

# CHAPTER 10-1

## ARTHROPODS: CRUSTACEA – COPEPODA AND CLADOCERA

---

### TABLE OF CONTENTS

SUBPHYLUM CRUSTACEA .....	10-1-2
Reproduction.....	10-1-3
Dispersal .....	10-1-3
Habitat Fragmentation.....	10-1-3
Habitat Importance.....	10-1-3
Terrestrial.....	10-1-3
Peatlands .....	10-1-4
Springs .....	10-1-4
Streams .....	10-1-5
Collection Methods .....	10-1-5
CLASS BRANCHIOPODA, ORDER CLADOCERA .....	10-1-6
Adaptations .....	10-1-6
Structural.....	10-1-6
Life Cycle Strategies.....	10-1-6
Habitats .....	10-1-6
Terrestrial.....	10-1-6
Peat Bogs .....	10-1-7
Aquatic.....	10-1-9
Lakes.....	10-1-9
Streams .....	10-1-10
CLASS MAXILLOPODA, SUBCLASS COPEPODA .....	10-1-10
Adaptations .....	10-1-11
Structure.....	10-1-11
Life Cycle Strategies.....	10-1-11
Feeding .....	10-1-12
Habitats .....	10-1-12
Terrestrial.....	10-1-12
Antarctic .....	10-1-14
Peat Bogs and <i>Sphagnum</i> .....	10-1-14
Aquatic.....	10-1-17
Mossy Tarns .....	10-1-17
Springs .....	10-1-17
Rivulets .....	10-1-18
Streams .....	10-1-18
Splash Zones.....	10-1-19
Cave Pool.....	10-1-19
Summary .....	10-1-20
Acknowledgments.....	10-1-20
Literature Cited .....	10-1-20

# CHAPTER 10-1

## ARTHROPODS: CRUSTACEA – COPEPODA AND CLADOCERA



Figure 1. *Simoecephalus* sp. with eggs in the carapace. Note the white *Vorticella* on the lower left edge of the carapace and near the base of the antennae. Photo by Jasper Nance through Creative Commons.

### SUBPHYLUM CRUSTACEA

Crustaceans (Figure 1) are those tiny arthropods that most of us have never noticed on the bryophytes. But in some habitats, and some parts of the world, the bryophytes – invaders of land – are home for such terrestrialized arthropods.

This large subphylum is mostly marine or aquatic, including such familiar animals as barnacles, crabs, crayfish, krill, lobsters, and shrimp (Wikipedia: Crustacean 2011). But it is mostly the smaller animals, the microcrustacea, that inhabit the bryophytes. The Crustacea are distinguished from other arthropods by their two-parted limbs (**biramous**; e.g. the pincers on the end of a crab claw or divided antenna of *Daphnia* or *Simoecephalus* – Figure 13) and a life cycle that includes a **nauplius** larva stage (first larval stage of many crustaceans, having an unsegmented body and usually a single eye, Figure 2), although most have additional larval stages after that. Almost all of them have a chitinous exoskeleton.



Figure 2. Nauplius of copepod. Photo from Wikipedia Creative Commons.

## Reproduction

Most crustaceans have separate sexes, but some change sex and many are **parthenogenetic**, with females producing viable eggs that develop into new organisms in the absence of fertilization (Wikipedia: Crustacean 2011). Eggs are generally released into the water column, but some **isopods** form a brood pouch and carry their eggs and young around with them. Many **copepods** form egg sacs that hang from the body until the young hatch. **Decapods** typically carry their eggs attached to their swimmerets. The **meiofauna** [small metazoans that pass through 500µm or greater sieves, but are retained on 40 or 62 or 40 µm sieves (Dražina *et al.* 2011)] of springs typically have shorter life cycles, permitting such groups as cyclopoid copepods to have a rapid recruitment ability (Robertson 2002) and other copepods and ostracods to develop rapidly compared to insects, completing their development in only a few months (Dole-Olivier *et al.* 2000).

## Dispersal

As with mites and other bryophyte dwellers, microcrustacea might be dispersed on a "magic carpet" – bryophyte fragments on which they are living. Sudzuki (1972) tested this hypothesis by exposing moss-soil samples to wind velocities of 2.9 m s<sup>-1</sup>. Sampling at distances of 100-400 cm from the "wind" source, they determined that even after 2 months, wind velocities up to 2 m s<sup>-1</sup> failed to disperse the Crustacea. Those animals dispersed were primarily protozoa. Nevertheless, encysted animals could get dispersed with bryophyte fragments or even with moss clumps that get carried by small mammals or wind.

## Habitat Fragmentation

Microarthropods must move from one leaf patch to another, or from hiding places to food sources. During this time, especially if disturbed during the daytime, they are vulnerable to desiccation. Gonzalez *et al.* (1998) experimented with such fragmented microcosms to determine parameters that led to success of the inhabitants. They found that when microecosystems were fragmented, species declines occurred. But when the patches were connected by habitat corridors, much as has been shown for large mammals, both abundance and distribution of the fauna experienced a rescue effect through immigration. Bryophytes can often serve as such corridors, providing places to replenish lost moisture and to hide from predators.

Gonzalez and Chaneton (2002) used bryophyte habitats for experimentation. They fragmented the bryophyte communities and found that this system likewise experienced loss of both faunal species richness and community biomass. Rare species were more likely to become extinct. Moss habitat corridors that connected fragments to a larger "mainland" of bryophytes permitted immigration and maintained microarthropod richness, abundance, and biomass in the fragments.

While we tend to view corridors as continuous suitable habitats, such continuity is probably not necessary for the larger arthropods like isopods. They can use the bryophyte clumps as islands of safety between larger suitable habitats such as leaf litter.

## Habitat Importance

Krebs (2001) reminded us that habitat heterogeneity is related to the creation of more ecological niches. Bryophytes can create many niches, providing protected space for the small microcrustaceans. Srivastava *et al.* (2004) contend that moss-arthropod ecosystems form natural microcosms that are useful for testing such concepts as fragmentation, metacommunity theory, and connections between biodiversity and ecosystem processes. Their small size, short generation times, hierarchical spatial structure, and contained, definable systems provide advantages in conducting field experiments that are subject to natural conditions and interactions with neighboring communities. The authors argue that "natural microcosms are as versatile as artificial microcosms, but as complex and biologically realistic as other [larger] natural systems."

## Terrestrial

Acosta-Mercado *et al.* (2012) found strong support for the hypothesis that abiotic factors (especially water chemistry of the bryophytes and pH) are important determinants of terrestrial microcrustacean diversity. They added that water-holding capacity is correlated with the morphology and canopy structure of the bryophytes. Roughness of the bryophyte canopy in the Bahoruco Cloud Forest, Cachote, Dominican Republic, was important in determining differences in species composition. For amoebae, the lowest species richness was on *Acroporium pungens* (Figure 3), a species with low roughness and faunal density, whereas *Thuidium urceolatum* had the highest roughness index, highest faunal richness, and highest species density. But for the 26 microcrustacean morphospecies among 11 bryophyte species, there was no detectable canopy effect on faunal richness or density. The lowest density of 1 individual per 50 cm<sup>2</sup> was on the cushions of *Leucobryum* (Figure 4) with a maximum of 6±3.37 on the same area of the thallose liverwort *Monoclea* (Figure 5), suggesting that openness of the community might play a role in diversity.



Figure 3. *Acroporium pungens* in the Neotropics, a species with low roughness and low faunal density. Photo by Michael Lüth, with permission.





Figure 4. *Leucobryum glaucum* cushion, a species with low faunal density. Photo by Janice Glime.



Figure 5. *Monoclea forsteri*, a liverwort that harbors a relatively high microcrustacean diversity. Photo by Jan-Peter Frahm, with permission.

## Peatlands

Peatlands, for our purposes those habitats dominated by *Sphagnum* and not including other types of peatlands (Figure 6), provide a mix of moist and dry mosses and pools influenced by those mosses. The "terrestrial plankton" are often sensitive to high CO<sub>2</sub> concentrations and low O<sub>2</sub> tensions such as those found among rotting leaves and other areas with high rates of decomposition (Stout 1963). For these organisms with good tolerance for low pH (sometimes below 4.0), *Sphagnum* provides a suitable habitat. Krebs (2001) found that the center of the *Sphagnum* moss mat had a higher species diversity than the edges, perhaps due to additional niches (habitat heterogeneity) resulting from the plant-associated species dwelling there.

On the other hand, the low pH created through cation exchange and organic acids produced by mosses in the genus *Sphagnum* (Figure 6) is detrimental to many organisms. Hillbricht-Ilkowska *et al.* (1998) examined the role of pH on Crustacea and other organisms by providing powdered lime to the system. Measurements after 1-4 years and 20-23 years indicated that both the water Ca and that of the sediment were permanently raised. This change coincided with a significantly increased rate of decomposition and an increase in species richness and diversity of crustaceans, among others. Overall diversity was doubled. The treatment eliminated peatmosses from encroaching on the lake but had no effect on those of the surrounding area.



Figure 6. Bohemia bog with *Sphagnum cuspidatum*, *S. denticulatum*, and others, showing the varied habitats of hummocks, hollows, and small pools available to bog fauna. Photo by Jonathan Sleath, with permission.

To add to this image of *Sphagnum* (Figure 6) as an unfriendly substrate, Smirnov (1961) stated that few animals were specialized to gain their nutrition by consuming emerged *Sphagnum*. He cited only one species of flies whose larvae are known to feed directly on *Sphagnum*. On the other hand, in such *Sphagnum* lakes the bladderwort, an insectivorous plant, traps and digests Crustacea such as *Daphnia* (Cladocera) – a not so friendly place for many.

But *Sphagnum* (Figure 6) may play a more positive role in the lives of these fauna. *Sphagnum* has long been known for its antibiotic properties; it was used as a wound dressing in WWI. Could it protect the crustaceans from fungal or bacterial attacks? Furthermore, for these invertebrates it may serve as a refugium – a place to escape predators (Kuczyńska-Kippen 2008), possibly due to its antifeedant properties as well as small hiding places.

## Springs

Among the favored habitats of limnoterrestrial (living in wet films on land) Crustacea are mosses of springs, *i.e.* these Crustacea are crenophilous, where temperature and pH were important determinants of community composition in four Northern Apennine springs (Bottazzi *et al.* 2011). Mosses in these springs usually had harpacticoid copepods and ostracods representing the Crustacea. The moss inhabitants had a seasonality, whereas drift assemblages did not. Bottazzi *et al.* suggest that the mosses were important in increasing the species diversity in these springs.

Springs are often a transitional habitat between aquatic and terrestrial systems. Even within the spring habitat, such a transition is typical, and moisture zones within the habitat can change as the seasons and weather change. Thus, the bryophytes of this habitat provide not only a refuge, but an avenue (more like a labyrinth) where macroinvertebrates can travel to escape the receding preferred moisture level.

Crustacea are not usually seen among bryophytes, but in some areas they can be quite abundant. For example, Michaelis (1977) reported that at Pupu Springs in New Zealand, there were ten species of bryophytes. The fauna included Crustacea among the most abundant groups. Suren (1993) suggests that the abundance of crustaceans in the New Zealand bryofauna may be due to the absence of some of the bryophyte dwellers found elsewhere, *i.e.* some families of Trichoptera (caddisflies), Plecoptera (stoneflies), and Ephemeroptera (mayflies).

Bottazzi *et al.* (2011) reported the **ostracods** and **Harpacticoida** (an order of copepods) among the three most abundant taxon groups among mosses in northern Apennine **rheocrene springs** (springs that become streams immediately upon emerging from the ground). Like Michaelis (1977) and Suren (1993), they suggested that favorable habitats, including mosses, accounted for the high diversity and the large numbers of these two crustacean groups.

Bottazzi *et al.* (2011) concluded that emergent mosses were important in increasing species diversity of these springs (see also Barquín & Death 2009; Ilmonen & Paasivirta 2005). Bryophytes act as an ecotone between the aquatic and terrestrial habitat by creating a range of microhabitats that vary both horizontally and vertically (Lindgaard *et al.* 1975; Thorup & Lindgaard 1977), including the **madicolous** zone (having thin sheets of water flowing over rock surfaces). These provide a range of moisture conditions that permit the meiofauna to migrate to a more suitable location as moisture conditions change. While providing a refuge from rapid flow (Madaliński 1961; Elliot 1967; Gurtz & Wallace 1984; Suren 1992; Glime 1994), bryophytes provide a variety of food sizes in trapped particulate matter (Habdija *et al.* 2004). Linhart *et al.* (2002c) demonstrated a direct association between harpacticoid copepods, including nauplii, and trapped organic and mineral matter among the mosses.

Lindgaard *et al.* (1975) found that in the Danish spring at Ravnkilde these vertical and horizontal differences among the bryophytes provided a source of diversity among the macroinvertebrates. They found that whereas the horizontal zonation sported different assemblages of species, the fauna of the neighboring stones had little influence on the moss fauna. More importantly, the flow rate and available detritus as a food source could account for the horizontal differences.

Lindgaard *et al.* (1975) found that the numbers of individuals fluctuated throughout the year, corresponding with changes in the life cycle stages of the dominate species. Bryophyte habitation is also seasonal in Northern Apennine springs, with a maximum in the spring and minimum in winter, whereas seasonal habitation is nearly constant in non-bryophyte areas sampled by the traps Bottazzi *et al.* (2011). On the other hand, permanent meiofauna had its minimum in autumn; temporary meiofauna of the mosses peaked in spring, then decreased thereafter.

## Streams

Bryophytes in streams create a rich source of invertebrate fauna, so much so that the aquatic moss *Fontinalis antipyretica* (Figure 7) was transplanted to streams in South Africa to increase the food source for

trout (Richards 1947). The bryophytes are able to provide a refuge from fast-flowing water and to increase stream heterogeneity (Tada & Satake 1994; Wulffhorst 1994; Dražina *et al.* 2011).



Figure 7. *Fontinalis antipyretica*. Photo by Jan-Peter Frahm, with permission.

Despite their seeming rarity among bryophytes, Amos (1999) included ostracods, cladocerans, copepods, and amphipods as "life in the torrent" in the UK – a description of the inhabitants of *Fontinalis* (Figure 7). His point was that "all was quiet" at the bottom of the moss clump despite the torrent occurring at the surface.

Linhart *et al.* (2002a), in Europe, found that regulated channels had a much greater meiofauna, including **Cladocera** and **Harpacticoida** (copepods), when the channel was overgrown by aquatic bryophytes, in this case *Fontinalis antipyretica* (Figure 7). In a different stream, the meiofauna of mosses was an order of magnitude higher than that in the surrounding mineral substrate (Linhart *et al.* 2000), but the crustaceans were not a significant part of this fauna. Rather, the density of the **Harpacticoida** was the second most abundant group in the gravel, where the fine particulate matter was also highest compared to that among the mosses. They further determined that high flow rates approaching the mosses had a negative impact on the crustaceans [**Cladocera**, **Ostracoda**, and **Cyclopoida** (an order of copepods)], although the velocity seemed to have no effect on the **Harpacticoida** (Linhart *et al.* 2002b, c). They suggested that fine detritus trapped by the *F. antipyretica* provided food for the **harpacticoid copepods**. It is interesting that in their 2000 study Linhart *et al.* suggested that it is "questionable whether *F. antipyretica* can serve as a refuge from the current for stream meiobenthos," a seeming contradiction to their conclusions in a different stream. It appears that food is the primary factor in distribution of the microcrustacea, but that does not rule out the role of the mosses as a refuge when sufficient food is present.

## Collection Methods

Methods of collection can have a biasing effect on the relative numbers of taxa collected. Copepods and other **Crustacea** in aquatic habitats can be collected by squeezing mosses into a collection bottle or squeezing the mosses in place and collecting the crustaceans downstream from the mosses with a plankton net (Gerecke *et al.* 1998; Reid 2001; Stoch 2007). Copepods, ostracods, and



amphipods may all be extracted from forest litter by the Berlese funnel, but as the litter dries out many will perish before they can escape (Stout 1963). Heat extraction can present the same problem. Chapman (1960) was successful in extracting terrestrial ostracods alive by slowly drying out the leaf litter (but it would work for bryophytes as well) in a Berlese funnel, using a water-jacket at 40° C to avoid overheating, in which case the ostracods close their valves and stop moving. The end of the funnel led to water rather than alcohol.

## CLASS BRANCHIOPODA, ORDER CLADOCERA

The class name of **Branchiopoda** literally means gill feet and refers to the **pereiopods** by which the aquatic species can swim. The order name **Cladocera** derives from the Ancient Greek κλάδος (kládos, "branch") and κέρας (kéras, "horn").

### Adaptations

#### Structural

Cladocera are a predominately aquatic group of small individuals known as water fleas (no relationship to the insect group of fleas). They swim using their antennae, using a series of jerks similar to the hops of a flea. Some have adapted to terrestrial habitats with free water, such as bromeliad basins. Others are able to use the film of water from the capillary spaces and leaf surfaces of bryophytes. Not only are the antennae important for swimming, but they are also powerful chemical sensory organs (Ecomare 2014). They can use these not only to find food, but also to detect the presence of enemies. The body of a cladoceran is a valve-like carapace that covers an unsegmented thorax and abdomen. Adults have a single compound eye.

#### Life Cycle Strategies

Cladocerans spend most of their lives as a female population that reproduces multiple times asexually by **cyclical parthenogenesis**. When conditions become unfavorable, they produce male offspring and subsequently reproduce sexually, producing resting eggs that remain within the carapace (*Daphnia*; Figure 8). In this state, they can dry out and travel long distances on wind currents or as hitch hikers on other travelling animals or even moss fragments. In fact, some of these dormant eggs are known to remain viable for 70-80 years in Lake Superior sediments (Kerfoot & Weider 2004) and can even survive the digestive tracts of birds (Figuerola & Green 2002).

### Habitats

Cladocera are primarily aquatic and marine, but a few are adapted to terrestrial living, taking advantage of films of water, pools in bromeliads, and other surfaces where they have easy access to water when they are active.

#### Terrestrial

Since Cladocera live primarily in fresh or marine water, living on land requires special adaptations for both water conservation and locomotion. It seems that few cladoceran species have accomplished this, or we simply

haven't found them yet. There are indications that appendage reduction is a terrestrial adaptation in this group. After all, why waste energy to make appendages that are not useful. Frey (1980) describes the non-swimming chydorid *Bryospilus* (Figure 9) from wet cloud forests as lacking a compound eye, a change that still requires explanation. The genus resembles the limnoterrestrial genus *Monospilus*, possibly through convergence. They exhibit reduced setation on their antennae and trunk limb, perhaps facilitating their slow crawl among wet bryophytes as high as 3-5 m above the forest floor.



Figure 8. *Daphnia pulex* with three eggs shown here to the right of the digestive tract. Photo by Paul Hebert, through Wikimedia Commons.

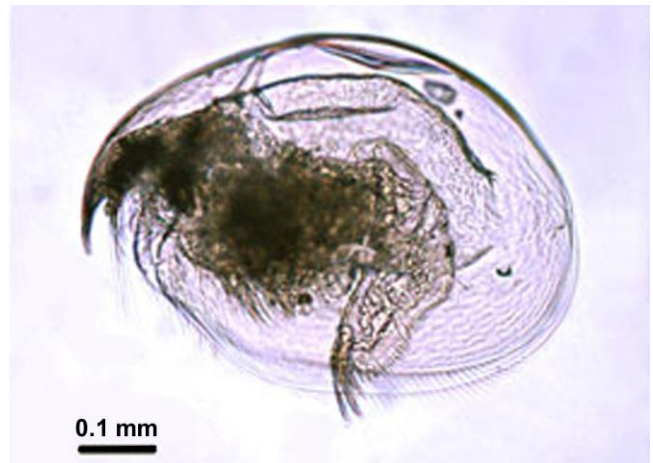


Figure 9. *Bryospilus repens*, a chydorid cladoceran that lives mostly in wet moss.. Photo by Francisco D. R. Sousa <Cladocera.wordpress.com>, with permission.

Existing 3-5 meters above the rainforest floor are Cladocera that crawl from place to place, unable to swim. Frey (1980) reported the cladoceran *Bryospilus repens* (Figure 9), a semiterrestrial species known from wet mosses in Puerto Rico, Venezuela, and New Zealand, and

*Bryospilus bifidus* from New Zealand, both in the same subfamily of Chydoridae as *Alona* (Figure 10-Figure 11), a common cladoceran from springs. Resting eggs are often buried in deep masses of vegetation (Powers & Bliss 1983) where they are protected from water loss. Dispersal of fragments of mosses they inhabit can aid in dispersal of both eggs and adults to new sites. Frey suggested that the mossy habitat in the rainforest exhibited the same continuity through time as ancient lakes, thus being a likely site for even more endemic species. Van Damme *et al.* (2011) consider *B. repens* (Figure 9) to be a "well known" species that lives in wet moss. They consider its occasional presence in river samples to be the result of individuals that got washed into the river from these mossy homes.

There may be more species of these tiny cladocerans hiding among bryophytes in terrestrial habitats. These organisms are typically studied by aquatic biologists who spend their time looking at plankton. Terrestrial bryophyte habitats are rarely studied with the aim of locating **Cladocera**. I have to wonder if somewhere there might be some Cladoceran species living in liverwort lobules.

### Peat Bogs

Living among *Sphagnum* (Figure 6) or in the bog pools requires a tolerance of low pH. Nevertheless, *Sphagnum* can increase the abundance of **Cladocera** by as much as tenfold in Swedish peatlands (Henrickson 1993). The heterogeneity of the *Sphagnum* habitat illustrated in Figure 6 provides shelter and refuge against predation while being a suitable foraging site. The bryophytes further contribute to this habitat through their production of antibiotics, organic acids, and cation exchange.

Bog lakes can support a number of species of Cladocera. Minelli (2004) listed *Alona quadrangularis* (Figure 10), *Alona affinis* (Figure 11), *Simocephalus exspinosus* (Figure 12), *S. vetulus* (Figure 13), and *Ceriodaphnia pulchella* as being among the common species in bog lakes in Italy. Hingley (1993) reported *Streblocerus serricaudatus* (Figure 14) and *Acantholeberis curvirostris* (Figure 15) swimming in UK peat pools. Macan (1974) likewise reported the latter species in *Sphagnum* (Figure 6). *Chydorus piger* (Figure 16) is typical of bare substrates such as rock or sand, but including *Sphagnum*, and is known from acidic pools in peatlands in Europe (Duigan & Birks 2000).

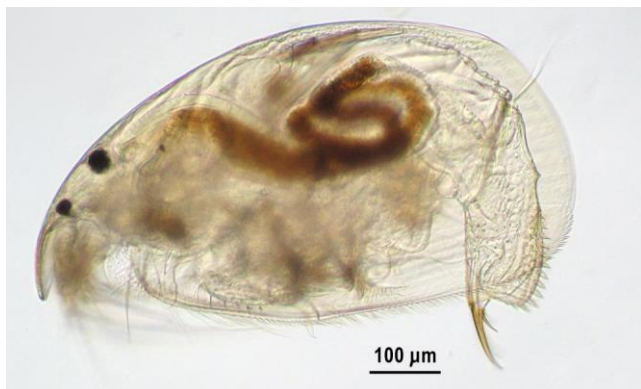


Figure 10. *Alona quadrangularis*, a common species in bog lakes. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 11. *Alona cf. affinis*, a common species in bog lakes. Photo by Yuuji Tsukii, with permission.



Figure 12. *Simocephalus exspinosus*, a common species in bog lakes. Photo by Malcolm Storey through <<http://www.discoverlife.org/>>, through online license.

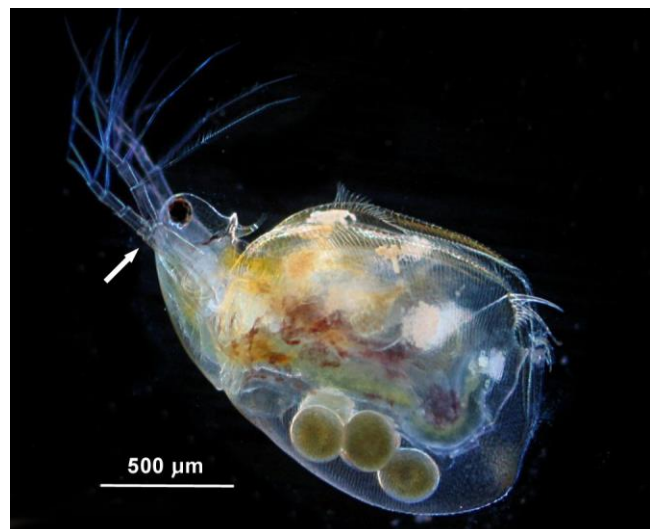


Figure 13. *Simocephalus vetulus*, a common species in bog lakes. Note the divided (biramous) antenna (**arrow**). Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



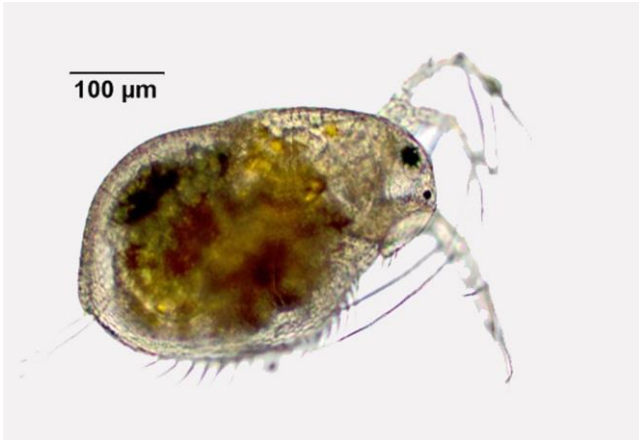


Figure 14. *Streblancerus serricaudatus*, a cladoceran that inhabits peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 15. *Acantholeberis curvirostris*, a cladoceran of peatland pools. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 16. *Chydorus piger*, a cladoceran from peatland pools. Photo by Angie Opitz, through online permission.

Kairesalo *et al.* (1992) considers the peatland habitat to be unsuitable for *Daphnia* (Figure 17) because the available food is "recalcitrant." In a lake in southern Finland that was bordered by the mosses *Warnstorfia* (Figure 18) and *Sphagnum* (Figure 6), the organic carbon excreted by *Warnstorfia* suppressed the growth of planktonic algae and provided little contribution to bacterial productivity. This meant that bacterial productivity was necessarily dependent on humic acids for their carbon source, resulting in decreased availability of this food source for the *Daphnia*. The predominantly particulate matter in the water was largely useless for the *Daphnia* as a food source.



Figure 17. *Daphnia*. Photo by Gerard Visser through Creative Commons.



Figure 18. *Warnstorfia exannulata*, a peatland moss that seems to be "recalcitrant," unable to provide food for the Cladocera living there. Photo from Biopix through Creative Commons.

Cladocera have played a role in reconstructing the history of some peatlands. Duigan and Birks (2000) report on *Sphagnum* (Figure 6) and other bryophytes from 9200 BP microfossils in western Norway with *Alonella nana* (Figure 19), *Alonella excisa* (Figure 20), and *Alona rustica* (Figure 21). *Alona rustica* is also known in peat bogs among mosses in Italy (Minelli 2004).



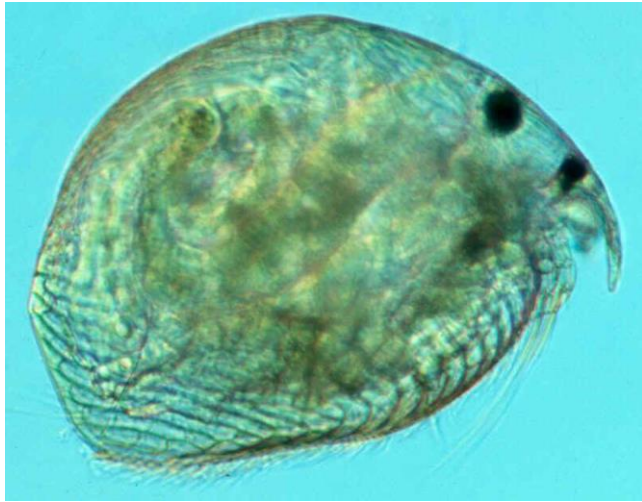


Figure 19. *Alonella nana*, a cladoceran from peat deposits in ~9200 BP. Photo from Great Lakes Research Laboratory, through public domain.



Figure 20. *Alonella excisa*, a cladoceran that occurs in peat deposits in ~9200 BP. Photo by Manuel Elias, ECOSUR, through Creative Commons.

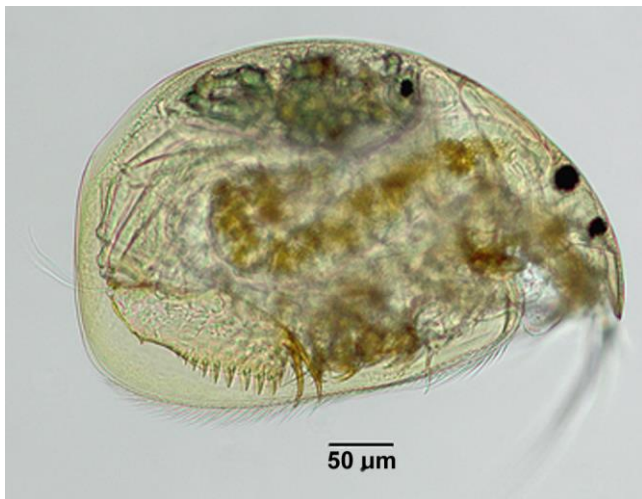


Figure 21. *Alona rustica*, a cladoceran that lives among bryophytes on stream banks. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

## Aquatic

### Lakes

Typically, cladocerans are rare among aquatic mosses, being adapted for planktonic life. However, in the subAntarctic lakes of South Georgia, the most common invertebrate was the cladoceran genus *Alona* (Figure 22), with 2544 individuals in a liter of water (Hansson *et al.* 1996). Several species in this genus were present, with the greatest numbers among mosses that extended into shallow lakes. In fact, the littoral mosses had the highest number of invertebrate species (20) and abundance (1539 individuals) of invertebrates in those lakes. With increasing UV levels reaching the shallow Antarctic lakes, mosses may provide refugia that protect these invertebrates from UV damage.



Figure 22. *Alona* sp., a genus with a number of terrestrial bryophyte-dwelling species. Photo by Yuuji Tsukii, with permission.

Van Damme *et al.* (2011) explain the absence of *Alona karelica* in littoral samples of European lakes by suggesting that it may actually be a terrestrial cladoceran that is normally associated with moss. This species has been reported twice from *Sphagnum* (Figure 6) in Europe (Flößner 2000; Kuczyńska-Kippen 2008) and its European distribution coincides with that of regions of high *Sphagnum* diversity (see Séneca & Söderström 2008; Van Damme *et al.* 2011). Another species of *Alona*, *A. bromelicola*, is from Nicaragua and lives in the basins of bromeliads (Van Damme *et al.* 2011). Yet another species, *Alona rustica* (Figure 21), is present in collections of bryophytes from stream banks in Italy (Margaritora *et al.* 2002), another transitional habitat. Such transitional habitats often have both higher diversity and density of organisms, a phenomenon known as the **edge effect** (Leopold 1933; Lay 1938; Good & Dambach 1943; Bider 1968; Wiens 1976).

Kuczyńska-Kippen (2008) examined the role of *Sphagnum* (Figure 6) compared to open water for zooplankton in a lake in Poland. The highest species diversity values occurred in the peat mat (mean = 0.67 for crustaceans compared to 1.76 for rotifers), whereas the



lowest values occurred in open water (0.36 and 0.99 respectively). The cladocerans present in the transition zone between the peat mat and the open water seem to relate to the presence of both invertebrate and vertebrate predators, and competition between the large cladocerans and smaller rotifers. For the cladocerans, *Sphagnum* (Figure 23) can serve as a refugium to protect them from other invertebrate predators.



Figure 23. *Sphagnum cuspidatum* mat (foreground) and nearby hummock (upper left), habitats where one can find more Cladocera than in the open water (upper left). Photo by Michael Lüth, with permission.

Cammaerts and Mertens (1999) discovered *Bryospilus repens* (Figure 9) in the **Palaeotropics** (tropical areas of Africa, Asia, and Oceania, excluding Australia) of western Africa, where it occurred in vernal pools of forests. This dispels the notion that this genus is strictly a moss dweller.

One problem in sorting out the Cladocera-bryophyte relationship is that species descriptions frequently fail to include the substrate, reporting only the general habitat, if even that.

### Streams

Stream drift, a popular topic in the 60's and 70's, is generally a phenomenon we relate to the insects and other macroinvertebrates. But microcrustacea can be part of this as well. For moss-dwelling Cladocera, this is a means to get from one moss clump to another in an unfriendly moving environment. Peric *et al.* (2014) found that of 60 invertebrate taxa in a moss-rich karst system in Croatia, six were annelids and arthropods from the meiofauna, representing 35% of the total drift, but among the most abundant drift organisms were several species of *Alona* (26.7%) (Figure 22), a cladoceran known for being a moss-dweller (Hansson *et al.* 1996; Van Damme *et al.* 2011). The drift was lowest in winter and highest in autumn and late spring to early summer.

## CLASS MAXILLOPODA, SUBCLASS COPEPODA

The name **Copepoda** comes from the Greek word *κοῦπιπποδ*, which literally means oar-feet (Wikipedia: Copepod 2014). Copepods are microcrustacea, mostly 0.5-2 mm (Encyclopaedia Britannica 2012), usually occurring as planktonic or benthic organisms and not ones we would

expect to be frequent in moss communities. The entire group comprises about 13,000 species with three of its ten orders being the most common (**Harpacticoida**, **Cyclopoida**, **Calanoida**) and containing the ones known from bryophytes (Wikipedia: Copepod 2014). Copepods have two pairs of antennae and a single red compound eye (in most). They are perhaps the fastest organisms alive, swimming in irregular spurts (Kiørboe *et al.* 2010). Some of the meiofauna taxa have switched to **direct development** (lacking the larval stage) and care of their young (Dahms & Qian 2004), traits that are absent in most copepods but that are beneficial in a terrestrial environment.

The **Harpacticoida** (Figure 24) have a short pair of first antennae (Figure 25), often a somewhat wormlike body, and are mostly benthic (living on the bottom) (Wikipedia: Harpacticoida 2013). Nevertheless, Dumont and Maas (1988) consider the harpacticoid copepods to be widespread in wet habitats such as wet mosses. The harpacticoid copepods include crawlers, walkers, and burrowers (Dole-Olivier *et al.* 2000), pre-adapting the crawlers and walkers to mobility in the water film of bryophytes.



Figure 24. Terrestrial **Canthocamptidae** male, a harpacticoid copepod. Photo by Walter Pfliegler, with permission.



Figure 25. *Canthocamptus*, a harpacticoid copepod showing antennae. Photo by Yuuji Tsukii, with permission.



The **Cyclopoida** (Figure 26) are mostly **planktonic** (live in water column and float or drift – can't swim against a current) (Wikipedia: Cyclopoida 2013). Their antennae are longer than those of Harpacticoida but shorter than those of Calanoida, reaching no farther than the thorax. They are capable of rapid movement.



Figure 26. *Cyclops vicinus*, a cyclopoid copepod carrying egg sacs. Photo by Ralf Wagner <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.

The **Calanoida** (Figure 27) are also mostly planktonic species (Wikipedia: Calanoida 2013). Unlike the short antennae of the Harpacticoida, the first antennae of the Calanoida extend about half the length of the body or more.

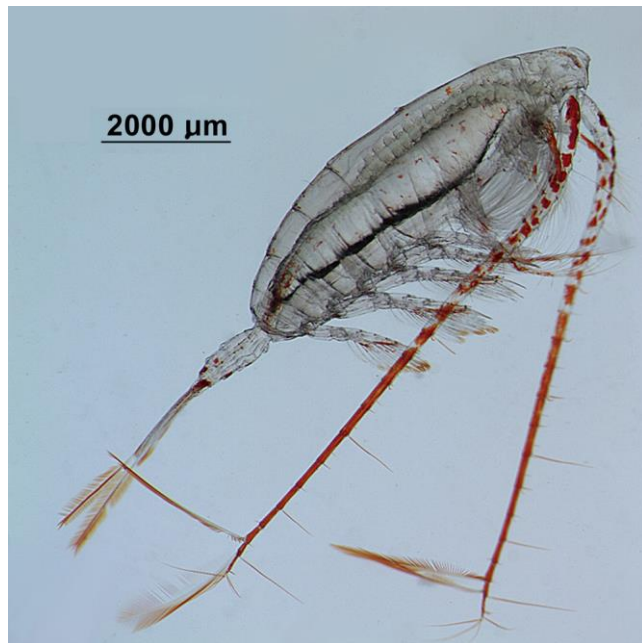


Figure 27. *Neocalanus cristatus*, a calanoid copepod showing the long antennae. Photo by Seward Line <[www.sfos.uaf.edu](http://www.sfos.uaf.edu)>, with online permission for educational use.

Copepods are known for their egg longevity, with some surviving as much as 322 years (Hairston *et al.* 1995).

## Adaptations

Copepods, like several other crustacean groups, have evolved to a terrestrial life style, but still live where water is generally available (Stout 1963). Bryophytes provide such a habitat. Stout suggests that through evolutionary time both copepods and ostracods moved from streams to adjoining moss carpets and currently are able to live among *Sphagnum* (Figure 23) as well as forest litter (Harding 1953, 1955).

Bryophyte-dwelling copepods are not very numerous, which probably explains, in part, the absence of descriptions of adaptations to the bryophytic habitat. Nevertheless, one might consider the adaptations to a terrestrial life style as exemplary of bryophytic adaptations. One such adaptation is the absence of hemoglobin (Green 1959). This is a stretch, because it appears that this pigment has evolved primarily in those species with a parasitic life style and a limited number of mud-dwelling taxa. Nevertheless, it suggests that oxygen is in adequate supply in the bryophytic habitat, so energy-requiring pigment development is not necessary.

## Structure

The moss-dwelling **nauplius** (larval stage; Figure 28) of the copepod uses its antennae for swimming and possesses a single eye that can disappear in some species in later developmental stages. The copepod eye, in at least some species, senses the direction of light and permits the copepod, by moving its tail, to keep its back oriented toward the light (Land 1988). This behavior furthermore permits the copepod to distinguish its own species from other species by the movement patterns. Directed movement in response to light seems to be useful in minimizing exposure to UV light in tidal areas (Martin *et al.* 2000). These light avoidance behaviors are probably less useful among bryophytes.

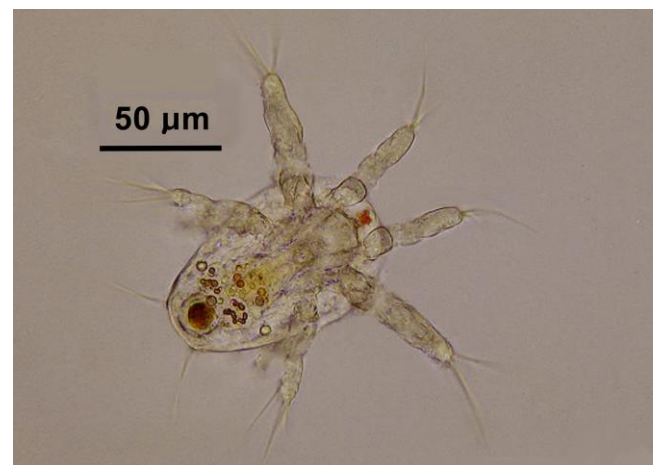


Figure 28. Copepoda nauplius, the immature state. Photo by Graham Matthews <[http://www.micromagus.net/microscopes/pondlife\\_copepoda.html](http://www.micromagus.net/microscopes/pondlife_copepoda.html)>, with permission.

## Life Cycle Strategies

Whether living in water that freezes, pools that dry up, or among mosses and other terrestrial habitats, life cycle strategies are important in enduring unfavorable seasons

(Santer 1998). Terrestrial habitats are all unstable. Evolution favors traits that help the copepods sense and prepare for these potentially deadly periods. These strategies include dormancy and migration as escape mechanisms, but also include synchronizing growth and reproduction with favorable periods.

Dormancy is a common trait among copepods, particularly in higher and temperate latitudes (Dahms 1995; Williams-Howze 1997). It permits them to survive periods of desiccation and other unfavorable conditions. The timing of dormancy varies with the species and can occur in different forms in multiple life cycle stages, including desiccation-resistant resting eggs, arrested larval development, **encystment** of juveniles and adults (Deevey 1941; Dahms 1995), and arrested development of adults (Dahms 1995; Williams-Howze 1997). Dormancy saves energy during a time when living conditions are unfavorable. In addition to facilitating copepod survival during desiccation, dormancy helps copepods escape unfavorable temperatures, insufficient oxygen availability, limited food availability, and predation.

Among these dormancy strategies, one potential adaptation is encystment. *Canthocamptus staphylinoides* (Figure 29) is a harpacticoid copepod that encysts (Deevey 1941). Some members of this genus are known from mosses in the aquatic environment and peat bogs, where encystment can permit them to survive not only desiccation but also unfavorable temperatures.



Figure 29. *Canthocamptus staphylinoides*. Photo from US Geological Survey, through public domain.

**Diapause** can be defined as a delay in development in response to regular and recurring periods of adverse environmental conditions. In its narrow sense, it is initiated and terminated by triggers such as photoperiod, temperature, chemical cues, population density, and physiological factors (Dahms 1995).

### Feeding

Fryer (1957a, b) considered chance encounter to be a primary mechanism in finding food for the mostly planktonic copepods. Nevertheless, chemoreceptors help them to distinguish edible from inedible food particles and thus may help somewhat in locating food. The carnivorous diet appears to be the primitive condition, with the change to an algal diet facilitating adaptive radiation.

### Habitats

Reid (1986, 1987, 1999, 2011) has contributed considerably to our knowledge of bryophyte-dwelling

copepods. She reported them from such overlooked habitats as mosses (including *Sphagnum* – Figure 23) and liverworts, as well as from tree holes (Reid 1986). She described the new species *Muscocyclops thersasiae* from Brazil, primarily from soils, but also from mosses. Reid (2001) considered the publications on the harpacticoids and small cyclopoids from mosses in humid climates to be so numerous that they were almost impossible to review. She found that such "aquatic" mosses as *Sphagnum* (Figure 23) and *Hypnum* (Figure 30) as well as those bryophytes from more humid habitats provide homes for their own unique communities of copepods. Stoch (2007) attributes the copepod abundance to the complex spatial structure and high availability of food resources among bryophytes. In their study on *Fontinalis antipyretica* (Figure 7) meiofauna in Central Europe, Vlčková *et al.* (2002) found that harpacticoid copepods were able to feed on organic matter in the size range of 30-100 µm trapped within the moss clumps.



Figure 30. *Calliergonella lindbergii* (= *Hypnum lindbergii*), a moss genus where copepods are known to live. Photo by Jan-Peter Frahm, with permission.

### Terrestrial

One would not expect a plankton organism like the copepods to occur on mosses on land, but a few have managed to venture into that habitat. Paul Davison (pers. comm. 9 November 2011) reported to me that harpacticoid copepods are well known from terrestrial mosses, but finding documentation of that has been challenging. Menzel (1921, 1925) reported both cyclopoid and harpacticoid copepods as moss dwellers. Bryophytes do not harbor a rich fauna, so they have not attracted much attention from the copepodologists. Nevertheless, those copepods that live among mosses can, at times, be important to ecosystem functioning. For example, the harpacticoid copepods are a first food source for the young salamanders living near and among the mosses (Paul Davison, pers. comm. 9 November 2011) (See Epiphytes below).

Scattered reports of terrestrial bryophyte-dwelling copepods, especially harpacticoids, occur in the literature (e.g. Olofsson 1918; Lang 1931), including mosses



(including *Sphagnum* – Figure 23) and liverworts as habitat.

The genus *Bryocamptus* seems to be among the more common taxa in the Eastern Hemisphere. *Bryocamptus pygmaeus* and *B. zschokkei* (Figure 31) occur primarily among mosses in Central Europe (Illies 1952). Harding (1958) reported *Bryocamptus stouti* from mosses in New Zealand.

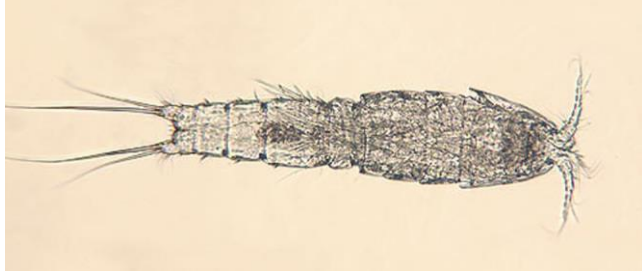


Figure 31. *Bryocamptus zschokkei* female, a moss dweller. Photo from US Geological Survey, through public domain.

Lewis (1984) reported twelve species of harpacticoid copepods from terrestrial mosses in forests and open areas in New Zealand. Lewis (1972a) found copepods in New Zealand among forest mosses that remained moist most of the year. These included *Elaphoidella silvestris* (see Figure 32), a copepod among damp mosses on the forest floor or nearby, but this species is limited to the damp conditions of higher altitude bush areas of North Island and dripping wet forests of the West Coast of South Island.



Figure 32. *Elaphoidella bidens*. Members of this genus live among damp mosses on the forest floor of New Zealand. Photo through Creative Commons.

Mrázek (1893) found the harpacticoid copepod *Maraenobiotus vej dovski* among mosses in Bohemia, and Harding (1953) reported them from woodland mosses in Scotland. These copepods are small and slender, permitting them to live an aquatic life in the water film among mosses (Harding 1953).

Scourfield (1939) reported *Bryocyclops* and *Muscocyclops* as living among mosses in Wales. With a name like *Bryocyclops muscicola*, one expects to find a moss-dweller. Reid (1999) reported this species, originally described from Indonesia, from a plant nursery in Florida, USA, apparently introduced with some of the plants, perhaps mosses. This is the only species of *Bryocyclops* known from continental US, although *Bryocyclops caroli* is known from Puerto Rico. In the Eastern Hemisphere the genus seems to be more common than in the Western Hemisphere, or perhaps just better known.

Menzel (1926) described the new species *Bryocyclops anninae* from moist mosses in Java and reported

*Bryocyclops bogoriensis* from the Fiji Islands among mosses and in tree holes. More recently, Watiroyram *et al.* (2012) listed ten additional wet moss dwellers in the genus *Bryocyclops* in Thailand, mostly near springs and waterfalls.

Harding (1953) reported that *Epactophanes* (Figure 54) and *Maraenobiotus* live in damp mosses in Europe. *Epactophanes muscicola* (in UK) avoids mosses that are very wet. Michailova-Neikova (1973) found that of the nine harpacticoid copepods living among wet mosses near water bodies on a mountain in Bulgaria, eight also lived among leaf litter.

In an apparently rare Western Hemisphere record of bryophyte dwellers, Rocha (1994) described *Metacyclops oraemaris* as a new species from moist moss in São Paulo, Brazil. In neighboring Suriname, Menzel (1916) found *Parastenocaris staheli* (see Figure 33) among mosses in the old leaf axils of the palm *Livingstonia*.



Figure 33. *Parastenocaris lacustris* female, member of a genus with species that live among epiphytic mosses. Photo from US Geological Survey, through public domain.

North American records seem to be almost non-existent. Nevertheless, Margaret (Maggie) Ray (pers. comm. 9 November 2011) told me that she found copepods in many of her bryophyte samples across North Carolina, USA. Paul Davison (pers. comm. 9 November 2011) likewise has often found them among bryophytic epiphytes in Alabama. Others have reported on them as a group (Camann 2011; Camann *et al.* 2011).

**Seepage Areas** – Seepage areas, typically with bryophytes, seem like a logical place to look for limnoterrestrial copepods. Scourfield (1932) found *Bryocyclops pygmaeus*, a common species, and *Speocyclops dimentiensis* among mosses of seeps on rock outcrops at Tenby in Wales. In New Caledonia, Hamond (1987) found *Fibulacamptus* among wet mosses as well as other wet terrestrial substrata.

Fiers and Ghenne (2000) suggested an interesting role for mosses in forests. They provide epigeal highways, especially for the tiny (~0.5 mm long) species, that help to connect the various patches of leaf litter and moist soils while also serving as a temporary or permanent habitat.

**Epiphytes** – It is interesting that one can see canopy food webs similar to those in the water, with bryophytes forming the habitat structure. In a (regrettably) rare North American study, Camann and coworkers (Camann 2011; Camann *et al.* 2011) report communities at 84 m above the forest floor in the redwood forest of California, USA. In these humus moss patches harpacticoid copepods dwell, encysting when conditions get dry. And further up the food web are Wandering Salamanders (*Aneides vagrans*; Figure 34), likewise bryophyte dwellers, that use the copepods as food. Most likely there are birds or other vertebrates that prey on the salamanders.



Figure 34. *Aneides vagrans*, a salamander whose larvae feed on terrestrial copepods. Photo by John P. Clare, through Creative Commons..

### Antarctic

Pesta (1928) described the harpacticoid copepod *Attheyella koenigi* (Harpacticoida: Canthocamptidae; see Figure 35) from mosses in a stream on the island of South Georgia in the Antarctic. Also on the island of South Georgia, it is likewise the family Canthocamptidae that has the only known copepod species living among mosses at the edges of shallow lakes (Hansson *et al.* 1996). Although only three larval forms were found, the mosses were the only location where these copepods appeared in that study of Antarctic lakes. Also among these Antarctic dwellers is the harpacticoid copepod *Marionobiotus jeanneli* (family Thalestridae) living among wet mosses (Pugh *et al.* 2002).



Figure 35. *Attheyella americana* immature. This genus has several bryophyte-dwelling species. Photo by US Geological Survey, through public domain.

### Peat Bogs and Sphagnum

Bog lakes and pools in peat bogs are often rich in copepod species (Minelli 2004). In the Italian bog pools and lakes (and likely throughout most of Europe as well), the copepods are represented by the orders Cyclopoida and Harpacticoida. The most abundant species are typically widespread predators, including *Megacyclops viridis* (Figure 36), *Macrocyclus albidus* (Figure 37-Figure 38), and *Diacyclops bicuspidatus* (Figure 39), and algal or detritus feeders including *Paracyclops fimbriatus* (see Figure 48), *Eucyclops serrulatus* (Figure 55), *Thermocyclops dybowskii* (see Figure 40), and *Tropocyclops prasinus* (Figure 41). *Megacyclops viridis* seems to have been introduced to the Great Lakes of North

America; in Austria it is commonly associated with salt pools (Kipp *et al.* 2012). The most common species in high-altitude peat bogs of Europe is *Acanthocyclops vernalis* (Figure 42), reaching an altitude of 2800 m in the Alps.



Figure 36. *Megacyclops viridis*, a widespread species whose habitats include peatlands. Photo by R. M. Kipp *et al.* at USGS, with permission.



Figure 37. *Macrocyclus albidus* female with egg sacs. Photo by Ralf Wagner at <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.



Figure 38. *Macrocyclus albidus* nauplius. Photo by Ralf Wagner at <[www.dr-ralf-wagner.de](http://www.dr-ralf-wagner.de)>, with permission.





Figure 39. *Diacyclops bicuspidatus* with egg sacs, a widespread predator that can be found on Antarctic bryophytes. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

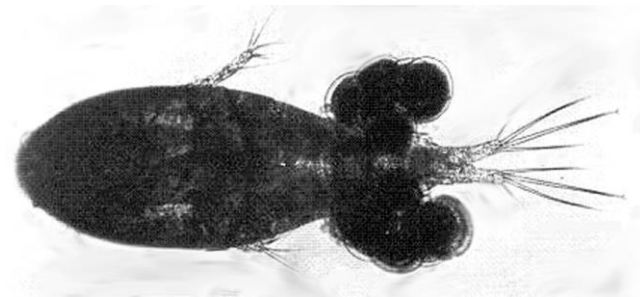


Figure 40. *Thermocyclops* sp. with egg sacs. Photo through Creative Commons.

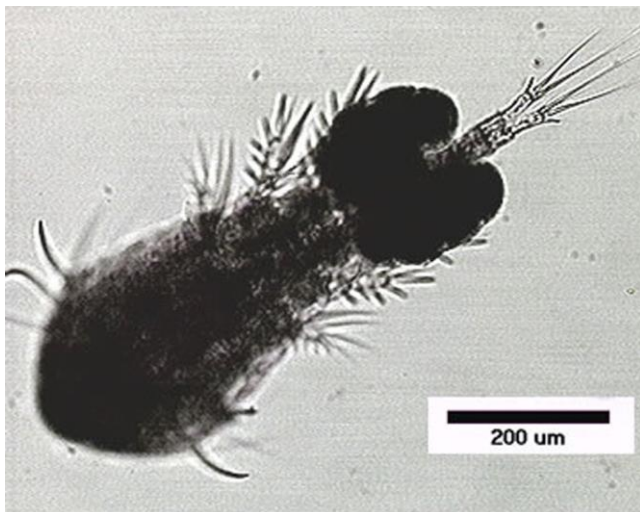


Figure 41. *Tropocyclops prasinus* with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 42. *Acanthocyclops vernalis* female with egg sacs. Photo from Haney, J. F. *et al.* 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.

Peat bogs, with a ground cover of *Sphagnum* species (Figure 43), provide the film of water needed by limnoterrestrial copepods. *Diacyclops languidus* and *D. hypnicola* (see Figure 44) are small species adapted to living in the water film on the mosses and characteristic of peat bogs in the Alps, Apennines, and central and northern Europe (Minelli 2004). Among European alpine *Sphagnum* and other moss cushions one can find *Bryocamptus pygmaeus*, *Epactophanes richardi* (Figure 54), and *Phyllognathopus viguieri*. Barclay (1969) found the latter species in New Zealand among mosses at the base of gravel piles in the winter when the mosses become quite soggy. A species of *Bryocyclops* is common in this same habitat.



Figure 43. *Sphagnum* blanket bog. Photo through Creative Commons.





Figure 44. *Diacyclops* sp., a genus of small copepods with some species adapted for living in the water film of bog mosses. Photo from USGS, through public domain.

Stoch (1998b) originally described the new species *Moraria alpina* and re-described *M. radovnae* (see Figure 45) from the Alps of Italy and Slovenia, where they occurred among mosses, in bogs, and in interstitial spaces in brooks. Additional European alpine species, for example *Bryocamptus veidovskji*, *Elaphoidella gracilis*, *Moraria mrazeki*, *M. alpina*, *Maraenobiotus veidovskji*, and *Hypocamptus brehmi*, live only in peat bogs and interstitial mountain habitats (Minelli 2004). In Britain, one can find *Moraria arboricola* among *Sphagnum* (Figure 43), as well as in leaf litter and tree hole pools (Fryer 1993). It seems none of these are strict **tyrphobionts** (living only in peat bogs and mires).



Figure 45. *Moraria laurentica* female, member of a genus including moss dwellers in the Antarctic South Georgia Island and known from mossy swamps and wet mosses on stream banks in the Great Lakes area, USA. Photo from US Geological Survey, through public domain.

Herbst (1959) reported *Metacyclops paludicola* and *Ectocyclops herbsti* (see Figure 46) from a *Sphagnum* bog in São Paulo, Brazil. Hingley (1993) reported *Moraria sphagnicola* (see Figure 45) and *Canthocamptus weberi* (see Figure 47) as associated with *Sphagnum* (Figure 43) in Europe. In addition to living in mossy tarns, *Attheyella* (*Delachauxiella*) *brehmi* and *Attheyella* (*Chappuisiella*) *maorica* (see Figure 35) occur among *Sphagnum* in New Zealand (Lewis 1972a).



Figure 46. *Ectocyclops phaleratus* with egg sacs, member of a genus in which some species occur in peat bogs. Photo from Haney *et al.* 2013, with permission

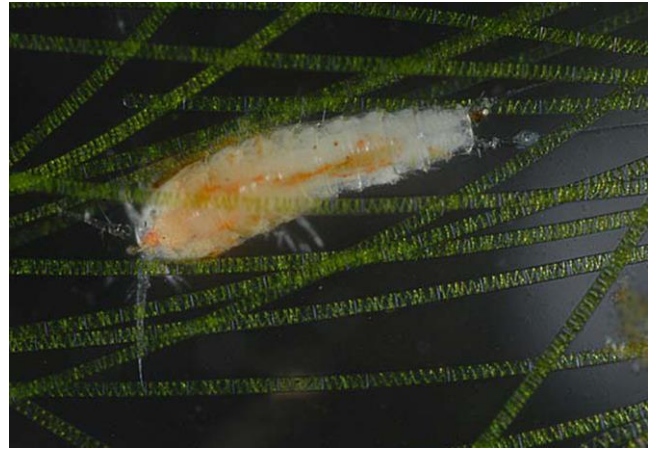


Figure 47. *Canthocamptus* sp. on the alga *Spirogyra*. Photo by Gerard Visser through Creative Commons.

In peatlands, the mosses can have an indirect influence on the fauna due to the tracheophytes they support. The rare North American copepod *Paracyclops canadensis* (Figure 48) is common in the pool of water in the leaves of the pitcher plant (*Sarracenia purpurea*, Figure 49) (Hamilton *et al.* 2000). In *Sphagnum* (Figure 43) peatlands, the mosses are a necessary habitat element to support the growth of pitcher plants.



Figure 48. *Paracyclops canadensis*, an inhabitant of pitcher plants. Photo from US Geological Survey, through public domain.



Figure 49. *Sarracenia purpurea* leaf amid *Sphagnum* where copepods can live in the pool formed within the leaf. Photo by Janice Glime.



## Aquatic

Reid (2001) reported that squeezing aquatic mosses would reveal small copepods such as members of *Acanthocyclops* (Figure 50-Figure 51), *Diacyclops* (Figure 52), and other small cyclopoid genera (Gurney 1932; Scourfield 1932, 1939). Aquatic bryophytes can provide cyclopoid genera with safe sites from strong flow, hide them from predators, and trap particulate matter that serves as food.



Figure 50. *Acanthocyclops venustoides*, genus of the small copepods that live among aquatic mosses. Photo by US Geological Survey, through public domain.



Figure 51. *Acanthocyclops robustus*, member of a genus of small copepods that live among bryophytes. Photo from Haney, J. F. *et al.* 2013. An Image-Based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <cfb.unh.edu>, with permission.



Figure 52. *Diacyclops navus*, genus of the small copepods that live among aquatic mosses. Photo from US Geological Survey, through public domain.

## Mossy Tarns

**Tarns** (Figure 53) are small mountain lakes. For the crustaceans, the mossy tarn habitat is similar in many ways to peatland pools, but it may differ in its pH and does not necessarily have *Sphagnum* (Figure 43) or may have different *Sphagnum* species. Several copepod species seem to prefer mossy tarns in New Zealand (Lewis 1972a). Among these are *Attheyella* (*Delachauxiella*) *brehmi* and *Attheyella* (*Chappuisiella*) *maorica* (species known to occur among *Sphagnum*; see Figure 35) and *Attheyella* (*Delachauxiella*) *bennetti*, genera known also from peatlands.



Figure 53. Tarn in Siskiyou Wilderness, CA, USA. Photo by Miguel Vieira, through Creative Commons.

## Springs

Stoch (2007) found that mosses in springs in Italy were particularly good habitats for copepods, supporting large numbers. This may be due to their complex structure and highly available food sources. At the same time, the spring-dwelling species are often not true **crenobionts** (occurring only in springs and spring brooks) (Stoch 1998a), also occurring in other damp or aquatic habitats such as the littoral zone of lakes, moist mosses elsewhere, in groundwater, and in the epirithral region (upstream stream region suitable for trout) (Gerecke *et al.* 1998; Jersabek *et al.* 2001; Galassi *et al.* 2002; Stoch 1998a, 2003, 2006, 2007). Within the springs, species often segregate into microhabitats that supply their needs, including hygropetric rivulets, mosses, and patches of sediments with different characteristics (Stoch 2003; Fiasca *et al.* 2005). Bottazzi *et al.* (2011) reported **crenophilous** ("loving" springs and spring brooks) crustaceans from mosses in the Northern Apennine **rheocrene** springs (springs that flow to surface from underground), with pH and temperature best explaining their distribution and diversity pattern. In fact, the harpacticoid copepods and ostracods dominated the moss fauna, along with stoneflies and Chironomidae. The mosses were important contributors to the biodiversity.

We know that the copepod genera *Moraria* (Figure 45) and *Bryocamptus* are associated with wet or submerged mosses in Europe, including springs (Harding 1953). In their Italian study, Bottazzi *et al.* (2008) used traps, tubes, and moss samples to determine the copepod fauna of **rheocrene springs** (those that exhibit flow immediately after emerging from the substrate). They found 63% of the copepod taxa in these springs were represented among the

mooses, including a species of *Moraria*, in this case, *M. poppei*. Some of the copepod taxa occurred only in the moss habitat (i.e., were not collected in traps). These were the harpacticoid copepods *Bryocamptus tatrensis*, *B. alpestris* (see Figure 31), *Moraria vej dovski*, *M. vej dovski truncatus*, *M. poppei*, *Epactophanes richardi* (Figure 54), *Attheyella crassa* (see Figure 35), and the cyclopoid *Eucyclops serrulatus* (Figure 55). *Bryocamptus* species were evenly recorded from both moss and trap samples.

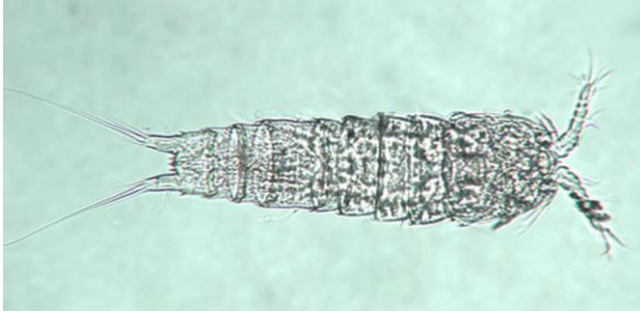


Figure 54. *Epactophanes richardi* female, a harpacticoid copepod of rheocene springs that seems to prefer mosses. Photo from US Geological Survey, through public domain.



Figure 55. *Eucyclops serrulatus*, a harpacticoid copepod that lives among mosses of rheocene springs. Photo by Fausto at <microscopio.it.gg>, with permission.

Bottazzi *et al.* (2011) also reported that the taxa most represented in the Northern Apennine rheocene springs were the harpacticoid copepods: *Bryocamptus zschokkei* (Figure 31) (mean number of individuals per sample = 2 for traps, 14 for mosses) and *B. pygmaeus* (1 individual/sample for traps, 5 for mosses). Out of their total of 3,284 invertebrates collected, **Ostracoda**, **harpacticoid Copepoda**, and **Diptera** were the most abundant among the 54 taxa. Bottazzi and coworkers considered the mosses to be a favorable habitat that contributed to the high species diversity.

### Rivulets

Rivulets, often as outflow from springs, often have mosses that serve as copepod habitats. Stoch (2003, 2007) reported copepods from mosses in **hygropetric** rivulets (having water forming a surface film on rocks). Genera such as *Moraria* (Figure 45), *Epactophanes* (Figure 54), *Arcticocamptus*, *Nitocrella*, *Parastenocaris* (see Figure 33), *Speocyclops*, and *Diacyclops* (Figure 52) occur among hygropetric rivulet mosses (Fiasca *et al.* 2005).

### Streams

It appears that copepods are important bryophyte inhabitants in mountain streams of New Zealand. In unshaded areas of the streams, Suren (1992) found *Canthocamptus howardorum*, *C. maoricus* (see Figure 56), *Attheyella stillicidarum*, *A. cf. brehmi* (see Figure 35), *Antarctobiotus elongatus*, and *A. cf. diversus*, all in the **Harpacticoida** (Figure 57). In 1992, Suren suggested that the large numbers of Copepoda found in association with bryophytes there may relate to the high food value of abundant periphyton that grow on the surfaces and the ability of the bryophytes to serve as safe sites against fast water currents. But in 1993, he refined his assessment to suggest that the copepods are especially important on bryophytes that are covered with detritus rather than periphyton (Suren 1993).

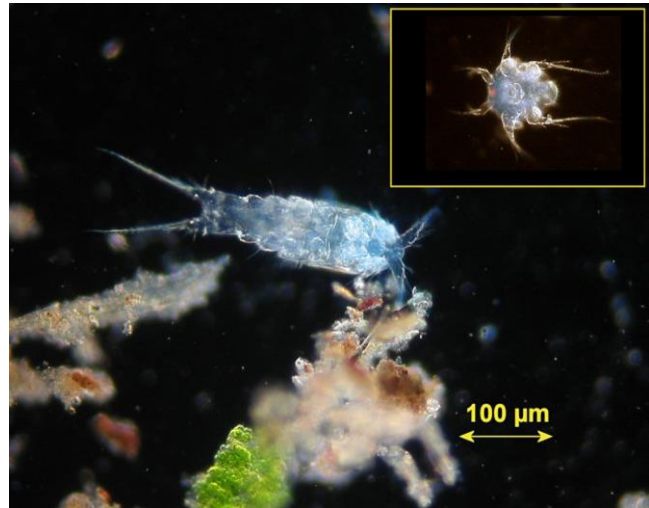


Figure 56. *Canthocamptus* from moss; note nauplius in insert. Photo by Graham Matthews <[http://www.micromagus.net/microscopes/pondlife\\_copepoda.html](http://www.micromagus.net/microscopes/pondlife_copepoda.html)>, with permission.



Figure 57. Harpacticoid copepod on leaf of *Fontinalis antipyretica*, demonstrating how tiny it is. Photo by Dan Spitale, with permission.

Leaf axils of bryophytes can be particularly protective against the current, but they also serve as collection sites for detritus. The differences in periphyton vs organic detritus may relate to location in sun vs shade. Cox (1988) found that bryophytes from an unshaded location had predominantly periphyton associated with them, whereas



those from the shaded site had predominately fine amorphous detritus associated with them. This is reasonable, as more light would promote greater algal growth. But flow rates will play into this as well, and oxygen content will differ with both flow rate and periphyton vs detrital matter.

Chironomidae (midges) are typically the dominant group on stream bryophytes [see, for example Williams (1989) in southern Ontario, Canada, and Nolte (1991) in Germany, who found that chironomids dominated on the submerged moss *Hygroamblystegium tenax* (Figure 58)]. In New Zealand alpine streams, Suren (1992) found that harpacticoid copepods and ostracods were among the most abundant groups of non-chironomids. Suren found that there was a "strong positive relationship" between copepod density and high water velocity, with densities among the bryophytes there reaching twice that of macroinvertebrates. At first, this seems like a contradiction because meiofauna are intolerant of high water velocity (Winner 1975) and avoid it by burrowing into the hyporheic zone (sediment). Suren (1992) pointed out that the copepods *Bryocamptus vej dovskyi* and *B. zschokkei* (Figure 31) in Minnesota, USA, can only be found in the hyporheos in fast-flowing streams. He suggests that the bryophytes provide a "biotic hyporheic zone." The studies by Suren (1992) in New Zealand are in sharp contrast to those of Cox (1988) who found that in streams in Tennessee, USA, it was rotifers that dominated the bryophytic "hyporheic zone" in the mosses *Fontinalis novae-angliae* (Figure 59) and *Platyhypnidium riparioides* (Figure 60).



Figure 58. *Hygroamblystegium tenax*, a submerged moss dominated by Chironomidae (midges - Diptera) rather than copepods in Germany. Photo by Barry Stewart, with permission.



Figure 59. *Fontinalis novae-angliae* at edge of stream, a moss that supports dominant rotifer fauna, not copepod fauna, in the hyporheic zone in Tennessee, USA. Photo by Janice Glime.



Figure 60. *Platyhypnidium riparioides*, a moss that supports a dominant rotifer fauna rather than a copepod fauna in the hyporheic zone in Tennessee, USA. Photo by Michael Lüth, with permission.

### Splash Zones

Stream edges and waterfall splash zones provide a suitable habitat for some limnoterrestrial copepods (Lewis 1972a). In New Zealand one can find such taxa as *Attheyella stillicidarum* (see Figure 35) among the mosses and liverworts, preferring either permanently dripping mossy banks or areas in the splash zones of streams, apparently requiring moving (fresh, not stagnant) water. *Attheyella humidarum* and *Attheyella fluviatilis* likewise prefer dripping mossy banks and damp "bush" moss. In addition to these *Attheyella* species, Lewis (1972b) also described six new species in the genus *Antarctobiotus* (*A. ignobilis*, *A. diversus*, *A. elongatus*, *A. australis*, *A. exiguus*, *A. triplex*) from damp mosses in New Zealand.

### Cave Pool

Galas *et al.* (1996) examined the decomposition of litter in a cave pool in Poland. These pools included copepods, among other fauna. Respiration released more energy by activity of microorganisms on mosses (*Polytrichum*, Figure 61) than on the litter of *Sorbus* and *Alnus* in the pool. This higher rate among the bryophytes suggests that they may have provided a better food source of fine particulates and microorganisms for small organisms such as copepods than that associated with the submersed leaf litter.



Figure 61. *Polytrichum commune* in a geothermal spring, Yellowstone, WY, USA. Photo by Janice Glime.

## Summary

Microcrustacea are primarily aquatic and marine, but some, including Copepoda and Cladocera, have developed characteristics that permit them to live on land in such habitats as wet bryophytes. Moisture, water chemistry, pH, and roughness of the moss habitat can be important determinants of microcrustacean diversity.

Adaptations to land may include separate sexes, ability to change sex, and parthenogenesis. Cyclopoid copepods have short life cycles that permits them to increase recruitment. They can sometimes disperse with their bryophyte substrate.

Truly terrestrial Cladocera are few, with *Bryospilus* being best represented among this group. Springs seem to be a transitional habitat between aquatic and terrestrial systems, with bryophytes serving as a refuge vertically and horizontally as moisture levels change. In streams, bryophytes can serve as a safety net to catch drifting organisms. The bottom of the moss clump provides a safe haven from the torrential waters above while being a collection site for food. Food is often fine detritus trapped by the bryophytes. In these aquatic and wet habitats, the bryophytes can contribute significantly to increasing the faunal diversity. Peatlands/*Sphagnum* bogs increase diversity by offering multiple niches both in the mosses and among the tracheophyte vegetation. *Alona* and *Alonella* are among the most common there; *Alona* is also the most common drift cladoceran in streams.

Cladoceran adaptations can include appendage reduction, shorter life cycle, eggs placed in dense masses of vegetation, and ability to swim in a thin film of water.

Copepods on land use their antennae to swim in the larval stage. Dormancy permits them to survive dry periods, including resting eggs, arrested development, and encystment of both juveniles and adults.

The ability of land-dwelling copepods to live among bryophytes is reflected in such names as *Muscocyclops*, *Bryocyclops*, and *Epactophanes muscicola*. Bryophytes can provide moist islands when copepods move from one location to another. Other species live among canopy epiphytes. Some even live among bryophytes in the Antarctic. *Attheyella* and *Moraria* are among the genera known from peat bogs, with genera such as *Paracyclops* found in pitcher plants there. Small copepods hide among the aquatic bryophytes. Harpacticoid copepods can dominate the moss fauna in springs, where temperature and pH are important factors in diversity. *Canthocamptus* and *Attheyella* are well represented in streams in New Zealand. Like the Cladocera, copepods often feed on periphyton or detritus among the bryophytes.

## Acknowledgments

I especially appreciate Dan Spitale for his contribution of the image of a copepod on *Fontinalis* and to Paul Davison for his anecdotal information, images, and

continued encouragement. Thank you to Larry Williams for numerous comments and suggestions that have improved the clarity of the manuscript. Thank you to all the photographers who have placed their images in Creative Commons on the internet.

## Literature Cited

- Acosta-Mercado, D., Cancel-Morales, N., Chinae, J. D., Santos-Flores, C. J., and De Jesús, I. S. 2012. Could the canopy structure of bryophytes serve as an indicator of microbial biodiversity? A test for testate amoebae and microcrustaceans from a subtropical cloud forest in Dominican Republic. *Microb. Ecol.* 64: 200-213.
- Amos, W. H. 1999. Life in the torrent – the moss *Fontinalis* and its tiny inhabitants. *Microscopy UK*, Accessed on 16 April 2008 at <<http://www.microscopy-uk.org.uk/mag/indexmag.html?http://www.microscopy-uk.org.uk/mag/artsep99/bamoss.html>>.
- Barclay, M. H. 1969. First records and a new species of *Phyllognathopus* (Copepoda; Harpacticoida) in New Zealand. *N. Z. J. Marine Freshwat. Res.* 3: 296-303.
- Barquín, J. and Death, R. G. 2009. Physical and chemical differences in karst springs of Catabria, northern Spain: Do invertebrate communities correspond? *Aquat. Ecol.* 43: 445-455.
- Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecol. Monogr.* 38: 269-308.
- Bottazzi, E., Bruno, M. C., Mazzini, M., Pieri, V., and Rossetti, G. 2008. First report on Copepoda and Ostracoda (Crustacea) from northern Apennine springs (N. Italy): A faunal and biogeographical account. *J. Limnol.* 67: 56-63.
- Bottazzi, E., Bruno, M. C., Pieri, V., Sabatino, A. Di, Silveri, L., Carolli, M., and Rossetti, G. 2011. Spatial and seasonal distribution of invertebrates in Northern Apennine rheocrene springs. *J. Limnol.* 70 (Suppl. 1): 77-92.
- Camann, M. 2011. Wandering salamanders choose direct route to good food. Old-growth redwood forest canopy arthropod prey base for arboreal wandering salamanders: A report prepared for the Save-the-Redwoods League. Accessed 8 November 2011 at <[http://www.savetheredwoods.org/research/grant\\_detail.php?id=12](http://www.savetheredwoods.org/research/grant_detail.php?id=12)>.
- Camann, M. A., Lamoncha, K. L., and Jones, C. B. 2011. Old-growth redwood forest canopy arthropod prey base for arboreal Wandering Salamanders. A report to Save-the-Redwoods League. Humboldt State University, Arcata, CA, 23 pp.
- Cammaerts, E. and Mertens, J. 1999. A new genus and two new species of Chydoridae (Branchiopoda: Anomopoda), from Korup National Park, Cameroon. *Belg. J. Zool.* 129: 327-337.
- Chapman, A. 1960. Terrestrial ostracods of New Zealand. *Nature* 185: 121-122.
- Cox, R. J. 1988. A Study of the Invertebrate Communities Associated with Real and Artificial Bryophytes in Lotic Ecosystems. unpublished PhD thesis, University of Tennessee, 163 pp.
- Dahms, H.-U. 1995. Dormancy in the Copepoda – an overview. *Hydrobiologia* 306: 199-211.
- Dahms, H.-U. and Qian, P. Y. 2004. Life histories of the Harpacticoida (Copepoda, Crustacea): A comparison with meiofauna and macrofauna. *J. Nat. Hist.* 38: 1725-1734.



- Damme, K. Van, Elías-Gutiérrez, M., and Dumont, H. J. 2011. Three rare European "*Alona*" taxa (Branchiopoda: Cladocera: Chydoridae), with notes on distribution and taxonomy. *Ann. Limnol.* 47: 45-63.
- Deevey, E. S. 1941. Notes on the encystment of the harpacticoid copepod *Canthocamptus staphylinoides* Pearse. *Ecology* 22: 197-200.
- Dole-Olivier, M.-J., Galassi, D. M. P., Marmonier, P., and Creuze Des Châtelliers, M. 2000. The biology and ecology of lotic microcrustaceans. *Freshwat. Biol.* 44: 63-91.
- Dražina, T., Špoljar, M., Primc-Habdija, B., and Habdija, I. 2011. Small scale patterns of meiofauna in bryophytes. In: 7th Symposium for European Freshwater Sciences, 27 June – 1 July 2011 in Girona, Spain.
- Duigan, C. A. and Birks, H. H. 2000. The late-glacial and early-Holocene palaeoecology of cladoceran microfossil assemblages at Kråkenes, western Norway, with a quantitative reconstruction of temperature changes. *J. Paleolimnol.* 23: 67-76.
- Dumont, H. J. and Maas, S. 1988. Five new species of leaf litter harpacticoids (Crustacea, Copepoda) from Nepal. *Zool. Scripta* 17: 55-68.
- Ecomare. 2014. Encyclopedia: Cladocera. Accessed 11 March 2014 at <<http://www.ecomare.nl/index.php?id=3631&L=2>>.
- Elliott, J. M. 1967. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* 63: 202-237.
- Encyclopaedia Britannica: Copepod. 2012. Last updated 25 April 2012. Accessed 14 March 2014 at <<http://www.britannica.com/EBchecked/topic/136547/copepod>>.
- Fiasca, B., Lorenzo, T., Laurentiis, P., Pantani, C., and Galassi, D. M. P. 2005. Biodiversità acquatica sotterranea nel Parco Nazionale del Gran Sasso-Monti della Laga: Analisi taxocenotica (Crustacea, Copepoda) e proposte di conservazione. *Studi Trentini di Scienze Naturali, Acta Biologica* 81: 157-166.
- Fiers, F. and Ghenne, V. 2000. Cryptozoic copepods from Belgium: Diversity and biogeographic implications. *Belg. J. Zool.* 130: 11-19.
- Figuerola, J. and Green, A. J. 2002. Dispersal of aquatic organisms by waterbirds: A review of past research and priorities for future studies. *Freshwat. Biol.* 47: 483-494.
- Flößner, D. 2000. Die Haplopoda und Cladocera (ohne Bosminidae) Mitteleuropas. Backhuys Publishers, Leiden.
- Frey, D. G. 1980. The non-swimming chydorid Cladocera of wet forests, with descriptions of a new genus and two new species. *Internat. Rev. Gesamt. Hydrobiol.* 65: 613-641.
- Fryer, G. 1957a. The feeding mechanism of some freshwater cyclopoid copepods. *Proc. Zool. Soc. Lond* 129: 1-25.
- Fryer, G. 1957b. The food of some freshwater cyclopoid copepods and its ecological significance. *J. Anim. Ecol* 26: 263-286.
- Fryer, G. 1993. The freshwater Crustacea of Yorkshire. Yorkshire Naturalists' Union.
- Galas, J., Bednarz, T., Dumnicka, E., Starzecka, A., and Wojtan, K. 1996. Litter decomposition in a mountain cave water. *Arch. Hydrobiol.* 138: 199-211.
- Galassi, D. M. P., Marmonier, P., Dole-Olivier, M.-J., and Rundle, S. 2002. Microcrustacea. In: Rundle, S. D., Robertson, A. L., and Schmid-Araya, J. M. (eds.). *Freshwater Meiofauna: Biology and Ecology*. Backhuys Publishers, Leiden, pp. 135-175.
- Gerecke, R., Meisch, C., Stoch, F., Aciri, F., and Franz, H. 1998. Eucronon-hypocronon ecotone and spring typology in the Alps of Berchtesgaden (Upper Bavaria, Germany). A study of microcrustacea (Crustacea: Copepoda, Ostracoda) and water mites (Acari: Halacaridae, Hydrachnellae). In: Botosaneanu, L. (ed.). *Studies in Crenobiology. The Biology of Springs and Springbrooks*. Backhuys Publishers, Leiden, pp. 167-182.
- Glime, J. M. 1994. Bryophytes as homes for stream insects. *Hikobia* 11: 483-497.
- Gonzalez, A. and Chanton, E. J. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* 71: 594-602.
- Gonzalez, A., Lawton, J. H., Gilbert, F. S., Blackburn, T. M., and Evans-Freke, I. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. *Science* 281: 2045-2047.
- Good, E. E. and Dambach, C. A. 1943. Effect of land use practices on breeding bird populations in Ohio. *J. Wildl. Mgmt* 7: 291-297.
- Green, J. 1959. Hæmoglobin and the habitat of the harpacticoid copepod *Elaphoidella gracilis* (Sars). *Nature* 183: 1834.
- Gurney, R. 1932. *British Fresh-water Copepoda*, Vol. 2. Ray Society, London, 336 pp.
- Gurtz, M. E. and Wallace, J. B. 1984. Substrate-mediated response of stream invertebrates to disturbance. *Ecology* 65: 1556-1569.
- Habdija, I., Primc-Habdija, B., Matoničkin, R., Kučomić, M., Radanović, I., Miliša, M., and Mihaljević, Z. 2004. Current velocity and food supply as factors affecting the composition of macroinvertebrates in cryophyte habitats in karst running water. *Biologia* 59: 577-593.
- Hairston, N. G. Jr., Brunt, R. A. Van, Kearns, C. M., and Engstrom, D. R. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76: 1706-1711.
- Hamilton, R. IV, Reid, J. W., and Duffield, R. M. 2000. Rare copepod, *Paracyclops canadensis* (Willey), common in leaves of *Sarracenia purpurea* L. *Northeast. Nat.* 7: 17-24.
- Hamond, R. 1987. Non-marine harpacticoid copepods of Australia. I. Canthocamptidae of the genus *Canthocamptus* Westwood s. lat. and *Fibulacamptus*, gen. nov., and including the description of a related new species of *Canthocamptus* from New Caledonia. *Invert. Taxon.* 1: 1023-1247.
- Haney, J. F. et al. 2013. An-Image-based Key to the Zooplankton of North America, version 5.0 released 2013. University of New Hampshire Center for Freshwater Biology. Accessed 21 March 2014 at <[cfb.unh.edu](http://cfb.unh.edu)>.
- Hansson, L.-A., Dartnall, H. J. G., Ellis-Evans, J. C., MacAlister, H., and Tranvik, L. J. 1996. Variation in physical, chemical and biological components in the subAntarctic lakes of South Georgia. *Ecography* 19: 393-403.
- Harding, J. P. 1953. The first known example of a terrestrial ostracod, *Mesocypris terrestris* sp. nov. *Ann. Natal Mus.* 12: 359-365.
- Harding, J. P. 1955. The evolution of terrestrial habits in an ostracod. *Bull. VII. Symposium on Organic Evolution*, National Institute of Sciences of India, New Delhi, pp. 104-106.
- Harding, J. P. 1958. *Bryocamptus stouti* and *Goniocyclops sylvestris*, two new species of copepod crustacean from forest in New Zealand. *Ann. Mag. Nat. Hist.* 13: 309-314.

- Henrikson, B.-I. 1993. *Sphagnum* mosses as a microhabitat for invertebrates in acidified lakes and the color adaptation and substrate preference in *Leucorrhinia dubia* (Odonata, Anisoptera). *Ecography* 16: 143-153.
- Herbst, H. V. 1959. Brasilianische Süßwassercyclopoiden (Crustacea Copepoda). *Gewäss. Abwäss.* 24: 49-73.
- Hillbricht-Ilkowska, A., Dusoge, K., Ejsmont-Karabin, J., Jasser, I., Kufel, I., Ozimek, T., Rybak, J. I., Rzepecki, M., and Weglenska, T. 1998. Long term effects of liming in a humic lake: Ecosystem processes, biodiversity, food web functioning (Lake Flosek, Masurian Lakeland, Poland). *Polish J. Ecol.* 46: 347-415.
- Hingley, M. 1993. Microscopic Life in *Sphagnum*. Illustrated by Hayward, P. and Herrett, D. *Naturalists' Handbook* 20. [i-iv]. Richmond Publishing Co. Ltd., Slough, England, 64 pp. 58 fig. 8 pl. (unpaginated).
- Illies, J. 1952. Die molle. Faunistisch-okologische Untersuchungen an einem Forellenbach im Lipper Bergland. *Arch. Hydrobiol.* 46: 424-612.
- Ilmonen, J. and Paasivirta, L. 2005. Benthic macrocrustacean and insect assemblages in relation to spring habitat characteristics: Patterns in abundance and diversity. *Hydrobiologia* 533: 99-113.
- Jersabek, C. D., Brancelj, A., Stoch, F., and Schabetsberger, R. 2001. Distribution and ecology of copepods in mountainous regions of the Eastern Alps. *Hydrobiologia* 453/454: 309-324.
- Kairesalo, T., Lehtovaara, A., and Saukkonen, P. 1992. Littoral-pelagial interchange and the decomposition of dissolved organic matter in a polyhumic lake. *Hydrobiologia* 229: 199-224.
- Kerfoot, W. C. and Weider, L. J. 2004. Experimental paleoecology (resurrection ecology): Chasing Van Valen's Red Queen hypothesis. *Limnol. Oceanogr.* 49: 1300-1316.
- Kjørboe, T., Andersen, A., Langlois, V. J., and Jakobsen, H. H. 2010. Unsteady motion: Escape jumps in planktonic copepods, their kinematics and energetics. *J. Royal Soc. Interface* 7: 591-602.
- Kipp, R. M., Larson, J., and Fusaro, A. 2014. *Megacyclops viridis*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Last updated 31 May 2012. Accessed 27 March at <<http://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=2723>>.
- Krebs, C. J. 2001. Ecology. The Experimental Analysis of Distribution and Abundance. Wydawnictwo Naukowe PWN, Warszawa, Poland, 734 pp.
- Kuczyńska-Kippen, N. 2008. Spatial distribution of zooplankton communities between the *Sphagnum* mat and open water in a dystrophic lake. *Polish J. Ecol.* 56: 57-64.
- Land, M. F. 1988. The functions of eye and body movements in *Labidocera* and other copepods. *J. Exper. Biol.* 140: 381-391.
- Lang, K. 1931. Schwedische Süßwasser- und Mooscharpacticiden. *Ark. Zool.* 22A: 1-84.
- Lay, D. W. 1938. How valuable are woodland clearings to birdlife? *Wilson Bull.* 50: 254-256.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York.
- Lewis, M. H. 1972a. Freshwater harpacticoid copepods of New Zealand. 1. *Attheyella* and *Elaphoidella* (Canthocamptidae). *N. Z. J. Marine Freshwat. Res.* 6: 23-47.
- Lewis, M. H. 1972b. Freshwater harpacticoid copepods of New Zealand. 2. *Antarctobiotus* (Canthocamptidae). *N. Z. J. Marine Freshwat. Res.* 6: 277-297.
- Lewis, M. H. 1984. The freshwater Harpacticoida of New Zealand: A zoogeographical discussion. *Crustaceana Suppl.* 7 Stud. Copepoda 2: 305-314.
- Lindegaard, C., Thorup, J., and Bahn, M. 1975. The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical and horizontal distribution. *Arch. Hydrobiol.* 75: 109-139.
- Linhart, J., Uvíra, V., and Birklen, P. 2000. Macronematofauna of an aquatic moss *Fontinalis antipyretica* and the surrounding gravel-bed material. In: Rulík, M. (ed.). Proceedings of the XII. Limnological Conference "Limnologie na prelomu tisíciletí," Kouty nad Desnou, Czech Republic, pp. 194-197.
- Linhart, J., Fiurásková, M., and Uvíra, V. 2002a. Moss- and mineral substrata-dwelling meiobenthos in two different low-order streams. *Arch. Hydrobiol.* 154: 543-560.
- Linhart, J., Vlčková, S., and Uvíra, V. 2002b. Bryophytes as a special mesohabitat for meiofauna in a rip-rapped channel. *River Res. Appl.* 18: 321-330.
- Linhart, J., Vlčková, S., and Uvíra, V. 2002c. Moss-dwelling meiobenthos and flow velocity in low-order streams. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium (2001-2002) Biologica* 39-40: 111-122.
- Macan, T. T. 1974. Freshwater Ecology. 2nd ed. John Wiley & Sons, New York, p. 60.
- Madaliński, K. 1961. Moss dwelling rotifers of Tatra streams. *Polsk. Arch. Hydrobiol.* 9: 243-263.
- Margaritora, F. G., Vagaggini, D., and Stoch, F. 2002. Two Chydoridae species (Crustacea, Cladocera) new to Italy: *Alona rustica* and *Camptocercus uncinatus*. *Italian J. Zool.* 69: 59-63.
- Martin, G. G., Speckmann, C., and Beidler, S. 2000. Photobehavior of the harpacticoid copepod *Tigriopus californicus* and the fine structure of its nauplius eye. *Invert. Biol.* 119: 110-124.
- Menzel, R. 1916. Über das Auftreten der Harpacticidengattung *Epactophanes* Mrázek und *Parastenocaris* Kessler in Surinam. *Zool. Anz.* 47: 145-152.
- Menzel, R. 1921. Beiträge zur Kenntnis der Mikrofauna von Niederländisch-Ost-Indien. I. Moosbewohnende Harpacticiden. *Treubia* 2: 137-145.
- Menzel, R. 1925. Over mos bewonende cyclopiden en harpacticiden en over vrij levende terricole nematoden van den Maleischen Archipel. Handelingen, Derde Nederlandisch-Indisch Natuurwetenschappelijk Congres, Buitenzorg, pp. 298-309.
- Menzel, R. 1926. Cyclopides muscicoles et bromélicoles de Java (Indes Néerlandaises). *Ann. Biol. lac.* 14: 209-216.
- Michaelis, F. B. 1977. Biological features of Pupu Springs. *N. Z. J. Marine Freshwat. Res.* 11: 357-373.
- Michailova-Neikova, M. 1973. Harpacticoida (Crustacea, Copepoda) reported from mountain waters in Bulgaria. III. Lyulin Mountain (water moss and wet forest leaves). *Ann. Univ. Sofia, Fac. Biol.* 65(1970/1971): 89-99.
- Minelli, A. (ed.). 2004. Mountain Peat Bogs – Relicts of Biodiversity in Acid Waters. Museo Friulano di Storia Naturale, Udine, Italy, 81 pp.
- Mrázek, A. 1893. Beitrag zur Kenntnis der Harpacticiden-Fauna des Süßwassers. *Zool. Jahrb. Syst.* 7: 89-130.
- Nolte, U. 1991. Seasonal dynamics of moss-dwelling chironomid communities. *Hydrobiologia* 222: 197-211.
- Olofsson, O. 1918. Studien über die Süßwasserfauna Spitzbergens. *Zool. B. Uppsala* 6: 183-646, 8 Pls.



- Peric, M. S., Drazina, T., Spoljar, M., Radanovic, I., Primc, B., and Habdija, I. 2014. Meiofauna constitute a considerable portion of invertebrate drift among moss-rich patches within a karst hydrosystem. *Biologia* 69: 363-380.
- Pesta, O. 1928. Eine Crustaceenausbeute aus Süd-Georgien (Antarktis). *Annalen des naturhistorischen Museums, Wien* 42: 75-86.
- Powers, L. W. and Bliss, D. E. 1983. Terrestrial adaptations. In: Vernberg, F. J. and Vernberg, W. B. *The Biology of Crustacea 8, Environmental Adaptations*. Academic Press, London, pp. 271-333.
- Pugh, P. J. A., Dartnall, H. J. G., and McInnes, S. J. 2002. The non-marine Crustacea of Antarctica and the Islands of the Southern Ocean: Biodiversity and biogeography. *J. Nat. Hist.* 36: 1047-1103.
- Reid, J. W. 1986. Some usually overlooked cryptic copepod habitats. *Syllogeus* 58: 594-598.
- Reid, J. W. 1987. The cyclopoid copepods of a wet campo marsh in central Brazil. *Hydrobiologia* 153: 121-138.
- Reid, J. W. 1999. New records of *Bryocyclops* from the continental U.S.A., Puerto Rico and Brazil (Copepoda: Cyclopoida: Cyclopidae). *J. Crust. Biol.* 19: 84-92.
- Reid, J. W. 2001. A human challenge: Discovering and understanding continental copepod habitats. *Develop. Hydrobiol.* 156: 201-226.
- Reid, J. W. 2011. Copepod Crustaceans of Great Smoky Mountains National Park: First Collections, Preliminary Impressions, and Results. Accessed 8 November 2011 at <<http://www.discoverlife.org/pa/ev/me/copepod.html>>.
- Richards, P. W. 1947. The introduction of *Fontinalis antipyretica* Hedw. into South Africa and its biological effects. *Trans. Brit. Bryol. Soc.* 1: 16.
- Robertson, A. L. 2002. Changing times: The temporal dynamics of freshwater benthic microcrustacea. In: Rundle, S. D., Robertson, A., and Schmid-Araya, J. M. (eds.). *Freshwater Meiofauna: Biology and Ecology*. Backhuys Publishers, Leiden, pp. 261-178.
- Rocha, C. E. 1994. New species of *Metacyclops* (Copepoda, Cyclopidae) from Brazil, with remarks on *M. campestris*. *Zool. Scripta* 23: 133-146.
- Santer, B. 1998. Life cycle strategies of free-living copepods in fresh waters. *J. Marine Syst.* 15: 327-336.
- Scourfield, D. J. 1932. A new species of *Cyclops* found on the cliff face at Tenby (*Cyclops (Bryocyclops) demetiensis*, sp. n.). *Ann. Mag. Nat. Hist. (Ser. 10)* 10: 559-570.
- Scourfield, D. J. 1939. Entomotraca in strange places. *J. Quekett Microsc. Club Ser.* 4 1: 116-122.
- Séneca, A. and Söderström, L. 2008. Species richness and distribution ranges of European *Sphagnum*. *Fol. Crypt. Est.* 44: 125-130.
- Smirnov, N. N. 1961. Food cycles in sphagnum bogs. *Hydrobiologia* 17: 175-182.
- Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munguia, P., Romanuk, T., Schneider, D. C., and Trzcinski, M. K. 2004. Are natural microcosms useful model systems for ecology? *Trends Ecol. Evol.* 19: 379-384.
- Stoch, F. 1998a. Fauna a microcrostacei (copepodi e ostracodi). In: Cantonati, M. (a cura di), *Le sorgenti del Parco Adamello-Brenta*. Documenti del Parco 11: 151-159.
- Stoch, F. 1998b. *Moraria alpina* n. sp. and redescription of *Moraria radovnae* Brancelj 1988, new rank, from Italian and Slovenian Alps (Crustacea, Copepoda, Harpacticoida). *Studi Trentini di Scienze Naturali, Acta Biologica* 73: 135-145.
- Stoch, F. 2003. Indagini ecologiche e faunistiche sulla meiofauna (Acari e Crostacei) di alcune sorgenti del Parco Naturale delle Prealpi Giulie (Italia nord-orientale). *Gortania, Atti Museo Friulano di Storia Naturale di Udine* 25: 239-250.
- Stoch, F. 2006. I Copepodi. In: Sambugar, B., Dessi, G., Sapelza, A., Stenico, A., Thaler, B., and Veneri, A. *Fauna sorgentizia in Alto Adige. Provincia Autonoma di Bolzano, Dipartimento all'Urbanistica, Ambiente e Energia*, pp. 322-323.
- Stoch, F. 2007. Copepods colonising Italian springs. In: Cantonati, M., Bertuzzi, E., and Spitale, D. *The spring habitat: Biota and sampling methods. Monografi e del Museo Tridentino di Scienze Naturali, 4. Museo Tridentino di Scienze Naturali, Trento*, pp. 217-235.
- Stout, J. D. 1963. The terrestrial plankton. *Tuatara* 11: 58-64.
- Sudzuki, M. 1972. [An analysis of colonization in freshwater micro-organisms. II. Two simple experiments on the dispersal by wind]. *Jap. J. Ecol.* 22(5): 222-225.
- Suren, A. M. 1992. Meiofaunal communities associated with bryophytes and gravels in shaded and unshaded alpine streams in New Zealand. *N. Z. J. Marine Freshwat. Res.* 26: 115-125.
- Suren, A. 1993. Bryophytes and associated invertebrates in first-order alpine streams of Arthur's Pass, New Zealand. *N. Z. J. Marine Freshwat. Res.* 27: 479-494.
- Tada, M. and Satake, K. 1994. Epiphytic zoobenthos on bryophyte mats in a cool mountain stream, Toyamazawa. *Jap. J. Limnol.* 55: 159-164.
- Thorup, J. and Lindegaard, C. 1977. Studies on Danish springs. *Folia Limnol. Scand.* 17: 7-15.
- Vlčková, Š., Linhart, J., and Uvíra, V. 2002. Permanent and temporary meiofauna of an aquatic moss *Fontinalis antipyretica* Hedw. *Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium (2001-2002)* Biologica 39-40: 131-140.
- Watiroyam, S., Brancelj, A., and Sanoamuang, L. O. 2012. A new *Bryocyclops* Kiefer (Crustacea: Copepoda: Cyclopoida) from karstic caves in Thailand. *Raffles Bull. Zool.* 60(1): 11-21.
- Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7: 81-120.
- Wikipedia: Calanoida. 2013. Updated 14 March 2013. Accessed 14 March 2014 at <<http://en.wikipedia.org/wiki/Calanoida>>.
- Wikipedia: Copepod. 2014. Updated 6 March 2014. Accessed 13 March 2014 at <<http://en.wikipedia.org/wiki/Copepod>>.
- Wikipedia: Crustacean. 2011. Updated 28 October 2011. Accessed 7 November 2011 at <<http://en.wikipedia.org/wiki/Crustacean>>.
- Wikipedia: Cyclopoida. 2013. Updated 14 March 2013. Accessed 14 March 2014 at <<http://en.wikipedia.org/wiki/Cyclopoida>>.
- Wikipedia: Harpacticoida. 2013. Updated 14 March 2013. Accessed 14 March 2014 at <<http://en.wikipedia.org/wiki/Harpacticoida>>.
- Williams, C. J. 1989. Downstream drift of the larvae of Chironomidae (Diptera) in the River Chew, SW England. *Hydrobiologia* 183: 59-72.
- Williams-Howze, J. 1997. Dormancy in the free-living copepod orders Cyclopoida, Calanoida, and Harpacticoida. *Ann. Rev. Oceanogr. Mar. Biol.* 35: 257-321.
- Winner, J. M. 1975. Zooplankton. In: Whitton, B. A. (ed.). *River Ecology*. Blackwell Scientific Publications, Oxford, pp. 155-169.

Wulforst, J. 1994. Selected faunal elements of the hyporheos and in submerged moss clumps (bryorheal) along acidification gradient in two brooks in the Harz Mountains, West Germany. Verh. Internat. Verein. Limnol. 25: 1575-1584.