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Chapter 9

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Bryophytes and Invertebrates

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*Mosses are useful to the insect tribe, countless numbers of
which find homes among their branches, and roam about in
their shades as in mighty forests, looking with their
thousand eyes upon the wonders of their leaves, and
summing their wings of purple and of gold, and burnishing
their shining armour upon the polished columns of their
urns*

Frances Tripp British Mosses, 1888

9.1 INTRODUCTION

These thousand eyes have also been looking upon naturalists for quite a while, but only few have looked back. Usually they were zoologists interested in specific groups which live on, in or under bryophytes; in the role these animals play during initial land colonization by cryptogams; in freshwater associations and in diverse other aspects. Botanists have published far fewer observations, these dealing mainly with fertilization or spore dispersal by invertebrates. Although scattered and uneven, taken as a whole the compiled data offer suggestive insights into the relationships between bryophytes and invertebrates, especially in regard to their co-evolution.

Ramazotti (1958) and Gadea (1964a), following Heins, distinguished between bryophilous and bryoxenous moss animals, including those which spend their entire lives in bryophytes in the former group, those that stay for only part of their cycle in the latter. These authors addressed themselves mostly to the microscopic water fauna (Protozoa, Rotifera, Nematoda and Tardigrada). Also considering larger invertebrates, it

becomes more useful to divide the fauna of bryophytes – the bryofauna – into four categories:

- (i) *Bryobionts*: animals which occur exclusively in association with bryophytes.
- (ii) *Bryophiltes*: animals which are usually found on bryophytes, but may survive elsewhere.
- (iii) *Bryoxenes*: animals which regularly spend part of their life cycle on bryophytes.
- (iv) *Occasionals*: animals which may at times be found in bryophytes, but do not depend on these plants for their survival.

The components of the bryofauna may also be categorized according to the humidity of the plants, thereby separating an aquatic from a terrestrial fauna (Travé, 1963). However, as some of the invertebrates occur in aquatic as well as terrestrial habitats, the faunas are not separately treated here. They are introduced in taxonomic order. Richards and Davies (1977) being the authority on the largest group, the insects. Concerning the names of organisms, it should be noted that the presented data were gleaned from a variety of botanical, zoological and ecological publications. Some discretion must therefore be exercised in applying scientific names.

9.2 INVERTEBRATES

9.2.1 Protozoa

Three of the four major divisions of the protozoa occur in bryophytes. These include the Sarcodina (rhizopods), characterized by moving with protoplasmatic flow or by pseudopodia; the Ciliophora (ciliates), which swim about with cilia, and the Mastigophora (flagellates), which use one or more flagella for motion.

The Sarcodina, and especially the testate or shell-bearing rhizopods, appear to be particularly abundant in moss and sphagnum, and were extensively studied there (Bonnet 1973, and many citations therein). The genera *Nebela* and *Hyalosphenia* and the species *Diffugia pyriformis* and *D. globularis* are considered as sphagnicolous (Bovee, 1979 and citations therein). Others, like *Euglypha ciliata*, *Trinema lineare* and *Diffugiella oviformis* were obtained from European as well as North American mosses (Bovee, 1979). The ciliates were recently studied by Grolière (1978 and citations therein). He concluded that *Cyclidium sphagnetorum* and

Bryometopus sphagni (among others) are sphagnophilic; as the former is only known from sphagnum, it may be considered a bryobiont. Data on protozoan groups in bryophytes were presented by Fantham and Porter (1945) and by Bovee (1979).

Sphagnum appears to be richer in species (and in their numbers) than other bryophytes; Bovee (1979) obtained 145 species of Protozoa from the former habitat, only 65 from forest mosses. Fantham and Porter (1945) recorded a maximum of 220 000 protozoans (mostly flagellates) from 1 g of *Sphagnum girgensohnii*, as compared to 4 maximum of 150 000 individuals from *Campyllum chrysophyllum*. Calculating differently, Heal (1962) estimated that there were about 16 million testaceans per m² of sphagnum sward. Populations of sphagnum-inhabiting protozoans also differ between alkaline fens and acid bogs, the former apparently being richer (Stout and Heal, 1967).

Protozoans living on *Sphagnum* have a vertical distribution which does not appear to be seasonal (Heal, 1962). This distribution is affected by tolerance to desiccation and to extreme temperatures, by animal size and food, as well as by various other factors (Bovee, 1979; Corbet, 1973). The effect of cryptogamic vegetation on the composition of ciliate populations in a sphagnum peat bog was explored by Grolière (1977). Ciliates in bryophyte-containing trenches resembled those from other *Sphagnum* areas, whereas those from algae-rich trenches were similar to populations inhabiting freshwater ponds. Much remains to be studied regarding the distribution of Protozoa in bryophytes; 'Every moss [including *Sphagnum*] in our collection had a different fauna of Protozoa' (Fantham and Porter, 1945).

Stout and Heal (1967) pointed out that in acid *Sphagnum* peat bacterial and fungal growth and metabolism are rather limited. The main growth activity in this habitat is due to rhizopods, which may play a direct role in the organic cycle.

The Protozoa probably invaded bryophytes via three major pathways: freshwater, by species colonizing land (Stout, 1963); air, by wind-borne, desiccation-resistant forms (Kühnelt, 1976), and soil, by protozoans moving into corticolous mosses (Bonnet, 1973).

The shells of Testacea enable their recognition even after many years. Štěpánek (1963) identified rhizopods in bryophyte samples collected even 80 years earlier. Grospietsch (cited by Corbet, 1973) showed that analysis of subfossil rhizopod tests in peat may supplement pollen studies.

Like some other microscopic components of the bryofauna, several Protozoa endure dry periods by forming cysts or other forms which resist desiccation. Cysts are wind-borne and thus widely dispersed. Alternatively, they may remain on the mosses until rewetted, when both groups of organisms resume their activities.

9.2.2 Turbellaria

These mostly non-parasitic flat worms usually – but not always – live within soil-water films. Little has been published about their specific relationships with bryophytes. Kühnelt (1976) mentions that *Acrochloridopsis* spp. live in very dry saxicolous mosses. Berg and Petersen (cited by Macan, 1963) found a few turbellarians in *Fomitulis dalecarlica* beds, and Lindgaard *et al.* (1975) reported 278 *Dugesia gonocephala* m⁻² of *Cranoneuron commutatum* and *C. filicinum* in a small Danish lake. Turbellarians may survive desiccation or saturation conditions by forming cysts (Kühnelt, 1976).

9.2.3 Rotifera

The rotifera or rotatorians, also called 'wheel animalcules', are small (c. 0.5 mm) animals whose anterior end is formed into a ciliary feeding apparatus (thus 'wheel') which crawl or settle on various substrates.

They appear to be associated with bryophytes mostly in alpine and polar regions (Heinis, 1959; Hyman, 1951), being rarer in the tropics (Donner, 1966). One group, the Bdelloidea, abound on bryophytes, especially those which are submerged, emergent or terrestrial with intermittent wetting

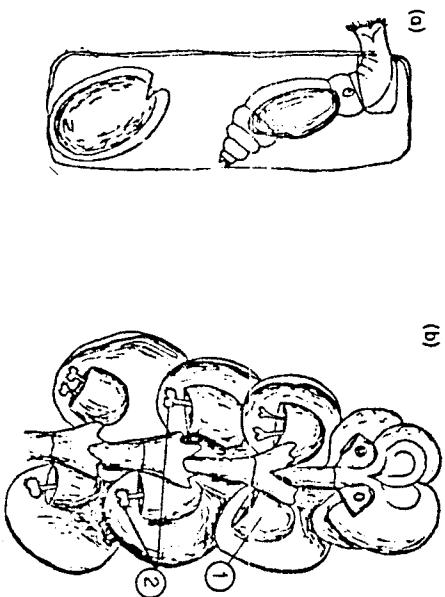


Fig. 9.1 (a) The rotifer *Habronocha reclusa* inside a cell of *Sphagnum*. (b), The rotifer *Mniobia symbiotica* (marked 1) inside postical lobes (marked 2) of leaves of *Frullania*. From *The Invertebrates* Vol. III by L. H. Hyman (1951). By permission of McGraw-Hill, New York.

(Pennak, 1978). Certain rotifers inhabit very specific positions on these plants. *Habronocha reclusa* and *H. roeperi* live inside hyaline *Sphagnum* cells (Fig. 9.1a), and *Mniobia symbiotica* dwells in the pitcher-like leaves of *Frullania* (Fig. 9.1b) (Hyman, 1951). *Pygura velata* settles only, but in large numbers, near the leaf tips of *Sphagnum erythrocalyx* (Edmonson, 1944). The rotatorians occur exclusively on the leaves' concave side, in the tubular part, so that they are almost entirely enclosed; only their anterior ends project above the edges. But *P. velata* was also collected from *Fomitulis* and angiosperms (Edmonson, 1944), therefore, despite its habitat specificity, it is merely a bryophilous species.

Terrestrial bryophyte-inhabiting rotifera are active only while their moss cushions are permeated with water; thus they actually lead an aquatic existence in the water films between plant parts. The ubiquity and survival of rotifera on bryophytes have led Hyman (1951) to write: 'Almost any bit of dried sphagnum will be found to contain desiccated rotifers'. Their ability to withstand desiccation is due to contracting, drying and shrinking their body contents and cuticle to the smallest possible volume, usually without forming cysts (Hyman, 1951; Pennak, 1978). During this period of anabiosis they are very resistant to extreme low or high temperatures, which explains rotatorian survival – for long periods – under harsh climatic conditions. The animals, along with their eggs, may then be blown about by winds over wide areas. Consequently, many species are cosmopolitan in distribution (Hyman, 1951). Recovery from anabiosis depends on immersion in fresh water, and can be quite rapid, requiring from minutes to one day.

Alpine moss-dwelling rotifers are often red, a colour imparted to them by carotenoids (Hyman, 1951). They may thus feed on particles of bryophyte origin. Rotifers may build up large populations in bryophytes. Fantham and Porter (1945) reported the following (numbers/g bryophyte): *Ceratonion purpureus*: 700; *Schistidium apocarpum*: 600; *Polyptrichum juniperum*: 1108; *Sphagnum fuscum*: 920; *S. girgensohnii*: 1160; *S. wulfianum*: 872.

9.2.4. Nematoda

The nematodes or roundworms are elongated, cylindrical animals which are parasitic in animals and plants, besides being very abundant in diverse aquatic and terrestrial situations. In the latter habitat, they may be associated with bryophytes, constituting an unspecialized, soil-derived fauna (Nicholas, 1975). Nematodes of the bryofauna occur all over the world; *Plectiscus cirratus* inhabits moss in the Galapagos Islands (Gadea, 1977) and high up in the Pamirs (Nicholas, 1975) as well as being abundant in European soils (Kühnelt, 1976). Several Dorylaimoidea, like *Dorylaimus macrodorus*, *D. stagnalis*, and *Eudorylaimus carteri* are often found in

bryophytes and some may feed on these plants (Gadea, 1964b). Another Dorylamoid recorded from mosses is *Funaria thornei* (Goodey, 1963).

Nematodes survive dry spells by forming resistant resting stages and by encystment. *Plectus rhizophilus*, abundant in dry moss, may at times remain as the sole nematode in shallow bryophyte cushions exposed to extreme climatic conditions. It is resistant to dehydration during its entire development (Nielsen, 1967). Vertical movements along the moss – up at night or during rain, down when it gets dry – also facilitate nematode survival. Their numbers in bryophytes approximate those of rotifers. The following values were reported by Fantham and Porter (1945) (animals/g bryophytes): *Brachyhectem acutum*: 510; *Ceraton purpureus*: 440; *Funaria hygrometrica*: 336; *Sphagnum girgensohnii*: 4680; *S. fuscum*: 740; *S. wulfianum*: 720. Nielsen (1967) counted 200 *P. rhizophilus* cm⁻² of *Tortula ruralis*, 330 cm⁻² of *C. purpureus*, both collected on a roof.

9.2.5 Annelida

This phylum, which comprises the segmented worms, includes such well-known animals as earthworms and leeches. The former belong to the class Oligochaeta and the latter to the class Hirudinea, and members of both are found in bryophytes. Lindegaard *et al.* (1975) counted 7520 *Nais elinguis*

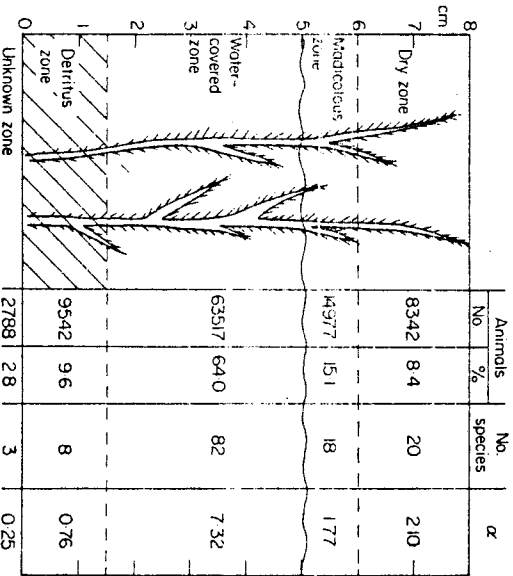


Fig. 9.2 Vertical zonation of a Danish *Cratoneuron* carpet. Number and percent of animals, number of species and Margalef's index of diversity ($\alpha = (S-1)/ln N$, where S is the number of species and N the number of individuals) for each zone. Data from Lindegaard *et al.*, 1975.

and 615 *Eiseniella tetraedra* (both Oligochaeta) in 1 m² of the detritous zone (Fig. 9.2) of *Cratoneuron* spp. in a Danish spring. Terrestrial oligochaetes were found under mosses on tree trunks (Larsson, 1978). Berg and Petersen (in Macan, 1963) reported 67 oligochaetes and five leeches per 1 m² of Scandinavian *Fontinalis*; members of both groups also occur in moss balls derived from *Fontinalis* and *Drepanocladus* (Luther, 1979). Finally, commercial leeches were packed and shipped while embedded in the moisture-retaining *Hypnum* (Thieret, 1956, citing Welch).

9.2.6 Mollusca

Representatives of two of the major molluscan classes, Gastropoda (snails and slugs) and Bivalvia (mussels and clams) associate with bryophytes. Some snails graze heavily upon *Octodieras fontanus*, preferring it to *Fontinalis* and *Drepanocladus* (Lohannar, 1954). This author consequently believed that the scarcity of *O. fontanus* in certain North European



Fig. 9.3 *Octodieras fontanus* growing on the live mussel *Anodonta cygnea*. From Lohannar (1954) used with the permission of Svensk Botanisk Tidskrift.

water bodies results from the snails feeding. On the other hand, *Octodierus* uses molluscs as a substrate. It grows on dead as well as live mussels, like *Anodonta cygnea* (Fig. 9.3), these sometimes moving about and thus possibly dispersing the bryophyte (Neumann and Vidrine, 1978). *Lepidodierium riparium* was also reported by these authors to grow on mussels.

Lindegard *et al.* (1975) collected 1247 gastropods (*Galba truncatula*) m^{-2} *Craioneuron* from the plant-water interface (madicolous zone in Fig. 9.2).

9.2.7 Tardigrada

The tardigrades or 'water bears' are small, eight-legged invertebrates closely related to the arthropods. They are very common in moss, less so in *Sphagnum*. Moss is believed to be the most favourable habitat for tardigrades, besides being well suited for population studies (Morgan, 1977). The largest numbers of tardigrades were reported by this author: as many as 2287 000 m^{-2} *Bryum argenteum* and *Ceratodon purpureus*, or 132 000 g^{-1} . Hallas (1975) estimated about 15 000 *Macrobiotus hufelandtii* m^{-2} *Hypnum cupressiforme*.

Under dry conditions tardigrades enter a state of diminished metabolism, or anabiosis. The body contracts in a regular manner, assuming a barrel shape which is called a 'tun' (Cuenot, 1949). Tuns are quite resistant to extreme climatic conditions and may survive for many years. Upon absorption of water there is a rapid return to normal life. During anabiosis, tardigrades are disseminated by winds, most species are consequently cosmopolitan (Morgan and King, 1976), but appear to be more abundant in temperate as compared to tropical regions (Mehlen, 1972). Moss tardigrades may also be disseminated by arthropods: Bertrand (1975) found them on carabid beetles and on 'Myriapoda' which frequent the same bryophytes (see also Ramazzotti, 1958).

Tardigrades on the whole do not appear to be host-specific but certain habitats contain more animals than others. Morgan and King (1976) stated that button and erect mosses (acrocarpus) harbour more tardigrades than those of creeping growth habits (pleurocarpus). Bertrand (1975) found that the relative abundance of several species differed between saxicolous and epiphytic bryophytes, and also between cushion-forming and 'carpet' mosses (i.e. *Polytrichum*, Hypnaceae). This author also reported that the numbers of *Diphascos* spp. in corticolous bryophytes were clearly affected by tree height.

Some tardigrades feed on bryophytes (Ramazzotti, 1958), others are predaceous or graze on bacteria and algae (Hallas and Yeates, 1972). The bryophagous tardigrades pierce host cells with their stylets and suck out the contents. *Racomitrium* and *Polytrichum* colonies contain very few

specimens, probably because of their more heavily protected cell walls (Morgan and King, 1976; Ramazzotti, 1958). Moss growth and architecture affect tardigrade populations. Morgan (1977) obtained correlations between prevailing daylight hours, temperatures and tardigrade numbers, indicating some links between the growth patterns of both groups of organisms. The arrangement of *Hypnum cupressiforme* leaves in a mat determines the amount of humidity available there after rain. When water bridges are formed, tardigrades may move vertically among the various layers (Hallas, 1975) and thus explore the entire mat.

9.2.8 Arthropoda

Arthropods, animals with segmented legs, are the largest phylum in the animal kingdom, and proportionately represented in the bryofauna. For the sake of convenience, they are discussed under the headings of Crustacea, 'Myriapoda', Insecta and Arachnida.

(a) Crustacea

Crustaceans, like crabs, shrimps and barnacles, are mostly aquatic animals, which either have a head, thorax and abdomen, or else the former two parts fuse to form a cephalothorax. They breathe through the body walls or by gills. Members of two subclasses, Copepoda and Malacostraca, often associate with aquatic bryophytes.

Copepods occur in fairly large numbers in moss-overgrown waters; Rylow (1963) recorded *Acanthocyclops nana* in populations up to 200 m^{-2} from this habitat. Fantham and Porter (1945), on the other hand, counted only 50 *Cyclops* g^{-1} of *Climacium dendroides*. A total of 18 copepod species was collected by Frost (1942) from an Irish river, of which eight were considered as normal components of the bryofauna. The tropical *Musocyclops* and *Bryocyclops* live in minute aquaria formed by epiphytic bromeliaceous leaves as well as in mosses (Lindberg, 1954; Vandel, 1965). The bryophyllous *Epaeciophanes* is resistant to desiccation, which facilitates its passive dissemination and explains its cosmopolitan occurrence in bryophytes (Menzel, 1921).

Few malacostracans are found in bryophytes. Lindegard *et al.* (1975) obtained 6819 *Gammarus* m^{-2} *Craioneuron* in a Danish lake. Berg and Petersen (cited by Macan, 1963) reported 198 *Asellus* m^{-2} *Fontinalis* in Lake Gribso. This isopod was also observed browsing on moss balls by Luther (1979).

Members of two other subclasses, the Branchiopoda and the Ostracoda may occur, in rather small numbers, in aquatic mosses (Frost, 1942).

(b) 'Myriapoda'

Members of three disparate groups, the Chilopoda, Diplopoda and

Symphyla, used to be combined within the Myriapoda. Although out-moded, this arrangement is retained here for convenience as well as due to the relative scarcity of the animals in bryophytes. 'Myriapoda' – elongated arthropods whose bodies consist of numerous similar segments each bearing one or two pairs of legs – may be collected from corticolous mosses (Larsson, 1978; Pschorn-Walcher and Gunhold, 1957) or in sphagnum peat (Pedroli-Christen, 1977). Little is known about their activities there. Stebaev (1963) believed that predaceous Lithobiidae (Chilopoda) were characteristic of the moss stage of soil colonization by plants in the Urals. Bryophyte-inhabiting tardigrades were collected from symphylians found in the same habitat, indicating that the latter were disseminating the former from one bryophyte habitat to another (Bertrand, 1975).

(c) Insecta

Richards and Davies (1977) recognized 29 orders within this class; members of 21 associate with bryophytes. Examples of the wingless insects – subclass Apterygota – come from the Thysanura (bristletails), Protura and Collembola (springtails). Great swarms of thysanurans, the most primitive of all insects, feed on dry moss, lichen and other plant material on high mountains (Mani, 1962); others associate with moist forest bryophytes (Larsson, 1978). The Protura, antenna-less soil dwellers, are often found in bryophytes (Nosek, 1973), but little is known about them. The moss springtails, on the other hand, were studied in regard to colonization, succession, habitat-specificity and feeding. Although they occur in fairly large numbers on temperate bryophytes (Lindgaard *et al.*, 1975, recorded 4182 *Isotomurus palustris* m⁻²; *Cratoneuron* from Denmark), collembolans really abound under harsh climatic conditions. Bengtson *et al.* (1974) working in Spitsbergen, compared springtail populations from lichens with those collected from mosses; there were 20 000–40 000 m⁻² in the former habitat, 243 500 m⁻² in the latter. Rather similar data were obtained by Chernov *et al.* (1977) from Cape Cheluskim, the northernmost mainland of Europe. Collembola also abound in high altitudes, where they live in and feed on the available colonizing mosses (Mani, 1962). Antarctic springtails like *Isotoma klovstadi* and *Gomphiocephalus hodgsoni* feed extensively on bryophytes available there, the latter preferring mosses to fungi (Prior, 1962; Wise *et al.*, 1964). Changes in collembolan populations consequent upon the succession of sphagna in a British bog were followed by Murphy (1955). Bonnet *et al.* (1975 and former papers) sampled bryophytes growing in various habitats and demonstrated contiguous changes in collembolan populations from soil to soil mosses to aerial mosses. Humidity preferences, as in Murphy's series, were believed to determine which springtail occurred in the various plants. Some species (i.e. *Xenylla milbergii*) appeared to be quite bryophyllous.

The Pterygota, winged or secondary wingless insects, are divided between those undergoing simple metamorphosis, the Exopterygota or Hemimetabola, and those with complete metamorphosis, the Endopterygota or Holometabola. Eleven Exopterygota orders are represented in bryophytes. The mayflies (Ephemeroptera) *Ephemera* and *Baetis* abound in aquatic mosses (Frost, 1942), both feeding mainly on algae, only occasionally on bryophytes (Chapman and Demory, 1963; Hynes, 1961). About 530 mayfly nymphs 200 g⁻¹ mosses were recorded by Frost (1942) from Ireland. Some Odonata (dragonflies), an order of predators, deposit their eggs into bryophytes (Macan, 1963), and their nymphs live there. Examples are the Himalayan *Calicnemis miles* (Kumar and Prasad, 1977) and the European *Leucorrhinia dubia* (Matthey, 1971). Plecoptera (stoneflies) may live in and feed on aquatic bryophytes; *Protonemura meyeri* is commonly found in *Fontinalis* (Hynes, 1941). Stonefly populations may reach substantial numbers: Lindgaard *et al.* (1975) counted 16 500 *Nemurilla pictetii* m⁻² *Cratoneuron*.

A member of the small, obscure order Grylloblattodea deposits its eggs in mosses (Richards and Davies, 1977). Orthoptera (crickets and grasshoppers) feed on *Sphagnum* (Vickey, 1969), *Hypnum* (Verdcourt, 1947) and other bryophytes; Uvarov (1977) believed that some grasshoppers may eat mosses because of their water content. The establishment of electric light in caves in New Zealand has stimulated moss growth there, on which local orthopterans browse (Richards, 1962). Among these is *Pallidopteron turneri*, which feeds on thick growths of *Marchantia*. Some Phasmida (stick insects), which are predaceous, closely resemble, by colour and in their foliate body and limbs, the epiphytic mosses on which they live and hunt (Robinson, 1969). A webspinner (order Embioptera) was collected from a moss cushion in Israel (unpublished data). The termite (Isoptera) *Hospitalitermes umbrinus*, which is unusual in feeding on live plants, prefers lichens but will also take bryophytes (Collins, 1979). Booklice (psocoptera), common on plants, may also feed on moss (Larsson, 1978).

Bugs (Hemiptera) are divided into the Homoptera and the Heteroptera, and members of both suborders occur in bryophytes. Peloridiidae, considered as the most primitive bugs and even 'living fossils', live and feed on southern-hemisphere mosses (China, 1962; Helmsing and China, 1937). Several aphids live on bryophytes, those of the subtribe Melaphidina forming galls on *Rhus* and migrating to mosses (Eastop, 1977). *Aspidaphium cuspidati* lives in water-logged *Calliergonella cuspidata* and *Drepanocladus aduncus* (Stroyan, 1955). Upon being placed on stems of *C. cuspidata*, nymphs of this aphid immediately moved below the water level (Müller, 1973). The latter author suggested that feeding on bryophytes was a secondary feature in aphid evolution, the transfer to

these plants having taken place several times in aphid history. Southwood and Leston (1959) listed bryophyte-associated bugs which attach their eggs to moss stalks (*Megalothous chiraga*), overwinter there (*Selinus biguttatus*) or feed on the plants (*Drymus sylvaticus*). Lacebugs of the genus *Acalypus* primarily feed on bryophytes, but under adverse conditions some move to phanerogams which thus serve as secondary hosts. This was interpreted as a case of incomplete transference to mosses (Horn *et al.*, 1979). A few thrips (Thysanoptera) occur in bryophytes, like *Lissolirrips muscurum* (Rhode, 1955) and *Bourmierothers*, only found in mosses (Bournier, 1979).

Representatives of seven out of the nine holometabolous orders associate with bryophytes. Lacewing (Neuroptera) larvae lurk about mosses in search of prey (Richards and Davies, 1977). Many Coleoptera (beetles), the largest of all animal orders, occur in bryophytes. Many find refuge in this habitat. Bordoni (1972) obtained 179 species belonging to 25 families from mosses in a Tuscan fen, but only a few were bryophilous. The Staphylinidae, known to feed on moss (Mani, 1962) were best represented there. Frost (1942) found many Elmidae in Irish bryophytes and stated that this environment was most favourable for the beetles. Other Coleoptera obtained from bryophytes are the Limnebiidae, called 'minute moss beetles', and the Sphaeriidae ('minute bog beetles') (Arnett, 1971). The hydrophilid *Cretinis punctostrata* is a true bryobiont, spending its entire life in *Sphagnum* (Matthey, 1977). Its eggs are deposited therein, larvae live there and pupation takes place in a cell formed from these bryophytes. The chrysomelid *Mniophila muscorum* is another bryobiont, living in ground litter and feeding on moss (Kühnelt, 1976). Many other bryophilous beetles subsist on epiphytic algae (LeSage and Harper, 1976). New Guinean weevils whose dorsum was extensively overgrown with bryophytes were discussed by Gressitt *et al.* (1968). Mosses (*Daltonia*) as well as liverworts (*Lejeunea*, *Metzgeria*) occurred on these beetles.

One family of scorpion flies (Mecoptera), namely the Boreidae, commonly occur in and feed on mosses. They are rather catholic in their tastes; *Boreus notoperates* was found on Grimmiaceae as well as Isoetiales (Cooper, 1974). Bryophyte texture may be a more important factor in determining boreid preferences. Mosses growing in low, compact cushions, whose rhizoids are tightly matted, usually contain more Boreidae than those growing as loose cushions (Penny, 1977). One reason may be greater predation pressure from carabid beetles in the latter bryophytes. Larvae and adults of *B. brunalis* eat mosses throughout winter in Ontario, presumably feeding on bryophytes even below snow cover (Shorthouse, 1979). *B. notoperates* survives dry Californian summers by hiding inside small insect-made earthen chambers which are hidden within bryophyte rhizoids (Cooper, 1974).

Chironomid (Diptera) larvae made up about five-sixths of the nearly 600000 organisms Frost (1942) collected from Irish submerged mosses. Lindegaard *et al.* (1975), who obtained about 100000 invertebrates m⁻² *Cratoneuron*, noted that flies made up more than 40% of the total. These data will emphasize that the Diptera (flies) is the insect order most intimately associated with bryophytes. The crane flies (Tipulidae) *Dolichopeza*, *Liogma* and *Trigona* live in and feed on mosses. Larvae of the latter two species remarkably resemble their host plants (Alexander, 1920), that of *D. americana* being green and irregularly marked with dark lines, so that it blends into its moss background (Byers, 1961). Other tipulid adaptations to life in bryophytes include the special anal papillae found in larvae confined to these plants (Brindle, 1957). Choice of specific moss species by *Dolichopeza* appears to depend mostly on bryophyte growth habit and leaf texture. Very compact-growing species, like *Bryum argenteum* or *Ceratodon purpureus*, hinder the larvae's tunnelling, while loose-growing mosses like *Climacium*, *Polytrichum* or *Plagiommium cuspidatum* are too diffuse for constructing suitable tunnels. Furthermore, coarse-leaved *Polytrichum* or thallose liverwort are also rejected in favour of softer leaves (Byers, 1961).

Larvae of many fly families of medical and veterinary importance occur in bryophytes. These include Psychodidae (sand flies) (Ouate, 1955), Culicidae (mosquitoes) (Fantham and Porter, 1945), Simuliidae (Snow *et al.*, 1958), Ceratopogonidae (Séguy, 1950) and Tabanidae (horse flies) (Teskey, 1969). Thomas (1971) developed a quick method to extract tabanid larvae from moss. Adults of coprophilous and dung loving flies, like *Sarcophaga* and *Scatophaga*, are attracted to the capsules of certain Splachnaceae and disperse their spores (Garjeanne, 1932; Ingold, 1965; Koponen and Koponen, 1978).

The caterpillars of a few Lepidoptera (butterflies and moths) live in bryophytes. Prominent among them are the primitive Micropterygidae. *Neomitropteryx nipponensis* deposits its eggs on the liverwort *Conocephalum conicum* and the larvae feed on its tissues (Yasuda, 1962). *Sabainca*, which also occurs in hepatics, resembles them in its greenish colour and large setae (Tillyard, 1922). Larvae of another primitive group, the Messinae, feed on lichens and mosses and incorporate fragments thereof in their cases, which thus resemble the substrate (Zagulyayev, 1970). The North European *Nudaria mundana*, which feeds on saxicolous lichens and liverworts (Forster and Wohlfahrt, 1960) and the Australian *Eudonia* (Anonymous, 1970), are examples of more advanced bryophyte-associated Lepidoptera. The hemlock looper, a forestry pest in North America, deposits its eggs on mosses, and special means had to be devised to separate them from this substrate (Shepherd and Gray, 1972). Caddis flies (Trichoptera), which live in bryophytes construct their cases from

§.3 BRYOPHYTES AS A HABITAT FOR INVERTEBRATES

9.3.1 General considerations

Bryophytes possess several attributes which affect the distribution and abundance of dependent invertebrates. They are among the earliest of soil colonizers (Kühnelt, 1976; Stebaev, 1963) and important components of high-mountain ecosystems (Mani, 1962). Bryophytes rapidly absorb large quantities of water, retain them, and thereby also retard the drying-out of their underlying substrate. They serve as insulation against heat, cold and wind (Corbet, 1973; Gressitt, 1967; Strong, 1967) thereby cushioning invertebrates which live within them against climatic changes. Bryophytes also muffle sounds in the 30–50 KHz frequency range (Kolb, 1976). Last but not least, due to the perennial life-forms of many bryophytes, they are there when invertebrates need them. On the other hand, bryophytes are usually inconspicuous, being in a subordinate position in most ecosystems (During, 1979). In this context, the concepts of 'apparentness' and 'unapparentness' (Feeny, 1976) will now be introduced. An 'apparent plant' is one which, due to its size, form, persistence and relative abundance in the community is 'bound to be found', or 'susceptible to discovery' by its enemies. An unapparent plant, then, is 'hard to find' or 'unsusceptible to discovery' by its adversaries. Bryophytes, as major components of the Forests of Lilliput (Bland, 1971), are rather unapparent. It is only under extreme climatic conditions, above the timber line or while colonizing new land that bryophytes dominate entire ecosystems, thus becoming apparent.

9.3.2 Physical effects

Different bryophytes have different life-forms and grow in different colonies. Strong (1967) and Tilbrook (1967), working in Antarctica, wrote that mats of *Polytrichum* and *Dicranum* are less wet and cold than those of *Pohlia*, and consequently harbour more arthropods. *Polytrichum* supports these animals to a greater depth probably due to its more developed rhizoid system. Mat compactness is important for larvae of the mecopteran *Boreus* and the crane fly *Dolichopeza*. *B. notoperates* avoids mosses with coarse and open clumps, which do not have a fine rhizoid mat (Cooper, 1974). *Dolichopeza* shuns *Bryum argenteum* and *Ceratodon purpureus* because their very compact mats are too resistant to its tunnelling. On the other hand, the framework formed by the loosely-growing *Climacium* or *Platniumium cuspidatum* is too diffuse for constructing suitable tunnels by these larvae (Byers, 1961).

Shape, texture and thickness of bryophyte leaves affect the associated invertebrates. The predilection of the rotatorian *Pygura relata* for the

curved leaves of *Sphagnum erythrocalyx* (Edmonson, 1944) has been noted in Section 9.2.3. The liverwort *Frullania dilatata* bears under its leaves minute pockets in which numerous rotifers occur (Donner, 1966). Given a choice, larvae of *Dolichopeza* prefer thin, soft-textured leaves like those of *Platniumium* to the coarse leaves of *Polytrichum* (Byers, 1961). Gerson (1972) correlated the inability of *Euxitigmaeus frigida* to feed on several thick-leaved Polytrichaceae with the mite's short mouth parts. Barr (1973) stated that more water mites may be obtained from fine-structured aquatic bryophytes than from those with larger leaves.

The tendency of bryophytes to accumulate plant debris provides the first stable microhabitat for many invertebrates in newly colonized soils (Kühnelt, 1976). Consequently, the bryofauna becomes quite varied (Stout, 1974). This matter will be further discussed in Section 9.6.1.

9.3.3 Shelter

Strong (1967) believed that bryophytes, widely spread in Antarctica, serve primarily as shelter for the arthropods found therein. This is supported by the data of Chernov *et al.* (1977), who reported that bare soils at Cape Cheluskin, sparsely populated with algae and lichens, harboured only 5–10% of the arthropod populations found in mosses there. Moving from cold to hot deserts, Hammer (1966) collected hygrophilous mites from small moss colonies in an oasis near the Red Sea. The mites are rather sensitive to low air humidities; their long-term survival was therefore believed to be wholly dependent on these moss enclaves.

In the milder regions, bryophytes still serve as refugia. Bordonni (1972) found 179 species of beetles in Tuscan moss cushions, from bryophilous to occasional species, most probably overwintering there. Bryophilous but predaceous Pselaphid beetles overwinter, as adults, in the interstices of frozen moss mats (Reichle, 1966). The water beetle *Hydroporus morio* lies in English sphagnum pools which dry out during summer. The beetle bores small round holes in the damp bryophyte 'floor' and aestivates in this moist microhabitat until rains come (Jackson, 1956).

9.3.4 Oviposition and pupation

Invertebrates which feed on bryophytes usually also oviposit their eggs there. Examples are the crane fly *Dolichopeza* and the mite *Euxitigmaeus* (Byers, 1961; Gerson, 1972). *E. frigida* places only a single egg on each leaf, but *E. schusteri* deposits 3–4, these eggs imparting a reddish hue to moss shoots. Another bryophyte feeder, the ground cricket *Pteronemobius*, punctures *Sphagnum* leaves with its ovipositor and places its eggs in the resultant cavity (Vickery, 1969). Several predators which hunt in bryophytes also deposit their eggs therein. These include the bug *Myndobia tenella*, which preys upon aphids (Southwood and Leston, 1959) and

the fly *Eurymogaster* (Williams, 1939). The water mite *Thyas barbiger*, a parasite of mosquitoes, begins its life as an egg deposited on water mosses (Mullen, 1977).

Insects associated with bryophytes may pupate therein, at times utilizing the plants for constructing special cells. Pupation of the water beetle *Crenitis punctatosriata* takes place within a small cell, which the larva had formed from decomposed *Sphagnum* (Matthey, 1977). Glime (1978) reported on blackflies which live among *Fontinalis* leaves and use them to support their pupal cases. Nägeli (1936) noted that larvae of a spruce-feeding sawfly preferred to pupate under *Hylacomium* and *Thuidium* as compared to *Polytrichum*.

9.3.5 Camouflage

Invertebrates which live in bryophytes gain an obvious advantage by camouflaging themselves with these plants. As such disguise favours them only while they remain within, or against the background of bryophytes, the use of this particular concealment may mark the stage at which some invertebrates become bryophiles (and mimicry, below, will denote bryobionts). Camouflage may be used by larvae which construct cases, building them from bryophyte pieces. Glime (1978) noted that the caddis *Palaeopterus celsus* always composed its cases from leafy liverworts. These were cut into nearly circular pieces and cemented together along their margins to form flattened cases, shaped like eyeglass cases. Larvae of another trichopteran, *Adicropheps hitchcocki* construct their cases from blades of *Fontinalis dalecarlica*, *Hygrohypnum* sp., *Chiloscyphus polyanthus* var. *rivularis* and *Plagiochila asplenoides* (Glime, 1978). Larvae of the crane fly *Dicranomyia badia* spin about themselves a web onto which they fasten bits of *Bryum* and *Amblystegium* (Alexander, 1920). The spider *Spilasma tubulofaciens* incorporates moss fragments into its retreat and web, but this may well be fortuitous (Quintero, 1974).

Gressitt *et al.* (1968) reported that bryophytes (and other cryptogams) were growing on the backs of New Guinean weevils (Curculionidae). The beetles, mostly of *Gymnopholus* subgenus *Symbiopholus*, are often structurally modified to promote plant growth; they have dorsal pits surrounded by ridges, stiff setae and produce a sticky secretion which may encourage cryptogam establishment there (Gressitt, 1966). *Daltonia angustifolia* was found on five species of *Symbiopholus*. Liverworts, apparently rare on these beetles, grew extensively on weevils of the genus *Poroplierus* living in the same habitat. *Odonotoleunea*, *Microlejeunea* and *Mezgeria* were reported from the latter animals. Most of these bryophytes grew on nearby plants, indicating their origin. Finding moss protonema on the weevils suggested that they originated from spores (Gressitt *et al.*, 1968). The beetle-cryptogam association apparently benefits both partners

(hence 'epizoic symbiosis'), the animals providing a suitable environment for the plants, the latter camouflaging the insects. Successful disguise was inferred from the scarcity of predation on the beetles, which feed on the upper shoots of various trees, thus being rather exposed. Another possibility was that the cryptogams made the beetles distasteful, a form of chemical protection.

As noted in Section 9.2.6, certain water bryophytes grow on live molluscs. The molluscs' shells are colonized like any other submerged calcareous substrate. However, as predation on Mollusca in aquatic environments may be visual (Heller, 1975), bryophyte overgrowth could be of advantage.

9.3.6 Mimicry

The moss-overgrown beetles and molluscs may also thrive without their masks of living plants, but invertebrates which mimic bryophytes will not survive elsewhere. Mimicry implies special coloration and/or special morphological modifications based on a model; without the latter, mimicry makes no 'evolutionary sense' and the imitating animals will disappear. Mimicry thus provides examples of bryobionts, but not necessarily also of bryophagy. Examples will be drawn from various insect orders. The predaceous phasmid *Trychopelplus laciniatus* has greenish foliations and lamellations on its body, which make it 'extraordinarily mossy' in appearance (Robinson, 1969). The peloridiid bug *Hemiodocus veichi* feeds on bryophytes, and with its cryptically shaped and coloured body it greatly resembles the plants' growing tips, being consequently rather difficult to see on the mosses (Helmising and China, 1937). Larvae of the primitive *Sabainca* (Lepidoptera) resemble hepatic leaves, carrying large setae similar to spines found on the host liverworts (Tillyard, 1922). Finally, crane flies which feed on bryophytes exhibit behavioural and morphological modifications which help them to blend into the plants' background. Larvae of *Phalacroera replicata*, carrying specialized outgrowths, are greenish and sluggish in their movements. Clinging to mosses and remaining almost motionless for hours, they closely resemble bryophytes. Larvae of *Trigona trisulcata* have rows of leaf-like appendages on their dorsal, pleural and ventral surfaces, making them quite similar to *Fontinalis* on which they live (Alexander, 1920).

9.4 BRYOPHYTES AS FOOD FOR INVERTEBRATES

Diverse invertebrates feed on bryophytes. Orthopterans, beetles and moth caterpillars bite and chew, whereas bugs, aphids and mites suck out the contents of moss cells. Ants feed on the spores within the capsule (Pitt, 1907) or harvest the entire capsule (Loria and Herrstadt, 1981). The

scorpion-fly *Boreus brunnalis* thrusts its rostrum into young moss shoots, chews off the apex, and eats its way down into the core (Shorthouse, 1979). Larvae of the fly *Dolichopeza* tunnel in bryophyte rhizoids (Byers, 1961), and those of *Lycoria* in the thallus of *Marchantia*. Gerson (1972) presented photographs of *Didymodon* cells sucked out by the mite *Eusitigmaeus*; the tardigrade *Echiniscus testudo* probably feeds in a similar way (Morgan, 1977).

These feeders, while restricted to bryophytes, are not particularly host-specific. Even aphids, usually quite narrow in their feeding choices (Eastop, 1973), have many moss species as hosts (Müller, 1973). Of eleven species of *Eusitigmaeus* collected by Gerson (1972) from Canadian mosses, those which were collected more than once were found in different bryophytes. Similar data were presented for the fly *Dolichopeza* (Byers, 1961) and for the scorpion fly *Boreus* by Cooper (1974) and Penny (1977). These and other authors concluded that habitat is probably more important than specific bryophyte host-plant in determining the distribution of invertebrates which feed on these plants.

Some bryophyte-consuming animals are not restricted to these plants. Fortuitous alternate feeding takes place when bryophytes and other plants – algae, lichens or even phanerogams – occur together, as in freshwater habitats (Chapman and Demory, 1963) or on mountain tops (Mani, 1962). An Antarctic springtail preferred moss to fungi (Wise *et al.*, 1964), while the termite *Hospitalitermes* selected lichens rather than bryophytes (Collins, 1979). Alternate feeding also occurs when the bryophyte host dries up, as happened when the lacebug *Aechlypta barberi* shifted from moss to hops (Drake and Latin, 1963). This case shows that, under certain conditions, bryophagous invertebrates may attain economic importance. Regular movement between moss and phanerogam constitutes the third mode of alternate feeding: aphids of the subtribe Melaphidina, which shift between bryophytes and *Rhus* (Eastop, 1977), are an example.

The digestion and metabolism of bryophytes in invertebrates, and the energetics of the association, are poorly known. Numbers of various animals occurring in bryophytes were presented above, and most of the cited sources contain additional data. Standing crop and/or annual production of some bryophytes were compiled by During (1979) and by Reiley *et al.* (1979). Data on bryophyte amounts ingested are available for an orthopteran and a beetle. Duke and Crossley (1975) tagged *Grimmia laevigata* with ^{13}C and showed that the rock grasshopper *Trimerotropis saxatilis* ingested 27.25 mg moss day $^{-1}$. They calculated that the entire population in the sample area consumed 391.2 mg moss m $^{-2}$ year $^{-1}$. Using a simple feeding technique, Smith (1977) offered various plants to the beetle *Ecomorrhinus similis*. It consumed 1.67 mg *Brachythecium ruabulum* per beetle day $^{-1}$, or 3–13% of the bryophyte's total production.

Frankland (1974) stated that 'consumption of bryophytes by animals appears to be insignificant'. Many invertebrates observed on these plants actually subsist on algae or detritus occurring on aquatic and terrestrial bryophytes (Glime and Clemens, 1972; LeSage and Harper, 1976; Matthey, 1971; Stout, 1974), and many, as noted, only shelter, oviposit, pupate or hunt there. And yet the data presented above show that members of a dozen insect orders, as well as some mites, gastropods and tardigrades, feed on bryophytes. On balance, it seems that more invertebrates feed on these plants than meets the eye; many others, however, do not. Crum's (1976) observations that 'In nature animals rarely eat bryophytes possibly because of their taste', and that *Preissia quadrata* when tasted, was hot enough to tingle the tip of the tongue and burn the back of the mouth, provide the clues. Taste, as well as smell, are imparted to plants by secondary chemical compounds, and it is this group of substances which are believed to protect plants against herbivores (Fraenkel, 1959; Swain, 1974), making the former unpalatable or even poisonous for the latter.

Bryophyte chemicals (including secondary substances) were reviewed by Markham and Porter (1978) and by Suire (1975). Some representative compounds known to affect arthropods are listed in Table 9.2, p. 324, but this is barely the tip of the iceberg. As bryophyte chemicals become better known, many additional substances will be found which repel, deter, inhibit or poison invertebrates. Certain animals, however, have managed to breach the chemical (and other) defenses of bryophytes by various ways – of which we are quite ignorant – and thrive on them. The archaic and the recent feeding associations of insects with bryophytes, as expounded in Section 9.2.8 (c), suggest that this breaching is of ancient as well as relatively modern origin. When Crum (1976) complained about the taste of *P. quadrata* he was probably savouring the bitter flavour of glycosides present in that liverwort (Markham and Porter, 1978).

Some of the secondary substance of bryophytes (Suire, 1975), like the terpenoids, pinene, limonene, camphene and cardinene, and the sterols, sitosterol and stigmasterol, induced the formation of mixed-function oxidases (MFO) in a moth caterpillar (Bratsten *et al.*, 1977). It was argued that MFO play a major part in protecting herbivores against chemical stress from secondary plant chemicals. These substances, then, while protecting bryophytes from some herbivores, may enable others to devour them.

A distinction should here be made between 'generalist' and 'specialist' herbivores (Feeney, 1976). The former are animals which attack plants of many chemically unrelated families, subsisting on most plants unless these are specifically repellent to them. Specialists feed on plant species only within one family, or group of families which are chemically related. Their

choice of food is strongly influenced by chemical signals from the host plant. Invertebrates devouring bryophytes and other plants (with the exception of aphids) are generalists. Peloridiid bugs, *Dolichopeza*, *Boreus* and *Eurigmatius* are examples of arthropods (drawn from diverse groups) specializing on bryophytes. Special adaptations to locate these plants, on the one hand, and to overcome their array of chemical (and other) defences, on the other, might most profitably be sought among these arthropods. Strict specialists, which exclusively feed on one diet (i.e., plants, wood, blood) require internal symbionts to supplement their fare with essential sterols and vitamins. Bryophyte specialists can therefore be expected to have them, and H.J. Müller (cited by Buchner, 1965) described the single symbiont of an archaic Peloridiid bug. Nothing is known about its specific role or how other bryophyte specialists obtain essential rare nutrients.

Certain bryophytes may absorb and store in their tissues heavy metals like copper, lead and nickel (Rühling and Tyler, 1970), elements toxic to all animals. If ingested by herbivores, the heavy metals will move along the food chain, continuously harming all participants. Much the same might happen when invertebrates consume mosses which had accumulated radio-nuclides (Lowe, 1978; Svensson, 1967).

9.5 INVERTEBRATE UTILIZATION BY BRYOPHYTES

9.5.1 Dispersal

Symbiophilus weevils which participate in epizoaic symbiosis (Section 9.3.5) carry their cryptogam gardens about. During their long lives (c. 5 years) the growths become cumbersome and may fall off as a result of fighting and mating (Gressitt and Sedlacek, 1970). Dispersal occurs when the gardens drop off away from their initial sites, and bryophytes then continue to grow. A similar mechanism may operate with freshwater mussels overgrown by *Ocotliceras*. The animals migrate with fluctuations in water levels, carrying their moss growth along (Lohammar, 1954; Neumann and Vidrine, 1978). Bryophyte dispersal in both cases is quite fortuitous, not dependent on animal presence, as the plants grow on other substrates in the same habitat.

The association between certain Splachnaceae and flies which disseminate their spores is another matter altogether. Its apparent long duration (Koponen, 1978), and the role insects appear to have played in the bryophytes' evolution, make it of special interest for those fascinated by plant-insect co-evolution.

Upon ripening the capsule of *Splachnum* (and some other Splachnaceae) remains fleshy, the hypophysis being large and coloured.

The sticky clumps of small, smooth spores, which are not air-borne (Crum, 1976), then become exposed. A 'musty' smell which attracts flies is emitted at that time (Erlanson, 1930, writing about *Tetraplodon montides*, described it as a 'strong and rank valerianic odour'). The odour apparently has two components, one resembling decaying protein (Faegri and van der Pijl, 1979), the other consisting of alcohols and acids (Pysalo *et al.*, 1978). The latter authors identified the feid butyric acid as well as rather specific 8-carbon compounds in some Splachnaceae; amount and distribution of these substances differed among the bryophytes assayed (Table 9.1). *Splachnum luteum* which has the largest hypophysis, contained more volatiles than the other species. The differences between the two *Splachnum* species suggest that others of this genus might also vary in their attractant substances. The entomophilous Splachnaceae are further characterized by enlarged, brightly coloured hypophyses, which, standing out against the generally green-mossy background, will likewise allure insects. Comparative observations on flower pollination by insects (Faegri and van der Pijl, 1979) suggest that odours preceded visual stimuli as attractants, and it is likely that the same sequence was followed in the Splachnaceae.

Table 9.1 Volatile compounds identified from several Splachnaceae (from Pysalo *et al.*, 1978).

Compound	<i>Splachnum luteum</i>	<i>Splachnum vasculosum</i>	<i>Tayloria tenuis</i>
1-octen-3-ol	+	+	+
3-octanone	+	-	-
3-octanol	+	-	-
2-octen-1-ol	+	-	-
<i>trans</i> -2-octenal	+	-	-
octanol	+	-	-
acetic acid	-	+	+
butyric acid	-	+	+
propionic acid	-	+	+

Koponen and Koponen (1978), who reviewed reports on insect attraction to Splachnaceae, baited traps with these mosses and caught several flies. Representatives of the families Muscidae, Sepsidae and Calliphoridae (which include the Sarcophaginae) were obtained. All belong to the more advanced order Cyclorhapha and are attracted to dung and cadavers, in which they oviposit and where their larvae (maggots) live. Dung and cadavers are the specific habitats of the entomophilous Splachnaceae. A representative list (Crum, 1976) includes cow, deer, horse, human and

moose faeces, cattle tracks, a site at which whales were slaughtered, wolf bones and owl pellets. Entomophilous Splachnaceae and the flies they allure are thus restricted to the same habitats, and the bryophytes appear to be making the most of it. They entice the insects by a two-component (odour and colour) system, and, as these arrive, their bodies and appendages become covered with sticky spores. Flies which later alight on dung or on cadavers and move around will cause the spores to fall off, thereby dispersing Splachnaceous propagules to their preferred sites.

Splachnum and its relatives, upon becoming adapted and then restricted to animal droppings and remains, were faced with the need to transport their spores to other similar habitats. Unlike a possibly analogous group, the copper mosses, *Splachnum* had adapted to growing on substrates which were inhabited by, and attractive to, highly mobile organisms like insects. Initially, the latter probably only rested on these bryophytes, but some spores could have adhered to them. Insofar as the insects then flew to animal dung or cadavers, and the spores dropped off there, dispersal was actually effected. The advantages accruing to Splachnaceae whose spores had thus been transported from one suitable habitat to another would then have exerted strong selective pressures to preserve and enhance this mode of dispersal. Consequently, *Splachnum* and its relatives evolved means to attract and hold flies on the hypophysis long enough for the spores to stick to them. In other words, steps in the evolution of the Splachnaceae towards entomophily were determined by insect response. The association between the entomophilous Splachnaceae and flies is therefore claimed as a case of bryophyte-insect co-evolution.

Many questions arise. A selection includes the specific role visual stimuli play in attracting flies: the variety of chemical attractants and the significance of 8-carbon compounds; a possible 'reward' for moss-visiting flies (such as high-energy and/or fecundity-promoting substances from the hypophysis) and whether there are any special behavioral or morphological insect modifications for spore dispersal. Whatever the answers to those (and many other) questions, the presence of specific fly allurements, the distinct growth sites of the mosses and the relatively large numbers of entomophilous species (Koponen, 1978) attest to the diversification and thus evolutionary success of the Splachnaceae. It is tempting to speculate that their unique relationship with insects has contributed to their success.

The remarkable morphological uniformity of entomophilous Splachnaceae obtained from various parts of the world, their similar habitats, and their associations with insects led Koponen (1978) to postulate a monophyletic origin for these mosses. Their strict entomophily precludes long-range dissemination, which suggests that the spread of the Splachnaceae to their present disjoint distribution could only have been along land connections in the geological past. This in turn indicated an

approximate era, about 200 million years ago, for the rise of these mosses (Koponen, 1978), a date not inconsistent with fossil evidence (Lacey, 1969). Two problems intrude here. The first concerns the original dung and cadavers producers, because cattle, moose and humans are rather recent newcomers to the geological scene. Koponen (1978) recognized this difficulty and suggested that reptiles were the early source of animal remains. The other problem concerns the disseminating insects. As noted, all flies baited or reported from Splachnaceae to date belong to the advanced suborder Cyclorrhapha. These are believed to have originated in the Cretaceous (Oldroyd, 1964), approximately 100 million years later than the entomophilous Splachnaceae. The difficulty may be overcome by assuming that these mosses originally attracted archaic flies, whose place was then taken by modern relatives. To sum up, as reptiles gave way to mammals, *Splachnum* and its relatives 'shifted' to growing on the latter's remains (Kühnelt, 1976, mentions a case of preferential moss growth on snail droppings - a possible early link). And as modern flies replaced ancient ones (or other insects), the bryophytes attracted them also. Should this model turn out to be generally correct, it would show that the entomophilous strategy of these Splachnaceae must have been quite successful, as well as constituting a rather long-running, extant case of plant-insect co-evolution.

9.5.2 Fertilization and fertilizers

Harvey-Gibson and Miller-Brown (1927) observed mites, springtails and other arthropods on the antheridia of *Polytrichum vulgare*, and noted that their bodies became smeared with male gamete-containing mucilage. Fertilization was believed to result from such activities. A more restrained point of view was expressed by Garjeane (1932), who noted that the conspicuous 'microscences' of the Polytrichaceae are not known to attract insects. More recent data on this potential bryophyte-invertebrate interaction are not available.

As the colonization of land passes from the initial lichen stage to the moss phase, a layer of humus is formed below the latter plants which enables many more invertebrates to live there (Kühnelt, 1976). This additional mass of dead animals and their excretions may well provide bryophytes with general and specific growth factors, thereby in turn enhancing their development. The case of a moss growing preferentially on snail droppings (Kühnelt, 1976) will serve to illustrate this point.

9.6 BRYOPHYTE-INVERTEBRATE COMMUNITIES

9.6.1 Colonization

While bryophytes participate in the early stages of plant succession, their associated invertebrates form similar stages in faunal succession (Gerson,

1969). The hardiest and most mobile animals arrive first, being later replaced by species of narrower ecological requirements but better competitive ability. Moss cushions developing on rock faces were first colonized by rhizopods, rotifers and tardigrades, nematodes and ciliates also occurring there (Kühnelt, 1976). As dead material formed under the cushions, rotifers and tardigrades became very abundant, nematodes also increased, and arthropods, like springtails and oribatid mites, began to appear. As a thicker decomposition layer formed below, rhizopods, rotifers and tardigrades declined, but nematodes, oribatids and springtails increased. 'Myriapods' appeared, the composition of the fauna becoming similar to that of the soil fauna. Other succession sequences involving bryophytes and invertebrates, but affected by other physical factors, were also described by Kühnelt (1976) and by Stebaev (1963).

The first bryophyte and invertebrate colonizers usually reach new sites by wind. The animals must therefore be able to withstand extreme temperatures, solar radiation and infrequent, widely fluctuating humidities. The ability of certain bryophyte-associated Protozoa, Turbellaria, Rotifera, Nematoda and Tardigrada to survive such conditions has already been mentioned (Section 9.2). To this may be added Kühnelt's (1976) remark that colonizing Collembola and Acari are usually drought-resistant. The end result of such strong selection is that disparate components of the bryofauna show remarkable convergence in their adaptation to harsh, unpredictable environments. Wind dispersal of the colonizing bryofauna partially explains its 'surprising' cosmopolitanism (Hesse *et al.*, 1951): seven of 12 Antarctic rotiferans, and most of the tardigrades, were already known from Europe and the Arctic. Nicholais (1975) remarked that common moss nematodes, like *Plecticus cirratus*, are found in very different parts of the world. Menzel (1921) noted the same in regard to bryophilus copepods.

Bryophytes play only a transitory part in plant colonization in most habitats, but retain a dominant role on high mountains or under very cold conditions, where succession cannot continue. Bryophytes may be the dominant producers in such situations and strongly affect their faunas. The dependence of Antarctic arthropods on mosses was emphasized by Janetschek (1967), who defined the bryosystem as one of the dominant Antarctic ecosystems. When this ecosystem matures, bryophytes become increasingly important and most of the fauna occurs in moss tufts and mats.

Under favourable conditions bryophytes form perennial colonies in many environments, thereby becoming apparent to feeders and predictable as habitats. This in turn causes a shift from r-selected to K-selected moss invertebrates. As noted above, the change from a colonizing moss tuft to a perennial cushion brings about a change from the small, mobile, rapidly reproducing r-selected Protozoa and Rotifera to larger, less

mobile, slower reproducing, K-selected arthropods. Year-round availability of bryophytes promotes monophagy, itself conducive to K-selection. Examining *Eustigmatus* mites, Gerson (1972) found species like *E. gersoni* and *E. rhodomela* to be associated with colonizing mosses, while *E. frigida* occurred only on perennial pleurocarpus species in forests and other humid situations. Life strategies of the host bryophytes thus impose themselves on their dependent faunas.

9.6.2 Succession, annual activity and exclusion

Changes in bryophyte composition affect the associated animals. This aspect of bryophyte-invertebrate inter-relationships was studied by Murphy (1955) in sphagnum bogs. Accumulations of acid peat are built up, at certain sites, by a complex of sphagnum hummocks and water-filled depressions which are constantly replacing and succeeding each other, with a concomitant change in *Sphagnum* species. Each of the latter tends to occupy a characteristic position relative to the water table and the age pattern of the hummock. The springtail *Sminthurus malinzeri* was associated with the most humid *S. cuspidatum* and *S. subsecundum*, *Folsomia brevicauda* and *Isotoma sensibilis* with the mesophiles *S. papillosum* and *S. magellanicum*, and other Collembolans with the drier *Calluna* and *Cladonia* habitat. Similar series were described by Tarras-Wahlberg (1952-53) for oribatid mites, and by Reichle (1966) for pselaphid beetles.

An interesting feature of some members of the bryofauna is their year-round activity, even under extreme cold conditions. Immatures and adults of the snow scorpionfly *Boreus bumalis* feed on mosses the year around, even below winter snows (Shorthouse, 1979). Active *Eustigmatus* mites were dug out of their 3-ft snow cover in eastern Canada by Gerson (1972). Upon being offered mosses in the laboratory, they immediately began to eat and oviposit. Morgan (1977) stated that tardigrades living in a moss on a roof in South Wales reproduced throughout the year.

Active cases of exclusion between bryophytes and invertebrates are rare. When *Fornitidis antipyretica* was introduced into South Africa, it quickly became established but caused a decline in the populations of the indigenous water-insect larvae. The latter were adapted for living on slime algae, and the blanketing of these microhabitats by *Fornitidis* did not enable the larvae to survive there (Richards, 1947). Another water moss, *Ocoidiceras fontanus*, is grazed by snails to the extent that they are mutually exclusive on some North European rock surfaces (Lohammar, 1954).

9.6.3 Specific communities

Four bryophyte-invertebrate communities will be discussed below briefly,

emphasizing the special environmental features of each. Readers interested in arthropods living in saxicolous mosses are referred to Bonnet *et al.* (1975) and Simon (1974).

Water bryophytes support large and varied, specialized and unspecialized invertebrate populations. The former include the primitive *Forninialis*—simulating crane fly *Trigona* (Alexander, 1920), the aphid *Aspidaphium cuspidati*, which feeds on *Calliergonella cuspidata* only below water level (Müller, 1973), and the tardigrade *Macrobiotus macronyx*, exclusively collected from submerged mosses (Morgan and King, 1976). Many of the unspecified, bryoxenous or occasional components of the aquatic bryofauna were found by Lindegaard *et al.* (1975) during their rather complete study of the animals on *Cratoneuron*. A special feature of their work was the comparison between invertebrates found in the various zones. These were defined as the underlying detritus zone, above it the one holding water-covered mosses, then the 'madicolous' zone ('just above the water surface where the moss is constantly wetted by capillary water') and uppermost, the dry zone (Fig. 9.2). One may thus see how the fauna changes from springtails, beetles, spiders and predaceous mites in the dry region to mainly flies, caddis flies and molluscs in the madicolous and water zones, to worms and more flies in the detritus. The water-covered zone harboured the largest numbers of both species and individuals as well as having the biggest diversity. A special aquatic bryofauna, developing around moss balls (formed from *Forninialis antipyretica* and *Drepanocladus tenuinervis*), includes the isopod *Asellus aquaticus*, oligochaetes and leeches (Luther, 1979).

Glime and Clemons (1972) compared number and diversity of insects found on *Forninialis* with those collected from similar but artificial substrates. They concluded that this moss probably serves only as a physical substrate for insects (which browse on accumulating detritus and algal growths). Studying submerged Antarctic mosses, Priddle and Dartnall (1978) reached a somewhat similar conclusion. The six rotifers which they investigated had clear settling preferences on various sites along the submerged stem of *Calliergon sarmentosum*, but none of the invertebrates found appeared to feed on the moss.

Sphagna in bogs have their own faunas, whose composition is determined by the special characteristics of these plants. Their acidity, for instance, limits the number of animal groups which may live there. Protozoa therefore abound in number as well as species (Bovee, 1979; Grolleté, 1978; Heal, 1962), while tardigrades are rare (Morgan and King, 1976). *Sphagnum* bogs undergo periods of drying out, which result in various invertebrate succession patterns (Section 9.6.2). Some of the plants actually float, thereby serving as habitats for oribatid mites (Karppinen and Koponen, 1973) and beetles (Dybas, 1978). *Sphagnum* 'carpets' can be

divided into two layers, the upper one consisting of the heads which, as they grow close together, form a smooth surface. Small animals may run there, and it effectively insulates the lower layer from temperature and humidity fluctuations (Nørgaard, 1951). The lower or stalk layer, on the other hand, is much thinner, being filled with small spaces and cavities in which animals live, rather protected from the surface. *Sphagnum* has hollow cells, in which some rotifers live (Fig. 9.1). And finally, these plants appear to be rather unedible to invertebrates (Smirnov, 1961), although odd feeders, like the ground cricket *Pteronemobius*, feed on sphagna (Vickery, 1969). *Sphagnum* peat is usually sterile *in situ*. However, as peat particles enter a bog, they are colonized by micro-organisms, which enhances their nutritional value and makes them edible to chironomid fly larvae (McLachlan *et al.*, 1979).

Arboreal bryophytes occur as continuous growth from the underlying soil, or as disconnected patches. In the former case, the plants serve as 'bridges' for the fauna between soil and trees; many animals are known to have followed bryophytes upwards (Bonnet, 1973; Larsson, 1978). The upper limit for such invertebrates is determined by the prevailing humidity, the animals arranging themselves according to their drought resistance at various tree heights (Pechorn-Walcher and Gunhold, 1957). Invertebrates in strictly arboreal bryophytes live in a biotype characterized by spatial and temporal discontinuity (Bonnet, 1973). Their fauna consists mainly of wind-borne species, capable of surviving intermittent humidities.

The only invertebrates living in bryophytes on roofs are very resistant species, which, having this environment all to themselves, may produce considerable populations. The tardigrades *Macrobiotus hufelandii*, *Hypsibius oberhauseri* and *Milnesium tardigradum* abound in British as well as Danish roof mosses (Morgan, 1977; Nielson, 1967). Another species very common in this habitat is the nematode *Plecticus rhizophilius*. Corbet and Lan (1974) recorded the protozoan *Arceella arenaria* and the rotifer *Mniodbia* from bryophytes growing on a west Norfolk roof.

9.7 BRYOPHYTES AS 'STEPPING STONES'

Bryophytes have been called the amphibians among plants (Richards, 1959), as they straddle, so to speak, the aquatic and the terrestrial worlds. This unique position has rendered them suitable to serve as 'stepping stones' or 'halfway houses' for invertebrates as these emerged from archaic water bodies onto land. The ability of bryophytes to live under intermittent wetting and drying was probably of considerable importance in this respect.

The transition of arthropods from aquatic to terrestrial habitats

probably began in the Silurian and the Lower Devonian (Kevan *et al.*, 1975), and was dramatically described by Størmer (1976): 'plants and animals of the seas, lakes and rivers were on their way to invade and conquer the land. The swamps, the early "mangroves" and the beaches with an abundance of plant litter were the "land of promise" for the animals struggling for life in the less nutritive waters along the shores'. Bryophytes (apparently present from the Devonian; Lacey, 1969) which grew at the water-land interface could also serve as a 'land of promise'. The ability of bryophytes to maintain high humidities might have been of special importance, as the dampness would protect newcoming invertebrates against desiccation, while enabling aquatic ones to breathe without drying out.

It is upon confronting change that organisms evolve. The intermittently-wetted bryophyte cushions constitute such changing, uneven habitats, their variability by itself exerting strong selection pressure. Such contingencies would favour animals capable of coping with them. The co-existence of invertebrates employing various respiratory mechanisms is likewise encouraged by moisture gradations available within the same cushion.

Emigration of animals from an aquatic to a semi-aquatic habitat will increase the weight placed upon the legs. Some aquatic arthropods walk on the bottoms of water bodies, the displaced volume of liquid taking some of the weight off their appendages. As these animals wander into bryophyte cushions, the humidity prevailing there will help them to 'take the weight off their feet'. Variable moisture encountered within such cushions would encourage stronger legs while affording the animals areas of 'rest', even of survival, between hours of walking. The newly colonized bryophyte environment, being partially dry, affords some animals sanctuary from wholly aquatic predators. The plants also offer an abundant, diverse food supply. For carnivores, many protozoans, nematodes and tardigrades are available, while the bryophytes themselves, their algal periphyton and the detritus accumulating underneath provide opportunities for phytophages and omnivores.

If bryophytes had indeed played a role in the colonization of land by invertebrates, we would expect to find primitive, relict animals still living in moss, sphagna and hepatics. The extant presence of some rather archaic insects in bryophytes thus lends support to the above hypothesis. The Peflorididae, for example, are a family of archaic moss-feeding bugs, regarded as 'living fossils' which have changed little since Triassic times (China, 1962). The two most ancient fly families, Tipulidae and Nymphomyiidae, are represented in bryophytes. Oldroyd's (1964) words are appropriate about the former family: 'We believe that flies, as a group, have arisen from ancestors whose larvae, though terrestrial, lived in wet

moss and so had, as it were, a foot in both worlds... Perhaps nearest to the ancestral way of life are those Tipulid larvae that live in moss'. The larvae of *Palaeopteron walkeri*, a member of the Nymphomyiidae, live among mosses in rapid streams (Cutten and Kevan, 1970). Among Lepidoptera, the Micropterygidae are the most primitive, and species of the genera *Micropteryx*, *Sabainca* and *Neomicropteryx* are found in bryophytes, on which they may feed (Tillyard, 1922; Yasuda, 1962).

Bryophytes serve as 'stepping stones' for arthropods moving in other directions also. The alpine water mite *Parnumia steinmanni* is a recent newcomer to water, and can still be found in moist as well as partially dry moss (Bader, 1969). Bryophytes were used in this case as a 'halfway house' on the mite's way into water. Cavernicolous copepods are believed to be relicts of a tropical fauna which flourished in Europe during the early Tertiary (Vandel, 1965, citing papers by Menzel). As the climate changed most tropical forms perished, except those which managed to adapt to subterranean waters. Mosses appeared to have a role as refugia during that adjustment period, because tropical copepods, like *Bryocyclops* and *Muscocyclops*, are closest to present-day cavernicolous species. Transition, through mosses, from an epigean to a cavernicolous mode of life may be observed in amphibious copepods. The genus *Morania*, for example, contains a series of species which live in dead leaves, in decaying wood, in bryophytes and finally in caves (Vandel, 1965). Another series begins with the beetle *Bathysciola*, which lives in mosses. Quite similar genera may be found in caves, these beetles having highly specialized, strictly cavernicolous, relatives (Vandel, 1965).

Passing to a totally different group, Stout (1963) believes that terrestrial Protozoa are freshwater species which had invaded land, probably via the moss-sphagnum of stream beds, and hence into forest litter and soil.

9.8 EFFECTS OF HUMAN ACTIVITIES

Modern technology is altering bryophyte distribution, abundance and composition, with resultant changes in the accompanying faunas. New habitats become available for cryptogams (bryophytes and algae) by installing electric lights in caves. Insects, mites and spiders – representing two additional trophic levels – rapidly colonize these plants (Dobat, 1972).

Bryophytes are sometimes considered to be weeds, necessitating chemical control. The effect of bryocides on the fauna would be mostly indirect, by reducing plant cover and biomass. Direct effects on animals can be expected upon using compounds like calomel (mercury chloride) (Pycraft, 1975) or chloroxuron and diuron (both of which contain urea) (Hackemesser and Liche, 1978). Calomel is a recognized insecticide, having been used against pestiferous maggots (Martin and Worthing,

1977), while urea is known to repel soil arthropods (Marshall, 1974). Residues of another pesticide, methoxychlor, were found in aquatic mosses several weeks after treating the water against simuliid flies (Wallace *et al.*, 1976). A broad-spectrum pesticide like this can be expected to have a severe influence on the non-target bryofauna.

More pernicious effects may be anticipated from accumulations of heavy metals and radionuclides. Grodzinska (1978) reported considerable concentrations of heavy metals (including the dangerous cadmium, nickel and lead) in *Pleurozium schreberi* and *Hylacomium splendens*. Increasing radionuclide levels were found in temperate as well as subtropical bryophytes (Svensson, 1967; Lowe, 1978). The effects of these types of pollution on the bryofauna are not known. Increased SO₂ levels are currently causing major changes in bryophyte cover and diversity. While most species decrease, some, like *Hylacomium splendens* and *Ptilium crista-castrensis*, increase their coverage (Winner and Bewley, 1978). Such changes are bound to alter the associated invertebrate fauna, decreasing the populations of many species while increasing those of few.

9.9 MISCELLANEOUS

Bryophyte-invertebrate associations have a few minor economic consequences, cited by Thieret (1956). Thus sphagnum was recommended for relieving itching caused by insect bites and even preventing them, and *Hypnum* was used for packing leeches for shipment as well as by anglers as a medium for scouring worms. Commercial use implies shipment; the lacebug *Acalypta sauteri* was intercepted by quarantine authorities at New York port, on moss used for packing nursery stock imported from Japan (Drake and Latini, 1963). The ubiquity of bryophytes suggested to Sayre and Brunson (1971) and to Corbet and Lan (1974) that these plants and their microfauna might be suitable material for classrooms.

Finally, an etymological note. Invertebrates were named after bryophytes (or musci) although often they were only occasional (i.e. the snail *Pupilla muscorum*, some Protozoa and other animals mentioned in Section 9.2). An entire phylum, Bryozoa ('moss animalcules') was given its name because their (mainly marine) colonies look like 'a mat of moss' (Pernak, 1978); they do not appear to be associated with bryophytes. The prefixes 'bryo' and 'musci', when applied to the names of invertebrates, therefore do not necessarily indicate a close relationship with bryophytes. On the other side of the fence, neither does the name *Ctenidium molluscum*, a moss sometimes growing on calcareous soil with molluscan remains (Marshall, 1979). Notwithstanding these reservations, one is struck by the congruence (in Latin) between *musca* (fly) and *muscus* (moss).

9.10 DISCUSSION

9.10.1 The origin of the bryofauna

The data presented indicate at least five sources of the bryofauna. Desiccation-resistant species came by winds. Others moved up from the underlying soil. Several invertebrates arrived from freshwater bodies. The phytophagous species originated from other host plants. The fifth group are relict species which apparently survived in bryophytes from archaean, their current distribution being quite disjunct (Hammer, 1965). The present diversity of the bryofauna probably reflects the disparate origins of its components.

9.10.2 The preponderance of flies in the bryofauna

Reviewing the bryofauna, one is struck by the variety of flies (Diptera) which occur on and in these plants. They predominate in numbers (Lindgaard *et al.*, 1975) and in diversity, being the only invertebrates to which mosses (i.e., Splachnaceae) have clearly adapted. And yet, the Diptera is neither the largest insect order (which is the Coleoptera) nor, among the major orders, the one most consistently associated with plants (which is the Lepidoptera). Three factors have probably contributed to the success of the bryophyte-fly relationship. The great versatility in the life style of the flies may have been one factor. 'No other order of insects present so great a diversity of larval habits as the Diptera' (Richards and Davies, 1977). To this should be added that in the context of another plant-insect association, namely pollination (mostly conducted by winged adults), the Diptera show more variation of habits than any other insect group (Faegri and van der Pijl, 1979). The need of most fly larvae for a more or less humid medium (Oldroyd, 1964), could have been another factor. Bryophytes have similar requirements, thus they co-exist with flies more often, and in a greater variety of situations, than members of other insect orders. The third factor may well have been the highly evolved position of the Diptera which have attained the highest degree of structural specialization (Richards and Davies, 1977).

9.10.3 Bryophytes as a factor in invertebrate evolution

Insects simulating bryophytes in their behaviour, coloration and even appendages were noted in Section 9.3.6. 'Epizoid symbiosis' (Section 9.3.5) is another instance of insects adapting to bryophytes (and other cryptogams) and the same might be said about case-building insects which use only bryophytes, even in the presence of other plant material (Glime, 1978). More subtle adaptations must have occurred in regard to feeding. As noted in Table 9.2, bryophytes have their array of secondary chemical substances, and invertebrates feeding on them would have to develop

*Table 9.2 Selected bryophyte chemicals (gleaned from Markham and Porter, 1978, and Suire, 1975) and their adverse effect on arthropods.

Chemical	Effect	Source
Oxalic acid	Repels moth caterpillars; repels a phytophagous mite	Dethier, 1947 Dubitzky and Gerson,
Lauric acid	May inhibit mite growth	unpublished
Limonene	Kills pine-feeding beetles	Rodríguez, 1972 R.H. Smith (in Levin, 1976)
Pinguisone	Inhibits feeding by a polyphagous moth caterpillar	Wada and Munakata, 1971
Sesquiterpene lactones	Inhibits feeding by moth caterpillars	Burnett <i>et al.</i> , 1974
Benzyl benzoate	Kills insects and mites	Brown, 1956

Other groups of bryophyte chemicals known to affect arthropods (Levin, 1976) include alkaloids, cinnamic acid derivatives, saponins and tannins.

mechanisms to overcome these nutritional defences. In this context, it will be repeated that bryophagous insects and mites usually feed on several, often unrelated bryophytes (Section 9.4); they do not appear to be specialists on any one moss species. This suggests that most bryophytes are protected by similar chemicals; breaching one thus means breaching all. Or else, coping with the defensive substances of one bryophyte enables the bryophages to cope with others also. The mixed-function oxidases (Bratsten *et al.*, 1977) noted in Section 9.4 may play an important role here. It is also noteworthy that some arthropods appear to feed only on bryophytes and lichens. The latter have their own rich and unique arsenal of secondary chemicals (Culbertson, 1969) which feeders would also have to overcome. One could speculate that invertebrates which live in these cryptogams have evolved the means to overcome both systems of defensive chemicals. This, however, goes against the tenet that changes in the host range of a particular feeder are most likely to occur among plant taxa sharing similar secondary substances (Feeny, 1976). More data are clearly required.

9.10.4 Invertebrates as a factor in bryophyte evolution

The presence of secondary substances of possible defensive function in bryophytes is also meaningful when seen from the other side. Their very occurrence suggests that they were evolved (or selectively favoured once synthesized) in response to invertebrate feeding pressure. Several other attributes of bryophytes may also be hypothesized to have arisen (or to have been encouraged) in answer to animal grazing. Bryophytes appear to

be deficient in such essential amino acids as methionine, tryptophan and tryptophane (Suire, 1975, Table 9.2). This could result from selection for inedibility, as postulated by Gordon (1959) for higher plants. Another conjectured protective mechanism could be the external leaf texture of several bryophytes, especially Polytrichaceae (Gerson, 1972; Ramazzotti, 1958). The role of plant surface texture in defending plants from their enemies was discussed by Levin (1976). The ability of some bryophytes to grow on and accumulate heavy metals in their tissue could well be another means of warding off feeders. Sphagnum growing in very acid surroundings may thereby be protected from herbivores. And finally, the rugose, sculptured, papillose spores of many bryophytes (Horton and Murray, 1976; Sorsa and Koponen, 1973) could protect them from attack by animals, or from the latter's alimentary system, when ingested (Kevan *et al.*, 1975). The oft-repeated observation that bryophytes are relatively free from arthropod attack attests to the success of these or other defence mechanisms, and their very presence implies that invertebrates, although by no means the only adverse factor, influenced bryophyte evolution.

9.10.5 Bryophyte-invertebrate coevolution

The last two sections strongly suggested that bryophytes affected the evolution of invertebrates, as well as the other way around. The relationship between some Splachnaceae and flies (Section 9.5.1.) provides firm evidence for actual coevolution.

The apparent antiquity of these mosses (Koponen, 1978) suggests that their mechanisms of attracting insects by odour and sight may have antedated those of the flowering plants. Another relevant question is whether the relatively rare known cases of bryophyte-invertebrate coevolution are due to the plants' slow rate of evolution (Crum, 1972) or to lack of observations. Answers to this question could be found in the tropics or subtropics, regions of continuous, year-round growth and invertebrate development.

9.10.6. Tropical considerations

Bryophytes abound in the humid tropics and additional data on the matter at hand could be sought there, but little information is actually available. Donner (1966) and Mehlen (1972) referring to rotifers and tardigrades, respectively, stated that these animals are rarer in tropical than in temperate mosses, an opinion with which Hesse *et al.* (1951) concurred. Lack of data could therefore also result from lack of some invertebrates in tropical bryophytes. On the other hand, this scarcity may reflect fewer collections. Unique associations were recorded from the tropics; the singular 'epizoid symbiosis' was already noted in Section 9.3.5. Another case is the rare fungous gnat (Diptera) which lives in and feeds on central

African bryophytes (Matile, 1972). Additional novel relationships between bryophytes and invertebrates, which could contribute to our understanding of the co-evolution between these two groups of organisms may therefore be expected to be found in the tropics. It is appropriate to recall here that evolution in the tropics operates in fundamentally different ways than in temperate regions (Dobzhansky, 1950).

9.10.7 Suggested topics for further research

This overview of what must sadly be admitted as mostly gaps in our knowledge has indicated some research areas in which additional information may have special interest.

(i) Invertebrate feeding on bryophytes, encompassing specificity to plants and to their various parts, and the occurrence of secondary chemicals in these parts. Also: effect and fate of these substances in herbivores; digestion and energetics; influence of heavy metals, pesticides and radionuclides, which had accumulated in bryophytes, on their various feeders.

(ii) The effect of urban and industrial pollution on bryophyte-invertebrate communities.

(iii) Associations in the tropics.

(iv) Dispersal of Sphacnaceae by flies.

(v) Aspects of economic entomology. A few pests, especially Diptera of medical importance, live in bryophytes. A better understanding of this specific association could lead to improved sampling and control measures.

This assay has hopped along the bryophyte-invertebrate interface, alighting here and there for specific topics but mainly skipping lacunae. One hopes that it will encourage others to look back at the thousand eyes which have been looking at us – askance – for so long.

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