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Moss-arthropod Associations[1]

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Abstract. *Mosses modify soil conditions and thereby affect the distribution of certain arthropods. Under extreme environmental conditions (such as those that prevail in Antarctica) arthropod survival and abundance often depend upon the mosses present. Several liverworts and a moss are symbiotic on New Guinean beetles, apparently conferring a degree of protection to the insects. Flies are attracted to the capsules of some Splachnaceae and disseminate their spores. Representatives of the insect orders Collembola, Diptera, Hemiptera, Hymenoptera, and Orthoptera, and the acarine orders Cryptostigmata and Prostigmata are known to feed on mosses. Bryophytes, along with other cryptogams, often constitute the initial stages in the plant succession series in newly colonized habitats, and it is postulated that their associated faunas form similar stages in the faunal succession.*

Mosses have often been studied from an ecological point of view. Among subjects of continuing interest are the role of mosses in the colonization of different land types, their succession in various habitats, and their value as indicator plants (Watson, 1964). More recently, mosses are being utilized as indicators of industrial air pollution in England (Gilbert, 1968). The associations between mosses and arthropods, on the other hand, have been largely neglected by botanical as well as zoological ecologists. The latter often ignore mosses as a habitat for arthropods. At best, this widely-occurring natural habitat is dismissed, as "it is clear that moss does not form a biotope with a stable microclimate" (Cloudsley-Thompson, 1967). The purpose of this review, which makes no pretence at total comprehensiveness is to discuss some moss-arthropod associations, and also to present a résumé of my recent work on moss-feeding mites (Acarina). A full report on this study will be published elsewhere. Gadea (1964) refers to certain other moss-associated invertebrates, such as Thecamoebae, Rotatoria, Nematoda and Tardigrada, especially in high-mountain biotopes.

Mosses may modify soil conditions and thus enable certain arthropods to survive better under extreme environmental conditions. Bryophytes may serve as food or

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shelter for these animals. Insects disseminate the spores of some mosses, and certain Bryophyta have recently been found to live symbiotically on Papuan beetles. These various interactions will be discussed separately.

The studies by Gressitt (1967), Strong (1967), and Tilbrook (1967) in Antarctica provide many data on the importance of bryophytes to arthropods under extremely low-temperature conditions where there is almost no other vegetation. Both Gressitt (1967) and Strong (1967) found that temperatures among mosses (*Polytrichum*, *Drepanocladus*) are consistently higher than the air temperatures just above them. Tilbrook (1967) concluded that, in the "maritime" Antarctic, *Polytrichum-Dicranum* mats harbor more arthropods than *Pohlia* mats, as the former are less wet and cold during summer. Thus, "it is felt that the mechanical structure of the bryophytes and the lichens is important in shaping the air spaces available for arthropods . . . The more open-textured mosses (*Polytrichum*) support arthropods to a greater depth than the more closely compact type (*Pohlia*)." (Tillbrook, 1967.) Strong (1967) concluded that mosses provide the most extensive and variable habitat types available, differing in their suitability for various arthropods, this variability being dependent on the dominant moss. The importance of the bryophytes to the animals, according to this worker, is mostly in providing shelter from the cold and wind. The dependence of Antarctic arthropods on their local moss flora was emphasized by Janetschek (1967), who defined the bryosystem as one of the dominant antarctic ecosystems. He also noted that, with the approach to climax, mosses become increasingly important, and the entire faunal spectrum of the system is to be found in the moss tufts and mats.

Nørgaard (1951) gave another example of how temperatures and humidities are modified by moss carpets and thereby affect the distribution of arthropods. Studying spider distributions in a Danish *Sphagnum* bog, he divided the moss carpet into two layers, the surface layer and the stalk layer. The microclimate of the former layer was very variable, daily temperature fluctuations exceeding 30°C, relative humidities being between 40% and 100%. In the stalk layer the relative humidity was constantly 100% and the daily temperature fluctuation only 5°C. One of the spiders studied, *Lycosa pullata* Clerck, lives on the moss surface, while the other, *Pirata piraticus* Clerck, inhabits the stalk layer. This spatial distribution is correlated with the higher temperature preference and the higher thermal death point of the former species and with the greater sensitivity of *P. piraticus* to low humidities.

The ability of mosses to provide a humid terrestrial microenvironment may have had a part in the evolution of flies (Diptera). Oldroyd (1964) believes that these insects, as a group, have arisen from ancestors whose larvae, though terrestrial, lived in wet mosses and so had "a foot in both worlds." Several species of crane flies (Tipulidae), considered to be among the most ancestral of living fly families (Oldroyd, 1964), live in and feed on mosses, including aquatic species, and assume their green color. Alexander (1920) records *Liogma* spp. living on *Rhytidiadelphus squarrosus* (Hedw.) Warnst. (called *Hypnum squarrosus* Bruch & Schimp. in Alexander's monograph), *Hypnum cupressiforme* Hedw., and related species. Another tipulid, *Triogma trisulcata* (Schum.) lives in mountain streams, where its larvae are attached to the stems of *Fontinalis antipyretica* Hedw. These larvae have various leaflike appendages arranged in rows on their bodies, which simulate the leaf arrangements of *Fontinalis*. As a result, the larvae resemble the moss on which they live to a startling degree (Alexander, 1920).

Perhaps even more archaic Diptera than the Tipulidae are the little-known, minute Nymphomyiidae. The larvae of this family, hitherto unknown, have recently been discovered and appear to be associated with moss in small rapid streams (Cutten & Kevan, in preparation). Among brachycerous Diptera, the subfamily Hemerodromiinae (Empididae) have aquatic or subaquatic larvae that live on mosses in or by fast-flowing streams (Brindle, 1964).

Larvae of other insect orders also feed on mosses. Chapman (1894) indicates that the caterpillars of the European *Eriocephala* (now *Micropteryx*) *calthella* (Fabricius) (Zeugloptera, Micropterygidae) feed on "mosses," although, according to Tillyard (1923), hepatics may be involved as the larvae of the related New Zealand genus *Sabatinca* feed on liverworts. Larvae of the primitive Australian mecopteran genus *Choristes* inhabit damp soil and appear to include mosses in their diet (Tillyard, 1926).

Collembola and hemimetabolous insects have also been reported to feed on mosses. Pryor (1962) found that a collembolan, *Isotoma klovstadi* Carpenter, fed extensively on moss. Food preference trials by Janetschek (1967) showed that another collembolan, *Gomphiocephalus hodgsoni* Carpenter, preferred moss over blue-green algae, a red lichen, and a *Penicillium* mold. Aquatic mosses are fed upon by certain may-fly naiads, such as those of the genus *Ephemerella* (Jones, 1949). The fecal pellets of the "grouse-locusts" *Acrydium vittata* Zetterstedt [now *Tetrix undulata* (Sowerby)] and *Tetrix subulata* (L.) were observed to contain remnants of *Hypnum* and other mosses (Verdcourt, 1947). The crickets *Pteronemobius palustris* (Blatchley) and *P. fasciatus* (De Geer) deposit their eggs in or on *Sphagnum* spp. (Swales, 1969; Vickery, 1969). Börner (1952) recorded several aphids from various mosses. Among them are members of the genus *Myzodium*, feeding on *Polytrichum* in Europe and North America, and *Muscaphis musci* Börner, found on *Polytrichum commune* Hedw. in Germany and Holland. Tingoid bugs of the genus *Acalypta* (which are found in mosses) were seen to feed on the capsules of *Climacium* from which the calyptra has fallen (Bailey, 1951).

Feeding on moss capsules was also recorded by Plitt (1911), who observed ants to gnaw the capsules of *Diphyscium foliosum* (Hedw.) Mohr [called *Webera sessilis* (Schmid.) Lindb. in Plitt's paper] and to remove the spores.

Various species of coprophilous flies are attracted to the capsules of the Splachnaceae, either by the secretion from special glands or by the colored apophysis (Garjeanne, 1932; Ingold, 1965). The spores of these mosses are sticky and adhere in masses to the flies' bodies and are thus disseminated. Many members of the Splachnaceae appear to be confined to growing on animal remains and droppings (Gams, 1932, and others), where such flies abound. Thus it may be postulated that this mode of spore dispersal is a complementary form of adaptation by these mosses to their particular habitat. The flies that visit these habitats not only disseminate the spores, but also transport them to other sites suitable for their subsequent development.

Several liverworts (*Lejeunea*, *Cololejeunea*, *Odontolejeunea*, *Microlejeunea*, and *Metzgeria*) and a moss (*Daltonia angustifolia* Dozy & Molk) were recently found on living curculionid beetles (weevils) in New Guinea (Gressitt, Samuelson & Vitt, 1968). The beetles—mostly of the subgenus *Symbiopholus* in the genus *Gymnopholus*—are often structurally modified to accommodate the various plants (which also include fungi, algae, and lichens) growing on them. These modifications are dorsal depressions surrounded by ridges, pubescent areas protected by tubercles, stiff scales, and modified setae. Furthermore, there is a dorsal secretion which appears to promote plant growth. Most of the plants are such as are found on nearby leaves and bark. They appear to be of survival value to the beetles, serving as camouflage or being distasteful to potential predators.

Mites (Acarina) have often been associated with mosses, and in fact one group, the Cryptostigmata (Oribatei), are commonly known as the moss-mites ("Moosmilben"). The exact relationships between the plants and the mites are, however, largely unknown, though it can be assumed that the bryophytes provide shelter as well as being a substrate for molds on which Cryptostigmata feed. Some of the latter have in fact been shown to feed on moss, and several were reared thereon (Woodring, 1963). I have observed unidentified oribateids to gnaw the capsules of various mosses and to feed upon the spores.

Mites of the genus *Ledermuelleria* (Prostigmata: Stigmaeidae), also, have often been collected in mosses in many parts of the world. A recent study (Gerson, in preparation) will show that several species of this genus feed on mosses. The mites sit on the stems and leaves of the gametophyte, pierce the tissue with their sharp cheliceral stylets, and suck out the contents of individual cells. The cell walls do not appear to be damaged. When the mites feed on a young shoot, it loses its green color, becomes silvery-gray, and may even shrivel. The mites are red, and they, their reddish eggs, and their blackish, shiny fecal droppings can often be observed in field-collected moss samples.

Transfer experiments showed that one species (to be described by me as new) of *Ledermuelleria* will feed upon and survive in many mosses. Reproduction, however occurs only while feeding on some of these, such as *Brachythecium* spp., *Hypnum* spp., *Didymodon tophaceus* (Brid.) Lisa, *Ceratodon purpureus* (Hedw.) Brid., and a few others. Polytrichales—such as *Polytrichum* spp., *Atrichum altecristatum* (Ren. & Card.) Irel., and *Pogonatum urnigerum* (Hedw.) Beauv.—did not support survival of the new species. On the other hand, species like *L. clavata* (Can. e Fan.) and *L. microsegnis* Chaudhri were found in *Polytrichum* mats, suggesting that they fed thereon. These mosses have lamellae on the upper side of their leaves and thickened cell walls on their lower surface (Parihar, 1965). Hence the inability of the new species of *Ledermuelleria* to survive on *Polytrichum*, as compared to the association of *L. clavata* and *L. microsegnis* with these mosses, may be correlated with the short (23μ) and thin (1μ) stylets of the former, and with the longer (40 and 32μ, respectively) and thicker (3–4μ) stylets of the latter.

To obtain a measure of the moss-mite association in the field, about 160 moss samples were collected from various localities, mostly in southern Quebec, Canada. Nearly half of these samples yielded mites, 13 *Ledermuelleria* species being thus obtained. Altogether, 55 moss species were collected, of which 38 harbored the mites. The most frequently sampled of these was *Ceratodon purpureus*, which was associated with *Ledermuelleria* in 15 out of 22 samples. The mite most frequently obtained from *Ceratodon* was *L. rhodomela* (Koch), which was also collected from several other colonizing mosses growing on open soil, suggesting a preference for this habitat. On the other hand, the new *Ledermuelleria* was recovered only from pleurocarpous mosses living in shady habitats, in turn indicating a different habitat preference. In this way some idea of the mites' distribution was obtained from data pertaining to the ecology of the mosses.

During January, 1969, some mosses (*Ceratodon* and *Bryum*) were dug out from beneath about five feet of snow at a previously-marked site on the Macdonald College campus, Montreal Island, Quebec, Canada. From these samples many live *Ledermuellaria* were recovered. These commenced to oviposit when transferred on to suitable mosses in the laboratory. Similar results were obtained from mites collected at snow thaw, March, 1969. The perennial nature of some mite colonies on moss mats was thus established.

The mite-associated mosses were evenly distributed between acrocarpic and pleurocarpic genera, including representatives from the orders Dicranales, Eubryales, Fissedentales, Funariales, Hypnobryales, Isobryales, Polytrichales, and Pottiales. This wide distribution among the various moss groups, and the high frequency of *Ledermuelleria* collections from mosses in other parts of the world (Wood, 1967), suggest that similar moss-*Ledermuelleria* associations also exist elsewhere.

Mosses and liverworts, together with algae and lichens, are the first plant colonizators of rocks, sand dunes, fallen logs and various other habitats, usually constituting the initial stages in the plant succession series. The remains of these plants contribute to humus formation, while the high humidity retained enables the seeds of many higher plants to germinate. At the same time, it is evident that these cryptogams support their own faunas. Thus, while the algae, lichens, liverworts, and mosses form the initial stages in the plant succession, their associated faunas form similar stages in the faunal succession.

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