathia*, *Valvognathia* and *Ratugnathia* are known from very restricted areas (Sterrer and Farris, 1975; Kristensen and Nørrevang, 1978; Sterrer, 1991).

Examples of more widely distributed species are found within the genus *Gnathostomula*. Along the European West Coast, *Gnathostomula paradoxa* is one of the most common and widely distributed gnathostomulid species. At the same latitudes, but along the North American East Coast, *G. armata* tends to be widespread and common, and further south, along the Carolinas, Florida and in the Caribbean, *G. peregrina* tends to be the dominant species.

Finally, some species appear to be true cosmopolitans; this is especially true among the filospermoid genera *Haplognathia*, *Pterognathia* and *Cosmognathia*, where the likelihood of cosmopolitanism is high. For example, the species *Haplognathia rosea* and *H. ruberrima* have been reported from the Southwest Pacific, the Central Pacific, the Caribbean, the Northwest and Northeast Atlantic, and Scandinavian waters, whereas *P. ctenifera* also is known from various localities in the Pacific, West Atlantic and Caribbean (Sterrer, 1968, 1991, 1997, 1998, 2001). These distributions indicate that all three species could be considered cosmopolitan. It is likely that molecular studies would indicate significant genetic distances between the populations and that all three would represent complexes of several cryptic species; this remains to be tested.

Currently it remains puzzling why some gnathostomulid species show great regionality whereas others have worldwide distributions. Nothing indicates that they should be specialised migrators, and since all species are strictly interstitial they would be unable to travel through muddy sediments. They are furthermore direct developers; as such there are no planktonic larvae that could serve as dispersal stages. Oviposition and egg development have only been described from a single species, *Gnathostomula jenneri*; here the egg is laid in the sediment and immediately attached to the substratum (Riedl, 1969), which disables the egg from spreading.

13.6 Nematodes

(Aldo Zullini)

Nematodes (Fig 13.4) are probably the most numerous metazoan group living on our planet. In non-desert soil there are, on average, about 2 million individuals per square metre, and at the sea bottom their abundance, following a conservative estimate, is about 100 thousand individuals per square metre (Lambshead, 2004); there are at least 10^{20} nematodes in the world. Assuming nematodes are on average 1 mm in body length, a queue of all these individuals would span a distance equivalent to 10 light years. The number of known species, in contrast, is not as impressive: there are about 27 000 nominal species, half of them free-living, and half plant and zooparasites. However, many authors think that the existing nematode species may be 10^5 or even 10^6 (Hugot et al., 2001). The biogeography of the

Fig 13.4 Anterior end of a soil nematode (*Mylonchulus* sp.), a predaceous species about 1.5 mm long. (Photo L. Poiras).

parasitic species depends on the hosts; therefore they obey macrofaunal dispersal logic. The biogeography of marine nematodes is still poorly known (Lambshead, 2004; Tchesunov, 2006) and goes beyond the scope of the present work. We consider the free-living soil and freshwater species only, remembering that a clearcut taxonomic distinction between these two nematode groups does not exist.

At a microscale level it is well known that soil nematodes exhibit an aggregate distribution tied to their limited dispersal and to the soil resource patchiness (Ettema and Wardle, 2002). But at the large geographic level, the existence of recognisable species patterns is still unclear. Much work was conducted on nematode dispersal; given that many soil species and some freshwater species are able to withstand dryness and low temperatures in cryptobiosis (anhydrobiosis) for many months or years, it has been postulated that nematodes in this state can be dispersed at great distances (Womersley et al., 1998; Wharton, 2004). Applying mathematical models, Carroll and Viglierchio (1981) found that dust-devil events can redeposit a significant number of nematodes within 0.5–1.5 km from a given vortex, whereas deposition

at longer distances (13–40 km downwind) are much rarer. They calculated that the nematode eggs are less transportable. The dispersion of nematodes by wind is possible for dry soils and this has been studied by catching transported soil in traps. In Texas, Orr and Newton (1971) placed traps 2 m above ground to catch the wind-transported sand; in total 28 genera of free-living and plant parasitic nematodes were collected. In the most ancient European desert (44°50′N, 21°10′E, near Belgrade) the sand caught by traps 1 m above ground contained from 2 to 9 nematodes per 100 ml, mainly Dorylaimida, Tylenchomorpha and Rhabditomorpha (Krnjaic' and Krnjaic', 1973). In the peanut-cropping area of Senegal, traps (pots opened at ground level) to collect wind-transported sand, captured nematodes (mainly mycophagous and bacteriophagous species, Dorylaimida and Tylenchomorpha being less numerous) especially during the dry season (Baujard and Martiny, 1994). On the coastal dunes in the Netherlands 30 nematodes per 100 g dry soil were found in the sand traps (de Rooij-van der Goes et al., 1997).

The McMurdo Dry Valleys, Antarctica, is the driest and coldest desert on Earth: air temperature averages –20 °C, and the area practically lacks snow and ice cover since precipitation is < 5 cm water equivalent annually and the wind speed can exceed 300 km h^{-1}. Wind-transported microfauna was collected (at 77°S, 162°E) by traps and from debris deposited on ice: 10 nematodes (of three species: *Eudorylaimus antarcticus*, *Plectus antarcticus* and *Scottnema lindsayae*, all Antarctic endemites) along with 82 tardigrades and 105 rotifers were found, on average, in 100 g of wind-transported soil. No microarthropods were present (Nkem et al., 2006). It is interesting to note that the inland nunataks of Ellsworth Land (at 75°–77°S, 70°–73°W) is the only known large area without nematodes: the sole existing metazoans are rotifers and tardigrades (Freckman and Virginia, 1997; Convey and McInnes, 2005). Similar nunataks with rotifer and tardigrade diversity, but devoid of nematodes, were found in an area at 73°–75°S, 11°–14°W (Sohlenius and Boström, 2005).

Water is another important dispersal mean for nematodes. Agriculturally polluted irrigation canals in south central Washington contain 150–16 000 nematodes per cubic metre of water; these were mainly free-living but there were also 5–12% of plant parasites: it was calculated that $2–16 \times 10^9$ nematodes per day were carried past a given point (Faulkner and Bolander, 1966, 1970). Densities of 50–222 nematodes per cubic metre were found in some irrigation canals in southern Italy (Roccuzzo and Ciancio, 1991). In northern Italy near Milan, about 300 million nematodes per day are drifted by the River Adda: 38 of the 40 identified species are typical of fresh water, the commonest nematode being *Paroigolaimella bernensis* (Zullini, unpublished data). Nematodes have been found to be dispersed via tap water: data from nine different papers record 1–41 nematode species present in drinking water, and about 0–156 individuals per litre (Dózsa-Farkas, 1965; Mott and Harrison, 1983; Lupi et al., 1994).

Phoresy seems to be much less important for free-living nematode dispersal. Their association with other animals can be internal (e.g. reproductive tract or trachea) or external. Nematodes involved are mainly Rhabditomorpha (*Caenorhabditis* species included), Diplogasteromorpha and Tylenchomorpha (Gaugler and Bilgrami, 2004). Internal phoresy (in the genital chamber) on certain Diptera and Coleoptera is physiologically obligatory for some, e.g. *Paroigolaimella coprophila* (Kiontke, 1996). An example of external phoresy is the transport of *Rhabditophanes schneideri* on the legs and pedipalps of pseudoscorpions (Curčic et al., 2004). More important is the transport via large mammals. It was observed that the Great Plains (large region extending from Canada to the Mexican border) hosts an almost identical nematode faunal diversity from north to south along its 3200 km. This region was, until 1870, inhabited by about 50–100 million American bisons; these roamed the Plains for thousands of years. They would often wallow in mud to protect themselves from swarms of flies: in this way they could carry around 5–20 kg of soil containing, of course, a lot of nematodes. These bisons would transport millions of tonnes of soil; such movement of mud has made for a uniform nematode diversity across the vast region (Thorne, 1968). At present, moreover, the anthropogenic transport of plants and soil is more frequent than ever.

All the factors mentioned above involving nematode dispersal can explain why many nematode species are cosmopolitan or nearly so. Nematode cosmopolitanism was in fact assumed as a general rule, but the bulk of new data suggests an alternate view, even if the existence of small-area endemism (like those observed for insects and terrestrial gastropods) has not yet been proved.

Sohlenius (1980), examining data from 81 sites encompassing the principal biomes, found that the abundance of soil nematodes was higher in temperate than in tropical or in cold regions (Fig 13.5A). His data were only indicative, given the few sites examined in tropical soils and the different methods used to extract nematodes. Examining this work and all the existing biogeographic literature, Procter (1984, 1990) published two papers asserting the following points:

(1) Nematode species richness, in contrast with the general rule valid for most animals and plants, reaches its maximum at higher latitudes. For example, a comparison of 18 soil samples gives an average of 81 species (range 33–162) in the tundra habitats, 56 species (31–95) in temperate grassland and forest habitats and 18 species (12–24) in tropical habitats.

(2) Genus *Plectus* is dominant, or nearly so, in high-latitude faunas, whereas it is insignificant in temperate and tropical areas. Other dominant genera in high latitudes include *Tylenchus*, *Dorylaimus*, *Eudorylaimus* and *Teratocephalus*. The same genera dominate at high altitudes.

(3) Nematode densities and biomass are both high at high altitudes, whereas they are very low in the tropical forests.
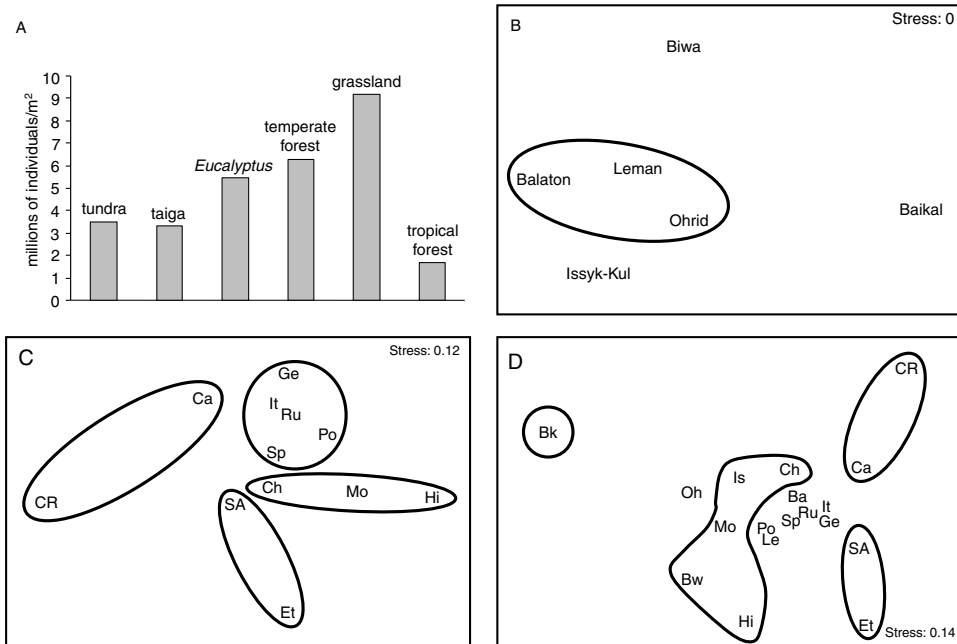
Fig 13.5 (A) Average density of soil nematodes (million individuals per square metre) in different biomes. Drawn from Sohlenius (1980) data. (B) MDS (multidimensional scaling) scatterplot of six lakes well known from the nematological point of view. (C) MDS scatterplot of freshwater regional nematofauna. America (Ca: Canada + USA; CR: Costa Rica), Europe (Ge: Germany + Austria; It: Italy; Ru: European Russia; Po: Poland; Sp: Spain), Asia (Ch: China; Mo: Mongolian waters < 5 per thousand salinity; Hi: Himalayas), Africa (SA: South Africa; Et: Ethiopia). (D) MDS scatterplot of freshwater regional nematofauna (abbreviations as before) encircling groups of five Asian faunas, two American and two African faunas, plus the nematofauna of six lakes (Bk: Baikal; Ba: Balaton; Bw: Biwa; Is: Issyk-Kul; Le: Léman; Oh: Ohrid). European fauna not encircled.

(4) At high latitudes many nematodes species (e.g. of *Plectus*, *Eudorylaimus* and *Dorylaimus*) are unusually large.

(5) Antarctic regions have lower nematode richness than do Arctic regions.

Since nematodes tolerate unfavourable conditions such as freezing and desiccation by means of an intermittent activity, Procter (1984) considers nematodes an invertebrate analogue of lichens (but see Chapter 10 for a detailed discussion on lichen biogeography). Moreover many nematodes, being often parthenogenetic (e.g. *Plectus*), can reproduce in habitats being very poor in nutrients, permitting only low population densities. The compelling short distance between individuals, usually necessary for sexual encounters, is not a

limiting factor for parthenogenetic nematodes. Procter's final interpretation of the above-mentioned facts was that most microfauna (mites, springtails, etc.), usually very active in tropical soils, are hindered in the cold climates owing to the arthropods' higher ecological requirements. Consequently nematodes experience little competition and therefore can maintain relatively high diversities and densities.

The rule that nematodes are larger in cold climates is often, but not always, confirmed: for example, the largest known species of *Tobrilus* (*sensu lato*) was found on Mount Kenya (*T. elephas*: almost 7 mm long), and many relatively large nematodes were found in the Himalayas from 5200 to 6100 m above sea level (Andrássy, 1964; Zullini, 1973). Boag and Yeates (1998), examining the existing literature on 134 soil samples at different sites across the world, found that soil nematode biodiversity is lower near the poles than in temperate and tropical regions. In particular, they found minimum values of species at 20°–30° latitude (north plus south) and at 60°–80° latitude, thus contradicting the suggestion of Procter (1984) about the scarce tropical nematode biodiversity.

The assessment of geographic patterns in nematodes is difficult for three reasons. First of all, the free-living species of many regions are understudied; only in Europe, and in some parts of India, is nematode diversity sufficiently known. Second, there are generally poor taxonomic descriptions of many species erected before 1950. The last reason is the yet unclear taxonomic relevance of nematode morphological variability: for example, *Dorylaimus stagnalis* and *Monhystera stagnalis* are species reported from lakes and rivers all over the world, but it is probable that these names include, in fact, a large complex of similar, but different species. Molecular analyses will perhaps resolve this and many other similar problems.

Despite these problems, it seems that some geographic patterns are evident. In 1964 Andrássy named Africa 'das Land der Actinolaimen'. In fact this family (whose species inhabit fresh water, moss and humid soil) containing 132 valid species, includes only two real cosmopolitan species. Africa hosts the largest number of Actinolaimidae (30%), followed by India (25%) and by Neotropic regions (23%). In total, 84% of the species of this family are known for the Gondwanian regions only. In 1970 Dao compared the two, at that time, best-known temperate and tropical soil faunas: the nematodes of the Netherlands (362 species) and Venezuela (113 species). Excluding the doubtful species and the Venezuelan non-tropical records (nematodes from above 1200 m), only 5% of the considered species were really eurytopic, i.e. common to both temperate and tropical areas. Loof (1971), in the same years, examined almost 25 000 nematodes from Spitzbergen (78°–79°N) and concluded that some genera (*Tylenchus*, *Teratocephalus*, *Cervidellus*, *Plectus*, *Ereptonema*, *Prismatolaimus*) are much more dominant on Spitzbergen than in the temperate regions. A surprising fact was the complete absence of Rhabditidae,

Diplogastridae, Mononchidae and Aporcelaimidae (less surprising was the absence of some families of plant parasitic nematodes). The Spitzbergen nemato-fauna was found to be very similar to that of northern Canada, Greenland and Novaya Zemlya.

The biogeography of freshwater species has received much less attention and thus entails many unsolved problems. One puzzling case is given by the nematodes living in freshwater habitats in the Galápagos archipelago: two of the 18 collected species were new, six were widely distributed in the southern hemisphere, and the remaining 10 were cosmopolitan. Since Galápagos are remote volcanic (therefore oceanic) islands 960 km away from the South American coast, the most likely vector of these nematodes, obviously in resistant stages, is the passive and very occasional transport by birds (Eyualem-Abebe and Coomans, 1995). The ability of freshwater nematodes to withstand harsh conditions, including long-distance transport, is illustrated by Hodda et al. (2006). The most dominant species in Alpine lakes are also cosmopolitan, but a survey on these lakes found that only three species (*Eumonhystera filiformis*, *E. longicaudatula* and *Tripyla glomerans*) were found in all the studied lakes (Traunspurger et al., 2006). Eyualem-Abebe et al. (2008) published an interesting paper on the global diversity of freshwater nematodes. They pointed out that this group of nematodes is only 7% of all the nominal nematode species and discussed the geographic distribution of the nematode orders including free-living species.

To find possible geographic patterns in freshwater nematodes, 102 papers and species lists from 1913 to 2003 were examined. After some taxonomic corrections, 717 nominal species were found; only strictly freshwater nematodes were considered, excluding the Tylenchomorpha (most of them being plant-parasitic). Comparing nematodes of six biogeographically important and well-studied lakes (Baikal: the most ancient lake and the richest in endemics; Balaton: a remnant of Paratethys; Biwa: the largest Japanese freshwater lake; Leman: the largest Alpine lake; Issyk-Kul + Sonkul: the largest endorheic lake; Ohrid: the most ancient European lake) by means of multidimensional scaling, a good propinquity (stress = 0) connects the three European lakes, whereas Baikal is placed well apart from all other lakes (Fig 13.5B). A well-studied lake for nematodes is the Königssee (Traunspurger, 1991), but in the following diagrams it is omitted since its placements practically coincide with the Léman: this means that these two Alpine lakes, whose distance apart is exactly 500 km, are extremely similar in their nematode fauna. Comparing the freshwater nematodes at the regional level (excluding the data of the above-mentioned lakes, and including rivers and other lakes), four distinct groups, at a continental level, emerge (Fig 13.5C). By including all data together (regional data plus the data of the six lakes) the following pattern emerges (Fig 13.5D): European faunas are well grouped together, excluding Ohrid (pliocenic

lake rich in unusual species) and Baikal, of which the latter is placed in an isolated position (Zullini, unpubl. data).

All these data prove that both the soil and the freshwater species (or freshwater groups of species) are not distributed randomly in the world.

It is one thing to discover natural patterns and it is another to tentatively intepret them. In our case, interpretation is based upon the distinction between environmental (ecological) and historical (evolutionary) factors: for the small eukaryotes, in particular, declaring that some 'species' are cosmopolitan might be approximately equivalent to saying that a genus or family of birds is cosmopolitan (Martiny et al., 2006). The concept of 'small' animal, and of the related microfauna concept, usually refers to the body length (generally defined as < 2 mm), but many soil and freshwater nematodes are outside the 2 mm length, and yet still remain within the frame of the microfauna. Therefore the maximum threshold (2 mm) should refer to the maximum body width and not to the body length. The geographic distribution of nematode species attacking roots of cultivated plants has been investigated (e.g. Navas et al., 1993; Coomans, 1996). Biogeographic analyses on soil free-living species were made by Ferris et al. (1976, 1981) adopting a plate tectonics perspective and using cladistic analysis. They analysed the family Leptonchidae because these hyphal and omnivorous feeders do not have cryptobiotic ability and their geographic distribution is rather clear. The genus *Tyleptus*, in particular, was regarded as a Gondwanian genus, except for one species present in Venezuela and in North America, which probably migrated northwards via the Central America land bridge. All other genera of this family radiated primarily in Gondwana areas, except *Funaria* which is of Laurasian origin. The fact that one of the cladograms (about *Tyleptus*) published by these authors presents species/continental area correspondences, could raise strong objections by many biogeographers, as a species level is generally considered a too low systematic level (= recent origin) to be correlated with the ancient tectonic splits. However, we must remember that species evolution in nematodes has a different pace: for example, the free-living soil nematodes *Caenorhabditis elegans* and *C. briggsae* (whose genome sequences were completed in 2002 and 2003, respectively) are morphologically almost indistinguishable, despite the fact that their most recent common ancestor existed about a 100 million years ago (Hillier et al., 2007).

In conclusion, it is still not clear what kind of geographic pattern is really true and important for the continental free-living nematodes, nor if there is a geographic parallelism between the soil and the freshwater species, nor if vicariance or dispersion are the main biogeographic factors. We can only foresee that new field collections and DNA data, that many laboratories are collecting with a constantly increasing speed, will permit us to define a picture of nematode distribution and history; one which is vaster and more correct than any we can conceive at present.

13.7 Flatworms

(Tom Artois)

Flatworms (Platyhelminthes) are a species-rich group of acoelomate, soft-bodied, protostome animals (over 20 000 species described). Traditionally they were subdivided into the parasitic Neodermata (*c.* 15 000 species) and the free-living or symbiotic 'Turbellaria' (*c.* 6500 species), this group included all the flatworms that do not replace the ciliated epidermis with a non-ciliated one (the so-called neodermis) during ontogenetic development. Phylogenetic analyses, based on molecular as well as morphological data, have made clear that 'Turbellaria' is not monophyletic (see Willems et al., 2006 and references therein). However, the term turbellarian is still commonly used as a vernacular name to indicate all non-parasitic free-living flatworms.

Until recently, four large taxa were recognised within Platyhelminthes: Acoela, Nemertodermatida, Catenulida and Rhabditophora (including Neodermata). However, it is clear now that Acoela and Nemertodermatida do not belong to the monophyletic Platyhelminthes, but are basal bilaterians (Hejnol et al., 2010). Here we will restrict the term microturbellaria to all species of the Catenulida and Rhabditophora that are free-living or symbiotic, and are less than a few millimetres in length (Fig 13.6). Hence Neodermata, triclads (planarians) and polyclads are not treated. Defined as such, microturbellaria includes about 3300 species. Microturbellaria all are simultaneous hermaphrodites, which
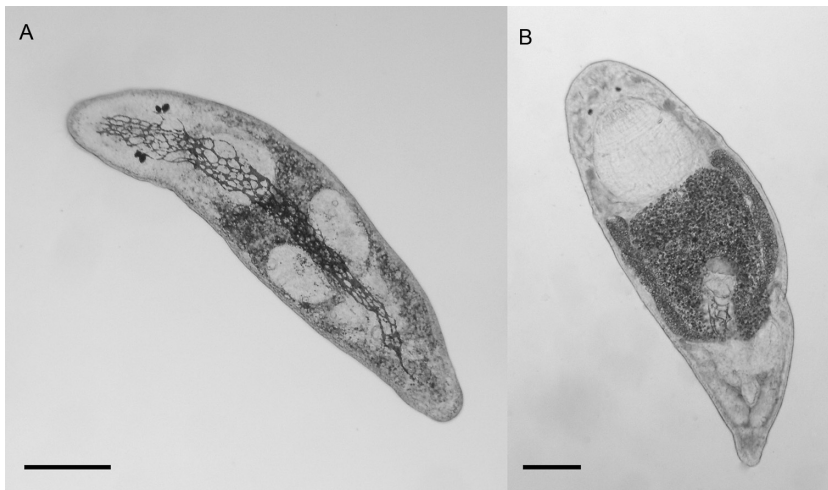
Fig 13.6 Two microturbellarians from India, December 2008. (A) *Trigonostomum franki* (marine) and (B) a new species of Dalyelliidae (freshwater). Scale bars 0.1 mm.

(probably) mostly cross-fertilise, although self-fertilisation can occur (Sekera, 1906). They have a direct development, without any free-living larvae. An overview of the world's distribution of freshwater turbellaria was recently provided by Schockaert et al. (2008). As yet, a worldwide review of marine turbellaria is not available.

Microturbellarians can be found in all types of wet environments all over the world: streams, ponds, salt marshes, sandy and rocky beaches and different kinds of sublittoral environments. They either live interstitially between the sand grains, epiphytically on algae and/or plants, or epizoically, e.g. on cnidarians and bryozoans. Whereas most turbellarians need wet habitats, about 50 species can occur in moist terrestrial environments. Very few species are described from dry environments (desiccated mosses), but recent collections have shown that at least rhabdocoel flatworms are ubiquitous in these temporarily dry environments (Van Steenkiste et al., 2010). These terrestrial rhabdocoels survive periods of extreme drought by encystment, often after the deposition of one or two eggs. A few days after excystment, the worms start laying eggs (for details, see Van Steenkiste et al., 2010). Encystment by adult worms, to survive adverse conditions, has also been reported in freshwater lecithoepitheliates and the freshwater species *Bothrioplana semperi* (see Luther, 1960). A number of limnic species produce resting eggs, which can survive periods of drought or cold. For example, mature specimens of five species of rhabdocoels were collected a few days after inundation of sediment containing resting eggs from a dried-out pool in Botswana (Artois et al., 2004). Such resting eggs have been reported from many taxa: Catenulida (Hyman, 1951), Macrostomida (Graff, 1913; Ingole, 1987), and Rhabdocoela (Graff, 1913; Luther, 1955; Young, 1974; Heitkamp, 1988).

Very little is known about the dispersal capacities of microturbellaria. Cases of worms in rafting material (such as coconuts, seaweeds, drifting algae and plants, driftwood) have been reported (Gerlach, 1977); this could be a major source of dispersal of the adult (and juvenile) worms, and of eggs. In polar areas, drifting sea ice could be an important carrier of flatworms. For acoels it has been known for a long time that they can survive in sea ice (see Gradinger et al., 1999; Janssen and Gradinger, 1999 and references therein; Friedrich and Hendelberg, 2001), and recently rhabditophorans have been discovered in the sea ice endofauna of the Weddell Sea (Melnikov, 1997; M. Kramer, personal communication). Worms as well as eggs could be displaced by animals that regularly visit moist habitats, such as waterfowl (Steinböck, 1931). Resting stages of limnic species, such as cysts and resting eggs, could be important stages for airborne or phoretic dispersal (Reisinger and Steinböck, 1927; Young and Young, 1976; Vanschoenwinkel et al., 2008a, 2008b, 2009). In a recent study, Vanschoenwinkel et al. (2008c) found a relatively high number of viable turbellarian propagules in the faeces of wild boars, and in mud from rubbing trees used by these animals, which indicates that large

mammal activity could be an important means of dispersal. Moreover, flooding has been shown to be important for the dispersal of microturbellarian resting stages (Vanschoenwinkel et al., 2008a). For interstitial marine microturbellarians, sand displacement by wave action and sea currents can be a means of egg and individual worm dispersal, which, together with the sand, are swept from their original location and deposited in a new location (Boaden, 1964, 1968). Moreover, and somewhat surprisingly, microturbellarians (and other meiofauna) are readily displaced while suspended in the water column (Palmer, 1988). They can enter the water column by accident, as a consequence of heavy wave actions, but they can also enter it actively. In an experiment carried out by Hagerman and Rieger (1981), specimens of several flatworm taxa, along with some other meiofauna taxa (predominantly nematodes), were retrieved from a meiofauna trap that was suspended in the water column. As such they can be dispersed by water currents, and colonise new areas. When mature, flatworms often carry one or more eggs, or have viable sperm stored from previous copulations, which can be used to fertilise eggs. Moreover, self-fertilisation can occur, although seldom does (Sekera, 1906). By these means, one individual can be responsible for the colonisation of a new locality. In more recent times, anthropogenic introduction of microturbellarians in new localities has occurred, for instance by the use of large bodies of sediment as counter ballast in sailing ships, or by the (international) trade of fauna and flora (Young and Young, 1976; Gerlach, 1977; Faubel and Gollasch, 1996).

Although the above-mentioned means of dispersal undoubtedly occur, it is far from clear how much these processes have influenced present-day distribution of microturbellaria. According to some authors, there are almost no boundaries to the spread of small interstitial animals, whereas others consider continental drift to be the major historical cause of the present-day distribution of these animals; the processes discussed above are only responsible for intracontinental rather than intercontinental dispersal (reviewed by Sterrer, 1973). At least the latter option seems conceivable for freshwater turbellarians; for these animals, large marine waters constitute an unbridgeable biogeographic barrier.

Based on the data sets compiled in the framework of the FADA-project (Balian et al., 2008; data set not publicly available yet), we calculated that about 50–80% (depending on the taxon considered) of the freshwater species are known from their type locality and the nearby vicinity only. Based on the data available in the Turbellarian taxonomic database (Tyler et al., 2006–2009) and on our own field experiences, the situation is comparable for the marine taxa. These high numbers of species with restricted distributions are reflective of our lack of knowledge as to the real distributions, rather than indicative of high levels of endemicity. In Europe, for instance, most species generally show a much wider distribution than species known from other continents; occurring in comparable habitats on the entire continent (including Russia). The obvious reason is sampling bias, since

most flatworm taxonomists in the past have been European, sampling predominantly in their own 'backyard'. Only Lake Baikal seems to be a real hotspot of microturbellarian endemicity (Schockaert et al., 2008).

On the other hand, there are many examples of species with a very disparate distribution. For instance, *Plagiostomum acoluthum* (Prolecithophora) is known from Hawai'i and Brazil (Karling et al., 1972), *Annalisella bermudensis* (Rhabdocoela) is recorded from Bermuda, Curaçao and Zanzibar (Artois and Tessens, 2008); these are but a few of numerous examples. More specifically, many species are known from localities in the European Northern Atlantic (Scandinavian and German Coast), the Mediterranean and Black Sea, and often the North American Atlantic Coast. Not coincidentally, these are the most densely sampled areas. Therefore, one could easily state that distribution maps of species of microturbellaria actually reflect the distributions of taxonomists, and the expeditions they have done. Without doubt, denser sampling will show that many species actually have a much wider distribution than is thought now.

In almost all taxa there are species that have an extremely wide or even cosmopolitan distribution. The most renowned example is *Gyratrix hermaphroditus* (Rhabdocoela). This 'species' occurs in freshwater, marine and brackish water habitats from the north pole to the south pole. However, populations (sometimes sympatric) can differ in the number of chromosomes, the morphology of the chromosomes and the detailed morphology and dimensions of the hard parts of the copulatory organ. This variation can even be found within populations. To what extent these differences indicate reproductive isolation and/or evolutionary differentiation is unknown, but it is clear that *Gyratrix hermaphroditus* represent a complex of species (see Curini-Galletti and Puccinelli, 1998; Timoshkin et al., 2004 and references therein). Most other 'cosmopolitan species' often belong to taxa in which species identification is extremely difficult (e.g. some species of *Mesostoma*, several taxa within Typhloplanidae, some species of *Macrostomum*, many species of Catenulida, etc.). A detailed molecular and morphological study of these taxa is certainly necessary to indicate whether these species are indeed cosmopolitan, or whether they form complexes of many cryptic taxa. The molecular study of cryptic biodiversity, however, has only very recently been started (e.g. Casu and Curini-Galletti, 2006).

It is clear that, at present, too few data are available to make any definitive inferences about patterns of distributions in microturbellaria. On one hand, it is clear that many species probably have a much wider distribution than is now known. On the other hand, many cosmopolitan species could represent complexes of sibling species, each with a much narrower distribution. Only intensive sampling, a combination of molecular and morphology-based taxonomy and experimental laboratory and field studies on the dispersal capacities of microturbellarians, will give a realistic image of their distribution patterns.

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