CHAPTER 4-2
INVERTEBRATES: SPONGES, GASTROTRICHS, NEMERTEANS, AND FLATWORMS

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Figure 1. This **planarian, *Polycladus gayi***, is navigating a mat of the liverwort ***Lepidozia cordulifera***. The planarian is a native of Valdivian rainforests of southern Chile, where it hunts for food on bryophytes and other substrata. Photo courtesy of Filipe Osorio.

Cnidaria

Members of the **Hydrozoa** (hydroids) are not common among bryophytes, but they can occur there. Jones (1951) reported ***Hydra viridissima*** (Figure 2) from ***Fontinalis antipyretica*** (Figure 3) on bedrock in the River Towy, Wales.

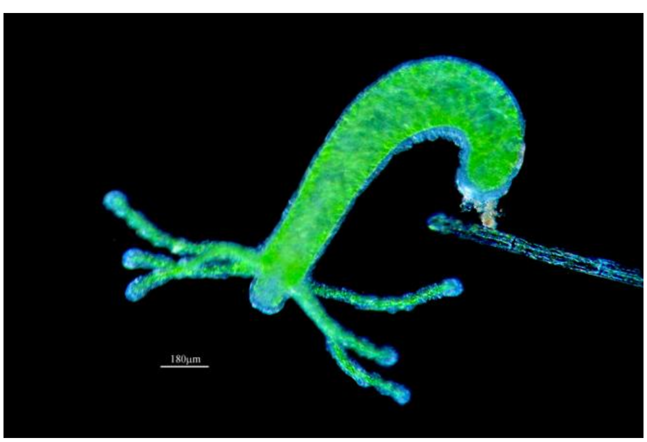

Figure 2. ***Hydra viridissima***, occasional bryophyte dweller. Photo from Proyecto Agua, with permission.

Figure 3. ***Fontianlis antipyretica*** growing in a stream where it can offer a protected substrate for a number of invertebrates. Photo by Andrew Spink, with permission.

Porifera – Sponges

Sponges don't seem to have any particular appreciation of bryophytes, being unknown from that habitat. However, it appears that the moss genus ***Fissidens*** has a special fondness for sponges. I know of no other bryophyte genus that finds this a suitable habitat, but ***Fissidens fontanus*** (Figure 4) in Europe is epizootic on **sponges** (Sowter 1972) and ***F. brachypus*** lives only on freshwater sponges in the Amazon (Buck & Pursell 1980). ***Fissidens*** seems to like animal habitats, living on the openings of wombat holes, termite mounds, and in this case, on a sponge.

Although a moss-sponge combination in nature is rare, humans seem to have found this combination useful. A patent application by Albert G. Morey, dated 13 October 1968, for an "improved mattress" extols the virtues of placing a large **sponge** (mattress) over a layer of only slightly spongy material such as moss. A three-layer mattress is considered to be superior, with the lower layer of moss sustaining the middle layer of woody fiber or excelsior, again with a layer of elastic **sponge** on top. It appears that this was a real sponge (or lots of them) and predates the use of cellulose sponges. The improvement seems to have been the addition of the moss and fibrous layers.

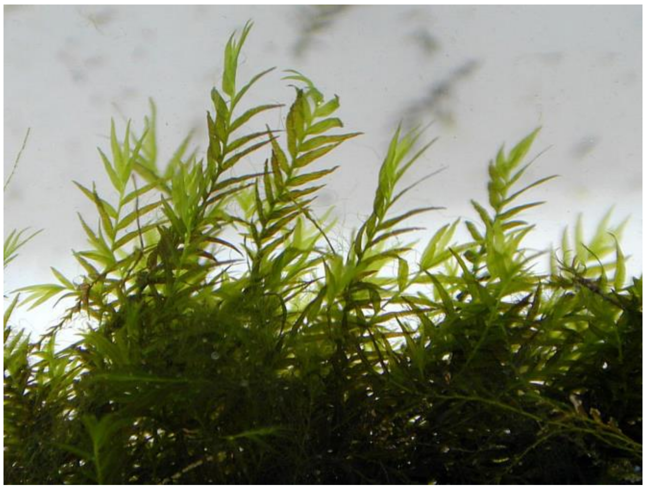

Figure 4. ***Fissidens fontanus***, a species that can be epizootic on **sponges**. Photo by Michael Lüth, with permission.

Gastrotrichs

These small animals with "hairs on their stomachs" use them to beat against such surfaces as moss leaves to glide forward (Figure 5-Figure 11; Hingley 1993). They lack a coelom, like flatworms, and move in a similar motion. Like nematodes, rotifers, and tardigrades, freshwater **gastrotrichs** are all **parthenogenetic**, producing viable unfertilized eggs. Adults are unable to go dormant, but when unfavorable conditions arise, they produce larger eggs with heavier shells that survive not only desiccation, but also low and high temperatures. They adhere using cement glands in two terminal projections (Gastrotrich 2009). One of the glands conveniently secretes a de-adhesion to release them.

They may be found occasionally on aquatic bryophytes. The **Dichaeturidae** is a rare family that has been found in cisterns, in underground water, and among mosses (Remane 1935-1936; Ruttner-Kolisko 1955). In the Czech Republic, Vlčková *et al.* (2001/2002) reported 2823 of these invertebrates on 100 ml of the aquatic moss ***Fontinalis antipyretica*** (Figure 3) in Bystřice, whereas in Mlýnský náhon there were only 371 per 100 ml. In Bystřice the mosses held a food source of organic matter in the size range of 30-100 µm. Linhart *et al.* (2002) found that abundance was negatively influenced by flow velocity in both of these streams, and the gastrotrichs were significantly fewer in riffles, suggesting that bryophytes could act as refugia in areas of high flow. On the other hand, sediment also was reduced in areas of high velocity, resulting in more available food in sediments in low velocity areas.

In a peatland complex in northern Italy, Balsamo and Todaro (1993) identified 21 species of **gastrotrichs**. Hingley (1993) found the following gastrotrichs among the peatlands mosses in her study of the British Isles:

Chaetonotus heterocanthus	*Chaetonotus zelinkai*
Chaetonotus maximus	*Heterolepidoderma ocellatum*
Chaetonotus ophiogaster	*Ichthydium forcipatum*
Chaetonotus polyspinosus	*Lepidodermella squamatum*
Chaetonotus voigti	*Stylochaeta fusiformis*

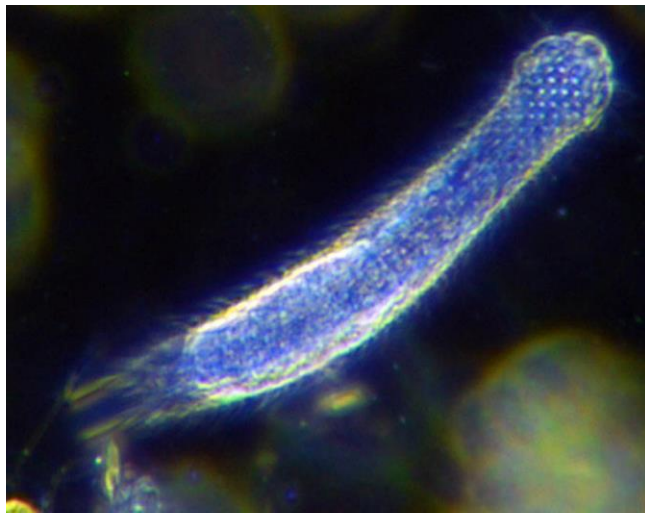

Figure 5. **Gastrotrich** showing two tails and cilia. Photo by Jasper Nance through Wikimedia Commons.

Figure 6. **Gastrotrichs** awakened from dry soil. Photo by Paul G. Davison, with permission.

Figure 7. ***Heterolepiderma***, a genus that has moss-dwelling gastrotrichs. Photo by Yuuji Tsukii, with permission.

Figure 8. ***Chaetonotus cordiformis*** next to a desmid. Photo by Yuuji Tsukii, with permission.

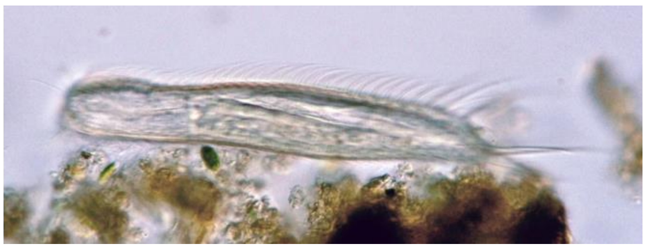

Figure 9. ***Chaetonotus zelinkai***, a moss-dwelling gastrotrich. Photo by Yuuji Tsukii, with permission.

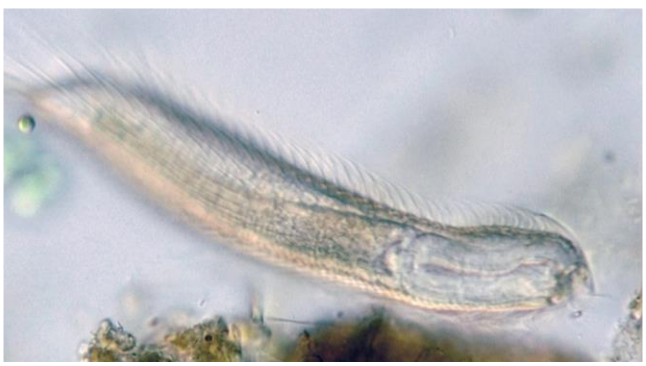

Figure 10. ***Chaetonotus zelinkai***, a peatland gastrotrich. Photo by Yuuji Tsukii, with permission.

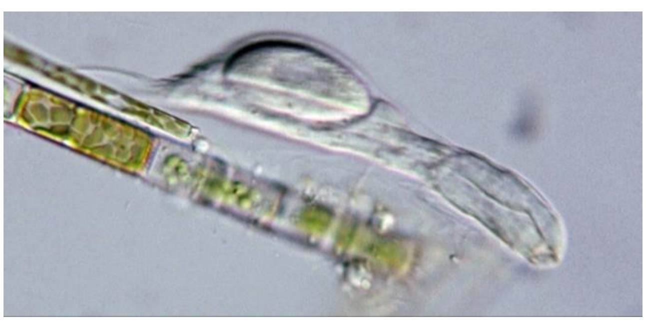

Figure 11. ***Ichthydium forficula***, a member of a genus that can occupy peatlands. Photo by Yuuji Tsukii, with permission.

Nemertea – Ribbon Worms

The ribbon worms are an unknown phylum to most of us. But those nemertines that live on land have learned about bryophytes. In 1915, Dakin described one of these as a new species *Geonemertes dendyi*, later moved to ***Argonemertes dendyi*** (Figure 12), from Western Australia. Anderson (1980) reported this species from Ireland, where it can be found among a thin layer of mosses on branches. Later, Anderson (1986) reported it from mosses and under bark in Ireland. Ribbon worms are clandestine species that one can rarely find in the open (Winsor 2001, pers. comm. 29 February 2012).

Argonemertes dendyi (Figure 12) is among the small fauna, measuring only 15 mm (Dakin 1915). It has multiple eyes, numbering as many as 30 or 40. As descendents from marine organisms, one of the major adaptations required by terrestrial nemerteans was a way to maintain sufficient hydration (Moore & Gibson 1985). The physiological mechanisms are not well understood but seem to involve mucous glands, blood and excretory system, and modulation of osmotic properties. These worms often travel with potted plants, and consequently they can be found in far-flung parts of the planet (Gibson 1995; Moore *et al*. 2001). Their hermaphroditic reproduction makes establishment of these travellers more likely to succeed.

Figure 12. ***Argonemertes dendyi***. Photo by Malcolm Storey through Creative Commons.

Leigh Winsor (pers. comm., 16 February 2012) is an avid seeker of terrestrial flatworms, but occasionally he also finds nemertines (Winsor 1985). He reports finding ***Argonemertes australiensis*** (Figure 13) under a thick mat of moss where it resided on a rotting log in a closed forest in southwest Tasmania. That is impressive for a worm that is 40 mm long (Hickman 1963; Moore 1975; Mesibov 1994). The egg capsules typically occur in rotting logs in August and March (Winsor 1996/97). These eggs are clear, jelly-like, and oblong, ca 10 mm long X 3 mm diameter.

Figure 13. ***Argonemertes australiensis*** extracted from moss on a log. Photo by Leigh Winsor, with permission.

This strange nemertine uses its proboscis to escape. When in a hurry, the worm quickly everts the proboscis and uses it as a muscled anchor to pull its body forward rapidly as the proboscis once again returns to its internal lodging (Figure 14). This rapid proboscis also out-paces its Collembola and other prey, permitting the worm to capture its dinner. This species comes in three very distinct color varieties (Mesibov 1994), most likely permitting it to survive in its diverse habitat where different predators may lurk in different locations, a phenomenon we will discuss later for tropical frogs.

Figure 14. ***Argonemertes australiensis*** with an extended proboscis. Photo by Leigh Winsor, with permission.

Platyhelminthes – Flatworms

Most of us in the pre-DNA-biology generations learned about flatworms in high school because it was easy to do experiments with ***Dugesia*** (see *e.g.* Saló & Baguñà 2002), known to most of us as *Planaria*. This animal has a distinguishable head with two eyes, and it was relatively easy to cut the head in half and watch two heads develop. This novel exercise opened discussions about development and other topics and provided a memorable experience that endeared the flatworms to us for life.

Most of the **turbellaria** (Figure 1), formerly a class within the phylum **Platyhelminthes**, are nocturnal and free-living, and it is among this group that one finds a small number of bryophyte-dwellers. The group is not monophyletic and is no longer recognized taxonomically, but the concept of **turbellaria** is useful for our purposes as all the bryophyte dwellers are in this group of non-parasites. The **turbellaria** lack a true body cavity and are shaped like a large ciliate protozoan and actually have a covering of cilia that permits them to glide (Hingley 1993). But they are multicellular, somewhat flattened, as their phylum name implies, where *platy* means flat and *helminth* means worm. This flattening permits them to obtain oxygen throughout their bodies, which lack circulatory and respiratory organs. They sport a simple digestive system, nervous system, and excretory system, and they seem to lack any sort of physiological or anatomical adaptations for conserving water, but they may be able to conserve water through alternative biochemical excretory pathways (Winsor *et al*. 2004). They even have eyespots and a simple brain (Hingley 1993).

Reproduction in the phylum may be by simple division (fission), whereas almost all turbellarians are **simultaneous hermaphrodites** (have both sexes at the same time). Among the family Typhloplanidae, the eggs may be thin-shelled in summer and hatch within days of being laid, but winter eggs are often thick-shelled and may be dormant (Pennak 1953; Domenici & Gremigni 1977; Hingley 1993). In the Typhloplanidae, these thick-shelled eggs can survive desiccation, whereas mature individuals might migrate to more moist, deeper levels. In other terrestrial flatworms, egg shells are typically thick (Figure 15), but the process of laying down the shell is different from those of the Typhloplanidae, and their ability to survive harsh conditions is unknown. These process differences may relate to differences between freshwater and terrestrial triclads (Winsor 1998a).

Figure 15. Eggs of a terrestrial flatworm. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Bryophyte Habitat Constraints

Leigh Winsor, who has spent more than 40 years studying terrestrial flatworms, says that in wet forests the bryophytes are generally too adherent to the substrate to permit the (large) flatworms to move beneath the moss (Leigh Winsor, pers. comm. 16 February 2012).

Furthermore, unlike many of the invertebrates that seek mosses to maintain moisture, the flatworms seek a fairly smooth surface to which they can adhere their ventral surface, thus minimizing water loss. I would suggest further that the hygroscopic mosses might actually absorb surface water from the flatworms in drying conditions, further drying them. Nevertheless, the bryophyte mats do offer a substrate where the flatworms can pursue their prey (Leigh Winsor, pers. comm. 16 February 2012). And some seem to solve the problem of water loss by twisting into a knot that glues the ventral surface to itself (Figure 16). On the other hand, in excessively wet conditions, the terrestrial flatworms may use mosses to prevent getting too wet by crawling up into the moss and away from **frank water** (obvious pools of water).

Figure 16. ***Australopacifica*** sp. in knot on moss in New Zealand. Photo by Alastair Robertson and Maria Minor, Massey University, Copyright SoilBugs, published by permission.

Following Schultze (1857), who suggested that terrestrial planarians are likely to exhibit a rich fauna concealed in damp mosses, under stones, and other habitats where moisture is sufficient to maintain them, Davison *et al*. (2008, 2009) report on bryophilous microturbellarians from northwest Alabama, USA. These smaller versions are able to live among mosses on tree trunks and rocks.

The terrestrial flatworm ***Tasmanoplana tasmaniana*** (Figure 17), a species widespread in a variety of habitats throughout Tasmania, has also been found beneath moss in a temperate rainforest near Fourteen Mile Creek, SW Tasmania (Leigh Winsor, pers. comm. 16 February 2012). The area was very wet and the bryophytes and logs were saturated with water.

Figure 17. ***Tasmanoplana tasmaniana***, a flatworm that lives in mosses in Tasmania. Photo by Leigh Winsor, with permission.

Bryophytes provide a moist habitat where zoospores of such parasites as the **chytridiomycosis** fungus ***Batrachochytrium dendrobatidis*** can survive (Dewel *et al.* 1985). This fungus can be lethal to some amphibians. One must wonder how bryophytes may play a role in harboring other parasites, or conversely, in providing antibiotics that deter them.

One mossy habitat that may be suitable for larger planarians is on leaves covered with epiphylls, as seen in ***Pseudogeoplana panamensis*** (Figure 18). The surface is relatively flat, and the mosses, liverworts, and other epiphylls can maintain greater moisture levels than a "clean" leaf surface. This relationship remains unstudied.

Figure 18. This flatworm, possibly ***Pseudogeoplana panamensis***, is on a palm leaf covered with lichens. Photo by Brian Gratwicke through Creative Commons.

Food Sources

When active, **microflatworms** feed on **protozoa**, **nematodes**, **rotifers**, **tardigrades**, **insect** larvae (Figure 19), and **algae** (Kolasa 1991; Davison *et al*. 2008) with which they share their mossy home. As suggested by Davison, it appears that one attraction for these **flatworms** in moss communities is the available **tardigrades** (Figure 20). **Flatworms** are known to eat **mosquito** larvae (Figure 19), so it is likely that they are able to eat **Chironomidae** (**midge**) larvae that live among the leaves of aquatic mosses and liverworts. Some **microturbellarians** are known to house green **algae** as symbionts (Kolasa 1991), presumably contributing to oxygen, but possibly also contributing carbohydrates. Such a relationship is unknown among moss-dwellers, but certainly it would be worthwhile to search for such symbionts. We do know that some of the tardigrades eat diatoms, a group of algae common on bryophytes, even in some terrestrial habitats, making algae part of the food chain (Bartels 2005).

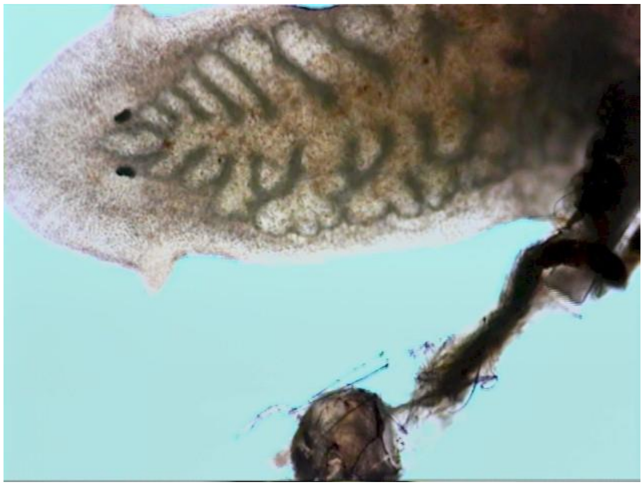

Figure 19. **Flatworm** feeding on a **mosquito** larva. Photo by Paul G. Davison, with permission.

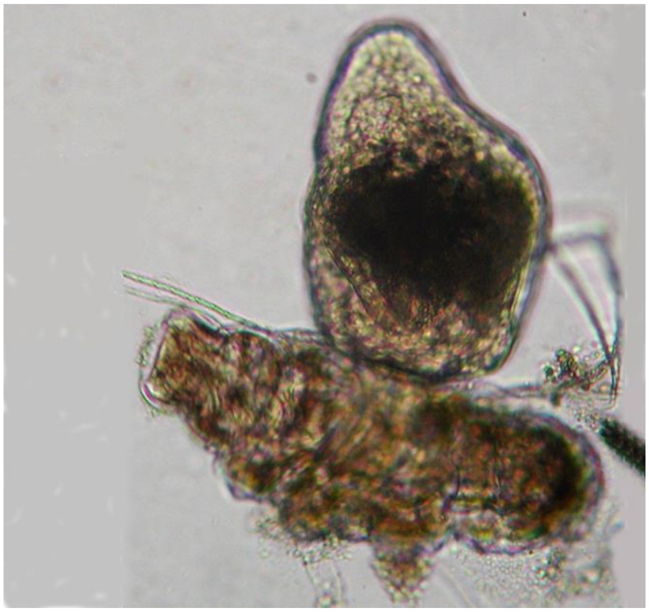

Figure 20. **Flatworm** eating **tardigrade**. Photo by Paul G. Davison, with permission.

Davison *et al*. (2009) experimented with prey choice among flatworms from epiphytic mosses in Alabama, USA. The flatworms had a strong preference for the rotifer ***Philodina roseola*** (Figure 21) over the nematode ***Panagrolaimus***, both of which occur on bryophytes (Hirschfelder *et al*. 1993; Shannon *et al*. 2005). They either ingested these prey or sucked the contents out.

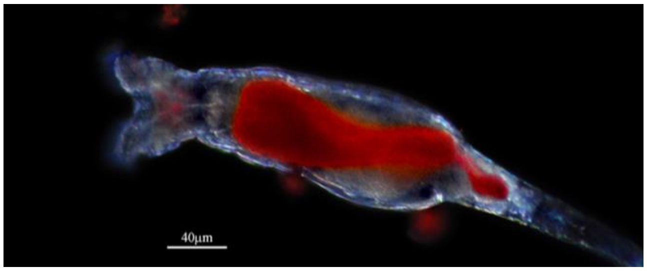

Figure 21. ***Philodina roseola***, a preferred prey organism for some flatworms. Photo from Proyecto Agua, with permission.

Protection or Predation?

The terrestrial flatworms seem to be relatively well protected from predation. Vertebrates seem to avoid them, most likely due to their mucous secretions when disturbed (Arndt & Manteufel 1925; McGee *et al*. 1996; Cannon *et al*. 1999). ***Arthurdendyus triangulatus*** (Figure 22) invokes violent reactions in earthworms when they make contact (Blackshaw & Stewart 1992 in Winsor *et al.* 2004). The flatworm wraps itself around the earthworm and secretes strong enzymes that turn the poor earthworm into soup! But then, earthworms are their primary source of food (Winsor *et al*. 2004). When this species is unable to find any food, it can survive more than 15 months at 12°C by digesting its own tissues – and shrinking (Blackshaw 1992, 1997; Christensen & Mather 1998a, 2001). However, at 20°C it dies within three weeks without food (Blackshaw 1992), so its presence at warmer temperatures needs to be timed with availability of a food source.

Figure 22. ***Arthurdendyus triangulatus*** on a bed of damp mosses. Photo © Roy Anderson, with permission.

Mosses can deprive the stoneflies of their flatworm prey. Wright (1975) found that flatworms in streams of North Wales were scarce on the undersides of stones and spent their lives confined to patches of mosses. Those that emerged from the mosses to venture to the undersides of rocks became easy prey for the stonefly *Dinocras cephalotes*.

Watch Out for Invasive Species

Arthurdendyus triangulatus (New Zealand flatworm, formerly *Artioposthia triangulata*; Figure 22) lives in damp terrestrial habitats such as those under logs, decaying wood, mosses, and leaves (Willis & Edwards 1977). ***Arthurdendyus triangulatus*** is a flatworm about 50 mm long, but can extend to 200 mm when in motion. Unlike the lab planaria with two large eyespots, ***Arthurdendyus triangulatus*** has a row of tiny black eyes extending down the pale-colored margin. These, as in planaria, are light sensitive and aid the animal in its navigation.

Arthurdendyus triangulatus (Figure 22) originated in New Zealand, but most likely hitch-hiked its way to Ireland among nursery plants, where it was able to spread to Scotland and Britain (Willis & Edwards 1977; Christensen & Mather 1998b; Baird *et al.* 2005). A member of this genus has also found its way to Macquarie Island in the subAntarctic (Winsor 2001). With its ability to travel at the rate of 28 cm per minute (Mather & Christensen 1995) and migrate as much as 20 m (Mather & Christensen 1998), there is concern about its spread in the British Isles where its habit of eating earthworms may be detrimental to their role in aerating the soil (Willis & Edwards 1977; Blackshaw 1990, 1997; Christensen & Mather 1995; Boag & Yeates 2001; Mather & Christensen 2001; Baird *et al.* 2005). One individual can eat about 1.4 *Eisenia foetida* earthworms each week (Blackshaw 1991) and has no species preference among earthworms. Furthermore, ***Arthurdendyus triangulatus*** thrives better in habitats with more earthworms (Mather & Christensen 2003).

Baird *et al*. (2005), concerned with its potential to drastically reduce the earthworm populations, studied the survival strategies of ***Arthurdendyus triangulatus*** (Figure 22) and its reproductive behavior under multiple conditions. As noted, planarians can survive for long periods of time without food, utilizing reabsorbed body tissue instead (Calow 1977; Ball & Reynoldson 1981). This permits them to survive winter and even allows them to lay eggs during that season (Baird *et al*. 2005). Whereas Christensen and Mather (1995) demonstrated that these flatworms could survive at least 15 months at 12°C without food, at lower temperatures (8°C), there was even less weight loss. In the lab, they had 100% survival under starvation for 4 weeks at 10°C, but at 15°C, 30% died during that time (Blackshaw & Stewart 1992). This greater loss of weight at temperatures above 14°C and the reduced survival at the warmer temperatures explains the greater spread seen in the northern compared to southern parts of the UK (Blackshaw 1992; Boag *et al*. 1993, 1995, 1998; Baird *et al.* 2005).

Because of these low temperature requirements, it is often necessary for these flatworms to burrow into the soil or travel down tunnels made by other invertebrates. The presence of bryophytes is likely to enhance the habitat by moderating the temperature and maintaining a greater level of moisture, but such bryophyte linkages have not been explored.

This species is a **K strategist** and is a hermaphrodite. Baird *et al*. (2005) demonstrated that ***Arthurdendyus triangulatus*** (Figure 22) could lay nine egg capsules in four months, with a mean of 4 eggs per capsule, producing 45 eggs per individual per year. It is able to store sperm after copulation (Baird 2002). Individuals cultured alone were able to produce eggs for up to eight months, indicating that sperm could be stored at least that long (Baird *et al*. 2005).

At temperatures above 10°C, there was a considerable decrease in hatching success, but eggs took longer to hatch at 10°C (Baird *et al*. 2000, 2005). These eggs, like the adults, can easily travel with potted plants from one country to another, and although the nursery trade is highly regulated, internet sales usually escape this close scrutiny.

Desiccation Tolerance

If there is a niche, there is most likely an organism to fill it. And eventually, there is most likely a biologist to study it, but for moss-dwelling **flatworms**, this has been a long time in coming. Although **flatworms**, known to most of us as human parasites and freshwater organisms, can be quite abundant among bryophytes, their presence there is barely known (Paul Davison, pers. comm., 8 August 2007).

Unlike rhizopods and other kinds of protozoa, moss-dwelling **microflatworms** are not known to enter a state of **cryptobiosis**. Davison has collected several ***Bryoplana xerophila*** (Figure 23) from mosses on a concrete wall and taken them to room-dry conditions, then revived them (Figure 24). These relatively unknown members of the bryophyte community do form cysts and resistant eggs (Figure 25-Figure 26) that permit them to survive the alternating wet and dry conditions found among bryophytes, especially those on tree trunks, despite the thinness of their mucous covering (Davison *et al*. 2008, 2009; Van Steenkiste *et al*. 2010). But for the Australian and New Zealand fauna, these cysts do not seem to occur on the bryophytes (Leigh Winsor, pers. comm. 16 February 2012). Winsor considers the bryophyte habitat there to be too exposed for the cysts or eggs and young to survive.

Figure 23. ***Bryoplana xerophila***, a moss-dwelling **microturbellarian** from Alabama. Photo by Paul G. Davison.

But for ***Bryoplana xerophila*** (Figure 23-Figure 26) survival on rocks is facilitated by the ability to encyst (Van Steenkiste *et al*. 2010). The cysts typically occur in concavities between moss leaves and the stem connection where interstitial water slows water loss. Once rewet, they begin moving within the cyst and within minutes (up to 15 minutes) break through the cyst wall and are on their way to an active life once again. They further ensure survival of the species by laying one or two eggs as they go into encystment.

Figure 24. Recently excysted terrestrial flatworm**,** ***Bryoplana xerophila***, and empty cysts. The dark brown eggs formed during encystment provide a second means of surviving. These **flatworms** were living in the moss ***Entodon seductrix*** (Figure 44) from a concrete block wall in Florence, Alabama, induced to encyst on a glass slide, then brought back to an active state. Photo by Paul G. Davison, with permission.

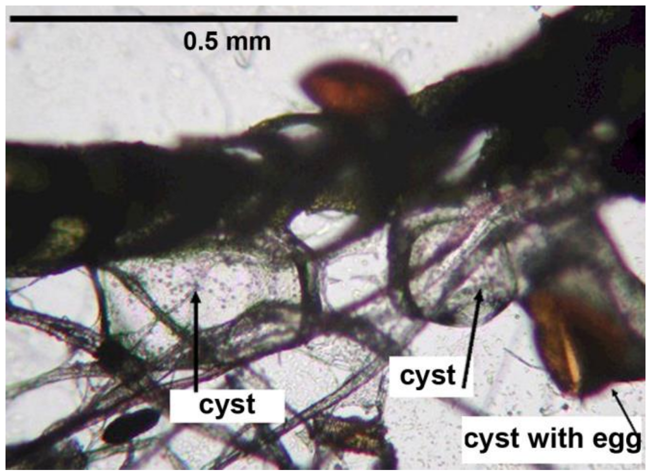

Figure 25. Cysts of flatworms, ***Bryoplana xerophila***, in desiccated state on moss. Photo by Paul G. Davison, with permission.

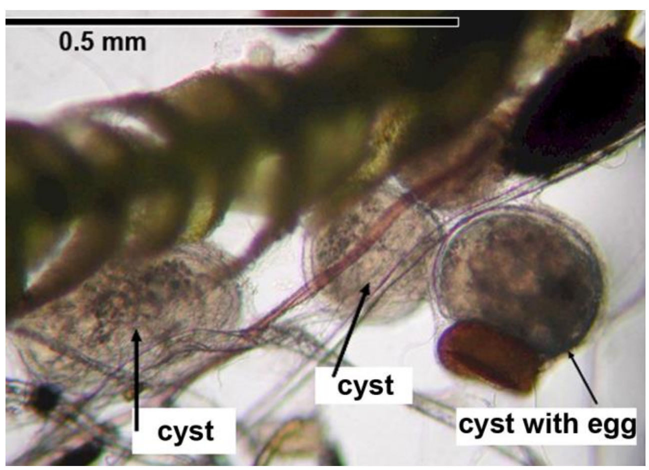

Figure 26. Cysts of flatworms, ***Bryoplana xerophila***, on a moss after rehydration. Photo by Paul G. Davison, with permission.

Terrestrial (Limnoterrestrial)

Fletchamia sugdeni (**Sugden's flatworm**, also known as **canary worm**; Figure 27-Figure 28) is a native of wet and dry forests in Victoria and Tasmania, Australia

(Winsor, 1977; Ogren & Kawakatsu 1991), where it can sometimes be found among bryophytes. Dendy (1890) noted that ***Fletchamia sugdeni*** was "remarkable for its habit of wandering about in broad daylight." That is truly remarkable for this bright yellow planarian. But the bright color might actually be a warning color that would be more useful in daylight.

Figure 27. ***Fletchamia sugdeni*** (**Sugden's flatworm, canary worm**), Victoria, Australia. Photo by Leigh Winsor, with permission.

Figure 28. ***Fletchamia sugdeni*** (**Sugden's flatworm, canary worm**) traversing a moss-covered substrate in Tasmania. This planarian certainly does not have camouflage on this bryophyte with its bright yellow color, but may gain protection with this warning coloration. Photo courtesy of Sarah Lloyd.

The bright yellow ***Caenoplana citrina*** (*C. barringtonensis* syn.; Figure 29) is known from mosses at Barrington Tops, New South Wales (Wood 1926). It resembles ***Fletchamia sugdeni*** (Figure 27-Figure 28), but has two stripes down its dorsal surface.

Wood (1926) noted that ***Caenoplana coerulea*** (Figure 30-Figure 31) was the commonest species collected near the Barrington River, New South Wales, being found on rocks, damp moss, the trunks of trees, and under rotten logs. Its thick-walled egg is in Figure 32.

Figure 29. A bright-colored flatworm, probably ***Caenoplana citrina*** (formerly *C. barringtonensis*), on a bed of mosses. Photo by Ian Sutton through Flickr Creative Commons.

Figure 30. ***Caenoplana coerulea***, a moss-dweller, among other habitats, displaying its blue color. Photo by Peter Woodard through Wikimedia Commons.

Figure 31. ***Caenoplana coerulea***, a moss dweller in a darker form. Photo from <www.aphotofauna.com>, with permission.

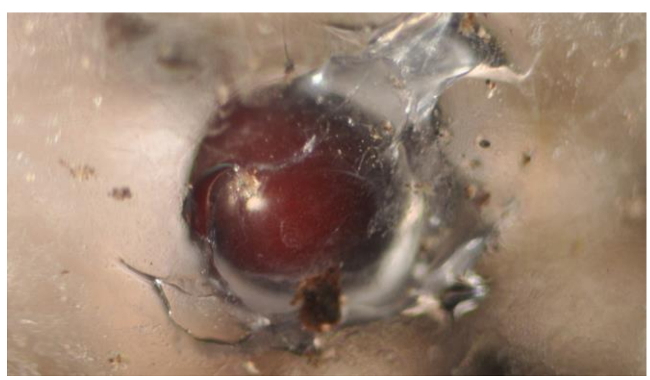

Figure 32. ***Caenoplana coerulea*** egg laid in captivity. Photo by Jacobo Martin through Flickr Creative Commons.

Elsewhere in Great Britain, McDonald and Jones (2007) compared habitat and food preferences for two species of ***Microplana***, a terrestrial flatworm. The habitat choices in the experiment were not germane to bryophytes, but in addition to the artificial cover, they did find cocoons at a 7 cm depth in ***Sphagnum*** in the garden. This genus is likely to occur among bryophytes elsewhere and thus should be sought there. The food preferences of ***Microplana terrestris*** (Figure 33) were gastropods [***Arion hortensis*** (slugs, Figure 34) and ***Discus rotundatus*** (snail, Figure 36)]. ***Microplana scharffi*** (Figure 37) preferred earthworms but also ate slugs. Both of these species avoided eating live animals and instead fed on damaged animals (see Figure 35). McDonald and Jones suggested that centipedes may contribute to that damage in nature.

Figure 33. ***Microplana terrestris*** in its grey form. Photo by Brian Eversham, with permission.

Figure 34. ***Arion hortensis***, a food source (when dead) for ***Microplana terrestris***. Photo © Roy Anderson, with permission.

Figure 35. Land planarians eating dead earthworm and dead springtails in a rainforest gully, Canberra, Australia. Photo by Andras Keszei, with permission.

Leigh Winsor (pers. comm. 16 February 2012) reports that some terrestrial flatworms have a "most unpleasant taste" (he tasted some species!) that may have a repugnatorial function. Whether brightly colored Australian flatworm species have a repugnant or toxic taste to birds or other predators is not presently known, but the yellow coloration could serve as either Batesian or Muellerian mimicry.

Figure 36. ***Discus retundatus***, a food source (when dead) for ***Microplana terrestris***. Photo by Francisco Welter Schultes through Creative Commons.

Figure 37. ***Microplana scharffi***, a flatworm that eats dead earthworms and slugs among bryophytes and elsewhere. Photo from <www.aphotofauna.com>, with permission.

Hyman (1957) reported the planarian ***Gigantea cameliae*** (identified at that time as *Geoplana cameliae* and moved to *Gigantea* by Ogren & Kawakatsu 1990) on wet mosses at night in Trinidad. This 25 mm, up to 50 mm (Hyman 1941), planarian is larger than most moss dwellers, especially among the terrestrial taxa. This species is also present in Panama (Hyman 1941), but there seem to be no reports of it from bryophytes there.

One mossy habitat where these **microturbellarians** seem to be quite rare, however, is in the Antarctic. Nevertheless, Schwarz *et al*. (1993) did find one **catenulid flatworm** inhabiting the mosses of flushes near the Canada Glacier on continental Antarctica.

Epiphyte Dwellers

The **microturbellarians** are those free-living flatworms (Platyhelminthes) generally <1 mm in length (*e.g.* Figure 23; Davison *et al*. 2008). They typically live in water films, making them essentially aquatic (**limnoterrestrial**). Bryophytes can provide such water films, so it is no real surprise that they (**Rhabdocoela**,

Typhloplanidae) are common 1-2 m above ground among epiphytic mosses. Davison *et al.* (2008) sampled longleaf pine-mixed hardwoods, *Juniperus* in limestone cedar glades, northern hardwoods above 1600 m elevation, dwarf oak forest, upland hardwoods-pine, and planted roadside pecan trees in the southeastern USA. They found that the tree trunk dwellers are rare in cool, mossy stream ravines, where one might have expected them, but are common in areas prone to rapid drying following rainfall – mosses on tree trunks fit this need well. In such locations, Davison *et al*. have found that flatworms are quite common in association with mosses on hackberries and other trees in Florence, Alabama, USA. These mosses include ***Leucodon julaceus*** (Figure 38) on *Cornus florida* and ***Clasmatodon*** (Figure 39) on *Paulownia tomentosa*, all at least 0.3 m above ground, as well as on trees of open, urban habitats, including *Catalpa* sp., *Celtis* sp., *Cornus florida*, *Fraxinus* sp., *Liquidambar*, *Magnolia grandiflora*, *Quercus* spp., and *Ulmus* spp. They survive these habitats by forming thin-coated transparent mucous cysts, a mechanism not familiar in other habitats.

Figure 38. Epiphytic ***Leucodon julaceus***, a known habitat for flatworms. Photo by Janice Glime.

Figure 39. ***Clasmatodon parvulus*** with capsule, a home for flatworms. Photo by Paul G. Davison, with permission.

Davison later collected **flatworms** from mosses on two white oaks in northern Tennessee, suggesting that they may be widespread, at least in these south temperate areas (Paul Davison, pers. comm. 12 January 2008). The collections were from the mosses ***Forsstroemia trichomitria*** (Figure 40) and ***Haplohymenium triste*** (Figure 41) growing 1.7-2 m above the ground. Although these had 10 and 6 turbellarians, a sample of ***Hypnum curvifolium*** (Figure 42) from the tree base produced only one flatworm. Davison suggests that the **water bears** (tardigrades) are important determinants of the location of the **flatworms** as a food source, and **water bears** were much less abundant at the tree base.

Figure 40. ***Forsstroemia trichomitria*** on a tree trunk, providing a suitable habitat for flatworms. Photo by Janice Glime.

Figure 41. ***Haplohymenium triste*** on bark, a suitable habitat for flatworms. Photo by Robert Klips, with permission.

Figure 42. ***Hypnum curvifolium*** on bark at base of tree, a habitat unsuitable for tardigrades and flatworms. Photo by Robert Klips, with permission.

Although **flatworms** are known from dry mosses on rocks, these observations by Davison and coworkers (2008, 2009) appear to be the first discovery of their living among epiphytic bryophytes. There is at least one report of moss-dwelling turbellarians (on ***Eurhynchium oreganum***, Figure 43) on a wet log (Merrifield & Ingham 1998), but that is hardly similar to the dry habitat of a tree trunk. The **flatworms** are seldom abundant, with four or fewer from a clump being common. However, they can be as abundant as 20 in a palm-sized patch of moss. Although they are not abundant, they are frequent, despite the apparent dispersal problems they are likely to have.

Figure 43. ***Eurhynchium oreganum***, sometimes home to flatworms. Photo by Matt Goff, with permission.

Epilithic Dwellers

The **epilithic** (rock) dwellers, like the epiphytic dwellers, must tolerate frequent drying on a very xeric habitat. For these limnoterrestrial microturbellarians, a bare rock is a challenge beyond their means. But bryophytes hold moisture and accumulate soil, making this austere habitat more turbellarian friendly. It was from this habitat that Van Steenkiste and co-workers (2010) described the new genus – ***Bryoplana***. They appropriately named the new species, the first in the genus, ***Bryoplana xerophila*** (Figure 23-Figure 26). This one was found among mosses, including ***Entodon seductrix*** (Figure 44), and soil on a concrete wall in northern Alabama, USA. Not only is it a new genus, but it is the first limnoterrestrial member of the **Protoplanellinae** to be found in North America and is among only a few rhabdocoels from a dry habitat. This species is easy to miss, measuring only 0.4-0.5 mm long.

Figure 44. ***Entodon seductrix***, a moss where the flatworm ***Bryoplana xerophila*** is known to encyst. Photo by Robert Klips, with permission.

These particular **microturbellarians** had guts filled with **bdelloid rotifers**, common inhabitants of mosses (Van Steenkiste *et al*. 2010). They ingested small ones within a minute, but for larger rotifers, they drained them instead, using a sucking action by the pharynx.

Other genera and species of limnoterrestrial turbellarian moss-dwellers include ***Acrochordonoposthia***, ***Adenocerca***, ***Chorizogynopora***, ***Haplorhynchella paludicola***, ***Olisthanellinella***, ***Olisthanellinella rotundula***, ***Perandropera***(?), and ***Rhomboplanilla bryophila*** (Van Steenkiste *et al.* 2010). Association of ***Acrochordonoposthia conica*** with mosses seems to be particularly well documented (Reisinger 1924; Steinböck 1932; Luther 1963). ***Rhomboplanilla bryophila*** is even named for its preference for a bryophyte habitat. The absence of images of these taxa on the internet is a testimony to how little we know of them.

Aquatic Bryophyte Habitats

Most of the non-parasitic **flatworms** (formerly **Turbellaria**) are known from aquatic habitats. Stern and Stern (1969) found numbers among cold springbrook mosses (***Fontinalis antipyretica***, Figure 3) in Tennessee to be similar to those on stones, ranging 1-5 per 0.1 m^2 on stones and 1-4 per 0.1 m^2 among the moss-algae associations. Frost (1942) found the fauna of **turbellarians** among mosses [mostly ***Fontinalis squamosa*** (Figure 45), ***F. antipyretica,*** and ***Platyhypnidium riparioides*** (Figure 46)] in her River Liffey Survey, Ireland, to be less than 0.1% of the non-microscopic fauna. Berg and Petersen (1956) reported ***Schmidtea lugubris*** (formerly *Planaria lugubris*; Figure 47) and ***Dendrocoelum lacteum*** (Figure 48-Figure 49) from beds of ***Fontinalis dalecarlica*** (Figure 51) in Store Gribsø Lake, Denmark. **Turbellarians** are not generally a dominant component of the aquatic bryophyte fauna.

Figure 45. ***Fontinalis squamosa***, a common habitat for stream fauna, including flatworms. Photo by Michael Lüth, with permission.

In a springbrook in Meade County, Kentucky, USA, flatworms were very abundant at one sampling station on the flattened moss ***Fissidens fontanus*** (Figure 52), ranging from ~92 per 0.1 m^2 in June to ~1200 in January, but at another station, the same moss had numbers ranging from ~7 to ~300 in November and March respectively. In the marl riffles, the highest number was 1, and in rubble riffles it was not found. The flatworm ***Phagocata velata*** (see Figure 53) was the most abundant flatworm on ***Fissidens fontanus*** as well as under flat stones, logs, twigs, and debris, always in fast currents.

Figure 46. ***Platyhypnidium riparioides*** in Europe. This species can be submerged or emergent. Photo by Michael Lüth, with permission.

Figure 47. ***Schmidtea lugubris*** **(**formerly ***Dugesia lugubris***) from Crowland, Lincs, UK. Photo by Roger S Key, with permission.

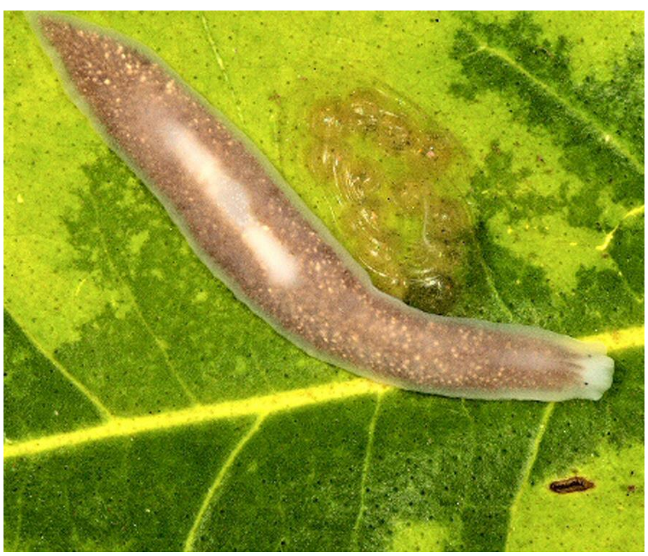

Figure 48. ***Dendrocoelum lacteum*** female in extended position. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 49. ***Dendrocoelum lacteum*** female in contracted position. Note the two eyes. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 50. ***Dendrocoelum lacteum*** female with recently deposited egg. Crowland, Lincs, UK. Photo by Roger S. Key, with permission.

Figure 51. ***Fontinalis dalecarlica***, suitable home for the flatworm ***Dendrocoelum lacteum***. Photo by Janice Glime.

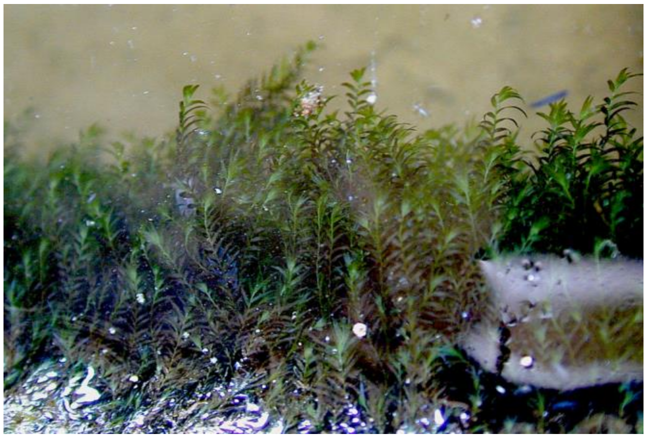

Figure 52. ***Fissidens fontanus***, showing the flat fronds. Photo by Michael Lüth, with permission.

The well-known planarian ***Dugesia dorotocephala*** finds "moss and sand quite acceptable," preferring them over silt, but less than rocks or leaves (Figure 54; Speight & Chandler 1980). ***Phagocata gracilis***, a moss-preferring species, selected temperatures of 4-22°C, preferring 14.8°C on rocks and 12.6°C on moss. I have to wonder if that was oxygen-related, with mosses taking up oxygen at night. ***Phagocata velata***, on the other hand, preferred living on rocks and migrated mostly to a temperature range of 16.0-20.5ºC, with a temperature preference of 17.8ºC.

Figure 53. ***Phagocata vitta***. Photo by Malcolm Storey through Creative Commons.

Figure 54. ***Dugesia*** sp. in its rock habitat, which is usually preferred to mosses. Photo by Janice Glime.

In a New Zealand springbrook, ***Neppia montana*** (Figure 55) seemed to have a preference for the ***Achrophyllum quadrifarium*** (=***Pterygophyllum quadrifarium***; Figure 56) over the other two mosses in the stream (***Fissidens rigidulus***, ***Cratoneuropsis relaxa***) (Cowie & Winterbourn 1979). The ***A. quadrifarium*** occurred in a zone extending from the stream margins on up the banks where it received spray from the rapidly moving water. This is a large, pleurocarpous moss with flattened branches.

Figure 55. ***Neppia montana***, a flatworm that prefers ***Achrophyllum quadrifarium*** over other moss species in its stream. Photo by Paddy Ryan, with permission.

Figure 56. ***Achrophyllum quadrifarium***, home of the flatworm ***Neppia montana*** in a New Zealand springbrook. Photo by Jan-Peter Frahm, with permission.

Extraction and Observation Techniques

The **flatworms** represent a little known fauna of terrestrial bryophytes. Brigham (2008) suggests that one reason for this may be the lack of a satisfactory extraction technique. She compared the traditional beaker extraction method with a Baermann funnel method modified by Paul Davison (see Vol 2, Chapter 4-1). Using the beaker method, she was unable to find any **microturbellarians** among the mosses. However, she found them in multiple samples using the modified Baermann funnel.

Since these organisms are too small and too numerous for quantification in the field, they must be transported to the laboratory for extraction. Examination of live organisms makes them both easier to locate and easier to identify (Kolasa 2000). Warm temperatures and lack of oxygen quickly become lethal, not to mention confined but hungry predators, so samples must be kept in a cooler (Stead *et al*. 2003) and processed within a few hours of collection. Preserved animals usually cannot be identified.

Winsor (1998b) suggests narcotizing the flatworms with 10% ethanol, then preserving them with a formaldehyde calcium cobalt fixative. They can be cleared for examination in terpineol, imbedded in paraffin wax, and serially sectioned. The sections can be stained to make internal systems more visible. Long-term storage may require 80% ethanol, and those for DNA extraction should be fixed in 100% ethanol.

Slowing down live animals for identification can be challenging, but Thorp and Covich (1991) recommend placing them in a small volume of water on ice. Alternatively, they can be anaesthetized with a mix of 7% ethanol, 0.1% chloretone, and 1% hydroxylamine hydrochloride.

One trick to help in identification of soft-bodied taxa when time is at a premium is to use a video camera on a sample under appropriate microscope magnification (Stead *et al*. 2003). Davison and Kittle (2004) suggest making a miniature aquarium using microscope slides as a housing for both culturing these organisms and examining them (Figure 57-Figure 59).

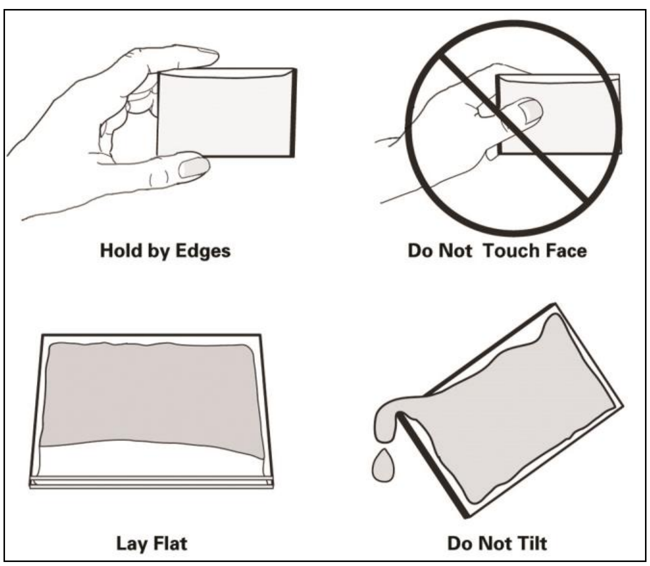

Figure 57. Method for constructing a microchamber for observing flatworms and other small invertebrates. Modified from Davison 2006.

Food choices in the lab may differ from those in the field where a wider array of choices is available. Gut analyses are used for larger organisms to determine diet in the field. But obtaining samples for gut analysis in flatworms and other tiny invertebrates is a bit more tricky than that used for insects and larger invertebrates. One can't pull or dissect the gut from the animal. Instead, Young (1973) sacrificed the animals another way. He squashed them with a coverslip on a glass slide. But first the flatworms had to take a bath by crawling around in tap water to remove adhering items that might look like food in the squash. Then they were placed on the "squash" slide, all within an hour of collection to avoid extensive digestion of the food items.

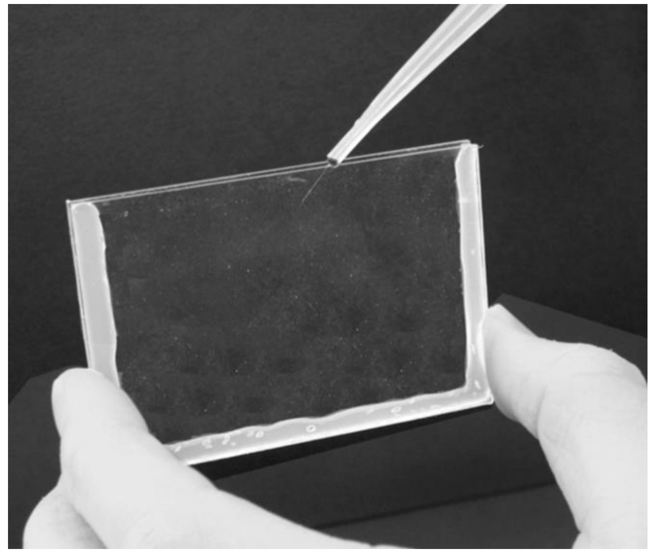

Figure 58. Filling completed microchamber built by above construction. Photo by Paul G. Davison from Davison 2006.

In 1979, Feller *et al*. demonstrated the usefulness of immunological techniques for identifying major taxonomic groups in the guts of these small organisms. Young and Gee (1993) used the precipitin test, a serological technique, to identify major taxonomic groups in the gut. Schmid-Araya *et al*. (2002) first anaesthetized the organisms with CO_2 to prevent regurgitation, although it was not clear if this method was used to identify flatworm gut contents. More recently, DNA extraction and amplification provide a means of identifying gut material from such small meiofauna (Martin *et al*. 2006), providing a potential tool for flatworms.

Figure 59. Occupied microchamber (with flatworms and moss). Image modified from Davison 2006.

Summary

Fissidens fontanus and ***F. brachypus*** can grow epizootically on **sponges**. Humans may enjoy a mattress made with mosses and sponges.

Gastrotrichs survive the dry stages of mosses by producing larger eggs that survive due to heavier shells. They seem to prefer lower velocity areas where sediments can accumulate and can be relatively common in peatlands.

Microflatworms are mostly from aquatic habitats where they are known from ***Fontinalis antipyretica***, ***F. squamosa***, and ***Platyhypnidium riparioides***. They survive winter and dry periods like the **gastrotrichs**, as thick-shelled eggs, but they can also form cysts, particularly among epiphytic mosses. They are actually more abundant on tree trunks that are prone to drying out than they are in cool, mossy stream ravines. These terrestrial species seem to be most abundant among the mosses where they can find **tardigrades** to eat. The triclad flatworm ***Phagocata gracilis*** actually prefers moss habitats.

A Baermann funnel seems to work best for extracting microturbellarians from terrestrial mosses.

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Paul Davison kept me informed of new finds, which were especially important for these groups where so little is known of their bryophyte relationships. Filipe Osorio added information on tropical Platyhelminthes. Sarah Lloyd has kept me in mind as she finds new invertebrates and takes pictures for me, including the canary worm. Yuuji Tsukii gave me permission to use his wonderful collection of images. Leigh Winsor has been invaluable in helping me to identify the flatworm and nemertine worm pictures, to understand these species better, and to review the revised chapter (February 2012). Thank you to Larry Williams for catching some of my errors and notifying me.

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