

CHAPTER 10-2

ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHIPODA

TABLE OF CONTENTS

CLASS OSTRACODA	10-2-2
Adaptations	10-2-3
Swimming to Crawling.....	10-2-3
Reproduction.....	10-2-3
Habitats	10-2-3
Terrestrial.....	10-2-3
Peat Bogs	10-2-4
Aquatic.....	10-2-8
Streams	10-2-8
Springs	10-2-8
CLASS MALACOSTRACA, ORDER AMPHIPODA	10-2-8
Adaptations to Land – and Bryophytes.....	10-2-9
Reproduction and Early Development.....	10-2-10
Food among the Bryophytes	10-2-10
Habitats	10-2-13
Terrestrial.....	10-2-13
Aquatic.....	10-2-14
Summary	10-2-15
Acknowledgments.....	10-2-15
Literature Cited	10-2-15

CHAPTER 10-2

ARTHROPODS: CRUSTACEA – OSTRACODA AND AMPHIPODA



Figure 1. Terrestrial amphipod on leafy liverworts from New Zealand. Photo by Paddy Ryan, with permission.

The amphipods (Figure 1) and ostracods (Figure 2) might be considered as mimics that live in the bryophyte world. The amphipods look like miniature shrimp and the ostracods look like miniature mussel shells with a shrimp inside instead of a mussel.

CLASS OSTRACODA

Mark Papp (pers. comm. 19 November 2011) reported to me that he had a very sore neck and shoulders, but no ostracods to report. He had been looking at roof mosses where he had originally taken many ostracods at Chalfont St. Peter, UK. Their identity as ostracods was confirmed by a marine ecologist. He did find the remains of a copepod. The ostracods are evasive, making it that much more delightful when you find them. Those on the roof had apparently moved on.

The name **Ostracoda** comes from the Greek *óstrakon*, meaning shell. Ostracods (sometimes known as seed shrimp) look like miniature clams (or seeds) with a tiny shrimp-like animal living inside the shell. They typically are marine and freshwater organisms, but some have

become terrestrialized. They are not common among bryophytes, but they do sometimes occur there.



Figure 2. Ostracod, showing internal digestive system through the shell. Photo by Anna Syme through Wikipedia Commons.

Adaptations

Harding (1953) claimed the first find of a terrestrial ostracod (*Mesocypris terrestris*) as a new species occurring among mosses at the source of a small stream on Mt. Elgon in Kenya. Another occurred among mosses in a waterfall. But this ostracod is too large and globular for close alliance to the aquatic environment, so Harding (1953) reasoned that it must be more truly terrestrial. This ostracod is blind, presumably surviving loss of eyes because eyes are of little use among the mosses, and their swimming setae are very reduced as well. Instead, the second pair of antennae is especially powerful and Harding suggested that it might aid in movement in the water film among the mosses, a movement typically accomplished on mosses and liverworts by crawling (Powers & Bliss 1983). Excretion seems to be poorly understood, but some form of nitrogenous waste is excreted through glands on the maxillae, antennae, or both (Barnes 1982). Their food includes diatoms, bacteria, and detritus (Miracle 2014), items found not only in aquatic habitats, but also among terrestrial bryophytes.

Swimming to Crawling

A loss of ability to swim seems to be the result of an evolutionary loss of setae on antennae and reduction of setae on antennules (Harding 1953; De Deckker 1983; Martens *et al.* 2004). Instead, the terrestrial ostracods use their antennae to move along solid surfaces, much as benthic ostracods move along the bottom surface (Harding 1953; De Deckker 1983). On a moss, the ostracod is surrounded by a film of water at the bottom of the carapace (shell). This water is trapped by numerous hairs, especially ventrally and laterally, to about mid-height. This mechanism seems to work only on moist substrates. When *Austromesocypris australiensis* (= *Mesocypris australiensis*) was placed on a dry Petri plate, it was unable to retain all of the water when it moved (De Deckker 1983). Whereas most ostracods lie on their sides when at rest, this moss-dweller remains upright. As members of this species dry, they migrate to wetter conditions, but when it is too dry they close their shells (compare Figure 3 to Figure 9) to curtail water loss.



Figure 3. Dead **ostracod** with its shell open, revealing the exoskeleton. When taken out of water, this shell immediately closes. Photo by Paul Davison, with permission.

Reproduction

About half the non-marine ostracod species belong to the family **Cyprididae** (Wikipedia 2014). Many of these occur in temporary water bodies, requiring a degree of terrestrialization, and have drought-resistant eggs, mixed sexual and parthenogenetic reproduction, preadapting them to terrestrialization, and to living among bryophytes (Powers & Bliss 1983). There seems to be a prevalence of asexual reproduction among terrestrial ostracods compared to their aquatic counterparts (Pinto *et al.* 2005a). Nevertheless, terrestrialization of some may include retention of the fertilized eggs, protecting them from desiccation. Observations by Chapman (1961) suggest that the developing embryos of the moss-dweller *Scottia audax* (= *Mesocypris audax*) may be retained within the shell of the mother until they become free-living juveniles.

Habitats

Terrestrial

Although most ostracods are marine or aquatic, some, such as *Mesocypris* spp., live in wet terrestrial habitats, including mosses (Introduction to the Ostracoda 2002). This genus seems to be widespread among bryophytes in the Eastern Hemisphere from the Russian Far East (I'm unable to confirm this record) to Australia (Martens *et al.* 2004). Terrestrial species also occur in South America (Pinto *et al.* 2005a, b).

Although Harding (1953) claimed the first record of terrestrial ostracods in Africa with his finding of *Mesocypris terrestris*, this one was still in the wet habitats of a waterfall and source waters of a stream among mosses. De Deckker (1983) collected *Austromesocypris australiensis* from Cammoo Caves in Queensland, Australia, from wet moss. De Deckker points out that although most ostracods are aquatic or marine, several species are able to live among leaf litter and mosses that are able to provide a moist environment. Among these, the type specimen of *Austromesocypris australiensis* was found among mosses, and others were living among *Sphagnum* (Figure 4) on the side of a road near a small creek in New South Wales, Australia. In fact, these individuals were unable to swim freely even in free water.



Figure 4. *Sphagnum cristatum* from a soil bank in New Zealand. Photo by Janice Glime.

In Queensland, the terrestrial ostracod *Scottia audax* (also known from mosses in New Zealand; Chapman 1961) occurred along with *Austromesocypris australiensis* in mosses (De Deckker 1983). *Scottia birigida* (Figure 5)

occurs among mosses in Japan (Robin James Smith, pers. comm. 31 March 2014). In Tasmania, *Mesocypris tasmaniensis* likewise occurs among mosses as well as litter (De Deckker 1983). Røen (1956) named *Bryocypris grandipes* from Africa (GBIF 2013), but I have only its name to suggest it dwells among bryophytes. De Deckker stated that terrestrial ostracods are known only from Gondwanaland: Africa, Madagascar, Australia, and New Zealand, but they have since been found in Europe (Pieri *et al.* 2009; Mark Papp, pers. comm. 19 November 2011) and South America, where *Caaporacandona iguassuensis* occurs among moist Brazilian forest mosses (Pinto *et al.* 2005a). Although members of the Cyprididae occur in North America, thus far terrestrial representatives seem to be undocumented. Nevertheless, Paul Davison (pers. comm. 31 May 2014) reports them from dripping cliffs (Figure 6) among algae and suspects they could inhabit bryophytes under similar conditions. Bryologists should watch for them!



Figure 5. *Scottia birigida*, a moss dweller in Japan. Photo by Robin James Smith, with permission.

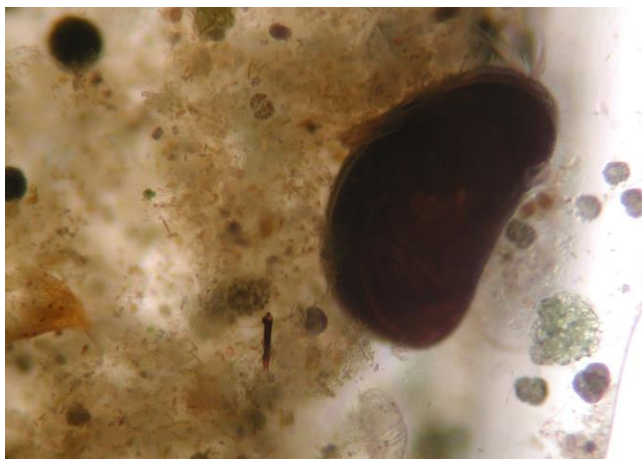


Figure 6. Ostracod from wet wall, a potential bryophyte dweller. Photo by Paul Davison, with permission.

Pieri *et al.* (2009), reporting on ostracods from Friuli Venezia Giulia, Italy, found three species distributed on mosses: *Cypria ophthalmica* (Figure 7), *Cyclocypris laevis* (Figure 8), *Cyclocypris ovum* (Figure 9). It is not clear what the habitat was for these mosses. *Cypria*

ophthalmica is known as a widespread species from the karst region of Italy (Wagenleitner 1990). All three species occur at the margins of lakes in the reed belt among the vegetation and on the sediment surface (Kiss 2007). The mosses were only examined from one site. One should note that these three species are also among the three most common taxa in the study (Figure 10), which included all the likely habitats for ostracods in the study area.

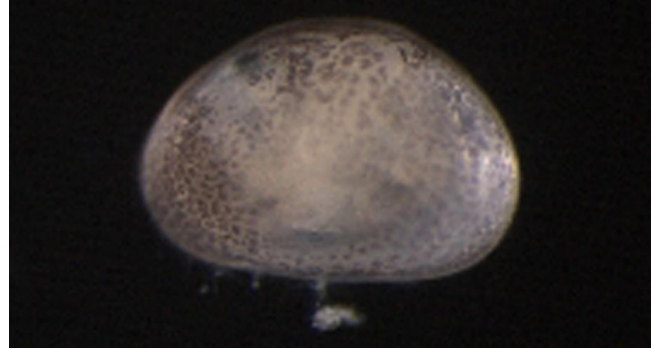


Figure 7. *Cypria ophthalmica*, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

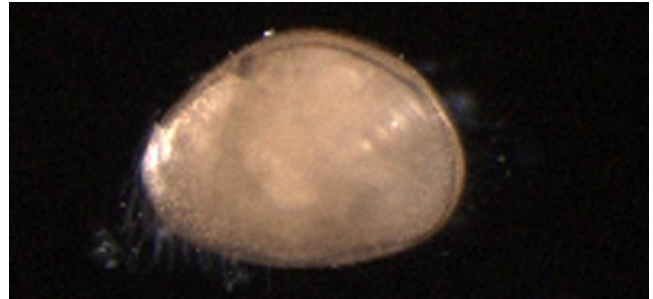


Figure 8. *Cyclocypris laevis*, a moss-dweller in Italy. Photo from Bold Systems through Creative Commons.

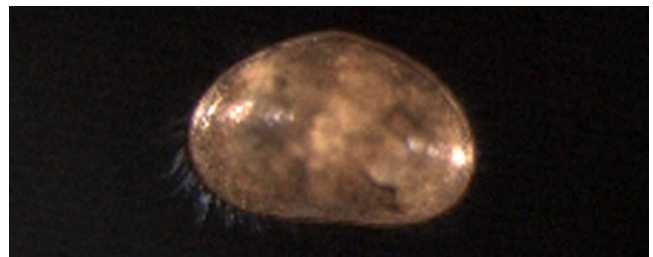


Figure 9. *Cyclocypris ovum*, a moss-dweller in Italy, with its shell closed. Photo by Bold Systems Creative Commons.

Peat Bogs

Peat bogs seem to be a rich site for ostracod species. Harding (1953, 1955) states that ostracods tend to occur in *Sphagnum* (Figure 11) as well as in forest litter. Bryophytes influence the species composition by creating a diversity of niches, from pools to dry hummock tops, and many microniches among the stems and leaves. Likewise, a gradation of pH can sometimes be found vertically and horizontally, providing more niche choices. Temperature differs between the surface and deeper portions of peat. Figure 10 shows the relationships of four environmental parameters with the five most common ostracod species in 200 sites in the sampling of surface, interstitial, and ground waters of Friuli Venezia Giulia, Italy (Pieri *et al.* 2009).

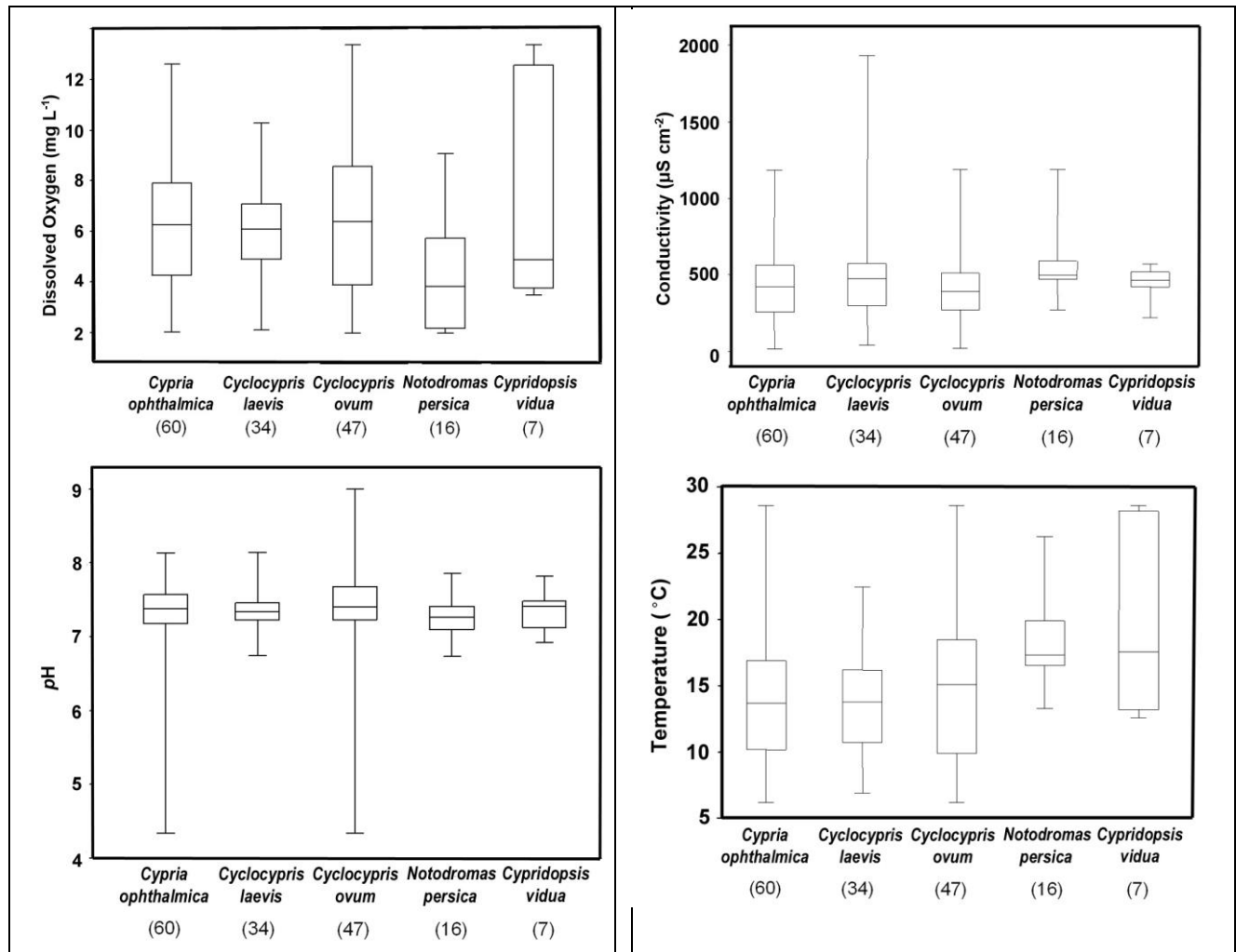


Figure 10. Comparison of environmental parameters for the five most common species in Friuli Venezia Giulia, Italy that also occur in peat bogs. The boxes show 25-75% quartiles. The horizontal line is the median, and vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al.* 2009.



Figure 11. *Sphagnum capillifolium* representing a genus that houses several species of terrestrial ostracods. Photo by Blanka Shaw, with permission.

At Friuli Venezia Giulia, Italy, the five most widespread and common species of ostracods also occurred in peatlands (Pieri *et al.* 2009). Pieri and coworkers reported 24 species in 16 genera from peat bogs (Table 1).

Table 1. Ostracod species among those at Friuli Venezia Giulia, Italy, that occurred in peat bogs. From Pieri *et al.* 2009.

<i>Darwinula stevensoni</i> Figure 12	<i>Cyclocypris ovum</i> Figure 9
<i>Penthesilenula brasiliensis</i>	<i>Ilyocypris bradyi</i> Figure 29
<i>Microdarwinula zimneri</i> Figure 13	<i>Ilyocypris inermis</i> Figure 19
<i>Pseudocandona lobipes</i>	<i>Notodromas persica</i> Figure 20
<i>Pseudocandona compressa</i> Figure 14	<i>Eucypris pigra</i> Figure 21
<i>Pseudocandona pratensis</i> Figure 15	<i>Herpetocypris</i> sp. Figure 22
<i>Pseudocandona</i> cf. <i>sucki</i>	<i>Herpetocypris reptans</i> Figure 22
<i>Cryptocandona vavrai</i>	<i>Scottia pseudobrowniana</i>
<i>Candonopsis scourfieldi</i> see Figure 16	<i>Cypridopsis elongata</i> Figure 23
<i>Cypria ophthalmica</i> Figure 7	<i>Cypridopsis vidua</i> Figure 24
<i>Cyclocypris globosa</i> Figure 17	<i>Cavernocypris subterranea</i>
<i>Cyclocypris laevis</i> Figure 18	<i>Metacypris cordata</i> Figure 25

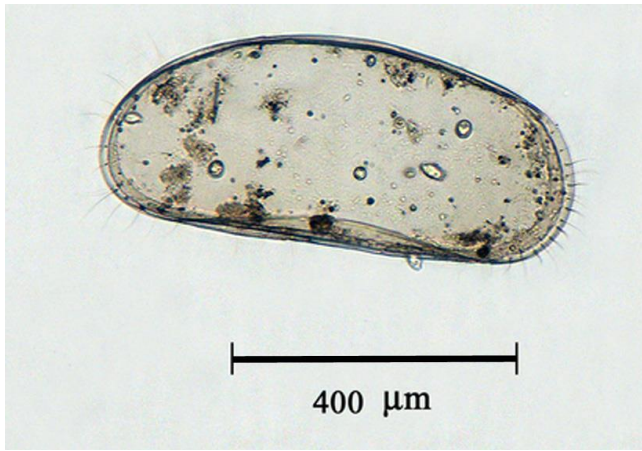


Figure 12. *Darwinula stevensoni*, an ostracod from mosses in peatlands in Italy. William Dembrowski through Creative Commons.

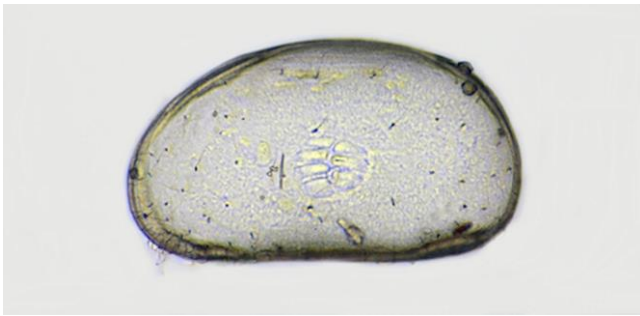


Figure 13. *Microdarwinula zimneri*, a peat moss ostracod. Photo by Robin J. Smith, with permission.

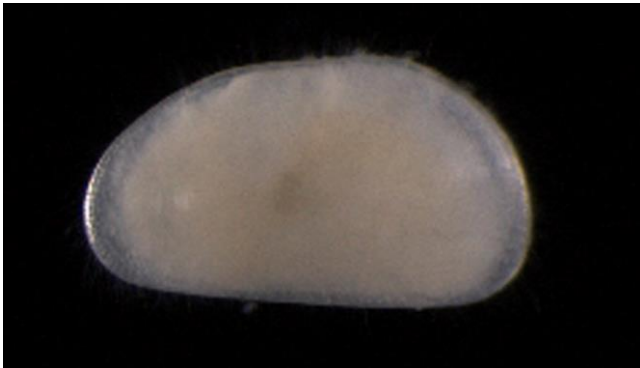


Figure 14. *Pseudocandona compressa*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 15. *Pseudocandona pratensis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 16. *Candonopsis kingsleii*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

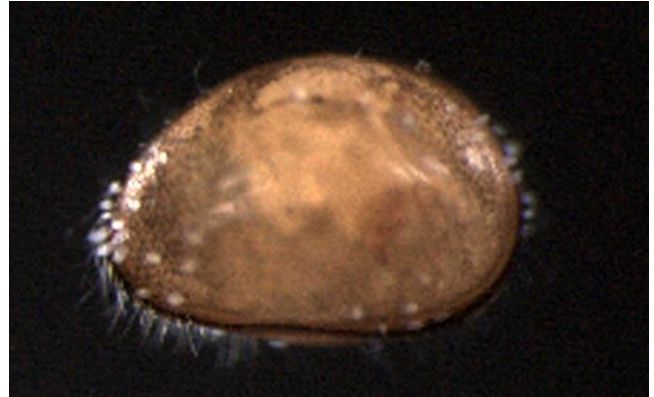


Figure 17. *Cyclocypris globosa*, a peat bog species in Italy. Those white ovals near its surface are attached protozoa. Photo from Bold Systems through Creative Commons.

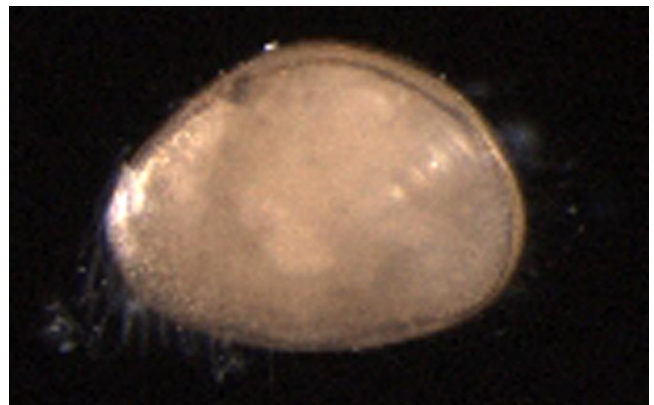


Figure 18. *Cyclocypris laevis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 19. *Ilyocypris inermis*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.



Figure 20. *Notodromus* sp., a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

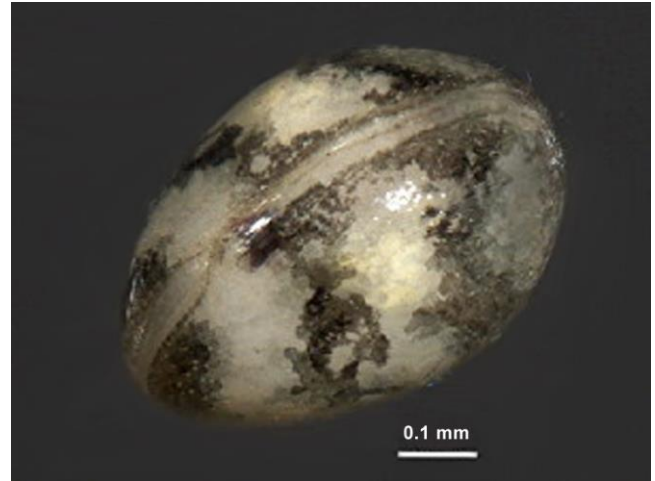


Figure 24. *Cypridopsis vidua*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

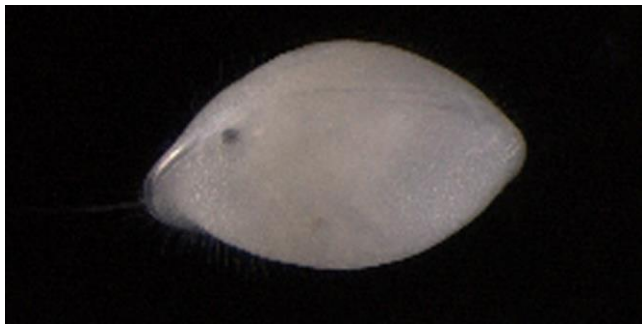


Figure 21. *Eucypris pigra*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

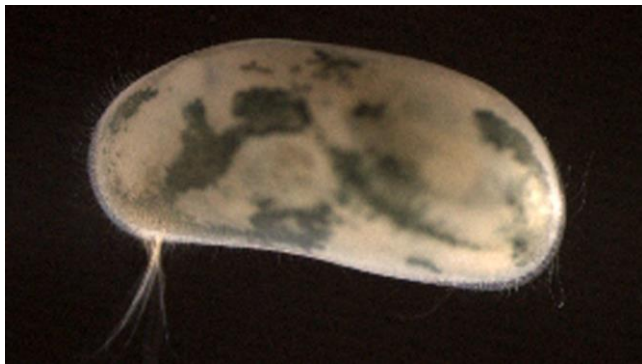


Figure 22. *Herpetocypris reptans*, a genus with members living in peat bogs in Italy. Photo from Bold Systems through Creative Commons.



Figure 23. *Cypridopsis elongata*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

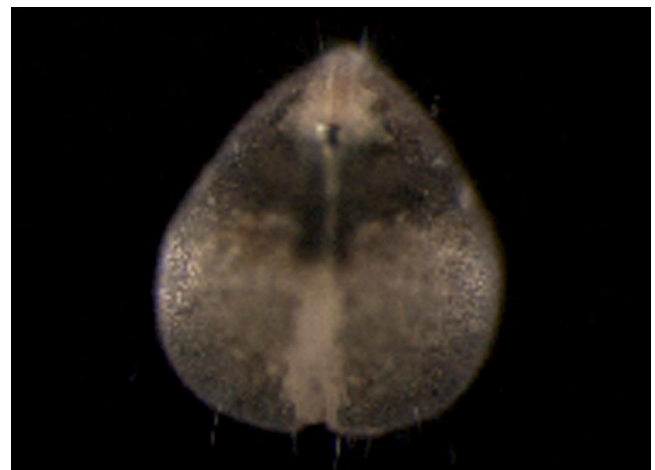


Figure 25. *Metacypris cordata*, a peat bog species in Italy. Photo from Bold Systems through Creative Commons.

It is interesting that some of these Italian bog-dwelling species are so widespread. For example, *Penthesilenula brasiliensis* is known on all the continents except Antarctica and North America (Pieri *et al.* 2009). Its wide range of habitats (rivers, streams, interstitial water, bromeliad basins, rain forest leaf litter, and bog mosses) may permit this widespread geographic distribution. Furthermore, three of the most common species in this part of Italy have a wide altitudinal distribution (Figure 26). Surely they occur among bryophytes in other European countries as well.

Some species seem to be restricted to bogs, making them **tyrphobionts**. In their study of Friuli Venezia Giulia, Italy, *Cavernocypris subterranea* and *Cryptocandona vavrai* were apparently restricted to peat bogs at high altitudes (Pieri *et al.* 2009). Barclay (1968) reported the new species *Penthesilenula sphagna* (= *Darwinula sphagna*) from New Zealand, living above the water among *Sphagnum* (Figure 4). Similar relationships of ostracods to *Sphagnum* are known from eastern Africa (Menzel 1916).

The importance of mosses in bogs can be indirect. In *Sphagnum* (Figure 11) peatlands, mosses are a necessary habitat element to support the growth of pitcher plants (*Sarracenia purpurea*; Figure 27). The leaves of these plants form pitchers of water that provide a suitable habitat

for some ostracods in North America (Hamilton *et al.* 2000), including those in Florida, USA (Harvey & Miller 1996).

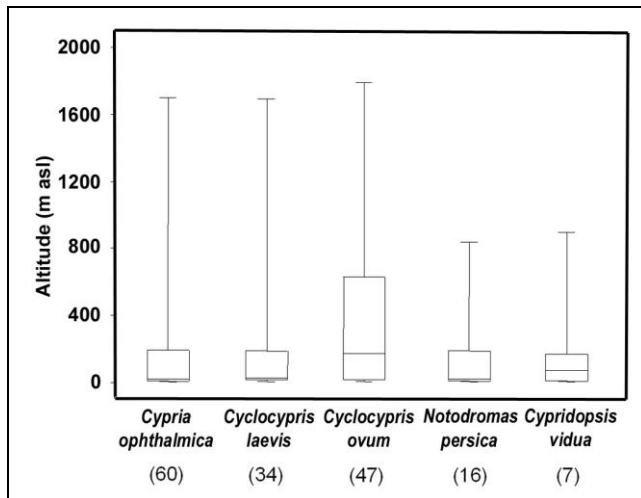


Figure 26. Comparison of altitudinal ranges of the five most common ostracods in Friuli Venezia Giulia, Italy, all five of which also occur in peat bogs. The boxes show the 25-75% quartiles. The horizontal line is the median, and the vertical bars (whiskers) show the maximum and minimum values. The numbers of analyzed samples appear in parentheses below the species names. Redrawn from Pieri *et al.* (2009).



Figure 27. *Sarracenia purpurea* in a *Sphagnum* bog. Photo from Wikimedia Creative Commons.

Aquatic

Streams

Potamocypris pallida (Figure 28) in Macedonia occurs in moss cushions on the sandy and rocky bottoms of mountain springs and brooks (Petrovski & Meisch 1995). In my own stream bryophyte collections in Appalachian Mountain, USA, streams, I rarely encountered ostracods and considered them to be accidental or temporary residents since they more commonly occur in quiet water.

Springs

Spring habitats have a number of features in common with peat bogs. They typically have a dominant bryophyte flora, and they can be dry during part of the year. But their

pH range can reach into basic values, creating conditions that favor different communities.

Bottazzi *et al.* (2011) compared ostracods collected in traps with those collected from mosses in **rheocrene** springs (where aquifer water reaches the surface) of the Northern Apennines. Ostracods were among the most abundant taxa, particularly among the permanent meiofauna. Such common inhabitants of springs can be called **crenophiles** (literally, spring-lovers). Only *Psychrodromus bertharrami* was collected in both traps and mosses, with similar numbers (20 individuals per sample in traps, 17 for mosses). *Ilyocypris bradyi* (Figure 29) was only recovered from mosses. All other taxa (except one of questionable identity) were collected in traps. Fryer (1955) described *Potamocypris thienemanni* (see Figure 28) as new to Britain, inhabiting bryophytes, including *Sphagnum* (Figure 11), in a spring. This species was also known from three springs in Germany.

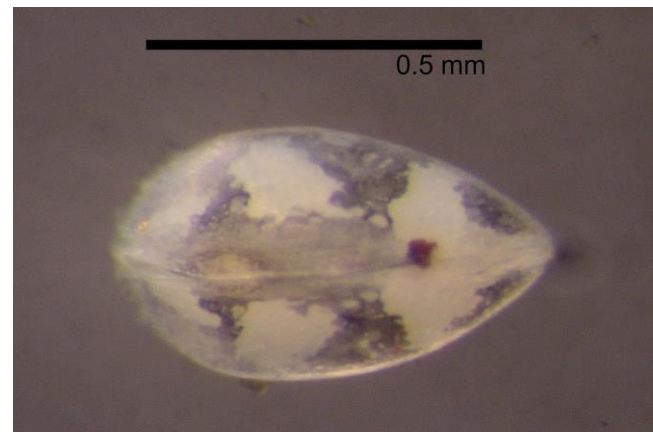


Figure 28. *Potamocypris pallida*, moss-dweller on sandy and rocky bottoms of Macedonian mountain springs and streams.. Photo by Elissa Dey, Zooplankton Project. Accessed 13 May 2014 at <http://www.biology.missouristate.edu/ostracods/Default.htm>.



Figure 29. *Ilyocypris bradyi*, an ostracod that in the northern Apennine springs seems to be limited to living among mosses. Note the hairy carapace that is typical of terrestrial ostracods. Photo from Bold Systems through Creative Commons.

CLASS MALACOSTRACA, ORDER AMPHIPODA

I have occasionally found amphipods in my collections of stream mosses, but they are more typically in quiet water

of larger streams. Nevertheless, it appears that in some cases they can be an important part of the aquatic moss faunal community (Minckley 1963; Minckley & Cole 1963; Matonickin & Pavletic 1964; Willoughby & Sutcliffe 1976). Badcock (1949) found *Gammarus* (Figure 30) to be most numerous in mosses and other protected niches, reporting an estimated fifty in a single tuft of moss (Cheney 1895). They are even known from terrestrial mosses (Merrifield & Ingham 1998).



Figure 30. *Gammarus pulex* showing the massive numbers in shallow pools. Photo through Creative Commons.

In some systems, amphipods can be quite abundant among the bryophytes. Wulffhorst (1994) found this to be true in two acid streams in the Harz Mountains, Germany, where they far exceeded those in the interstitial spaces (Figure 31).

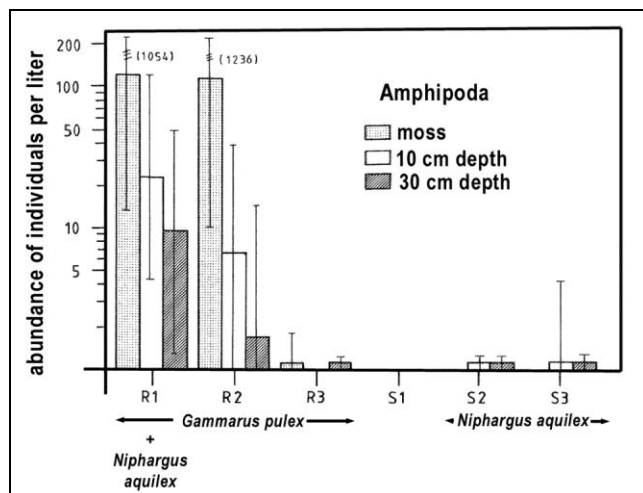


Figure 31. Abundance (number of individuals per liter) of the amphipods *Gammarus pulex* and *Niphargus aquilex* (Figure 32) among mosses and the interstitial spaces at 10 and 30 cm depth at six stations in two Harz Mountain streams. Bars indicate 95% confidence interval; n = 14 for mosses and 28-36 for interstitial spaces. Redrawn from Wulffhorst 1994.



Figure 32. *Niphargus aquilex*, a moss dweller. Photo by Grabow-Universität Koblenz-Landau, permission pending.

Adaptations to Land – and Bryophytes

Stout (1963) summarized three evolutionary pathways for terrestrial plankton. Among these, Hurley (1959) proposed that amphipods moved from the **supralittoral** (splash zone) fauna directly to the forest floor. Another suggestion is that fauna such as amphipods may have originated in freshwater streams, extended to the wet mossy banks and *Sphagnum* (Figure 11) bogs to the forest floor and ultimately to mineral soil. Stout considers the latter route to be the most convincing.

Hurley (1959, 1968) reported that all the terrestrial species of amphipods are in the family **Talitridae**, occurring in damp habitats. To survive in these terrestrial habitats required several morphological and behavioral changes, not to mention the physiological changes needed. They needed to become air breathers, jump instead of swim (accomplished by reduced **pleopods**, *i.e.* swimmerets, – to stumps in some species), adapt their life cycle to the changes in the seasons (Hurley 1959), and excrete uric acid instead of ammonia (Dresel & Moyle 1950). But they can have more than 50% ammonia excretion (Hurley 1959), perhaps releasing their ammonia as a gas like the isopods (O'Donnell & Wright 1995). It appears that they may have evolved different solutions to some of these problems from those of some of the other crustacean groups.

We can understand the small number of terrestrial amphipod species by comparing them to the isopods, where both aquatic and terrestrial species likewise exist. Terrestrial amphipods are less adapted to their terrestrial life than the isopods, being restricted to more narrow niches (Hurley 1968). The amphipods lack the isopod advantages of evaporative cooling at high temperatures and have exoskeletons with greater permeability, leading to greater risk of desiccation (Hurley 1959). Terrestrial isopods have lost their antennae, whereas in amphipods they are merely simplified. Both groups have modified their behavior to stay where it is cool and moist.

In wet leaf litter, the amphipods may move upward, a behavior we should look for among mosses (Hurley 1968). It is interesting that in the Fiordland of New Zealand the high level of rainfall and saturated ground has driven the amphipods to living among mosses or under bark of trees rather than their usual habitat of leaf litter. Avoidance of leaf litter there seems to be especially true for *Arcitalitrus sylvaticus* (= *Talitrus sylvaticus*; Figure 33). Its relative

Arcitalitrus dorrieni (Figure 34) also occurs with mosses on bark in Australia.



Figure 33. *Arcitalitrus sylvaticus*, an amphipod that avoids leaf litter and lives among mosses in the New Zealand Fiordland. Photo by Arthur Scott Macmillan through Creative Commons.



Figure 34. *Arcitalitrus dorrieni* on bark among mosses. Photo by Dluogs through Creative Commons.

Obtaining water, no problem for aquatic species, requires special behavioral techniques for the land dwellers. It is interesting that the water-obtaining behavior is similar to that of the terrestrial oniscid isopods. The terrestrial amphipods both gain and eliminate water by dabbing the uropod tips (tails) onto wet or dry substrata, respectively (Moore & Richardson 1992). The water is exchanged rapidly in or out of the central channel through the capillary spaces between the body parts. Beating **pleopods** (abdominal appendages also known as swimmerets) transfer water from the abdomen to the thorax in most terrestrial taxa. Water that pools beneath the tail is taken in by anal drinking.

Reproduction and Early Development

Among amphipods, the male is typically larger than the female and mounts her dorsally when she is ready to molt (Sutcliffe 1992). This behavior of having the male carry the female beneath him, known as **mate guarding**, helps to protect her during the crucial mating molt while

she is more vulnerable to predation, and on land to desiccation. The eggs are deposited in the external brood pouch when she molts, followed by deposition of the sperm by the male. Following fertilization, embryos are carried by the female, but hatchlings, resembling miniature adults, are on their own. The terrestrial *Talitrus saltator* (a sandhopper; Figure 35) lays its eggs four days after molting, compared to laying them immediately after copulation (Figure 36) in the aquatic *Gammarus* (Hurley 1959). The latter species can hold the spermatozoa in a brood pouch for up to four days. The aquatic male *Gammarus* carries the female under him for several days (Figure 36), whereas the terrestrial male of *Talitrus saltator* does not carry the female, a behavior difference that seems backwards until you realize he is jumping around on the sand and the female would get in the way. The 1-10 terrestrial eggs are much larger than the small and numerous aquatic eggs. The eggs of the terrestrial species furthermore remain in the brood pouch longer, affording them greater protection from desiccation.



Figure 35. *Talitrus saltator*, a sand hopper that holds its eggs four days after molting. Photo by Arnold Paul through Wikimedia Commons.



Figure 36. *Gammarus pulex* copulating, with the larger male on top. Photo by J. C. Schou, with permission.

A further means to conserve both energy and water is **neoteny**. *Orchestia* (Figure 37) reaches sexual maturity at an earlier growth stage and smaller size (Powers & Bliss 1983). This results in fewer offspring. They have a female bias, somewhat compensating for the smaller number of offspring, and females are larger than males, which is atypical for amphipods. Stephensen (1935) reported *Orchestia floresiana* from moss in Java, where it grows in waterfalls, rivulets, and fountains.



Figure 37. *Orchestia cavimana* at Colwick Park, Notts, UK. This terrestrial genus has females larger than males. Photo by Roger S. Key, with permission.

Food among the Bryophytes

Felten *et al.* (2008) found that some aquatic amphipods, or at least *Gammarus fossarum* (Figure 38), eat mosses, and that the relative proportion in the diet increases as they grow from 2 mm to 4 mm, increasing only slightly after that (Figure 39). Conversely, the proportion of fine amorphous detritus steadily decreases as the amphipods grow. Felten *et al.* suggest that the younger (smaller) amphipods do not have mouth parts that are developed well enough to eat the larger food items like bryophytes. The proportion of bryophytes in the diet also depends on where they are living, with those living among bryophytes eating a greater proportion of bryophytes (Figure 40). It is interesting that those in the detrital pools have a greater proportion of minerals, suggesting that they are unable to sort out the nutritious items from the non-nutritious items that surround them. It was unclear if the detrital pool populations were actually nibbling on the bryophytes or just eating fragments that had collected where they were.



Figure 38. *Gammarus fossarum*, an aquatic amphipod that eats mosses when its mouth parts are developed well enough to do so. Photo from BioLib.cz through public domain.

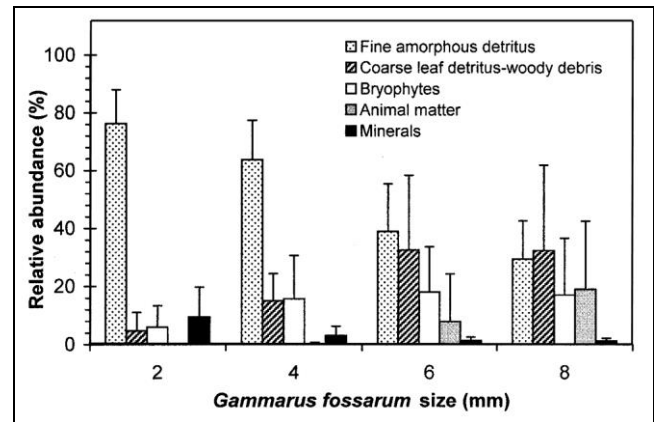


Figure 39. Comparison of mean percentage food types \pm SD. of *Gammarus fossarum* as it relates to size. Modified from Felten *et al.* 2008.

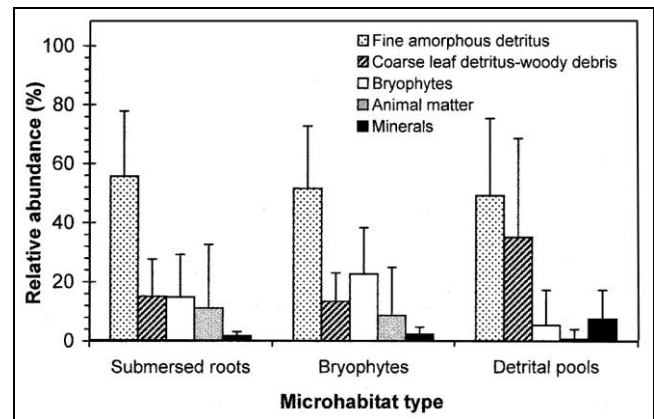


Figure 40. Comparison of mean proportion (\pm SD) of bryophytes vs other food items eaten by *Gammarus fossarum* in three habitat types. Modified from Felten *et al.* 2008.

Gladyshev *et al.* (2000) examined the gut contents of *Gammarus lacustris* (Figure 41) and found that they ingested mostly seston, obtaining omega 3 fatty acids from bottom sediment particles. They also consumed cells of the green alga *Botryococcus*. This alga not only survived the digestive tract, but its photosynthetic activity increased. They considered this activity to contribute to the dispersal of the alga, causing blooms in the littoral zone. Could this also be true of bryophytes they consume?



Figure 41. *Gammarus lacustris*, an amphipod that consumes mostly seston. Photo by Bold Systems Creative Commons.

Food particle size can determine which species are able to survive in a habitat. Graca *et al.* (1994) found that *Gammarus pulex* (Figure 30-Figure 36) occupies different zones in rivers from those of the isopod *Asellus aquaticus* (Figure 42). The researchers found that the selection of substrate by *G. pulex* was based on size, with larger individuals choosing larger-sized substratum particles; juveniles were mostly associated with plants, including mosses. The substrate choices were most likely food choices. For the aquatic amphipods, it is likely that the detritus collected by the mosses serves as a food source. It would be interesting to determine the role of food sources in the choices of terrestrial amphipods for particular bryophytes.



Figure 42. *Asellus aquaticus*, an aquatic isopod shown here on leaf litter. Photo by Malcolm Storey through Discover Life.

Acosta and Prat (2011) partially supported the idea of mosses as food collectors for the amphipod *Hyaletta* sp. (Figure 43) in the headwaters of a High Andes river. Those living among layers of travertine had 69.5% fine particulate organic matter (FPOM), but even the bryophyte-dwellers had 56.8% FPOM. Those from leaf litter, on the other hand, had 68% of their gut contents from coarse particulate organic matter, suggesting a high level of flexibility in the diet.



Figure 43. *Hyaletta azteca*, a common bryophyte dweller in streams and rivers. Photo by Barbara Albrecht at <<http://www.ipm.ucdavis.edu/WATER/U/hyaletta.html>>, with permission.

One hypothesis is that increased density of bryophytes would increase available organic detritus and thereby increase invertebrate abundance. However, Suren and Winterbourn (1992) found that reducing stem density of mosses had little effect on periphyton biomass, but that the detrital biomass was reduced on low-density artificial mosses. In any case, stem density had little effect on invertebrate abundance. Nevertheless, detrital and periphyton availability seemed to be the determining factor for invertebrate density.

Gladyshev *et al.* (2012) examined the gut contents of gammarids as part of a food chain study including *Fontinalis antipyretica* (Figure 44). Following Kalachova *et al.* (2011), they used acetylenic acids, considered as biomarkers for *Fontinalis antipyretica*, to trace the food through the mosses, periphyton, Trichoptera, gammarids, and Siberian grayling (Gladyshev *et al.* 2012). Gladyshev *et al.* (2012) found small amounts of consumption of the mosses among both the Trichoptera (caddisflies) and the gammarid *Eulimnogammarus* (*Philolimnogammarus*) *viridis*. The latter species had the highest concentrations of acetylenic acids in the winter and the lowest in summer (Kalachova *et al.* 2011), suggesting a shift to mosses in winter. It is likely that both the caddisflies and gammarids ate the moss to gain the periphyton and detritus accumulated there. The moss and associated periphyton and detritus are especially important in winter when other food sources are scarce (Gladyshev *et al.* 2012).



Figure 44. *Fontinalis antipyretica* var *gracilis*, home for the amphipod *Eulimnogammarus* (*Philolimnogammarus*) *viridis*. Photo by Des Callaghan, with permission.

But Parker *et al.* (2007) found that even when the moss *Fontinalis novae-angliae* (Figure 52) was cleaned of particulate matter, the amphipods still ate significant quantities of it. Earlier studies by Minckley and Cole (1963) likewise indicated that amphipods ate mosses. On the other hand, Mulholland *et al.* (2000) found that the amphipod *Gammarus minus* (Figure 45) depended on fine benthic (bottom) organic matter, despite the presence of bryophytes.

One feeding possibility in nature that might not be evident in laboratory studies is the role of fungi. Barlocher and Porter (1986) demonstrated that *Gammarus tigrinus* (Figure 46) was able to digest plant polysaccharides and release sugars from maple leaves. They also had the right enzymes to break down glycosidic linkages in small molecules, much as that done in microbial decomposition.

Furthermore, fungal carbohydrases ingested with the food of the *Gammarus* remained active in the gut. The implication seems to be that *Gammarus* could benefit from fungi associated with bryophytes in the field. Similarly, Sarah Lloyd (pers. comm.) has documented that terrestrial amphipods eat slime molds that live on mosses (Figure 47).

It appears that at least some bryophytes are not suitable food for *Gammarus* (Figure 30-Figure 36). Willoughby and Sutcliffe (1976) conducted feeding experiments on *Gammarus pulex* (Figure 30) from the River Dutton. They found that those provided with only the liverwort *Nardia* sp. (Figure 48) were unable to grow or survive.



Figure 45. *Gammarus minus*, an amphipod that seems to prefer fine benthic organic matter over bryophytes. Photo through Creative Commons.



Figure 48. *Nardia scalaris*, a leafy liverwort genus in which a European species failed to sustain *Gammarus pulex* as a food source. Photo from Europe by Michael Lüth, with permission.



Figure 46. *Gammarus tigrinus*, an amphipod that can digest fungi from leaves. Photo by Hugh MacIsaac, with permission.

Habitats

Terrestrial

Terrestrial amphipods are rare, but bryophytes can provide the kind of moist habitat needed for them to survive. Merrifield and Ingham (1998) found amphipods in their Oregon Coast Range, USA, study of the fauna of *Eurhynchium oregonum* (Figure 49). In most months they were not evident, but in the December collection their numbers rose to 1 per gram of moss in 10 5-cm samples. The second "peak" was in April, with 0.6 per gram. Sarah Lloyd (pers. comm.) found what appears to be *Keratroides*, possibly *K. vulgaris*, among mosses in a wet eucalypt forest in northern Tasmania.



Figure 47. Amphipod, probably *Keratroides*, possibly *K. vulgaris*, eating a slime mold (probably *Diderma* sp.) on moss. Photo by Sarah Lloyd, with permission.



Figure 49. *Eurhynchium oregonum*, a moss that is known to house amphipods in North America. Photo by Adolf Ceska, with permission.



Figure 50. Terrestrial amphipod, probably *Keratoides*, possibly *K. vulgaris*, on mosses in wet sclerophyll (eucalypt) forest at Birrallee in Northern Tasmania, Australia. Photo courtesy of Sarah Lloyd.

Friend (1987) described the new species *Orchestiella neambulans* from litter that accumulated between mosses in Tasmania.

The Antarctic seems to be the most likely place to find limnoterrestrial Crustacea among mosses, but the amphipods are poorly represented. Pugh *et al.* (2002) found only one (*Makawe insularis*) in their study, a species with a broad niche of wood, leaf litter, lichens, tussock grass, under stones, penguin nests, and...among mosses.

Aquatic

Rocky streams are often dominated by mosses and liverworts in extensive mats over the rocks. These provide a foothold that protects their inhabitants from being swept away. Macan and Worthington (1951) found that amphipods such as *Gammarus* (Figure 30-Figure 36) were more likely on mosses that were not so thick, whereas thicker mosses were dominated by Chironomidae. They found that fish food organisms increased in number when the streams had rooted plants or mosses. One problem faced by the inhabitants of tracheophytes is that the plants begin die-off in late summer and the amphipods must find a new substrate with sufficient periphyton and detritus to provide food. *Gammarus* is among the slow colonizers (Fontaine & Nigh 1983), so it might benefit from the stable year-round habitat of bryophytes as a source of shelter and detrital and periphytic food.

Elliott (2005) found that *Gammarus pulex* had significant day-night differences in its habitat distribution. These were explained by dry weights of bryophytes, leaf material, organic detritus, distance from bank, water depth, water velocity, and particle size class. The bryophyte weight correlated positively with larger particle sizes and negatively with smaller particle sizes, perhaps explaining some of the choices by *G. pulex* for bryophytes. But this correlation may have been due to the preference of

bryophytes for larger stones. Juvenile densities in the daytime correlated positively with smaller particles and negatively to larger particles, also correlating with the weight of bryophytes. However, at night the densities were unrelated to particle sizes or bryophyte weight.

Parker *et al.* (2007) found that the amphipod *Crangonyx gracilis* (see Figure 51) was a common inhabitant of the brook moss *Fontinalis novae-angliae* (Figure 52), where it used the moss shelter as a food source. Badcock (1949) found that *Gammarus* (Figure 30-Figure 36) species were more numerous in sheltered sites such as mosses. Minckley (1963) found *Gammarus* among the moss *Fissidens* sp. (Figure 53) in a Kentucky, USA, stream. It not only lived there, but ate the moss that served as its home (Minckley & Cole 1963).



Figure 51. *Crangonyx pseudogracilis*, relative of *C. gracilis* that lives among *Fontinalis novae-angliae* and also eats it. Photo from Discover Life - Creative Commons.



Figure 52. *Fontinalis novae-angliae*, shelter for *Crangonyx gracilis*. Photo by Janice Glime.

In an unlikely place, the depths of Yellowstone Lake, associated with active geothermal vents, *Fontinalis* abounds (Lovalvo *et al.* 2010). Associated with this unusual inhabitant are, among other invertebrates, the amphipods *Hyalella* (Figure 43) and *Gammarus* (Figure 30-Figure 36, Figure 41, Figure 45).



Figure 53. *Fissidens fontanus*, both a home and food for some species of *Gammarus*. Photo by Michael Lüth, with permission.

Summary

Both Ostracoda and Amphipoda are primarily marine, with fewer species in freshwater and much fewer in terrestrial habitats. Nevertheless, ostracods are known from roof mosses, and the genus *Mesocypris* is a common terrestrial moss dweller, especially in the Southern Hemisphere.

Their adaptations to living among bryophytes (and other terrestrial locations) include swimming instead of crawling, small size, loss of eyes in some, reduced setae (used for swimming), excretion of nitrogenous waste from maxillae, antennae, or possibly through the carapace (perhaps as gaseous ammonia), drought-resistant eggs, and parthenogenesis. Food often consists of detritus, algae, and bacteria, but some amphipods eat bryophytes as well.

Bogs offer habitats where ostracods can migrate vertically or horizontally to find suitable conditions as the temperature and moisture change. Some are even true **tyrphobionts**. But there appear to be few, if any, records for amphipods. Some ostracods live among the pitcher plants in the bogs.

Few ostracods are known from among mosses in streams, but several amphipods can be found there. However springs seem to be suitable habitats for several species in both groups.

The microcrustacea may have advanced onto land through wet mosses of springs and stream banks. They are represented by few families, the **Cypridae** among the ostracods and the **Talitridae** among the amphipods.

Terrestrial amphipods are not well known, and thus far their presence among *Sphagnum* does not seem to be documented.

interesting images and identifying the organisms. Robin James Smith not only gave me permission to use his images, but provided me with another moss record of an ostracod in Japan. Paul Davison has provided constant support with his interest, his images, and in this subchapter providing a critical review.

Literature Cited

- Acosta, R. and Prat, N. 2011. Trophic ecology of *Hyaella* sp. (Crustacea: Amphipoda) in a High Andes headwater river with travertine deposits. *Internat. Rev. Hydrobiol.* 96: 274-285.
- Badcock, R. M. 1949. Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* 18: 193-208.
- Barclay, M. H. 1968. Additions to the freshwater ostracod fauna of New Zealand. *N. Z. J. Mar. Freshwat. Res.* 2: 67-80.
- Barnes, R. D. 1982. *Invertebrate Zoology*. Holt-Saunders International, Philadelphia, pp. 680-683.
- 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.
- Chapman, M. A. 1961. The terrestrial ostracod of New Zealand, *Mesocypris audax* sp. nov. *Crustaceana* 2: 255-261.
- Cheney, A. N. 1895. Food for fishes. In: Davis, B. H., Lyman, H. H., Weed, W. R., Babcock, C. H., and Thompson, E. (eds.). *First Annual Report of the Commissioners of Fisheries, Game and Forests*, pp. 99-117.
- Deckker, P. De. 1983. Terrestrial ostracods in Australia. In: Lowrey, J. K. (ed.). *Papers from the Conference on the Biology and Evolution of Crustacea*. Australian Museum Memoir 18: 87-100.
- Dresel, E. I. B. and Moyle, V. 1950. Nitrogenous excretion of amphipods and isopods. *J. Exper. Biol.* 27: 210-225.
- Elliott, J. M. 2005. Day-night changes in the spatial distribution and habitat preferences of freshwater shrimps, *Gammarus pulex*, in a stony stream. *Freshwat. Biol.* 50: 552-566.
- Felten, V., Tixier, G., Guerold, F., Crespin De Billy, V. De, and Dangles, O. 2008. Quantification of diet variability in a stream amphipod: Implications for ecosystem functioning. *Fund. Appl. Limnol.* 170: 303-313.
- Fontaine, T. D. and Nigh, D. G. 1983. Characteristics of epiphyte communities on natural and artificial submersed lotic plants: Substrate effects. *Arch. Hydrobiol.* 96: 293-301.
- Friend, J. A. 1987. The terrestrial amphipods (Amphipoda: Talitridae) of Tasmania: Systematics and zoogeography. *Records of the Australian Museum, Supplement* 7: 1-85.
- Fryer, G. 1955. XVI. – *Potamocypris thienemanni* Klie, a little-known spring-inhabiting ostracod new to Britain. *Ann. Mag. Nat. Hist.* 8: 121-124.
- GBIF. 2013. The Global Biodiversity Information Facility: GBIF Backbone Taxonomy. *Bryocypris* Røen, 1956. Last updated 1 July 2013. Accessed 14 May 2014 at <<http://www.gbif.org/species/4808141>>.
- Gladyshev, M. I., Emelianova, A. Y., Kalachova, G. S., Zotina, T. A., Gaevsky, N. A., and Zhilenkov, M. D. 2000. Gut content analysis of *Gammarus lacustris* from a Siberian lake using biochemical and biophysical methods. *Hydrobiologia* 431: 155-163.
- Gladyshev, M. I., Sushchik, N. N., Kalachova, G. S., and Makhutova, O. N. 2012. Stable isotope composition of fatty

Acknowledgments

Sarah Lloyd and her colleagues have been of invaluable help in this chapter by providing me with

- acids in organisms of different trophic levels in the Yenisei River. PLoS one 7(3), e34059.
- Graca, M. A. S., Maltby, L., and Calow, P. 1994. Comparative ecology of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.) I: Population dynamics and microdistribution. *Hydrobiologia* 281: 155-162.
- 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.
- 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.
- Harvey, E. and Miller, T. E. 1996. Variance in composition of inquiline communities in leaves of *Sarracenia purpurea* L. on multiple spatial scales. *Oecologia* 108: 562-566.
- Hurley, D. E. 1959. Notes on the ecology and environmental adaptations of the terrestrial Amphipoda. *Pacific Sci.* 13: 107-109.
- Hurley, D. E. 1968. Transition from water to land in amphipod crustaceans. *Amer. Zool.* 8: 327-353.
- Introduction to the Ostracoda. 2002. University of California Museum of Paleontology. Accessed 6 November 2011 at <<http://www.ucmp.berkeley.edu/arthropoda/crustacea/maxillopoda/ostracoda.html>>.
- Kalachova, G. S., Gladyshev, M. I., Sushchik, N. N., and Makhutova, O. N. 2011. Water moss as a food item of the zoobenthos in the Yenisei River. *Central Eur. J. Biol.* 6: 236-245.
- Kiss, A. 2007. Factors affecting spatial and temporal distribution of Ostracoda assemblages in different macrophyte habitats of a shallow lake (Lake Fehér, Hungary). *Hydrobiologia* 585: 89-98.
- Lovalvo, D., Clingenpeel, S. R., McGinnis, S., Macur, R. E., Varley, J. D., Inskeep, W. P., Glime, J., Neelson, K., and McDermott, T. R. 2010. A geothermal-linked biological oasis in Yellowstone Lake, Yellowstone National Park, Wyoming. *Geobiology* 8: 327-336.
- Macan, T. T. and Worthington, E. B. 1951. *Life in Lakes and Rivers*. Collins, London, 272 pp.
- Martens, K., Deckker, P. De, and Rossetti, G. 2004. On a new terrestrial genus and species of Scottiinae (Crustacea, ostracods) from Australia, with a discussion on the phylogeny and the zoogeography of the subfamily. *Zool. Anz.* 243: 21-36.
- Matonickin, I. and Pavletic, Z. 1964. Postanak i razvoj najmladin sedrenih tvorevina u rijeci Uni s biologskog stanovista. *Jugoslav. Akad. Znan. Umjetn. Krs. Jugoslavje* 4: 103-112.
- Menzel, R. 1916. Moosbewohnende Harpacticiden und Ostracoden aus Ost-Afrika. *Arch. Hydrobiol.* 11: 486-489.
- Merrifield, K. and Ingham, R. E. 1998. Nematodes and other aquatic invertebrates in *Eurhynchium oreganum* (Sull.) Jaeg., from Mary's Peak, Oregon Coast Range. *Bryologist* 101: 505-511.
- Minckley, W. L. 1963. The ecology of a spring stream Doe Run, Meade Co., Kentucky. *Wildl. Monogr.* 11: 1-126.
- Minckley, W. L. and Cole, G. A. 1963. Ecological and morphological studies on gammarid amphipods (*Gammarus* spp.) in spring-fed streams of northern Kentucky. *Occ. Papers C. C. Adams Center Ecol. Studies., W. Mich. Univ., Kalamazoo*, 35 pp.
- Miracle. 2014. Ostracods. Accessed 31 March 2014 at <<http://www.ucl.ac.uk/GeolSci/micropal/ostracod.html>>.
- Moore, M. L. and Richardson, A. M. M. 1992. Water uptake and loss via the urosome in terrestrial talitrid amphipods (Crustacea: Amphipoda). *J. Nat. Hist.* 26: 67-77.
- Mulholland, P. J., Tank, J. L., Sanzone, D. M., Wollheim, W. M., Peterson, B. J., Webster, J. R., and Meyer, J. L. 2000. Food resources of stream macroinvertebrates determined by natural-abundance stable C and N isotopes and a ¹⁵N tracer addition. *J. N. Amer. Benthol. Soc.* 19: 145-157.
- O'Donnell, M. J. and Wright, J. C. 1995. Nitrogen excretion in terrestrial crustaceans. In: Walsh, P. J. and Wright, P. (eds.). *Nitrogen Metabolism and Excretion*. CRC Press, Boca Raton, FL, pp. 105-118.
- Parker, J. D., Burkeile, D. E., Collins, D. O., Kubanek, J., and Hay, M. E. 2007. Stream mosses as chemically-defended refugia for freshwater macroinvertebrates. *Oikos* 116: 302-312.
- Petrovski, T. K. and Meisch, C. 1995. Interesting freshwater Ostracoda (Crustacea) from Macedonia. *Bull. Soc. Nat. Luxemb.* 96: 167-183.
- Pieri, V., Martens, K., Stoch, F., and Rossetti, G. 2009. Distribution and ecology of non-marine ostracods (Crustacea, Ostracoda) from Friuli Venezia Giulia (NE Italy). *J. Limnol.* 68: 1-15.
- Pinto, R. L., Rocha, C. E. F., and Martens, K. 2005a. On new terrestrial ostracods (Crustacea, ostracods) from Brazil, Primarily from São Paulo State. *Zool. J. Linn. Soc.* 145: 145-173.
- Pinto, R. L., Rocha, C. E. F., and Martens, K. 2005b. On the evolution of the genus *Microdarwinula* Danielopol, 1968 (Ostracoda, Darwinulidae) with the description of a new species from semi-terrestrial habitats in São Paulo State (Brazil). *Crustaceana* 78: 975-986.
- 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.
- Stephensen, K. 1935. Terrestrial Talitridae from the Marquesas. *Bernice P. Bishop Museum Bull.* 142: 19-34.
- Stout, J. D. 1963. The terrestrial plankton. *Tuatara* 11: 58-64.
- Suren, A. M. and Winterbourn, M. J. 1992. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. *Freshwat. Biol.* 17: 327-339.
- Sutcliffe, D. W. 1992. Reproduction in *Gammarus* (Crustacea, Amphipoda): Basic processes. *Freshwat. Forum* 2: 102-129.
- Wagenleitner, H. 1990. Morphology and evolution of *Cypria cavernae* n. sp. (Ostracoda, Crustacea). *Bull. Soc. Nat. Luxemb.* 90: 199-226.
- Wikipedia. 2014. Ostracod. Last updated 22 March 2014. Accessed 31 March 2014 at <<http://en.wikipedia.org/wiki/Ostracod>>.
- Willoughby, L. G. and Sutcliffe, D. W. 1976. Experiments on feeding and growth of the amphipod *Gammarus pulex* (L.) related to its distribution in the River Duddon. *Freshwat. Biol.* 6: 577-586.
- 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.