THE OCCURRENCE OF RADIAL INFECTION PATTERNS IN COLONIES OF POLAR BRYOPHYTES

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ABSTRACT. Prominent rings of moribund shoots, up to 20 cm. in diameter, are described from bryophyte colonies in the maritime Antarctic and on Ellesmere Island, northern Canada, and their development is compared with that of previously reported rings in mosses on Jan Mayen.

Rings in *Drepanocladus uncinatus* on Signy Island, South Orkney Islands, developed from small aggregations of moribund shoots through radial expansion of the infected area accompanied by progressive revival at the centre. Fungal hyphae were abundant on the stems and leaves in a narrow zone coinciding with the leading edge of the rings, and intracellular penetration of stem and leaf tissue occurred. Cell contents in the upper parts of the moss plants forming the rings were largely decomposed, while inside the rings most of the original stem apices were missing. The moss in the centre of the ring systems was recovering through the production of lateral shoots.

Rings in other Antarctic mosses were similar in most respects to those in *D. uncinatus*. Occasional pairs of concentric rings in several species appeared to result from two waves of infection. The perfect stages of a previously undescribed taxon, *Thyronectria antarctica* var. *hyperantarctica*, and an undetermined species, probably a plectomycete, were each recorded on rings in several species, but the two fungi were not seen in the same ring.

FUNGAL attack on bryophytes in temperate regions is well documented and probably widespread (Nicholas, 1932; Prior, 1966). In mosses, circular patterns of infection have been described by Wilson (1951) in *Rhacomitrium canescens* (Hedw.) Brid. var. *eriodes* (Brid.) B.S.G. on Jan Mayen in the Arctic and a similar occurrence has been reported briefly from the maritime Antarctic (Longton, 1966). The purpose of this paper is to amplify the latter account, and to record the occurrence of rings in mosses on Ellesmere Island in the Canadian Arctic.

In the maritime Antarctic, rings of infection were found to occur in most areas which supported substantial bryophyte vegetation, having so far been recorded from Candlemas Island, South Sandwich Islands, in the north to Avian Island, Marguerite Bay, in the south. In general, they were most abundant in wet habitat communities of the moss-carpet subformation (Longton, 1967), being particularly frequent in vegetation dominated by species of *Brachythecium*, *Calliergon* and *Drepanocladus*. They were also widespread in cushion-forming mosses on wet rock ledges, for example in colonies formed by species of *Ceratodon* and *Dicranoweisia*, but they were less frequent in communities of the moss-turf sub-formation and other dry-ground vegetation.

The most detailed observations were made on rings in *Drepanocladus uncinatus* (Hedw.) Warnst. at Factory Cove on Signy Island, South Orkney Islands. *D. uncinatus* is widespread and often abundant throughout the maritime Antarctic forming carpets of slender, erect, sparingly branched leafy shoots which arise from a prostrate basal layer. Rings are a characteristic feature of the carpets and those at Factory Cove appeared to be typical.

RINGS IN *Drepanocladus uncinatus* AT FACTORY COVE

At the Factory Cove site the rings ranged from small aggregations of white moribund shoots less than 1 cm. wide to white rings and arcs between 2 and 15 mm. wide and up to 20 cm. in diameter (Fig. 1). In places the affected areas were so abundant that adjacent rings merged to form intricate patterns over the surface of the vegetation, as indicated in Fig. 2. The moss carpet was often brownish in colour immediately inside the ring of white shoots, but usually reverted to the normal green colour towards the centre. The relative width of the green and brown zones was variable and the latter was often absent. The surface of the carpet in the centre of the ring systems was normally depressed compared with that at the margins (Fig. 3).

The development of the rings was followed in a carpet of *D. uncinatus* situated at *c.* 20 m. altitude on a wet, west-facing slope overlooking Factory Cove, by recording the internal and external diameters, in north–south and east–west directions, for four examples from December

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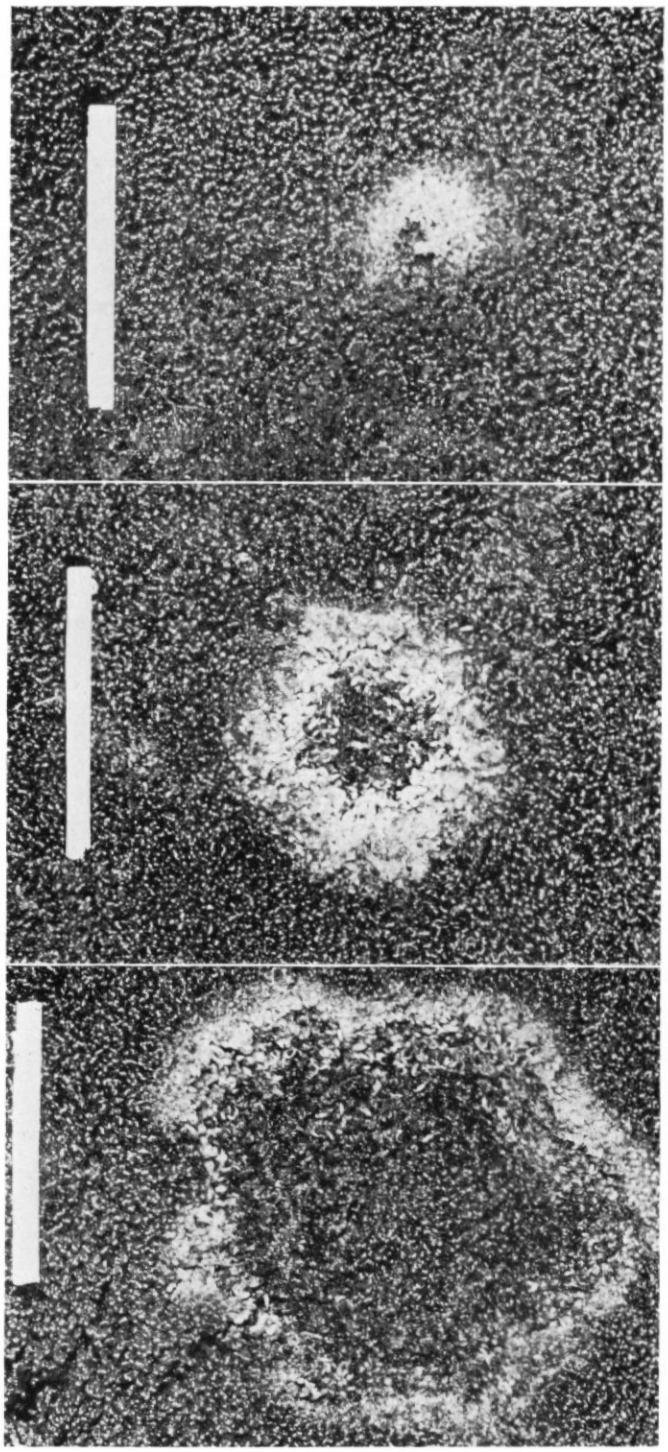

Fig. 1. Three ring systems at different stages of development from a carpet of *Drepanocladus uncinatus* at Factory Cove, Signy Island, after *c.* 15 hr. in a warm laboratory. The grey zone surrounding each ring of white shoots indicates the presence of abundant external hyphae. The scale object is 3 cm. long.

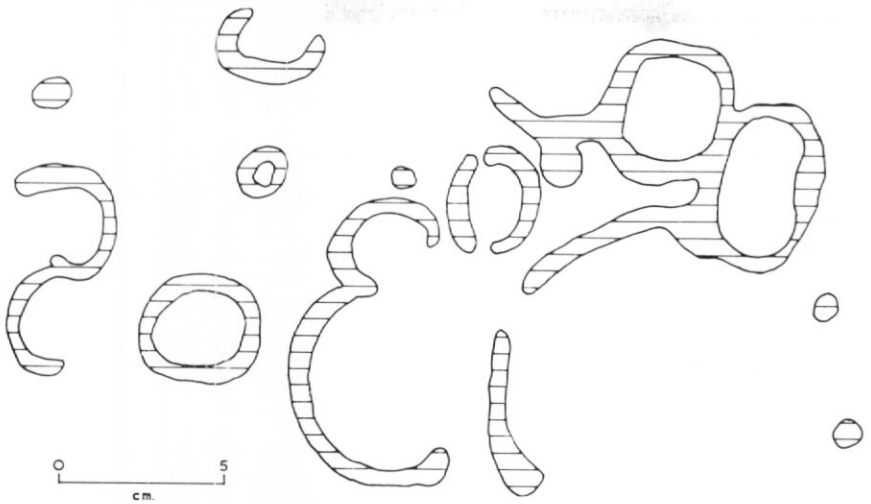

Fig. 2. Distribution of white rings (hatched) in a carpet of *Drepanocladus uncinatus* at Factory Cove, Signy Island. The brown zones present in many of the rings are not indicated.

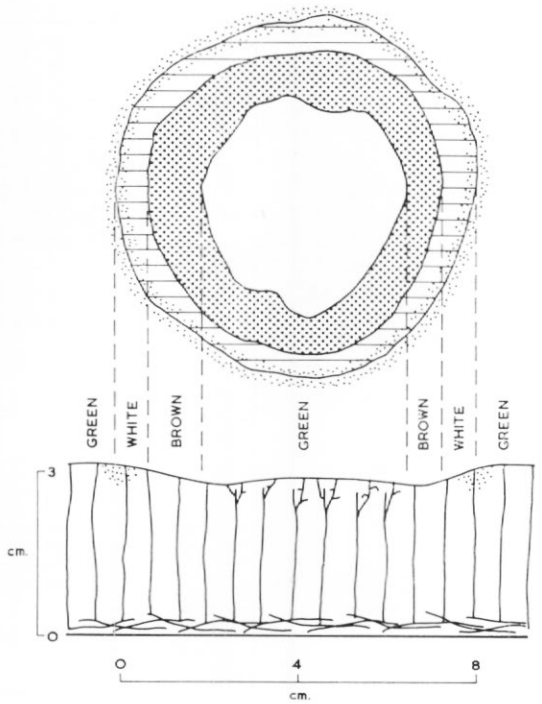

Fig. 3. Diagram of a single ring system in *Drepanocladus uncinatus* at Factory Cove, Signy Island. The distribution of abundant external hyphae is indicated by stippling.

1964 to February 1965. From the results summarized in Table I it can be seen that ring 1 expanded radially during the period of observation, and by early February its advancing

TABLE I. CHANGES IN DIAMETER OF RINGS IN *Drepanocladus uncinatus* AT FACTORY COVE, SIGNY ISLAND

Ring number	*Diameter measured*	*Length of diameter on date shown* (mm.)		
		5 December 1964	*6 January 1965*	*3 February 1965*
1	External N–S	81	90	93
	Internal N–S	70	73	75
	External E–W	84	90	—
	Internal E–W	71	72	77
2	External N–S	13	17	22
	Internal N–S	—	7	8
	External E–W	25	29	34
	Internal E–W	—	12	15
3	External N–S	12	15	18
	Internal N–S	—	—	8
	External E–W	12	12	18
	Internal E–W	—	—	7
4	External N–S	60	—	—
	Internal N–S	45	—	—
	External E–W	53	—	—
	Internal E–W	47	—	—

N–S North–south. E–W East–west.

western edge had merged with the eastern side of an adjacent ring. Examples 2 and 3 initially consisted of small aggregations of white plants with only a few scattered green shoots in the centre; in these cases radial expansion of the white areas was accompanied by the recovery of plants in the centre, as indicated in Fig. 4. In contrast, ring 4 had become very narrow and indistinct by early January, and disappeared completely by the beginning of February.

These measurements, combined with less detailed observations of other rings, indicate that rings are formed when small areas of white moribund shoots extend radially while the central region regains its green colour. Subsequently, the gradual extension of both white and green areas gives rise to rings up to 20 cm. in diamter, and adjacent rings may merge to form complex patterns such as that illustrated in Fig. 2.

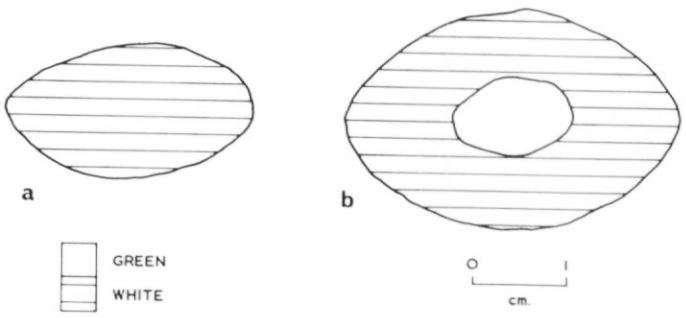

Fig. 4. Development of marked ring number 2 at Factory Cove, Signy Island.
a. 5 December 1964; b. 3 February 1965.

The recorded rates of expansion were low, however, as the increases in diameter ranged from only 6 to 12 mm. during 2 months, suggesting a maximum increase of *c.* 25 mm. during a 4 month growing season. It is, therefore, probable that the larger rings took several years to develop, unless there was activity under winter snow cover. Moreover, it is clear from the observations on ring 4 that under certain conditions the rings may disappear, and it may be noted that there was a general decrease in the frequency of rings at the study site during the period of measurement.

Distribution of hyphae

In the field, abundant fungal hyphae were noted among moss stems in a zone 5–8 mm. wide comprising the leading edge of the ring and the region immediately outside (Fig. 3). The hyphal belt could be seen with a $\times 10$ hand lens in fresh material, and became clearly visible to the naked eye when intact rings were left overnight in a warm laboratory (Fig. 1). To investigate further the distribution of the fungus in these rings, and any morphological changes in the plants of *D. uncinatus* associated with the passage of the infection, material from the carpet was examined microscopically either when fresh or after storage in lactophenol.

Infection of shoots outside a ring

It was found that hyphae were largely confined to the upper, actively growing parts of the moss plants. Thus, in the region immediately outside a ring, the bright green leaves and stems of the moss near the surface of the carpet were covered with dense wefts of hyphae, but the fungus was barely detectable among the brown or greenish brown leaves more than 5 mm. from the stem apices. The hyphae, which stained dark blue in picro-nigrosin, were found to be sparingly branched, septate and *c.* 2·0–3·7 μm. in diameter.

Many of the moss stems just outside the rings were discoloured, having a narrow region of brown cells *c.* 5 mm. from the apex, while, in addition, the apices themselves were often brown in colour. In general, the upper leaves retained their normal colour but, in some of them, the cell contents had disintegrated over restricted areas of the lamina.

Intracellular hyphae were noted in almost every cell in the damaged parts of the leaves, including those adjacent to cells with intact protoplasts. The hyphae were normally lying parallel to the long axes of the cells and showed constrictions where they passed through the cell walls. Intracellular hyphae were also noted within the stem tissue, particularly in the region immediately below the stem apex.

Infection of shoots forming a ring

The stems of almost all the shoots forming the rings had brown apices, with a white zone extending for *c.* 5 mm. below, and followed below that by a narrow brown region up to 2 mm. wide. Some stem apices had become detached at various distances above the lower brown band. Most upper leaves were white in colour and the protoplasts had almost completely disappeared, while some leaves were partially fragmented indicating a break-down of the middle lamellae. Where a shoot apex remained intact, the white length of stem between the two brown zones was sometimes profusely permeated by the fungus. In some cases, presumably representing a stage immediately prior to the fall of the apex, the stem tissue just below the terminal bud had almost completely disintegrated leaving a dense mass of hyphae. The stem tissue below the lower brown zone appeared to have escaped infection.

Large numbers of asci were noted on the shoots forming some of the rings. They were spherical, *c.* 11–15 μm. in diamter and normally contained four hyaline spores. Most of the asci were lying singly on stem and leaf surfaces near the shoot apices, but occasional small groups were enclosed within simple spherical cleistocarps. No conidia were noted. The density of both external and intracellular hyphae observed towards the inside of the rings was lower than around their outer margins, possibly due to the disintegration of the older hyphae or their failure to take up the stain.

Infection of shoots inside a ring

In the central region, surrounded by the ring of white shoots, it was found that almost all the shoot apices had fallen, exposing the brown or greenish brown leaves lower on the stem

and thus resulting in the brown zone seen inside many of the rings. In most ring systems, however, the central area was green due to regeneration of the carpet, and it was found that one or two erect-growing, lateral shoots had developed on most shoots at or just below the lower brown region. The width of the brown zone in the ring systems may thus be determined by the rate of advance of the infection together with the time interval between the fall of the white shoot apices and the development of the laterals. The lateral shoots were at first conspicuously freely branched compared with the almost simple shoots characteristic of the uninfected parts of the carpet (Fig. 5), suggesting that the flow of growth substances from the

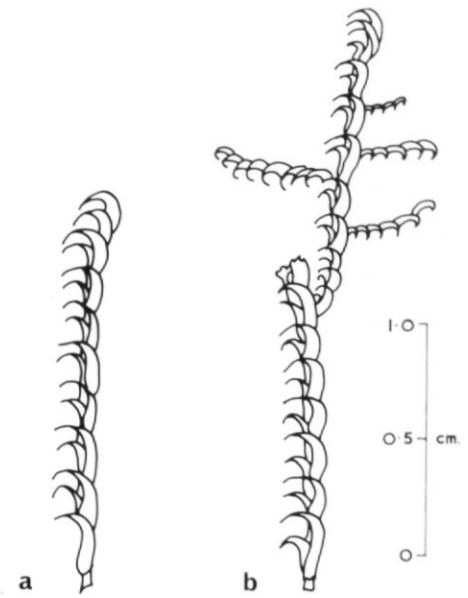

Fig. 5. Diagram of typical *Drepanocladus uncinatus* shoots at Factory Cove, Signy Island.
a. Normal shoot from uninfected carpet; b. Reviving shoot from the centre of a single ring system.

young shoot apices may be different from that in older stems. Many of the lateral shoots had small brown spots on their stems but it seems clear that most survive in view of the generally healthy appearance of the carpet within most of the larger ring systems.

Hyphae were only sparsely distributed on the moss plants forming the green and brown zones inside the rings, although young asci were sometimes present among leaves on the detached stem apices.

Rings at Other Antarctic Localities

Fungal rings were seen in *Drepanocladus uncinatus* and a variety of other mosses at several localities on Signy Island and elsewhere in the maritime Antarctic. Most of the features observed in the Factory Cove study site were noted, including the local abundance of hyphae, discoloration of the moss leaves, the presence of brown regions on the stem, death of the stem apices and regeneration by lateral shoots in the central area of the ring system. A number of minor differences were observed, for example, the rings in some species were brown not white, while in cushion-forming species they tended to be smaller than in carpet-forming species, seldom exceeding 5 cm. in diameter. Unlike the situation in *D. uncinatus*, the lateral shoots developing in the central parts of rings in the cushion-forming species were simple or sparingly branched, while occasionally, particularly in species of *Dicranoweisia*, there was no evidence of recovery.

The occurrence of pairs of concentric rings was an unusual feature in some carpets of *D. uncinatus* and other species on Signy and Avian Islands. The concentric systems were up to

20 cm. in diameter and contained three distinct zones of green shoots which differed morphologically as shown in Fig. 6. In the outermost green zone, the uninfected moss plants had the typical erect, simple or sparingly branched stems with intact apices, while in the second green zone, situated between the two white rings of infection, the original stem apices were missing but one or two lateral shoots had developed on most stems. In the third green zone, located inside the inner ring, the original stems and their first series of lateral shoots had lost their apices but a second series of green, apparently healthy laterals had arisen from the first. Both white rings had wefts of hyphae at their leading edges and this, coupled with the evidence of two phases of regeneration, suggests that the inner ring was formed from a re-infection at the central area.

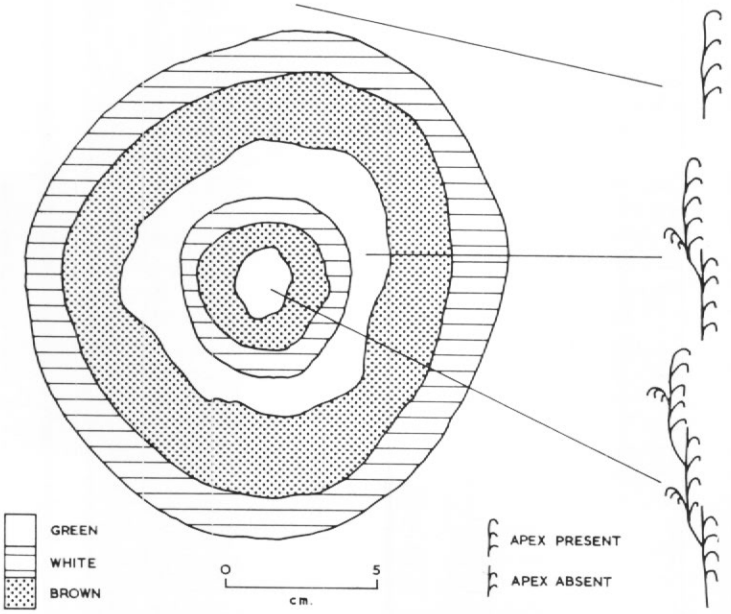

Fig. 6. Diagram of a concentric ring system in *Drepanocladus uncinatus* at North Point, Signy Island.

Outside of Factory Cove, moribund plants were not examined microscopically for penetration by the fungus but spherical asci resembling those at the Factory Cove site were recorded on rings in *D. uncinatus* from other parts of Signy Island and from Deception Island. On Signy Island they were also seen in mixed carpets where moribund plants of *D. uncinatus* and species of *Brachythecium* and *Calliergon* contributed to a single ring. In contrast, small pink perithecia were recorded in a narrow zone among the mosses around the inner margins of rings in a species of *Brachythecium* on Galindez and Petermann Islands. Similar perithecia were associated with concentric pairs of rings in *D. uncinatus* on Avian Island and in a species of *Bryum* on Signy Island. Perithecial material from Signy and Galindez Islands has been determined as a previously undescribed taxon, *Thyronectria antarctica* (Speg.) Seeler var. *hyperantarctica* Hawksw. (Hawksworth, 1973), while the fungus at Factory Cove is probably a plectomycete but has not been positively identified.

Ring Systems at Arctic Sites

At an Arctic site on Ellesmere Island single ring systems up to 10 cm. in diameter were locally common during July 1967 in deep spongy cushions of *Bryum cryophyllum* Mårt. growing in shallow mountain streams at an altitude of 700 m. on the northern slopes of Mount McGill. Septate hyphae of an unidentified fungus, which lacked clamp connections and reproductive bodies, were abundant in a narrow zone around the outer margin of each ring,

but in contrast to the position in the Antarctic systems, the greatest concentration of hyphae was at distances of 5–10 mm. below the stem apices. Above this level the plants within a ring had brown stems bearing white or yellowish leaves in which most protoplasts had disintegrated. The apices were dead but commonly remained intact, even when lateral shoots bearing healthy, dark red leaves were formed on the main axis below the level formerly enveloped by hyphae. Some cells in the apical leaves contained bodies resembling resting spores of species of the Plasmodiophorales but as similar structures were noted in uninfected colonies of *Bryum cryophyllum* it seems unlikely that they were the direct cause of ring symptoms.

Finally, it may be noted that in June 1969 single ring systems were recorded in colonies of *Tortula ruralis* (Hedw.) Gaertn. at Alert on the north-east coast of Ellesmere Island (personal communication from G. R. Brassard).

Discussion

It has been established that the prominent rings of white moribund shoots characteristic of *Drepanocladus uncinatus* carpets in the maritime Antarctic are associated with a radially spreading fungal infection combined with the progressive recovery of the plants. The sequence of events appears to be that once infection is established in a carpet, hyphae spread outwards by forming dense wefts on the surface of actively growing apical parts of the moss plants where they penetrate the stem and leaf tissues of virtually every shoot. At about the same time a brown discoloration develops locally on the stems and the leaf protoplasts begin to disintegrate. Later, almost complete break-down of the protoplasts results in the upper parts of the infected plants turning white in colour, but the lower brown stem region appears to act as necrotic tissue preventing the infection spreading down a shoot. Asci may develop at this stage among the upper leaves and the hyphae disintegrate, while the apices of the infected shoots die and become detached. Meanwhile the fungus continues to spread outwards, while shoots in the centre of the original area of attack regenerate by the production of laterals, these two processes resulting in the circular patterns. Rings in other Antarctic mosses appear to develop in a comparable manner.

Frequent re-infection of the recovering plants by spores or hyphae persisting in the central area might be expected, but evidence of re-infection was seen only in the rather rare cases of colonies with pairs of concentric rings. Thus, in the absence of experimental evidence, the possibility of the fungus causing a secondary infection following initial damage by other, less conspicuous agencies should not be overlooked. At least two fungi, *Thyronectria antarctica* var. *hyperantarctica* and an unidentified species, probably a plectomycete, were present on different rings but it appears that neither is entirely host specific.

All the bryophyte ring systems so far described have in common the presence of abundant hyphae around their margins, but the development of the Antarctic rings differs in several important respects from those on Jan Mayen studied by Wilson (1951). On Jan Mayen, multiple systems comprising up to 12 concentric annual rings of dead moss as much as 2 m. in diameter were formed, and they were associated with a fungus which spread radially throughout the growing season but only caused severe damage to the moss in the autumn, when the attack was lethal. Except in species of *Dicranoweisia*, the Antarctic mosses were not killed, and where concentric rings occurred they appeared to be due to re-infections, rather than a seasonal effect of a single infection. Moreover, the Antarctic rings were associated with ascomycetes, whereas those on Jan Mayen were apparently caused by a basidiomycete. It is interesting to note that the rings in *Bryum cryophyllum* on Ellesmere Island resembled more closely those in Antarctic mosses than the examples from Jan Mayen.

Wilson (1951) indicated that fungal ring systems may be widespread in Arctic mosses, a view supported by the present records from Ellesmere Island. This, combined with their frequent occurrence in the maritime Antarctic and the absence of published records from elsewhere, suggests that radial patterns of infection in bryophyte colonies may be a characteristically polar phenomenon. They appear not to be restricted to high latitudes, however, as similar patterns have been casually observed in mosses in the Great Smoky Mountains of the United States of America, and in Alberta, Canada (personal communication from A. J. Sharp). Further observations are required to establish fully their distribution pattern and their relationship to the well-known fungal induced "fairy rings" of temperate grasslands.

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