ON THE PROBLEM OF SUBARCTIC BASIDIOLICHENS I.

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During the last ten years the problem of basidiolichens has been notably widened, mainly due to the investigations of GEITLER (1955, 1956), POELT (1958, 1962, POELT and OBERWINKLER 1964), and GAMS (1962). Thus, besides the tropical *Thelephorolichenes* two other groups of basidiolichens are discussed viz. the *Clavariolichenes* and the *Agaricolichenes*, the members of which have an wide extratropical distribution. In addition to these, some fungi belonging to the *Corticiaceae* may also be lichen components (POELT and OBERWINKLER 1964, p. 399).

While the actual nature of these relationships between algae and the Basidiomycetes is for the present unsettled, it cannot yet be decided whether a parallel might be drawn between the Basidiolichenes and the Ascolichenes. The present situation in the study of the Basidiolichenes resembles that which existed in the investigation of the Ascolichenes before their double nature was finally proved by a synthesis. Until then there was at least a theoretic possibility to take a doubting attitude, as the Finnish botanist Elfving did. In addition to synthesis, other approaches such as statistical ecological probability and anatomical evidence can be employed in seeking the final solution. In this investigation we use the concepts Basidiolichenes, Agaricolichenes etc. knowing well the possible inexactness included in such terms. If this symbiotic relationship of an alga and a fungus — already statistically shown — will be found to differ so much from the old concept of a lichen that it is better to give a new name to it, the terms used here will only serve to present evidence of research history.

In Finland, attention has been paid to these subjects for some time (GAMS 1962, p. 377), but virtually nothing has been published except mention of the relation between certain *Omphalinas* and the «hemilichen« *Botrydina vulgaris* and *Coriscium viride* by KALLIO and KANKAINEN (1964, p. 198—9). Therefore, more extensive information is obviously needed. During the last two years this problem has attracted our notice; we have made observations and collected material principally in the northernmost part of Finland (Inari Lapland) and the adjacent Norwegian Finnmark. Some preliminary work in the laboratory has also been done.

I. FIELD OBSERVATIONS

1. Agaricolichenes

Among agarics only the genus *Omphalina* has been taken as a component of *Basidiolichenes*; a case of *Russula* has been discussed, too, but in this instance there was obviously only a casual occurrence of algae involved (GEITLER 1955, p. 145). Several *Omphalina* species have been supposed living in symbiosis with green algae of the genus *Coccomyxa* and forming two different kinds of double organisms: the homeomerous *Botrydina vulgaris* and the heteromerous *Coriscium viride* (GAMS 1962, p. 379).

A. Botrydina vulgaris Bréb.

History. The name Botrydina vulgaris was given by Brébisson (1839, p. 3), who placed it in Nostocales.

Though he regarded it as a green alga, his view of its structure was quite near to the present one, as appears in his description: «Fronde globuleuse, gélatineuse, formée de cellules alvéolées, remplies de granules formant plus tard, en devenant libres, de nouvelles frondes. Les globules muqueux ou plutôt gélatineux de cette plante, composés de cellules soudées et rapprochées en forme d'alvéoles remplies de granules verts reproducteurs, rappellent très-bien la forme et la disposition des globules polliniques ou *spermatocystes* des *Chara* vus dans leur état de jeunesse. Leur consistance est beaucoup plus ferme que celle des groupes d'Anacystis. ---«

Since the year 1909, when Acton's study was published, *Botrydina* has been regarded as a kind of double organism. — As a result of her investigation, Acton (1909 b, p. 583), a student of the famous G. S. West, stated: *«It (Botrydina) consists of an alga and a fungus growing symbiotically, and is therefore a lichen.* It is certainly a primitive type of lichen; yet the union at an early stage of several smaller thalli shows a tendency towards the formation of a large thallus, though the diameter never exceeds 500 μ . It differs from the soredial stage of a typical lichen in the complete absence of any trace of hyphae in many adult specimens, and in the cellular nature of the envelope. ---«. The alga was identified as *Coccomyxa subellipsoidea* Acton.

Another theory was presented by JAAG (1933 a), whose opinion was that, at least in the specimens he had studied (from the Alps of Switzerland and Austria), the colourless envelope was formed by a moss protonema. He thought that the colourless protonemal branches of the moss *Georgia (Tetraphis) pellucida* (L.) were living as parasites on *Coccomyxa*-algae.

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GEITLER (1956 b) refuted JAAG's arguments giving proof that there were distinct differencies in the cells between the *Georgia* protonema and the colourless *Botrydina* component. In addition he remarked that *Botrydina* lives abundantly also in localities where *Georgia* is not found. He regarded the contested component as a fungus and thus confirmed ACTON's lichen theory.

GAMS (1962) was the first investigator to assign *Botrydina* to the *Basidio-lichenes*. He drew attention to the fact that *Botrydina* is always found with certain *Omphalinas* and concluded that specifically these fungi make up the lichen together with *Coccomyxa*-algae. In the collective species *Botrydina vulgaris* he also included the double organisms formed by certain fungi of the *Clavariaceae* (*Lentaria mucida* and *Clavulinopsis*) and *Coccomyxa*-like green algae.

Distribution. Though several versions have been given of the nature of Botrydina, its identification has not caused any difficulties, and investigators have been unanimous as to its morphology. Acton's material was «growing indiscriminately amongst a moss and an hepatic, covering the shoots with a layer of dark green globular structures just visible to the naked eye.« (1909 b, p. 580). Similarly JAAG'S (1933 a), specimens were mostly found in moss tufts. According to him Botrydina seems to favour mountain regions and prefers a relatively high moisture of the surroundings. He presumed that it is spread all over the world at least in the temperate zones. ACTON (1909 b, p. 585) reported it as «not uncommon in the mountainous districts of the British Islands«. In the list of POELT and OBERWINKLER (1964, p. 400) there are localities for Omphalina-Botrydina in Sweden, Germany (Silesia, Bavaria), Austria, Czechoslovakia, Italy and Nepal. In 1963 the author Kallio collected Omphalina ericetorum and Botrydina at Northwest River, Newfoundland, Canada.

In Finland, *Botrydina* was first reported by Hävrén (1944, 1945 a, b) from Uusimaa, in the communes of Tuusula and Espoo.

According to our own observations, *Botrydina* generally grows so abundantly around the fruit-bodies of *Omphalina* that the green mass is easily visible to the naked eye; especially on rotten wood and often also on the earth it covers an area of several square centimetres. It often lives on leaves and stalks of mosses, at the base of the fruit-bodies and sometimes even on the foot. On *Sphagnum* it often occurs more sparsely, and the single globules seem to be somewhat smaller, too. The structure of the *Botrydina* specimens we have studied corresponds in all details with the descriptions given by the previous authors (ACTON 1909 b, JAAG 1933, GEITLER 1933 and 1956 b, POELT and OBERWINKLER 1964). Fig. 1.

Some «raw cultures« were made by setting whole *Botrydina* globules in Petri dishes and test tubes containing MS- (WARIS 1953), Kari- (KARI 1936, p. 12), and Hagem agar. Most of them were badly infected by molds and bacteria, but it could be seen, however, that the alga multiplied quite rapidly and soon formed colonies of its own, while no expansion of the fungus could be noticed. In only

one case was there some tendency of the components to keep together. The algae grew on the agar as an elevated mass, under which the fungus formed a sclerotium, and this had not spread farther than in the immediate vicinity of the algae.



Fig. 1. Two Botrydina globules of different ages (SW-Finland, Yläne). The Coccomyxaalgae appear as dark spots within the colourless cellular envelope formed by the fungus. A bit of the hypha is visible under the small globule. (Magnification about 500 x).

In another test, *Botrydina* globules were set on sterile strips of filter paper, and these were placed by means of wadding in test tubes so that one end of the strip reached the MS-solution on the bottom, while the globule was on the higher part above the solution. These cultures, too, were soon occupied by algae and most of them were likewise infected. Taken with its substrate, *Botrydina* thrives well in the «culture rooms« of the Institute, particularly in those with a temperature about 5°C.

Fungal component. GAMS (1962, p. 377–8) regards Omphalina umbellifera (L. ex Fr.) Quél. (= O. ericetorum (Pers.) M. Lange) as the most important Botrydina-forming agaric, but mentions that also other species of Omphalina seem to form it, especially O. fibula (Bull. ex Fr.) Quél. POELT and OBER-WINKLER (1964, p. 399) call the Botrydina-fungus in their material «Omphalina pseudoandrosacea (Bull. ex Fr.)«. According to our observations, O. ericetorum in our research area is al w a y s a Botrydina component. The same opinion we have about O. luteovitellina Pilát & Nannf. In our only find of O. velutina (Quél.) Quél. this fungus was also associated with Botrydina.

Omphalina ericetorum (Pers.) M. Lange [=O. umbellifera (L) Quél.] Plate 1. According to M. LANGE (1955, p. 25) the species is «exceedingly common in arcto-alpine areas«. In Finland, too, it is found very frequently; already KARSTEN (1889, p. 94) stated that it occurs from Uusimaa to northernmost Lapland, growing on peat soil and rotten wood. According to STENLID (1947, p. 84) it occurs very frequently already in spring and early summer and is quite a «character plant« in many places in the outermost archipelago southwest of Finland. He presumes that O. ericetorum is one of the agarics which extend

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furthest out in the outermost barren isles, and he finds this fact especially interesting, because the same species is one of the fungi that grow highest up on the fjelds. The authors have collected specimens in SW-Finland (Åland/Ahvenanmaa: Eckerö and Geta; Rymättylä, Yläne, Tampere); and in the herbarium of Turku University there are collections from the southwestern (Korppoo, Kemiö, Lappi) and middle part (Toivakka) of Finland.

In Inari Lapland observations made during several years have shown that the species is very common and abundant, both in the communes of Inari and Utsjoki as well as in the north adjacent Norwegian Finnmark (cf. KALLIO & KANKAINEN 1964, p. 198 and 1966, unpubl.). Its fruit-bodies are often found already in June, but are most frequent in July and August. They occur on rotten wood, on mosses in woods and on rocks, on pathsides, and in bogs, both in moist places on *Sphagnum* and on drier hummocks (also on «palsas«).

O. ericetorum varies greatly in appearance as regards its form, size and colour. The cap (about 0.7 — even 3 cm in diam.) may have an attractive umbrella-like form, may be distinctly infundibuliform, or may be intermediate between these; the gills are very deeply to moderately decurrent; the stem is slender and tall or (more unusually) rather short and sturdy; and the colour of the fungus may vary from brownish-yellow to whitish, generally having a darker tinge at the top of the stem. NANNFELDT described the same thing in Swedish Lapland (PILÁT and NANNF. 1954, p. 22): «It is very variable as to shape and colour, while microscopical features are stable. The variability is to large extent due to environmental conditions.« The environmental factors surely cause a great deal of this variability, but the matter seems to be quite complicated, because no distinct connection between the different types and habitats could be established. Spores were measured from four dried specimens collected in different localities, and their mean values (of 100 spores) varied between $5.8-6.5 \mu$ in length and $4.3-4.5 \mu$ in breadth (Fig. 3a.).

In view of the wide variation of our material, we find it unnecessary, like NANNFELDT (PILAT and NANNFELDT 1954, p. 22) and M. LANGE (1955, p. 25), to try to separate *O. pseudoandrosacea* and *O. ericetorum*, as Möller (1945, p. 259—260) did. Poelt and OBERWINKLER (1964, p. 399) call the *Botrydina* fungus *O. pseudoandrosacea*, describing two types of it: the typical 2-spored type occurring in bogs and in higher habitats, and the mostly 4-spored one, generally in lower habitats. The latter seems to us to be rather like a typical *O. ericetorum*.

Quite apart from the habitat, variety or form of *O. ericetorum*, careful observations made during the two last summers on several hundred specimens have shown that *Botrydina* always grows together with its fruit-bodies. Older herbarium samples in the Botanical Museums of the Universities of Helsinki (H) and Turku (TUR) also showed this connection.

 $Omphalina \ luteovitellina \ Pilát & Nannf. [= O. flava (Cooke) Möller.]$

Utsjoki: Ailigas 10.8.-64, Tshuomasvaara (alpine region) 13.8.-63, Tsharsjoki 17.9.-63, Puksalskaidi 2.8.-62, 5.8.-62, Kotkapahta 18.8.-62, 27.7.-65, Kenespahta 10.8.-63, east of Piikkijärvi 24.8.-65. — Inari: Kätkipassitunturi 17.7.-65, west of Laurivaara 29.7.-65, Pystykurkkio 30.7.-65, shore of Stuorraboggijärvi 1.8.-65. — Finnmark: north shore of Pulmankijärvi 22.7.-65. All are in the subalpine region.

In the Scandinavian literature BLYTT (1905, p. 41) made reference to a yellow Omphalina — he called it O. umbellifera var. flava (Cooke) —, which is found higher up on the fjelds than O. ericetorum proper. LANGE (1946, p. 166) reported a similar fungus from the Abisko district. Later, PILAT and NANNFELDT (1954, p. 22) described a new yellow species from Swedish Lapland, O. luteovitellina: «Species pulchra, O. ericetorum similis, sed colore laete vitellino, lamellis angustioribus, margine pilei diu involuto sporisque angustioribus discrepans. [P]« (p. 24). Concerning its distribution, they wrote: «--- probably common in the reg. alp. throughout the whole of the Scandes, though its fruit-bodies are very scattered in occurrence.« They assumed that the statements of BLYTT (1905) and M. LANGE (1946) might in part refer to this species. MöLLER'S (1945, p. 260) O. flava they regarded as a synonym, but changed the name because of nomenclatural reasons. KÜHNER and ROMAGNESI (1953, p. 123) and FAVRE (1955, p. 43) reported O. flava Cooke, ss. Möller from the Alpine district. LANGE (1955, p. 25 and 1957, p. 63) has found the species in Greenland.

In Finland, the species has been reported by KALLIO and KANKAINEN (1964, p. 198), but because of nomenclatural confusion many of the collections given as O. luteovitellina do not represent this fungus but rather O. luteolilacina. We have usually found the small bright yellow Omphalinas growing on mosses on vertical rocky walls. They are often single in occurrence or in groups of two or three fruit-bodies. They look somewhat hygrophoroid; the whole fungus is glossy bright yellow, the cap (about 1 cm) may be somewhat irregular in shape, the gills distant, thick and rather deeply decurrent, the stem quite short and often curved, often minutely pubescent, ending at the base in a white mycelium. Those specimens correspond best with FAVRE's (1955, p. 43-44) description. Sometimes we have found in subarctic bogs a bright yellow Omphalina with a somewhat longer and straight stem and an attractive regular cap. The spores (of one dried specimen from Utsjoki, east of Piikkijärvi) measured $7.6 \pm 0.7 \times 3.7 \pm 0.5 \mu$, and are thus relatively narrower than the spores of O. ericetorum. This agrees with the description of O. luteovitellina by PILAT and NANNFELDT (1954). Our specimens of this type correspond fully to the holotypus of O. luteovitellina Pilát & Nannfeldt from Katterjåkk, Torne Lappmark in the Herbarium of Uppsala University. Professor Nannfeldt has seen a photograph of this type and regarded it as a typical O. luteovitellina (cf. Plate 1.)

Around the fruit-bodies of this species we have always obtained an abundant green mass of *Botrydina*.

Omphalina velutina Quél. [= O. grisella (Weinm.) Karst.]

Utsjoki: birch grove at the mouth of Tsharsjoki 16.8.-65.

During an excursion of the Kevo mycological symposium in summer 1965, two specimens of a beige-coloured small *Omphalina* were found which resembled very much a delicate *O. ericetorum*. The distant gills were somewhat lighter than the cap and the stem, the latter was pubescent with white hairs. The basids proved to be two-spored. Dr. D. M. Henderson (Edinburgh) kindly examined and named the species. — The fungus was growing on decayed wood and was accompanied by abundant *Botrydina*.

This species was reported twice by KARSTEN, first (1879, p. 133) as a variety (var. grisella Weinm.) of O. ericetorum from Russia, Finland and Scandinavia; later (1889 Tillägg I, 194) as an independent species, (O. grisella). Von SCHULMANN (1960, p. 17) encountered it in Tuorila (by Karkkila), Tammisaari, and Åland.

J. LANGE (1936, p. 59) has described O. grisella in Denmark, KÜHNER and ROMAGNESI (1953, p. 127) and FAVRE (1955, p. 44) in the Alpine district, REID and AUSTWICK (1963, p. 289) in Scotland. According to CEJP (1936, p. 27) it has also been found in Germany, Austria, Czechoslovakia, France, Italy, and Great Britain.

According to our observations, the other Omphalinas found in Lapland are not — at least not constantly — Botrydina-components. O. luteolilacina (Favre) Henderson is associated with Coriscium viride. No algae have been noticed in connection with the fruit-bodies of O. viridis (Fl. Dl.) Lange, O. pyxidata (Bull.) Quél, and O. rustica (Fr.) Quél., species which have been thoroughly studied. In association with O. sphagnicola (Berk.) Karst. Botrydina was once found in a South Finnish collection (from Yläne), but never in Lapland. A small grayish-brown Omphalina species, resembling O. camptophylla (Berk.) Sacc. (see KALLIO and KANKAINEN 1964, p. 199), grows on the thallus of Blasia pusilla and does not belong to the Botrydina-formers.¹ According to GAMS (1962, p. 377) Gerronema fibula (Bull.) Sing. [= Omphalia fibula (Bull.) Fr.] is a Botrydinacomponent; we have sometimes observed algae around it, but only once Botrydina. Furthermore, in this case Clavulinopsis septentrionalis grew nearby, and the Botrydina obviously belonged to it. Gerronema setipes (Fr.) Sing. [= Omphalia Swartzii (Fr.) Quel.] is not found to be a lichen component.

Hygrophorus violeipes M. Lange 1955.

Utsjoki: Erdigvaara, alpine region 1.9.-60, Kevonniemi 21.8.-64, mouth of Kevojoki 26.8.-64, bog along the shore of Vetsikkojärvi 15.8.-64, between Voddijärvi and Piikkijärvi 24.8.-65, northwest of Tuöldivaldimroavvi 25.8.-65, near by Kuktsjoki fall 25. 8. -65. — Inari: Petsikko «palsa« bog 16. 8. -64. — Finnmark: Rastegaissa, subalpine region 24. 8. -64.

During several years we have found this fungus in Lapland, and its characteristics agree in all details with those described by M. LANGE (1955, p. 18—19) in material from Greenland. Later (1957, p. 63), however, he changed the name to H. lilacinus (Laest.) M. Lange and gave as synonyms Agaricus lilacinus Laestadius and Omphalina luteolilacina Favre. It is very difficult to decide whether the concise footnote of LAESTADIUS (1860, p. 45) really means this fungus; there is actually nothing against it. INGELSTRÖM (1940, p. 155) reports Omphalia lilacina Laest. from Abisko (not rare). NANNFELDT (PILAT and NANNF. 1954, p. 22) mentions that he has never seen A. lilacinus Laest. in nature, but he assumes that it is one of the «genetically based colour races« of O. ericetorum. All the museum samples of O. lilacina studied by him proved to be similar to O. ericetorum in their microscopical features. Because H. violeipes microscopically differs distinctly from O. ericetorum (e.g. having clamp connections), these collections could not represent the latter.

FAVRE'S (1955, p. 45) Omphalina luteolilacina and Hygrophorus violeipes M. Lange in our opinion are quite separate fungi (the former has no gelatinous cap surface, its stem is distinctly pubescent, it has no clamp connections, etc.). Because of this confusion we prefer using here the original name H. violeipes, even though the author subsequently changed it.

KALLIO and KANKAINEN (1964, p. 199) have reported the species in Finland, but on account of these nomenclatural misunderstandings it was listed as *Omphalina luteolilacina* Favre. In the same paper there is the statement: «Also this species is a component of 'hemilichenes'.« This opinion was based on a single find where *Botrydina* was growing around the fruit-body; later it has not been observed. It is thus quite questionable whether *H. violeïpes* might be a facultative lichen component or whether this *Botrydina* was by mere chance growing nearby and had another fungal component.

Cultures. We have made a great many attempts to obtain a pure culture of Lapponian Omphalinas, especially the lichenised ones, but we have not succeeded, neither in starting with spores nor in planting sterile pieces of fruitbodies (from the middle of the point where the stem joins the cap). Dr. V. Hintikka (Helsinki) kindly supplied us with a culture of a South Finnish O. ericetorum (from Loppi). It originated from a piece of a fruit-body of this species obtained under sterile conditions, but nevertheless it is quite possible that the growing mycelium could represent some other organism. Formation of fruitbodies seemed to us the only way to obtain certain identification, but all the experiments attempted for that purpose were unsuccesful (cultivation in different constant and rhythmic light and temperature conditions; in different agar mediums - Hagem, Kari, MS - and on sterilised rotten wood pieces; alone and together with Coccomyxa-algae of Botrydina). In the living Botrydina and Coriscium tufts in the culture rooms $(+5^{\circ} \text{ and } +17^{\circ})$ fruit-bodies, however, appeared several times, and they were easily recognizable as Omphalina ericetorum (on Botrydina) and O. luteolilacina (on Coriscium), though the caps were not completely developed. Thus the light and temperature conditions were not unfavourable.

¹ In many respects it agrees with M. LANGE'S (1955, p. 23) description of *Omphalina* demissella. (cf. Plate 1).



Fig. 2. Ring structures in a MS-agar culture (at $+17^{\circ}$ C) of a fungus which was probably (although not finally proved to be) Omphalina ericetorum. Fig. 3. Spores of a) Omphalina ericetorum (Utsjoki, Kevonniemi) with average measurements (100 spores) $9.2\pm1.1\times5.5\pm0.6\,\mu$ b) Omphalina luteolilacina (Utsjoki, east shore of Kevojärvi), measuring $7.7\pm0.5\times$ $4.5\pm0.5\,\mu$. (Fresh material.)

The cultivated fungus has submersed, branched, septate hyphae without clamp connections, measuring usually 2—5 μ , but its most striking character is the inclination to form curious, often quite complicated ring-structures in cultures (Fig. 2.) The simplest resemble those of the *Botrydina* fungus described and illustrated by ACTON (1909 b, p. 584). According to her they «suggested the first coil of a spiral conidium«, and because of them she placed the fungus in *Helicosporae* of *Mucedinaceae*.

In the cultures where the fungus was growing together with *Botrydina* algae, no *Botrydina*-formation could be observed, nor was there any clear relation between them: they seemed to grow quite independently of each other.

Algal component. The algal component of Botrydina belongs to the genus Coccomyxa; all investigators since ACTON (1909b) have been unanimous about this. The genus was established by SCHMIDLE (1901) and later investigated more thoroughly especially by CHODAT (1913) and JAAG (1933 b). In JAAG's monograph are described more than thirty species, some of them free-living (fresh water, marine, or aerial), others epiphytic on lichens or endophytic within lichens, and one species a parasite of echinoderms (C. ophiurae). Concerning the position of the genus within Chlorophyta, several opinions have been presented. ACTON (1909 a, p. 575) placed her Coccomyxa in Palmellaceae (likewise FRITSCH 1935, p. 137), while OLTMANNS (1922, p. 268) referred the genus to Scenedesmaceae and PRINTZ (1927, p. 104) to Pleurococcaceae. In the newer literature its family is named Coccomyxaceae; SMITH (1950, p. 132) placed it in Tetrasporales, LEWIN (1962, p. 833) in Chlorosphaerales.

The diagnosis of the genus, modified by CHODAT (1913, p. 224) from that of SCHMIDLE (1901, p. 23) reads: «Cellulae baculiformes vel anguste ellipsoidae libere natantes, vel gelatina aggregatae, divisione contentus cellulae matricalis

transversa dein obliqua multiplicatae. Sporae demum elongatae cellulae matricali similes i.e. autosporae binae vel quatuor.«

ACTON who was the first to describe the *Botrydina* alga (1909 b, p. 582), stated as follws: «These proved to be a unicellular green alga. The cells were usually elliptical in form, about 6—8 μ in length by 3—4 μ in breadth, though many of them were flattened and angular and others curiously twisted. The chloroplast was parietal, but did not extend over the whole cell, one side of the cell being colourless. There was a single pyrenoid in the centre of the chloroplast. --- The alga multiplied by oblique fission, freshly liberated cells often showing this condition. ---« She identified the alga with *Coccomyxa subellipsoidea*, which name she had given (1909 a) to a free-living alga that forms slimy, dark-green stratum on damp rocks and stones in subaerial habitats. She stated that it forms zoogonidia, and this fact together with the presence of a pyrenoid, aroused the suspicion that there were two organisms confused. E.g. WILLE (1910, p. 301), CHODAT (1913, p. 244, footnote) and JAAG (1933 a, p. 174) assumed that these characters belong to *Chlamydomonas*, which was mixed in the *Coccomyxa* material.

JAAG (1933 a, p. 180) made a new description of the species — without the pyrenoid and zoospores — (Coccomyxa subellipsoidea Acton ss. Jaag), and in addition he described another Botrydina alga, C. Pringsheimii (botrydinae) Jaag, which is more variable, generally smaller and often shows four-celled fission stages in culture. For C. subellipsoidea, JAAG (1933 b, p. 129) gave the average length: $7.2\pm0.65 \mu$ and the ratio breadth: length = 1: 1.8 ± 0.25 . This material was from the Swiss Alps and Austria (Innsbruck) and the collections of C. Pringsheimii were from Finland (cf. JAAG 1933 b, p. 116; as a more exact indication of the locality the name «Skuja« is given, but this must be based on some misunderstanding).

HÄYRÉN (1944, p. 5 and 1945 b, p. 47) named the algal component of his Botrydina finds (Tuusula, Espoo) C. subellipsoidea.

The algae in our *Botrydina* material are principally broadly ellipsoidal with average measurements in situ (200 cells) length $7.5 \pm 0.7 \mu$, breadth $3.8 \pm 0.4 \mu$, and ratio breadth: length = 1: 2.0 ± 0.02 . These numbers agree quite well with JAAG's measurements of *C. subellipsoidea*. In cultures, however, our alga corresponds better with the description and figures of *C. Pringsheimii* as regards the shape of the cells, but four-cell stages were only rarely observed.

These phycobionts of *Botrydina* are easily cultivated in several mediums, both in solution as well as on agar. We have mainly used the mineral MS-agar and the agar of Kari containing glucose (2 %) and asparagine (0.5 %). In these cultures the alga formed glossy dark green, round colonies with a very narrow yellow-green margin. Viewed from the side, they look shallowly conical with a small top in the centre. JAAG (1933 a, p. 178; b, p. 118) mentioned that the top

point of the colonies on glucose agar (1/3 Knop + 2% glucose, 1933 a, p. 8-9) always turned gradually apple green, while the edge remained dark green; this phenomenon could not be observed in our Kari-agar cultures.

The shape and size of the cells vary widely also in culture, but in spite of this great individual variation, the influence of sugar in the medium could be seen. As JAAG (1933 a, p. 180; b, p. 119) has shown, the cells in a glucose-containing medium are on the average more slender and longer than in a medium without sugar; in our cultures, however, they were not so slender as C. subellipsoidea in JAAG's glucose agar cultures. The growth was also somewhat faster in our cultures.

As for the influence of temperature, we cultured the algae at $+5^{\circ}$, $+9^{\circ}$, $+17^{\circ}$ and $+21^{\circ}$ C. The intermediate temperatures seemed to be most suitable. At $+5^{\circ}$ the growth was very slow, while at the highest temperature it was most rapid but a great many of the cells were abnormal in shape and size. JAAG (1933 a, p. 182; b, p. 121) regarded temperatures of 6—15°C as optimum.

B. Coriscium viride (Ach.) Vain.

History. In the year 1890 WAINIO (p. 188, footnote) established the genus for this species, which had earlier been referred to various genera (Endocarpon, Verrucaria, Normandina, Lenormandia, cf. GAMS 1962, p. 378).

VAINIO (1921) referred *Coriscium* to *Lichenes imperfecti* because no apothecia were known. It is very interesting to note that as early as in 1890, in connection with *Cora* (p. 240), he pointed out the similarity between *Coriscium* and *Corella*. He tried thus to prove that *Cora* and *Corella* were not basidiolichens, but in any case this is apparently the first time when *Coriscium* is mentioned in association with this group. Later *Coriscium* has been referred to the *Pyreno-lichenes* (e.g. MIGULA 1931, p. 510, v. KEISSLER 1938, p. 455, MATTICK 1954, p. 211).

GAMS (1962, p. 378) was the first investigator who regarded *Coriscium* as a basidiolichen, formed by *Omphalina umbellifera* and *Coccomyxa*-alga. This opinion has been accepted by POELT and OBERWINKLER (1964).

Distribution. In Central Europe Coriscium is found in mountain districts as well as in the bogs of the North German plain (MIGULA 1931, p. 510) and also in Denmark (MAGNUSSON 1937, n:o 30). ZAHLBRUCKNER (1905, p. 4, 1909, p. 401) reported it from the Dalmatian Isles of Yugoslavia, even on Olea europaea, which GAMS (1962, p. 378) finds somewhat doubtful. The species is common in the mountainous regions of the British Isles (WATSON 1953, p. 87: England, Wales, Scotland, Ireland). In the arctic-subarctic district it is obviously circumpolar (AHTI 1964, p. 27); there are finds from North America (HALE 1954, p. 264, AHTI 1964, p. 27, REDFEARN and THOMSON 1965 who reported it from Adirondack Mountains in N. Y., KALLIO and KÄRENLAMPI 1966), Greenland (DAHL 1950, p. 32), Siberia (VAINIO 1909, p. 157), and Fennoscandia (FRIES 1860, p. 256, VAINIO 1921, p. 232, MAGNUSSON 1937, n:o 30, 1946, p. 28, and 1952, p. 78, RÄSÄNEN 1943, p. 104, AHLNER 1944, p. 16, HAKULINEN 1965, p. 35).

In Finland the species seems to have a northern distribution; the only find which has been made in the south was by Lindberg in Åland (VAINIO 1921, p. 232). Its southern range seems to be in association with its Swedish occurrences in the coastal regions of Uppland (HAKULINEN 1965, p. 36). In Lapland *Coriscium* is much more common than the earlier finds have shown; inconspicuous as it is, it has certainly often escaped attention. The fruitbodies of the fungal component have proved to be a great help in discovering it.

Our finds of *Coriscium viride* (Ach.) Vain. and *Omphalina luteolilacina* (Favre) Henderson are the following.

Utsjoki; Ailigas 23. 7. -65, west of the church (alpine region) 16. 8. -62, Tshuomasvaara (alpine region) 13.8.-63, Skallovaara 26.8.-65, west of Juovuskalluvaara 3. 8. -64, 10. 8. -64, Jesnalvaara 9. 8. -62, Tsharsjoki 10. 8. -59, mouth of Kevojoki 26. 8. -64, Kevonniemi 15.8.-61, 8.8.-62, 26.8.-64, 14.9.-64, 11.8.-65, 15.8.-65, east shore of Kevojärvi 15. 8. -61, 14. 8. -65, 27. 8. -65, Tshieskulvaara 15. 8. -64, Tshieskuljoki 25. 7. -62, 20. 8. -65, Puksalskaidi 30. 6. -63, 11. 8. -64, 27. 7. -65, Kotkapahta 3. 7. -64, Kenespahta 8.8.-64, west shore of Vetsikkojärvi 14.8.-64, west of Vetsikko 15.8.-64, east side of Tshuoggajoki 1.7.-63, northwest of Tuöldivaldimroavvi 25.8.-65, west of Tsoagis Karbuljärvi 24.8.-65, shore of Piikkijärvi 24.8.-65, bog area between Voddi- and Piikkijärvi 24.8.-65, Karigaskaideroaivi 18.7.-65, Rassiotshokka 18.7.-65, valley of Stuor Avdshijoki 18. 7. -65. — Inari: 3. 8. -62, 4. 8. -64, 10. 8. -64, 16. 8. -64, 17. 7. -65, «palsa« bog by Aksujärvi 19.7.-65, Syrminiemi 8.8.-65, 9.8.-65, west of Heikkilä 4.8.-65, west of Lauravaara 2.8.-65, shore of Stuorraboggijärvi 1.8.-65, southern Skietshoaivi 30.7.-65, west of Laurivaara 29.7.-65. — Finnmark: Vadsö, Kiby 6.8, -64, Skallely 7.8, -64, Nesseby 22.7, -65, 19.8, -65, Rastegaissa (subalpine and alpine region) 24.8.-64, 25.7.-65, 17.8.-65.

As for the habitus and structure of our *Coriscium* material, they correspond fully with earlier descriptions (VAINIO 1890, 1921, PLESSL 1963, p. 256, POELT and OBERWINKLER 1964, Abb. 1). A special feature in the vertical section of the thallus is the *Botrydina*-like structure of the *«Coccomyxa*-packets« surrounded by fungal hyphae. This similarity has already been mentioned by PLESSL and by POELT and OBERWINKLER.

Fungal component. According to GAMS (1962, p. 379) the fungal component of Coriscium is Omphalina umbellifera (= ericetorum), the same species which also forms most Botrydinas. POELT and OBERWINKLER (1964, p. 368) observed that two different species were concerned and therefore they called the fungal component of Coriscium «Omphalina ericetorum (Fries) M. Lange (pro parte?)« and that of Botrydina «O. pseudoandrosacea (Bull. ex Fries)«, emphasizing that this decision was only temporary. Our opinion thus seems to differ only nomenclatorally. We already discussed our attitude about separating O. pseudo-

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androsacea and O. ericetorum (especially in the case of the four-spored variety), and, in addition, we have found Botrydina growing together with all types of O. ericetorum. As for the fungal component of Coriscium, our observations in the summer of 1964 revealed that in most cases it was a species of its own, different from O. ericetorum. For lack of anything better we referred it to O. luteovitellina Pilát & Nannf. (KALLIO and KANKAINEN 1964, p. 198), although it clearly differs from the bright yellow types described earlier. A few specimens which were not microscopically investigated were also confused with O. ericetorum, and therefore Coriscium was mentioned in connection with this species, too. In the summer of 1965 during the Kevo mycological symposium Dr. Henderson solved this problem by identifying the Coriscium fungus with FAVRE'S (1955) Omphalia luteolilacina. In Scotland this species had previously been found to grow «always in association with lichens« (REID-AUSTWICK 1963, p. 289). We have never found this species without Coriscium, and if we sometimes have noticed the lichen first, there have usually been at least some remains of the fruit-body. In one case only O. ericetorum was found in the neighbourhood of Coriscium (in Kenespahta 15.6.-65), but Botrydina was also growing nearby. Furthermore, O. luteolilacina was known from the same locality, so this surely is no exception to the rule. These two fungi often grow in the same locality, but each one seems to have a separate lichen of its own. Among the older museum samples of O. ericetorum and O. luteovitellina in TUR, specimens of O. luteolilacina were also found, and if there was some substratum attached to the foot, Coriscium could always be observed.

Omphalina luteolilacina (Favre) Henderson (Plate 1).

In our material the c a p is convex-umbilicate or flatly infundibuliform, mostly about 1.5 cm (exceptionally even 2.5 cm) in diam., with a minutely pubescent surface, especially in young specimens, cream-coloured or tinged with yellowish-orange, older whitish, the edge often somewhat pellucido-striate and folded. Gills : same colour as the cap, not very narrow, distant (12–20 in number, 0–3 small ones between), mostly rather shortly decurrent. Stem : rather short and sturdy, sometimes slightly thickened at the base, straight or somewhat curved, measuring 1.5–2.5 cm \times 2.5–3 mm; entirely pubescent with short white hairs; the colour is whitish, often but not always tinged with violet, very seldom clearly lilac. S p o r e s : hyaline, elliptical. They were measured from 10 dried specimens, collected in three localities, and the mean values (of 100 spores each) varied between 6.2–7.3 µ in length and 3.1–3.6 µ in breadth.

The species differs from *O. ericetorum* especially by the whitish, sturdy, pubescent stem (in dried specimens the contrast between the strongly yellow gills and the whitish stem is a characteristic feature), the less deeply decurrent gills and narrower spores. (In *O. luteolilacina* the ratio breadth: length of the spores usually is about 1: 2, by *O. ericetorum* about 1: 1.5. Fig. 3.) In distinguis-

hing from O. luteovitellina the spores do not seem to be useful, but the glossy bright yellow colour of the entire fungus and the less clearly pubescent and less sturdy stem of O. luteovitellina are distinctly different from those of O. luteolilacina in fresh material.

In Finnish Lapland and Norwegian Finnmark O. luteolilacina is most abundant in «palsa« bogs and on «palsa« hummocks but is often found also on rocks and fjelds (in subalpine and alpine regions). The fruit-bodies occur either on *Coriscium viride* or on bare ground or mosses (mostly *Dicranum elongatum*) — also then in the immediate vicinity of *Coriscium*.

In the subalpine-alpine zone it might be circumpolar like *Coriscium*. In addition to our collections from northern Finland and Norway, the author Kallio has found this species in Labrador, Canada (Ungava peninsula, Irony mountain, in reg.alp. 5.8.-63). Furthermore, in the herbarium of Uppsala university he has seen some Swedish and Canadian specimens which obviously belong to *O. luteolilacina*. Particularly a sample collected by Gunnel and Hugo Sjörs in «Ontario, Hudson Bay lowlands near Hawley Lake, Palsa bog, W of Lake in cracks of palsa« in 1957 is a most characteristic *O. luteolilacina*. Dr. T. E. Hasselrot has kindly sent us two *Coriscium* samples from South Sweden, both having a typical *Omphalina luteolilacina* attached: 1. Uppland: Blidö sn, Rödlöga Åsmansboda, Storskär, N-ändan, över mossor på klippvägg i nordbrant, rikl. 27. 6. -51 (on moss carpet on rockwall N-exp., abundantly) and 2. Västergötland: Österbitterna sn, mossen N on Ramnö, dike o. rester av torvupplag vid torvlada, rikl. 23. 7. -63 (Bog, along ditch and on peat blocks lifted for drying).

FAVRE (1955, p. 45) described O. luteolilacina in Parc National suisse, where it occurs at an elevation of 2640 m. According to REID and AUSTWICK (1963, p. 288) «it is an alpine species which has been found on several Scottish peaks«. It certainly is more widely distributed than the information up till now has shown. The figure (Abb. 3) and the description of POELT and OBERWINKLER (1964) give good reasons to believe that the fungus of their Coriscium material might also be O. luteolilacina. Furthermore, in the lichen herbarium of H. there is a Coriscium sample: «Omphalia umbellifera (L. ex Fr.) Quel. 4-sporige Form, syn. Coriscium viride (Ach.) Vain.; vide H. GAMS in Österr. bot. Z. 109: 376—380 (1962). — Ammergauer Alpen, Oberbayern: Gipfel der Notkarspitze, auf dicken Rohhumuslagen der Westseite, ± 1885 m. 6. 1962. leg. J. Poelt« — Besides the lichen the sample includes three fungi, which seem to be typical Omphalina luteolilacinas as well in macroscopic as in microscopic characters. — The author Heikkilä has found the species together with Coriscium in a bog in Denmark (Jutland, Rold Skov, Øks-sø 26. 9. 1965).

Algal component. VAINIO (1921, p. 232) wrote about the algal component of Coriscium viride: «Gonidia coccomyxoidea aut dactylococcoidea (nec 'poly-

coccoidea', ut ab autoribus nonnullis indicatur), ---«. In spite of this many authors (e.g. ZAHLBRUCKNER 1926, p. 90, MIGULA 1931, p. 510, v. KEISSLER 1938, p. 445) regarded the alga as *Polycoccus*. Nowadays most investigators refer it to *Coccomyxa* (MATTICK 1954, p. 211, GAMS 1962, p. 379 etc.). According to PLESSL (1963, p. 256) the species is *Coccomyxa ichmadophilae* Jaag. According to JAAG (1933 b, p. 109-114) a characteristic of this species is that the cells already in situ are very slender, unlike the *Coccomyxa* gonidia of other lichens (*Botrydina* is no lichen in his opinion!).

In our material the *Coccomyxa* of *Coriscium* differs very little from that of *Botrydina*. In situ the cells have quite the same shape and dark green colour, and their average measurements (200 algae) were: length $8.0\pm0.7 \mu$, breadth $4.3\pm0.5 \mu$ and ratio breadth: length is 1: 1.9 ± 0.03 . In cultures on MS- and Kari-agar this alga formed similar round dark-green colonies. In older cultures, however, their surface often became rough (this never occurred in *Botrydina-Coccomyxa*); JAAG described a similar character of *C. icmadophilae*. In other respects the alga seemed to be very near to that of *Botrydina*, both morphologically and physiologically. No such curiously curved («gebogen«) forms were produced on glucose-containing Kari-agar, as JAAG (1933b, p. 113) observed with *Coccomyxa ichmadophilae* on «glucose agar«.

2. Clavariolichenes

In this century many investigators have studied the genus *Clavaria*, but GEITLER (1955) was the first author to positively show that one of its species was a lichen component, *C. mucida* Fr. [= *Lentaria mucida* (Fr.) Corner], which already much earlier (e.g. FRIES 1821, p. 476) was known to be «phycophilous«. According to GEITLER (1955, 1956) the green stratum around the fruit-bodies is formed by fungal hyphae and algal packets. In this thallus there are several kinds of algae occurring freely without any connection with the hyphae, but within these packets a certain kind of *Coccomyxa*-like alga is always observed. The envelope is formed by *Lentaria*-hyphae which have formed large-celled pseudoparenchyma. The fungus also penetrates into the interior of the packets between the algal cells. GAMS (1962, p. 377) refers these formations to *Botrydina vulgaris* (as a collective species).

POELT (1959) reported a similar symbiosis in *Clavulinopsis septentrionalis* Corner. He also mentioned that the closely related species *C. vernalis* (Schw.) Corner might also be lichenized (POELT 1959, p. 600, 1962, p. 87). CORNER (1950, p. 394) described its habitat: «On bare earth covered with *Cyanophyceae* and moss protonemata.«

All these three species, according to POELT (1962), are rare. In addition to

Europe (Sweden, France, Bavaria, Austria, east Slovakia, Soviet Union, North Italy), *Lentaria mucida* has according to CORNER (1950, p. 442) also been found in North America (USA, Canada), Central and South America (Panama, Columbia), Asia (Japan and Siberia), and possibly in Australia. *Clavulinopsis septentrionalis* was described from Sweden (CORNER 1956) and later found in the Alps (POELT 1959). *C. vernalis* has according to CORNER (1950) been discovered in Europe (Holland, France) and North America (USA; also Canada, cf. KALLIO and KANKAINEN 1964, p. 186).

In Finland, *Lentaria mucida* (Fr.) Corner has been found by LAURILA (1939, p. 3) in Noormarkku and Kankaanpää. He also called attention to its algal symbionts and wrote: «Algae chlorococcoideae (?) in eodem substrato semper inveniuntur et forsan functionem gonidiorum habent.«

Clavulinopsis septentrionalis Corner has been reported by KALLIO and KAN-KAINEN (1964, p. 187) in Finnish Lapland and Finnmark.

In addition to the sites mentioned by them the species has been found in the following localities in 1965:

Utsjoki: S-shore of Kevojärvi 18.8.-65. — Inari: near Kietsimäjoki, dry pine heath 31.7.-65, Lemmenjoki Aug.-65.

The habitat is on sandy or peat soil with only sparse cryptogamic vegetation (*Polytrichum piliferum*, *P. juniperinum* and *Pogonatum urnigerum*). The conditions correspond closely to those described by POELT (1959, p. 601) in the Alps.

All the characteristics of the fungus agree with those described by CORNER (1956) (cf. KALLIO and KANKAINEN 1964, p. 187). The green lichen stratum was always observed around the fruit-bodies. The structure of the thallus corresponds with the description of GeITLER (1955—56) and POELT (1959).

Clavulinopsis vernalis (Schw.) Corner.

Utsjoki: Saarela farm (south of the church) 22.8.-63. — Inari: Petsikko fjeld (subalpine region) 1.8.-62, 10.8.-64, 25.8.-65. — Finnmark: Geidnogaissa (alpine region) 20.8.-63.

This species also was first reported in Finland by KALLIO and KANKAINEN (1964, p. 186). In our finds no evidence could be obtained for an eventual lichen formation in nature. Some *Gloeocapsas* and Nostocaceous algae were noticed during microscopical study, but this was the only «phycophilous« feature. In laboratory conditions, however, *Botrydina*-like formations were found surrounding the fungus on the natural substrate.

II. ECOLOGY OF CO₂ ASSIMILATION

Since the distribution of the above-described basidiolichens clearly emphasizes their adaptation — as is characteristic in general of all lichens — to conditions

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of low temperature and short growing season, it is essential to determine the ecology of their primary energy production. We have considered it most advantageous to study the processes of assimilation under laboratory conditions, where it is possible to establish the general correlations of these processes to external factors, and subsequently on this basis the ecological reasons for their geographical distribution can readily be understood. At the present stage of the investigations we have been limited to determining only the relative temperature curves of assimilation. This is due mainly to the fact that — especially with *Botrydina*, which cannot be cultured pure — it is necessary to take the specimen together with its substrate (in this case a very thin layer of rotten wood); and this substrate contains other organisms whose respiration affects the results. However, we regard this as having only a minor influence on the shape of the temperature curve.

Method. Assimilating lichens were placed in cylindrical cuvettes made of copper and having a diameter of 15 cm and height of 4 cm. They were covered with a perspex-glass («Finn Acryl«) lid and had a removable screen bottom which facilitated the free passage of gas. The entry and exit gas tubes as well as the conducting wire of the thermocouple were led into the cuvette. The cuvette was placed in an ethylene-glycol temperature bath, whose temperature was adjusted by means of a heater, cooler and stirrer to the desired value with a precision of ± 0.1 °C. Owing to radiation heat, the temperature in the thallus was not exactly the same as in the bath. In addition to the delay in temperature change, the final difference could sometimes exceed 0.1°. Since, however, constant readings were made by means of the thermocouple in the cuvette, the difference in temperature between the heating bath and the cuvette is only of technical importance. On the other hand, there was a more important temperature difference between the upper and lower surface of the thallus caused by the illumination. This was naturally dependent upon the light intensity, but at the intensities used in determining the temperature curves, this difference was about 0.2°C. Evidently the difference in temperature between the upper surface of the lichen and the gonidial layer was smaller than this. In the present trials the latter temperature error was not taken into consideration.

Illumination was provided by a high-pressure mercury lamp Philips H PLR 700 W, and the light intensity was held constant at 5200 lux, which is somewhat below the «half-value« for assimilation.

The air used in the trials came from flasks and thus its CO_2 content was constant, generally close to the average of 0.03 vol. %. The speed of gas flow was 10 l/h. Determinations of the CO_2 content of the gas were made by means of a Hartmann & Braun URAS gas analyser.

In general the temperature tests were begun at -5° C and the temperature was raised in intervals of 5 degrees. At least one hour was required for each

change, and readings were not taken until they had remained constant for about 15 minutes. Consecutive determinations of CO_2 concentration were made both in the dark and light. Thus, obtaining the entire curve required a trial series lasting 16—18 hours. As was shown by e.g. LANGE (1965), under constant conditions assimilation remains the same. This was confirmed in the constant lighted conditions during 18 hours.



Fig. 4. Temperature curves (at light intensity of 5200 lux) for the apparent photosynthesis (white spots) and respiration (black spots) of a *Botrydina* specimen (from SW-Finland, Yläne 10. 9. -65), kept for a month before the experiment at +17 °C and 2300 lux. — The ppm CO₂ values are relative; because of the irregular thickness of the *Botrydina* layer and the remnants of the stratum in it, the exact area of the assimilating surface could not be calculated. This also concerns the other curves.

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Fig. 5. Temperature curves (at light intensity of 5200 lux) for the apparent photosynthesis (white spots) and respiration (black spots) of a *Botrydina* specimen (from SW-Finland, Yläne 10. 9. -65), kept for three weeks before the experiment at $+5^{\circ}$ C and 800 lux.

Botrydina. The curves in Figures 4 and 5 show the apparent photosynthesis and respiration of two specimens taken from Yläne; these curves are presented as relative changes in CO_2 content. The difference between two specimens is that no. 4 was kept before the trial for three weeks at $+17^{\circ}C$ and light intensity of about 2300 lux, while the temperature of the corresponding pre-treatment of no. 5 was only $+5^{\circ}C$ and light intensity 800 lux.

The curves show that the temperature optimum of apparent photosynthesis in both cases was close to 0°C. Photosynthesis continued actively below this temperature to at least -5° . The pre-treatment had no great effect, and similarly both of the respiration curves resembled one another closely.

The Coccomyxa-alga of Botrydina was pure-cultured in Petri dishes on a substrate of Kari-agar. Two specimens were tested, one from Geta on Åland, lat. about $60^{\circ}N$ (Fig. 6) and the other from Kevo in Utsjoki, lat. about $70^{\circ}N$ (Fig. 7). The curves of both of these specimens reveal that over a wide range photosynthesis is relatively insensitive to changes in temperature. Worthy of note is the great difference in response of the two specimens investigated. Whether

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Fig. 6. Temperature curves (light intensity 5200 lux) for the apparent photosynthesis (white spots) and respiration (black spots) of Coccomyxa-algae of a South Finnish Botrydina (Åland, Geta). The specimen was a thin green algal film on Kari-agar in a large Petri dish, cultured for 3 1/2 months, of which the first two were at +17°C (800 lux) and the final $1 \frac{1}{2}$ months before





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Fig. 7. Temperature curves (light intensity 5200 lux) for the apparent photosynthesis (white spots) and respiration (black spots) of Coccomyxa-algae of a Lapponian Botry-dina (Utsjoki, Kevonniemi). The specimen was a $2\frac{1}{2}$ month old Kari-agar culture in a large Petri dish, kept during the first two months at $+17^{\circ}$ C (800 lux) and for two weeks before the experiment at $+5^{\circ}$ C (800



lux).

Fig. 8 (above, left). The recovering of Botrydina (Yläne 20. 10. -65) after freezing (20 hours at -28°C.) The broken lines indicate the situation at +5°C and 5200 lux before freezing. The curves show the changes in apparent photosynthesis (white spots) and respiration (black spots) under the same conditions for several days after freezing. - Fig. 9 (above, right). Curves (at 5200 lux) for the apparent photosynthesis (white spots) and respiration (black spots) of Lapponian Coriscium viride. The specimen was collected in mid-August, kept dried

for 2 1/2 months at room temperature, and for one week before the experiment it was kept moist at +5°C and 800 lux. - Fig. 10. The recovering of Coriscium viride (same specimen as in Fig. 9.) after freezing (14 hours at -28° C). The broken line indicates the situation at $+5^{\circ}$ C and 5200 lux before freezing. The curves show the changes in apparent photosynthesis (white spots) and respiration (black spots) under the same conditions during four days after freezing.

there is a difference which indicates a «southern« and a «northern« type of response may be proved with larger material.

When Botrydina was held overnight at -28°C, its photosynthesis required







Fig. 11. The relation between the apparent photosynthesis (Aa) and the respiration in darkness (Rd) at various temperatures, by Botrydina vulgaris (white spots = the specimen kept at $\pm 17^{\circ}$ C before the experiment, Fig. 4; black spots = kept at $\pm 5^{\circ}$ C, Fig. 5) and Coriscium viride (= crosses, kept at $\pm 5^{\circ}$ C, Fig. 9).

Fig. 12. The relation between the apparent photosynthesis (Aa) and the respiration in darkness (Rd) at various temperatures, by the *Coccomyxa*-algae of *Botrydina* from South-Finland = white spots, Fig. 6) and Lapland (= black spots, Fig. 7).

a relatively long time in order to recover from this freezing treatment (Fig. 8). Not until the third day did the values approach those originally obtained. The recovery of respiration took place within two days. This is considerably longer than the recovery of *Cetraria nivalis* mentioned by LANGE (1962).

Coriscium viride. A sample of Coriscium from Utsjoki showed a photosynthesis temperature curve (Fig. 9) which was quite similar in shape to that of *Botrydina*. There was a gently sloping optimum region close to 0° with compensation points at about -10° and $+13^{\circ}$.

The recovery of *Coriscium* after 14-hour freezing at -28° was likewise slow. (Fig. 10). Three days were required to attain the normal values of respiration (at $+5^{\circ}$) and slightly longer for photosynthesis.

A characteristic feature of the lichens is the typical low relation between the net assimilation and the respiration in darkness, which is regarded as a kind of adaptation to northern conditions (cf. STÅLFELT 1937, p. 53); Fig. 11 and 12.

The frost resistance of different specimens of Goccomyxa was investigated in preliminary tests by freezing liquid cultures at -29° C for 24 hours, after which Petri dish cultures were made both with the treated material and untreated controls. It was found that such freezing did not weaken the vigour of the organisms. This result agrees with the studies made by Holm-HANSEN (1963) on the algae of antarctic regions.

Plate 1. — Above: (left) Omphalina luteolilacina with Coriscium viride, hanging on a slope, Inari, Syrminiemi 8. 8. -65; (right) Omphalina luteovitellina, Utsjoki, east of Piikkijärvi 24. 8. -65. — Middle: (left) Omphalina luteovitellina with Botrydina (the dark green mass), Finnmark, north shore of Pulmankijärvi 22. 7. -65; (right) Omphalina ericetorum with Botrydina, Aland, Geta 20. 9. -64. Below: (left) Omphalina sp. on Blasia pusilla, Utsjoki, mouth of Kevojoki Aug. -62; (right) Gerronema sp. on Marchantia, Utsjoki of Piikkjärvi 24. 8. -65 (KALLO and KANKAINEN 1966, Rep. Kevo Subarctic Sta 3). — The colour of the Table somewhat too reddish.

III. DISCUSSION

1. Some aspects of taxonomy

The problem of northern Agaricolichenes seems to be limited only to the genus Omphalina. In this genus it includes the subarctic obligatory lichen components O. ericetorum (Pers.) M. Lange, O. luteovitellina Pilát & Nannfeldt and O. luteolilacina (Favre) Henderson. These species are usually recognizable although there have been several obscurities in the fungal taxonomy at this point; including some which have not yet been unravelled. These species are morphologically close to each other, and one thus could assume that their taxonomical and ecological evolution might have progressed in parallel.*) On the other hand it has to be kept in mind that e.g. O. viridis, which has often been regarded as a variety of O. ericetorum, is ecologically quite different. It grows on rather bare ground and belongs to the well lighted microassociation of Polytrichum piliferum habitats, where competition is quite insignificant. It often occurs together with Gerronema fibula and Omphalina pyxidata, which according to our observations are not lichenised either. It is naturally possible that there might be some facultative Botrydina formation, although we do not know of any really convincing case. Botrydina was once observed (at Yläne) in the vicinity of Omphalina sphagnicola, even on the base of its stem, but it is still possible that O. ericetorum, perhaps growing in the same site, might be the fungal component. The habitat was a small boggy place on rock, and O. ericetorum often grows in such places. At Yläne, on Sphagnum nemoreum on the side of a cliff, which is a typical habitat of O. ericetorum, both O. ericetorum and O. sphagnicola were observed. In each of the 28 O. ericetorum samples found there in 1965, Botrydina was also present, while it did not occur in any of the 11 samples of O. sphagnicola, even though the shortest distance between the fruit-bodies of these two species was about 20 cm. The habitat factor thus might not have a direct influence in Botrydina formation, but rather a genetic character is concerned.

From the standpoint of elucidating the special peculiarities of lichens as a whole, it is noteworthy that certain species of a taxonomically entirely different fungal group, *Clavariaceae*, with a similar distribution as *Omphalina*, have both morphologically and ecologically arrived in their evolution at the same end result as the latter. This phenomenon is currently being studied in greater detail.

2. The subarctic-arctic ecological aspect of the problem of B a s i d i o l i c h e n e s

The biological problems of the subarctic zone are related to its unique climatic conditions (cf. MATTICK 1950, 1953; LANGE 1965). The short growing period and the low temperature limit the supply of available energy; this is the essence of the general biological aspect of the subarctic-arctic problem. The number of agarics declines sharply where the forest ends, a fact which may be associated with the decrease of litter and the distributional limit of hosts for many mycorrhiza fungi. On the other hand, the forest line indicates a certain stage in climatic changes. As one ascends above the pine line in the subarctic region or moves into the arctic zone, the fungal flora diminishes radically. On the contrary, an isolated pine district is — as Kevo shows — also mycofloristically almost as rich as the more southern woodlands, even if some important forest fungi cannot extend to these separate tracts. One of the most important ecological factors in this respect is the lower temperature in the north which slows the process of litter decay.

The fact that Omphalina species are among the last macrofungi in the Arctic (e.g. SINGER 1954, p. 453; DEARNESS 1923, p. 16; M. LANGE 1955) might be related to their ability to use light energy through the agency of the Coccomyxa-alga. All three closely related basidiolichen Omphalinas (O. ericetorum, O. luteovitellina and O. luteolilacina) seem to extend quite far both into the mountains and into the arctic region.¹ In addition, their southern limit may reach a good distance outside of the Arctic. They may possibly have a new distributional center in the mountains, like so many other northern species. In Finland, however, like so many other northern species, O. luteovitellina and O. luteolilacina seem to have their southern limits quite near to the Subarctic. NANNFELDT (1959, p. 176) also refers the former to the fungi with southern limits in Scandinavia. The occurrences of Coriscium in Aland and the Archipelago of Stockholm as well as the find of it and O. luteolilacina in Denmark (furthermore *Coriscium* in North Germany) show that this basidiolichen is not merely subarctic-arctic and mountainous by nature. In Finland, however, it is certain that the center of its distribution is in the north.

As with lichens in general, basidiolichens also show a distinct adaptation of their photosynthetic activity to a comparatively low temperature. LANGE (1965) has studied many northern lichen species and found a wide temperature range in their assimilation, which means a great adaptability. On the other hand, even in the tropics some lichens are able to assimilate at very low temperatures.

^{*)} The taxon *Omphalina luteolilacina* is according to the nomenclatural scheme of THOMAS (1939) synonymous to «Corisciomyces viride«. On the other hand «Botrydinomyces vulgaris« is ambiguous because it may be synonymous to *O. luteovitellina*, *O. ericetorum* etc.

¹ GAMS' statement (1965, p. 102) seems quite strange to us: «It seems, that *Botrydina* results only in warmer climates, in cooler climates (in the Alps, ---, in Northern Europe, ---) the association is less intimate. ---«

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Coriscium- and Botrydina-thalli are primarily plants of localities with a winter snow cover. It is possible that the typical habitats of Coriscium — the «palsa« hummocks — may partly be snow-free, but at least the characteristic Botrydinahabitats are those of chionophilous species. Their photosynthetic curves show continued activity even at temperatures below 0°C. These lichens are very well adapted to the subarctic-arctic summer. However, since they have a slow recovery after being chilled to very low temperatures, their adaptation to the chionophobous winter conditions is not as good as that of many epiphytic lichens in more southern areas (LANGE 1962; c.f. KALLIO and VIRRANKOSKI unpubl.).

The symbiotic relationship between fungi and photosynthetic plants is especially characteristic of the arctic-subarctic area, particularly when we think of the dominating position of the ascolichens in its flora. The basidiolichens show how the same principle is accomplished in a different way in systematically separate groups.

There may be even other phenomena of the same ecological category, where adaptation has thus led to an immediate preservation of energy of the fungus through the agency of a green plant. One such case, which has not been more closely investigated, is the connection between *Omphalina sp.* and *Blasia pusilla* (cf. KALLIO and KANKAINEN 1964). This relation has also been observed in North America (in Labrador by the author KALLIO), and it might be quite common; at least in Finland it has been seen also in the south (by the authors in Tampere and Masku), but even seems to be normal in Lapland. This connection is obviously not facultative but obligatory by nature. It is still unsolved whether this is a question of an immediate association between *Blasia* and the fungus, or a more complicated one: *Blasia* — *Nostoc* — *Omphalina*.

IV. SUMMARY

Preliminary research has been done on the group *Basidiolichenes* in Finland, especially in Inari Lapland. Attention has been mainly paid to *Agaricolichenes*: to the «double organisms« *Botrydina vulgaris* Bréb. and *Coriscium viride* (Ach.) Vain. formed by *Omphalina*-species and *Coccomyxa*-algae. *Omphalina ericetorum* (Pers.) M. Lange and O. *luteovitellina* Pilát & Nannf. were always found in association with *Botrydina* and thus seem to be obligatory lichen components. The fungus of *Coriscium viride* is O. *luteolilacina* (Favre) Henderson. Among the other Lapponian representatives of the genus Omphalina only O. velutina (Quel.) Quel. might belong to the obligatory lichen (= *Botrydina*) formers; some of the others (e.g. O. *sphagnicola* (Berk.) Karst.) could possibly be facultative ones although this matter remained quite uncertain.

In Finnish Lapland the group Clavariolichenes is represented by Botrydina-

like structures with *Clavariadelphus septentrionalis* Corner as the fungal component. *Clavulinopsis vernalis* (Schw.) Corner needs further investigations.

Some work was also done in laboratory, mainly by cultivating the algal components and studying their photosynthetic activity by means of a URAS gas analyzer.

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ON THE MACROECOLOGY OF SOME RUST FUNGI*

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I. INTRODUCTION

The effects of environmental conditions on plant pathogenic fungi have been thoroughly studied in many instances by plant pathologists (see, e.g., WALKER 1957, p. 544; STAKMAN & HARRAR 1957, p. 301; COLHOUN 1964). It is well known that many of the epidemics caused by parasitic fungi are correlated with favourable climatic conditions. In particular, much attention has been devoted to the economically important phycomycetes, to *Puccinia graminis*, and to *Erysiphe graminis*.

In natural populations the ecology of parasitic fungi has been much less studied. The purpose of this paper is not to present a review of the subject; it only aims to point out some general features in the ecology of parasitic fungi, with some examples mainly from the rust flora of Lapland. These will reveal that the ecological responses of parasitic fungi are much more delicate and complicated than a simple host-parasite relationship suggests, and that these responses can also be studied in the field. At least in Fennoscandia, very few studies exist on this problem; apparently LAGERHEIM (1909) was the first to draw attention to the climatic requirements of parasitic fungi (he stated that Uromyces sommerfeltii (U. solidaginis) and Puccinia virgae-aureae on Solidago virgaurea mainly occur on arctic-alpine areas). Many excellent ideas about the ecology of fungi are to be found in the review of HINTIKKA (1931), which, however, is written only in Finnish.

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