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On the Apothecia in the Lichen Family *Umbilicariaceae.*

By

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(12 Textfigures and 5 Plates.)

A discussion and valuation of the proposed divisions of the *Umbilicariaceae* into various genera have in late years particularly been given by Frey (1929, 1931, 1933), in his publications on this family. In accordance with earlier investigators like Nylander and Tuckerman he is of the opinion that there should only be maintained one genus, *Umbilicaria* Hoffm. in the family *Umbilicariaceae.* The characters on which divisions were formerly based, namely multilocular or simple spores and pustulate or non-pustulate thallus are found to be insufficient as a basis for generic distinction. I also agree that generic distinction on these premises, particularly the characters of the spores, is untenable in practice. However, when I am of the opinion that the *Umbilicariaceae* should be divided into at least 4 genera, it is the result of a study of the apothecia of these lichens, which in part are extremely remarkably built, and which have attracted the attention of previous investigators only to a very small extent, especially from a taxonomic point of view. In the following I am going to demonstrate how the species of *Umbilicariaceae* examined may be arranged in 4 different, partly large groups, according to the structure of the apothecia.

The 1st group (genus *Umbilicaria*, cf. p. 19), which has the most simple apothecia (fig. 1), is characterized by its regular lecideine apothecia with smooth disk. Noteworthy are the young apothecia which open like a saucer with a more or less concave bottom which is completely and uninterruptedly covered by the ascogenous hymenium. In older apothecia the disk may sometimes secondarily crack so that more ore less angular and branched fissures are formed, bordered by a small, elevated, sterile margin.

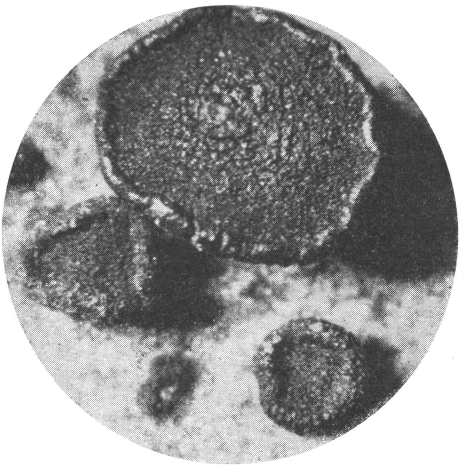


Fig. 1. Young and old apothecia of *Umbilicaria* type (1st group). The young disks without central sterile column, uninterruptedly covered by the ascogenous hymenium. *U. subglabra* Harm. France. Magn. 22 ×.

To this group belong a series of species, of which the Scandinavian ones are *U. rigida, leiocarpa, Lyngei* (cf. p. 19) and *pustulata*, the latter with multilocular spores.

The 2nd group (genus *Omphalodiscus*, cf. p. 32), differs from the 1st group particularly in the young apothecia. These do not open like saucers as in the first group but, at an early stage, the sterile, not ascogenous central part of the apothecium shoots out like a small column or button in the middle of the young apothecium (fig. 2, 3). The ascogenous hymenium develops about this central column like a ring, the opening of the young hymenium being marked by the circular furrow between the central column and the apothecial margin (cf. also Pl. II fig. 1 and 2; Pl. IV fig. 8). This characteristic, sterile, prominent central column persists on the full-grown apothecium either as such, e. g. in *O. spodochrous* (cf. Pl. II fig. 2), or commonly as a more or less wavy, frequently branched fissure bordered by a sterile, narrow margin such as seen in fig. 2 and 4. Similar but mostly smaller fissures frequently develop also later at various places in the fertile hymenium between the central fissure and the apothecial margin. If many of them are present a profusion of fissures bordered by their elevated margins may finally develop, and between these the faces of the ascogenous hymenium (fig. 4 *a*). In older apothecia all traces of these fissures may have vanished

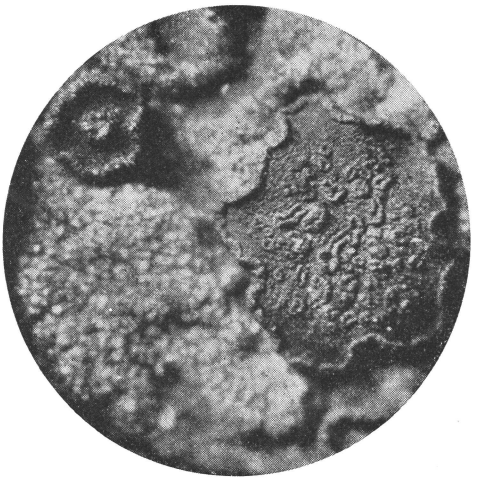


Fig. 2. Young and old apothecia of *Omphalodiscus* type (2nd group). The young disk with a ring-shaped ascogenous hymenium around a sterile central column. The old disk with the central column transferred into a central fissure, and with secondary fissures between this and the margin. *O. Kraschenininikovii* (Sav.) Schol. N.E. Greenland. Magn. 22 ×.

so that a quite plane, structureless disk is developed as in the preceding group (fig. 4 *c*). But a minute investigation of such apothecia under high magnification will, as a rule, reveal remains of the central fissure. Particularly in *O. virginis*, however, it may at times be lacking, even in some young apothecia. In Scandinavia four representatives of this group are known, viz *O. decussatus*, *virginis* and two species with multilocular spores *O. crustulosus* and *spodochrous*.

We then have the two last groups, the remarkable apothecia of which have given rise to the generic name *Gyrophora*. The first of these, the 3d group in all (genus *Gyrophora*, cf. p. 26), seems to be the group containing more species than any other group of *Umbilicariaceae*. The disk consists of a series of, in principle, concentrically arranged folds separated by fissures (fig. 5). In order to understand this picture better we shall at once examine a section, for instance through an apothecium of *G. proboscidea* (fig. 6), which has been carefully located so that it cuts the fissures and folds perpendicularly. Under the microscope we see that the light coloured areas at the top of the folds constitute the ascogenous hymenium, the surrounding, more or less dark coloured tissue being sterile. In other words we understand that the fertile hymenium is placed as in a groove at the top of the folds, and we see how they open outwards by a small furrow

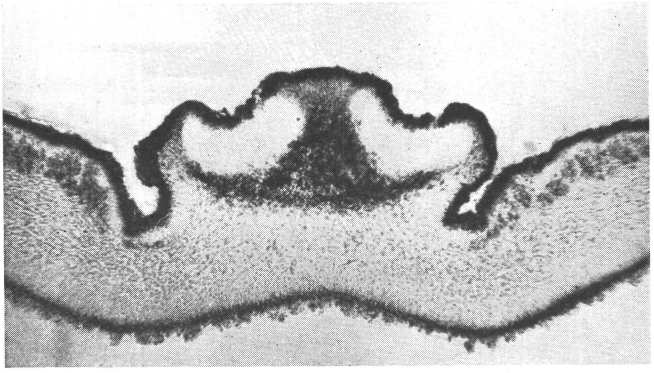
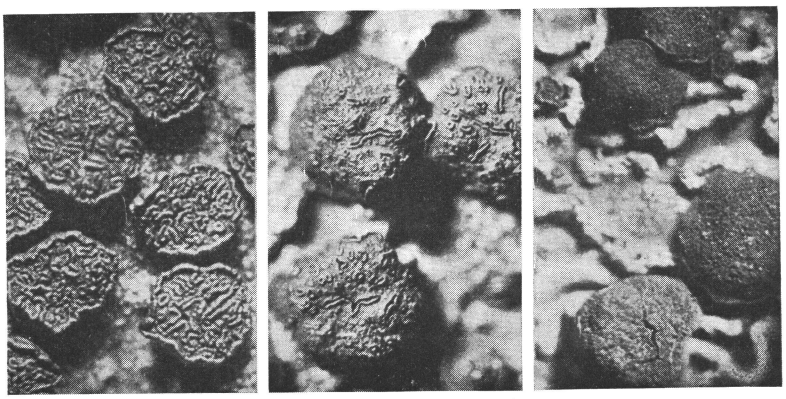


Fig. 3. Section through a young *Omphalodiscus* apothecium showing the sterile central column and the two section-faces of the ascogenous hymenial ring. *O. decussatus* (Vill.) Schol. Spitsbergen. Magn. 83 ×.

at the top. This structure, consisting of a fold which at the top encloses an ascogenous hymenium opening outwards by a small, middle furrow we shall designate a gyrus. The immersed, ascogenous, hymenial stripes at the top of the gyri are homologous with the open faces of ascogenous hymenium present between the margins of the fissures in the apothecium of the second group. In the 3d (and 4th) group the opening face of the ascogenous hymenium as seen in the 2nd group, has been reduced to the small opening furrow at the top of the gyri.

These long and narrow gyri are formed in a characteristic, stereotypic way. If we examine a section through e. g. the *vellea* apothecium (Pl. V fig. 6) we see how some of these light-coloured hymenia at the top of a gyrus are in the act of dividing along the middle, the fertile, light coloured tissue being pierced by sterile, dark tissue, which by further growth divides at the middle. From this it is easy to understand how this apparently complicated structure of the apothecia is developed, namely by a successive dichotomous division, during growth, into more and more gyri. That this explanation is correct is directly apparent from the numbers 2, 4, 8 in the groups of gyri, and from the mutually symmetric arrangement always to be observed in gyri of well formed apothecia.



a *b* *c*

Fig. 4. *Omphalodiscus* apothecia with a varying development of secondary fissures, from copiously in *a* to almost entirely effaced in the old apothecia of *c*. In a single of these old apothecia (*c*) remains of the central fissure is seen; they are distinct in the young ones. *O. Krascheninnikovii* (Sav.) Schol. N. E. Greenland. Magn. ca. 10 ×.

The development of an apothecium such as the one figured in fig. 6 is best demonstrated by a series of drawings (fig. 7 *a*, *b*, *c*, *d*). The ascogenous hymenium originates here as a small ring around a central sterile column (*a*, cf. also Pl. III fig. 2), just as in the preceding group, or it may primarily originate as a small, frequently somewhat curved gyrus. By an early fissure in the eventual central column (*b*) this disappears totally as such. One has to look for its theoretical remains in the opposite grooves of the two young (v. l. one ring shaped) complete gyri developed by the splitting of the central colum. During simultaneous growth these two hymenial stripes split longitudinally, producing four new gyri (*c*). Each one of these splits again longitudinally into two daughter gyri so that eight gyri are produced (*d*), i. e. an apothecium corresponding to fig. 6. On account of this manner of growth of the hymenium by repeated, dichotomous formation of gyri it becomes clear that the surface of the apothecium continually increases in size, and it is easily explained why these apothecia are always stalked and why they frequently acquire a convex surface when old. Furthermore the apothecia are

Fig. 5. Old apothecium of *Gyrophora* type (3d group). Ascogenous hymenium immersed in concentrically arranged, long, narrow gyri, the opening-furrows of which are to be seen as the thinnest grooves. In many places the gyri are seen in a state of dividing. *G. cylindrica* (L.) Ach. var. *Delisei* Despr. Jan Mayen. Magn. 22 ×.

bordered by a more ore less continuous common margin formed by the outermost gyrus. It is also clear that the deepest slits to be seen in the apothecium are the oldest ones, the next deepest slits the next oldest ones, and so on.

By examining such an apothecium in direct light (fig. 5, 8, 9) we shall now be able to interprete more easily what we see. We clearly see that the grooves are of different sizes. From the section (fig. 6) we now know that the narrowest grooves are the opening furrows of the gyri, and that we have corresponding to these, and here only, the ascogenous hymenium. In several places in fig. 5 and more easily in the higher magnified figs. 8 and 9 we may follow in detail the dichotomous splitting of a gyrus into two new daughter gyri. We here see how the top furrow with its ascogenous hymenium during growth splits longitudinally whereby at the same time the margins of the fissure proliferate forming the internal margins of the two daughter gyri, whereas the margins of the primary gyrus form the external margins of the two new gyri.

It is noteworthy that by a local inhibited growth, by necrosis, or for other reasons, it not rarely occurs that a gyrus is interrupted or at this point loses its power of dividing. In this way a chain-structure is formed, especially common in older apothecia (cf. figs. 5 and 8). The chain was originally a con-

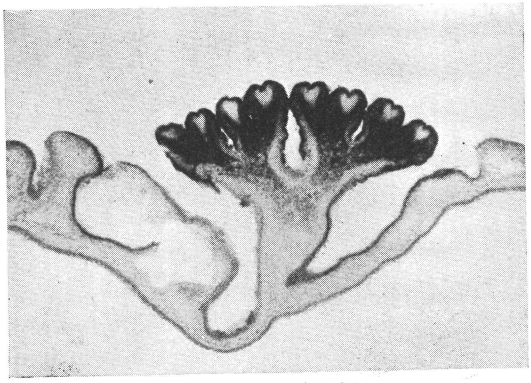


Fig. 6. Section through a *Gyrophora* apothecium. Note the symmetrical apothecial structure, formed through a dichotomous branching. In the top of the gyri the thin openingfurrow is seen leading down to the immersed stripe of light ascoge- nous hymenium. *G. proboscidea* (L.) Ach. Norway. Magn. 32 ×.

tinuous gyrus. If this chain formation, v. l. gyrus fragmentation, is prominent the apothecia may frequently be difficult to interpret. Such a localized inhibition of the division, especially of the initial ring-shaped gyrus, is also the cause of the zonation of the apothecia into 2—3 (-many) dividing centres such as is commonly seen (cf. Pl. III fig. 3).

At this point we may look into some of the strange conceptions of the umbilicariacean apothecium, contained in the six pages of text where Frey in his otherwise thorough and most valuable publication treats the apothecia in general (1933 p. 229—236). Here he points out forcibly (p. 233): »Diese allmähliche Verdunklung ist auch ein Beweis für die Unrichtigkeit der Ansicht, daß ein Parathecium nur als solches unterschieden werden könne, wenn es dunkel ist«.

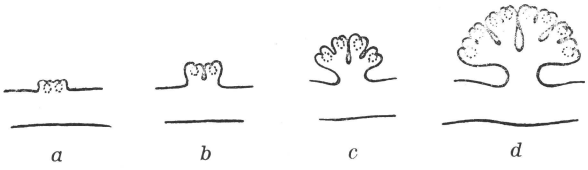


Fig. 7. Stages in the development of a regular *Gyrophora* apothecium. From the initial ringshaped ascogenous hymenium in *a*, the two gyri of *b* have been formed by a splitting of the central column. By a further dichotomous splitting during the growth the four gyri of *c* have been formed, and by a repeated splitting the eight ones of *d*.

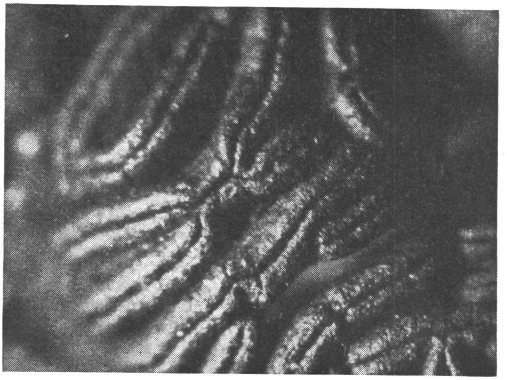


Fig. 8. Detail picture of dividing gyri in a *Gyrophora* apothecium. Cf. next fig. *G. hyperborea* Ach. Norway. Magn. 45 ×.

We may leave this point open, but when he thinks that his figure (fig. 33 l. c. p. 231) proves the point it is due to a misunderstanding. Frey's figure 33 g is a drawing of a young apothecium of *O. virginis* entirely corresponding to my figure 3. Frey writes here (l. c. p. 233): "Besonders deutlich zeigt sich diese nachträgliche Verdunkelung nach unten bei F. 33 g (p. 231). Hier sind zwei Apothecien nahe beieinander angelegt worden. Es besteht kein Zweifel, daß sie zuerst selbständig sich entwickelten. Nachträglich aber ist zwischen den zwei benachbarten Gehäusen ein verbindendes Gewebe enstanden, das sich nicht nur durch die Verdunkelung erkennen läßt, sondern auch durch die dichtere Textur".

However, Frey's illustration is evidently a central section of a young apothecium in which is included the sterile central column which I have described above (p. 2). The "two" hymenia which have misled him to this incorrect explanation are the two section-faces of the hymenial ring (cf. fig. 3). Frey then continues, unfortunately, on the same false premises: "Dieses Beispiel ist noch aus einem zweiten Grunde interessant. Es ist nämlich ein Beweis dafür, daß die Kompliziertheit der gyrophoren Früchte nicht ausschließlich durch die Aufteilung durch die Hymenien entsteht, sondern daß auch die Verschmelzung mehrerer Anlagen die Ursache sein kann. Im oben erwähnten Fall der F. g wird man später kaum mehr entscheiden können, ob das Apothecium durch Verschmelzung oder durch Aufteilung

Fig. 9. Diagram of the type of gyral division in *Gyrophora*. Corresponding to the opening-furrow the immersed ascogenous hymenium splits longitudinally whereby the fissure margins prolify, forming the internal margins of the daughter gyri, the margins of the initial gyrus forming the external margins of them. In *c* a gyrus fragmentation is seen, being the starting point for a later chain formation if the fragments begin a gyral division.

enstanden ist. Immerhin ist die Aufteilung viel häufiger", an example which, however, on account of the false premises proves nothing. On page 234 Frey gives the following obscure statement of the formation of the gyrose apothecia: "Bei den stark gerillten Früchten bilden sich nicht Risse, sondern das rein vegetative Palisadenplechtenchym verdrängt die Hymenien, wächst stärker als dieselben, weshalb diese einsinken. So entstehen auf ganz einfache Weise die Rillen durch ein Wechselspiel der vegetativen und generativen Tendenzen. Bei den konzentrisch gerillten Früchten entsteht in der Mitte eine Säule von solchem vegetativem Palisadengeflecht, darum herum sinkt ein erster Ring Hymenium ein. In demselben können sich Lamellen von derbem Palisadengeflecht bilden, die die anfänglich einfache Rille ringsum tangential teilen. So entstehen weitere konzentrische Rillen". However, the essential part of the picture is the regular, dichotomous splitting of the hymenium under growth into gyri. A central column is present in the gyrose species only as a very transitory formation in the very youngest apothecia. A gyrus is frequently formed primarily without the formation of a central column.

The following statement seems to be untenable (l. c. p. 234): "Häufiger aber als diese konzentrische Rillung ist die unregelmäßige. Hierbei wächst der amphitheciale Thallusrand zunächst nur buchtenartig in die Schale des Gehäuses hinein, greift immer tiefer und teilt dieses auf. So ist auf Längsschnitten

sogar das Hypothecium durch amphitheciale Rindeneinsenkungen geteilt (vgl. z. B. F. 44d, 47h)". The figure references are partly to sections of *A. polyrrhiza* (cf. Pl. V fig. 8) to which I shall return later, partly to sections of a very regular and fine apothecium of *G. cylindrica*, similar to Pl. V. fig. 6 of my own illustrations. That the so-called amphithecial thallus edge has got nothing to do with the formation of gyri is clear when we remember that these structures, i. e. gyri with separating grooves, in all cases are developed by growth and dichotomous splitting which takes place concentrically within the intact amphithecium (cf. figs. 5 and 6) i. e. between the thallus edge and the central column or fissure. The fact that a new small apothecium in a series of species may be regenerated almost anywhere in the hymenial layer of older apothecia shows that these cells are still strongly plurivalent, and that the thallus cortex, contrary to the opinion of Frey (l. c. p. 232, 233), is not a necessary constituent of an amphithecium, even if this perhaps is the rule in the lower parts. There is no anatomical difference between the upper part of the amphithecium, i. e. the margin of the apothecium, on one side, and the margins of the gyri in the apothecia of the 3d and 4th groups and the margins of the fissures of the apothecia of the 1st and 2nd groups on the other side. They are all really homologous structures.

The kind of monstrous apothecial sections that may be obtained when no attention is paid to the methodically fundamental point of locating the section perpendicularly on the gyri may be seen in Frey's illustrations l. c. fig. 41, 49, 51 and 53. The right side of my section of *G. polyphylla* (Pl. V fig. 5) shows a similar thing and is due to the same cause. With a knowledge of the genesis of the gyri it is clear that the apothecium of *G. cylindrica* figured in Zahlbruckner: Lichenes, in Die Natürlichen Pflanzenfamilien 1926 p. 211, Fig. 100 is free imagination as far as the gyri are concerned.

Note should also be made of the fact that the grooves which occur in the apothecia of certain *Graphideae* (cf. Frey 1933 p. 237) in principle are quite different from the gyri of the *Umbilicariaceae*, and not comparable to these at all. The stripes to be seen here are only due to a periodic renewal of the amphithecium from within, in which way the older one is pressed out. At the

same time no splitting of the hymenial stripe takes place. Likewise are the fissures, which may be observed in the apothecium of *Icmadophila* and others not comparable to the "Rillung" (Frey 1933 p. 11) of the *Umbilicariaceae*.

After this diversion we may sum up the characteristic features of the apothecia of the 3d group: the ascogenous hymenium occurs in concentrically arranged gyri which are formed and reproduced by a dichotomous, longitudinal splitting taking place simultaneously with the growth. The apothecia are stalked and surrounded by a common, (more or less) entire margin formed by the outer margin of the outermost gyrus. — To this group belong the majority of our Scandinavian species: *G. arctica, cinereorufescens, corrugata, cylindrica, deusta, erosa, fuliginosa, hirsuta, hyperborea, murina, polyphylla, proboscidea* and *vellea*.

We now arrive at the 4th group (genus *Actinogyra*, cf. p. 28) which is numerically the smallest one. It bears important points of resemblance to the preceding group as the ascogenous hymenium is here also immersed in typical gyri, which open by a small middle furrow at the top (figs. 10 and 11). But the similarity goes no further. In contrast to the preceding group we here see that the gyri are radially arranged. On account of the radial growth over the thallus it is clear that the apothecia are stalkless and without continuous margin, lying like cushions on the thallus. In contrast to all the others they also lack a common excipulum. As it appears from the illustration fig. 10 the gyri are placed close together along the entire perifery, and it is therefore clear that they are continuously multiplying, not only growing in length, otherwise they would be growing apart as the apothecium increases in size. This reproduction of gyri is of a somewhat different kind than the splitting described for the preceding group. In the perifery of the apothecium we observe how (figs. 10 and 11) the gyri divide in the shape of a Y. During further growth the two Y branches approach each other more or less closely, and soon the tips of these branches again divide in the same manner. In this way new gyri are reproduced at the periphery to the extent that space allows. A longitudinal splitting as described for the preceding group

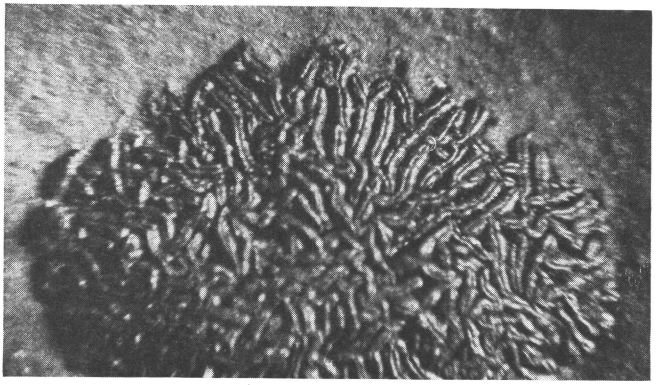


Fig. 10. Apothecium of *Actinogyra* type (4th group). Ascogenous hymenium in radially arranged gyri, multiplying by a Y branching of the peripheral ends. *A. polyrrhiza* (L.) Schol. Norway. Magn. 28 ×.

occurs here also, just as indication of a forking also may occur in the preceding group, particularly in the joungest stages of the development of the apothecia. However, each one is characteristic of its own group.

Between the radial gyral lamellae themselves, as well as between the lamellae and the thallus, splits very easily arise on account of uneaqual rate of growth (cf. Pl. V fig. 8). These splits may in part loosen the apothecium and may make the sectioning very difficult if, as in the methods here employed, no imbedding medium has been used.

In principle these apothecia originate from a single, small, frequently star-shaped initial gyrus. A central, distinct, column like that in 2nd and 3d group is only rarely seen. However, it is clear that two or more closely placed embryonic apothecia may unite to an aggregate, a process which we may observe in the apothecia of most lichens. But this has fundamentally nothing to do with the gyrose structure, contrary to the opinion of Frey (l. c. p. 234). Likewise it has nothing to do with the concentric or radial arrangement of the gyri. No more are the apothecia of the 4th group formed by any "amphitheciale Rindeneinsenkungen", which is the opinion of Frey (l. c. p. 234).

To sum up the most important characters in the structures of the apothecia of this 4th group we may state that its apo-

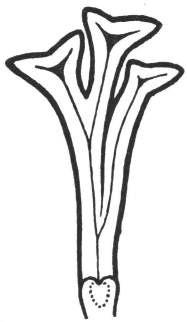


Fig. 11. Diagram of the type of gyral branching in *Actinogyra*. During the radial growth the peripheral ends of the gyri repeatedly branch.

thecia are characterized by an ascogenous hymenium in radially arranged gyri which multiply during growth by a Y shaped branching of the peripheral end of the gyrus. The apothecia are sessile, cushionshaped, with the greater part of their lower surface united with the thallus. A common excipulum and a continuous margin around the apothecium are lacking.

In the Scandinavian flora there is only one representative of this group, *A. polyrrhiza*, which is frequently sterile. From other parts of the world I have seen only two additional species, namely *A. Mühlenbergii* and *A. pulvinaria*. Most of the specimens of *U. angulata* Tuck. which I have examined belong here also, but they appear to me identical with *A. polyrrhiza*.

How great taxonomic importance is to be attached to the characters here described? I have already pointed out that these characters are typical group characters, according to which the very greater part of the species examined may be arranged naturally and unrestrained. The constancy of these characters is very great. However, in some specimens, especially within a few certain species exceptions may occur, but statistically these exceptions play a quite subordinate part. I shall here describe those cases of more or less distinct transitions between the 4 different groups which I have observed.

In the 1st group the nearest relatives of *U. pustulata*, viz. *U. pennsylvanica*, *caucasica* and *porphyrea* sometimes show one or another young apothecium with a small central, superficial tap-formation, which frequently drops off later and does

not seem to be a startingpoint for any later fissure formation in the older apothecia. Neither have I observed in these apothecia the characteristic, secondary fissure formation of the apothecia of the 2nd group. The irregular structure of this small tap, and its rare occurrence only in certain apothecia of certain individuals seem to point to abnormities. In any case, they do not leave any doubt as to which type the apothecium belongs to. These three cases are the only certain ones I have seen which may be designated as exceptions. It is of interest that all of them occurred within the very natural group *Lasalliae*, which is characterized by pustulate thallus and multilocular spores. This group may possibly in the future again be raised to generic rank. The secondary fissurre formation sometimes to be observed in older apothecia of the *Anthracinae* group is quite analogous with the one of the second group. However, there is no question of any transition as the central column of the young apothecium (v. l. the central fissure in the old apothecia) is always lacking (cf. Frey 1933 Figs. 58 a, b, d; 59 b; 61 d).

As in the 1st group deviations similarly occur also in the 2nd group. In *O. virginis*, especially as it seems in Himalayan specimens (*U. lecanocarpoides* Nyl.), and rarely also in *O. decussatus* and *Krascheninnikowii* the central column may sometimes be lacking in certain apothecia so that they get a quite plain disk. However, on careful examination remains of the central fissure may frequently be demonstrated. Young apothecia without umbilicus do occur though. However, in my opinion there can be no doubt as to the classification of the apothecia of *O. virginis*, and much the less so in the other species mentioned. In a single instance I have seen apothecia transitional from the 2nd to the 3d group, viz. in some specimens of *O. crustulosus* from Central-Europe. It was here observed in certain apothecia that a concentric splitting of the ascogenous hymenium into few, very coarse and not very typical gyri, had taken place around the strong, persistent, more or less cracked central papilla (cf. Frey 1933 p. 260, Fig. 35 a, c). All the other specimens of *O. crustulosus* which I have examined show apothecia typical of the 2nd group (cf. Pl. II fig. 1). If gyrose apothecia should prove to be general in material from Central Europe it seems to point towards

specific difference. In any case I have not observed anything like that in the copious material from Scandinavia.

In the 3d group, with its concentrically arranged gyri, apothecia, which are distinctly transitional to those of the 2nd group occur particularly in *G. cylindrica* var. *Delisei*, and also, as far as I can see from my scanty material, in *G. phaea* and *aprina*. In some apothecia or sometimes in all apothecia of one specimen may be seen an entirely incoordinated, irregular splitting of the hymenium so that the complicated, regular formation of gyri has come to a standstill, so to say. Such apothecia may in many cases hardly be distinguished from an apothecium of the 2nd group in which a strong secondary fissure formation of the ascogenous hymenium has taken place (cf. fig. 4 *a*). Altogether, there are perhaps only few species of the 3d group that may not exceptionally show single apothecia with this unsuccessfull gyrus formation, although perhaps no species shows it relatively so frequently as just the above mentioned *G. cylindrica* var. *Delisei*. On the other hand we should note that exactly in this variety *G. cylindrica* var. *Delisei* perhaps the greater part of all specimens has apothecia of the most characteristic, concentrically gyrose type there is to be seen (cf. fig. 5), and this is just the point. — From this it will appear that in certain cases it may not be possible from single specimens to decide to which of the groups 2 or 3 a species is to be referred. Before this is decided one ought always to have seen rather ample material with fully grown apothecia, preferably as large as possible.

A certain connection between the concentrically gyrose apothecia of the 3d group and the radially gyrose apothecia of the 4th group is conceivable when looking at the young apothecia in certain species. Especially in *G. erosa* and, as it seems, even more distinctly in some specimens seen of the American complex *G. angulata* (excl. of *A. polyrrhiza*) the apothecia are frequently triangular to angularly star-shaped when quite young. The apothecia of the 4th group could easily be considered as derived from such apothecia by a radial growth of the corners of the triangle with further dichotomous branching and union with the substratum. If, on the other hand, a strong longitudinal splitting (ad mod. 3rd group) of the radial gyri has taken place the radial

structure may naturally be more or less effaced. This I have seen in some specimens of *A. Mühlenbergii* from Siberia and also, really not fully so distinctly, in apothecia of *A. pulvinaria*, as seen in pl. III fig. 5.

The exceptions mentioned above in the form of more or less distinct transitional apothecia which may appear in certain individuals of certain species or varieties are of great interest as they seem to reflect a relationship between the four groups, connecting them in a natural way, at the same time not being able to obliterate the border lines between them. These characters of the apothecia are of fundamental importance for the classification of the *Umbilicariaceae* and can not be dispensed of in practice. I have had ample opportunity to demonstrate this in material from almost all over the world. Furthermore, as these characters are connected with the organs of fructification proper they should, a priori, be considered as of a high systematic importance. For these reasons I mean that a generic division is just as natural as it is desirable and necessary. In accordance with this the four groups will in the following discussion be designated by their resp. generic names *Umbilicaria*, *Omphalodiscus*, *Gyrophora* and *Actinogyra*, corresponding resp. to 1st, 2nd, 3d and 4th group.

It seems natural to conclude that these four genera are phylogenetically connected with each other, in such a way that the one is derived from the other in an order corresponding to the presentation given on the preceding pages and in the diagram fig. 12. The first genus, *Umbilicaria* has the most simply built apothecia. From such forms *Omphalodiscus* forms have probably arisen through the ages, viz. by the formation of a sterile central column in the apothecium. The tendency towards a lack of this central column, occasionally to be seen especially in *O. virginis*, might be interpreted as an atavism or rather a reminiscence, pointing to its descendancy from some old *Umbilicaria* form. However, it naturally follows that one cannot deny the possibility of the reverse being the case, viz. that we are here dealing with a phylogenetical process of reduction, eliminating a primary

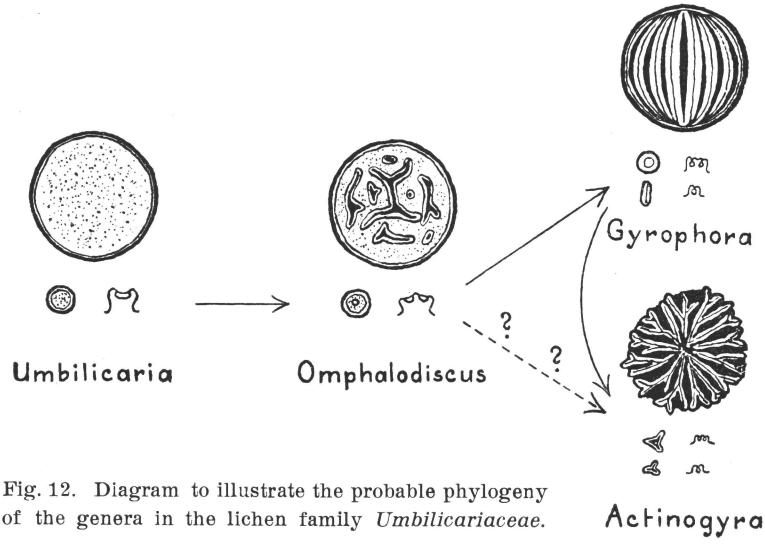


Fig. 12. Diagram to illustrate the probable phylogeny of the genera in the lichen family *Umbilicariaceae*.

central column. If so, such a phylogenetic reduction should not be compared with the secondary ontogenetic effacement of the central fissure which is sometimes seen in old apothecia of specimens where all the young ones are normally developed with a central sterile column (cf. fig. 4 *c*, p. 5). By a successive coordination of the incoordinated fissure formation in the *Omphalodiscus* apothecium and the simultaneous reduction of the hymenial faces to the opening furrows of the gyri we may picture the derivation of the *Gyrophora* apothecium. Here also the already mentioned occurrence of transitional apothecia back to the *Omphalodiscus* genus might be interpreted as reminiscences from this. A species, such as *G. phaea* where this occurs so relatively frequently may from this point of view be interpreted as a species which, phylogenetically regarded, has not yet wholly reached within the genus *Gyrophora*. In which manner the *Actinogyra* apothecium naturally may be thought to have been derived from the *Gyrophora* apothecium I have already described (p. 15), viz. by a radial growth of the small initial gyrus and its further forking. This development might well be thought to have occurred also directly from a young *Omphalodiscus* apothecium. However, this hypothesis offers certain difficulties,

namely the occurrence now and then of typical *Gyrophora* splitting in the radial gyri of the *Actinogyra* apothecium, as described on p. 11. This fact is best explained if we consider it a reminiscence, v. l. relict genes, from an earlier passing through the *Gyrophora* stage. To judge from the young apothecia, a species such as *G. erosa*, or the remarkable forms belonging to the American *G. angulata*-complex (cf. p. 15), seem to be species which have already taken their first step in their phylogenetic wandering towards *Actinogyra*. A matter which to a specially high degree links the three last mentioned genera *Omphalodiscus, Gyrophora* and *Actinogyra* together is that the young apothecia in all of them (±distinctly in *Actinogyra*) are omphalodiscous, i. e. with the ascogenous hymenium originating ring-shaped around a sterile central column (cf. fig. 12).

In which way are now the different representatives within each genus genetically connected with each other? This matter is assuredly complicated, but one could imagine the following way: the genus *Umbilicaria* with the most simple apothecia is to be regarded the primeval genus of the *Umbilicariaceae*, partly persisting up to this day. In the course of time it has, probably repeatedly, split off *Omphalodiscus* forms which partly yet persist. These forms have likewise through the ages split off *Gyrophora*-(possibly also *Actinogyra*-) forms, which persist in great numbers. Some few forms of these have gone yet further and developed into *Actinogyra* forms. In addition to these relatively different forms (presumably section types), which are directly and rectilinearily derived from forms belonging to the phylogenetically nearest lower genus, the genera at present also contain forms which are the result of a species formation within the genus, such as in all probability is the case with closely similar forms, e. g. *G. arctica — corrugata — hyperborea* or *G. hirsuta — murina* and others.

In other words it will be understood that within each genus all those, phylogenetically more or less related, forms are gathered which, morphologically regarded, have today reached the same stage of their phylogenetic evolution, the last obtainable stage of which at the present day seems to be *Actinogyra*. The genus abstractions *Umbilicaria, Omphalodiscus, Gyrophora*

and *Actinogyra* are themselves the four morphologically well characterizeable stages in this line of evolution. — In many instances of taxonomy, and also here, it may regrettably but nevertheless assuredly sometimes happen that two species which are placed in different genera of what we call a natural system may in reality be more nearly related than two species classed together in the same genus.

In the following list of species which I have had the opportunity to study more closely, I am giving the species in alphabetical order within the various genera, or just indicating a more natural grouping. The final division into subgenera, sections, or even more genera I am for the present leaving open. With regard to nomenclature I have not at all points followed the works of Frey as I have found it desireable to be somewhat less radical. As to the complete synonymy I may especially refer to the works of Zahlbruckner and Frey.

Genus *Umbilicaria* (Hoffm.) emend. Schol.

Thallus foliaceus, mono- vel polyphyllus, ad substratum umbilico adfixus. Apothecia lecideina, stipitata, marginata. Apothecia juvenilia disciformia, discus omnino hymenio ascogeno tectus, papilla centrali sterili destitutus. Discus laevigatus vel in aetate deinde fissuris secundariis, irregulariter dispositis, angulatis instructus.

According to the structure of the apothecia the following species belong to this genus:

Umbilicaria laevis (Schaer.) Frey.

Umbilicaria leiocarpa D. C.

Umbilicaria Lyngei Schol. spec. nov. Pl. I fig. 1 and Pl. IV fig. 1. (Pl. III fig. 3, 4 and Pl. VI fig. 4, in Lynge and Scholander 1932, sub. nom. *Gyrophora decussata* (Vill.) Zahlbr.). Syn. *Gyrophora discolor* Th. Fr. f. *perforata* Lynge in Stud. on the Lich. Flora of Norway. Vid.-Selsk. Skr. I. Mat.-Nat. Kl. No. 7, 1921 p. 91.

Thallus tenuis, mono- vel subpolyphyllus, diam. vulgo 3—10 cm, superne minute elevato-reticulatus vel interdum sublaevigatus, praecipue peripheriam versus, colore cinerascens vel obscure cinereus, saepe p. p. fuscescens, madefactus fuscus et subpellucidus. Laciniae

secundariae epithallinae rarissimae, thallus etiam isidiis sorediisque destitutus. Thallus in margine tenuis, saepe perforatus, haud revolutus, sed in margine vulgo subadscendens, et saepe in margine morbose cinereus et laciniatus. Thallus inferne rhizinis destitutus, minute et irregulariter fuliginosus, vulgo hinc inde efuliginosus et ibi pallide fuscescens vel pallide rosaceus, et ab umbilico plicis radiatis sat profundis instructus.

Apothecia raro evoluta, peripheriam thalli versus sparse disposita, stipitata, diam. 1—2 mm., discus laevigatus, papilla centrali vel fissura centrali destitutus, margo tenuis, elevatus, deinde subevanescens. Hymenium 80—110 μ altum, sporae octonae, simplices vel interdum uniseptatae, 9—16 × 3—7 μ.

Typus: North East Greenland: Kap Humboldt, leg. Schol. August 3, 1930. Hb. Oslo. This specimen is figured in Lynge and Scholander 1932, Pl. IV fig. 1 and Pl. III fig. 3.

The thallus is 100—250 μ thick. Upper cortex 20—60 μ thick, built up of densely interlaced, thick-walled hyphae, in its exterior part brown, and covered by a more or less distinct and very uneven, uncoloured stratum of decomposed, dead hyphae, increasing in thickness towards the centre of the thallus. The stratum gonidiale is not well developed, discontinuous, with more or less scattered gonidia. The stratum medullare is composed of loosely contexted, thin-walled hyphae, it is also poorly developed, thin, 20—70 μ in thickness, gradually passing into the lower cortex. The hyphae of the latter are thick-walled, sclerenchymatic, densely contexted and not distinct. The lower cortex is 50—100 μ in thickness, in its exterior part unequally thick, built up of irregular, dark-brown, relatively thin-walled hyphae with numerous dead and deformed hyphae immixed, the whole of this exterior part composing the more or less uneven, fuliginous under side of the plant. Hypothecium 100—200 μ thick.

Habitat: cliffs and boulders, preferably in screes at high altitudes (found up to 1300 m altitude in N. E. Greenland), not nitro- or ornitho-coprophilous, in contrast to *Omphalodiscus decussatus* (cf. p. 23). I have seen well determined plants from the following areas (a detailed list of localities will be published later): Novaya Zemlya not common; Svalbard rather common; Scandinavia (sterile) very rare; N. E. Greenland very common, West Greenland, Ellesmereland. Probably it also occurs farther

west in the arctic to subarctic America (Rocky Mountains). The species seems to have its greatest distribution in west arctic regions. Whether it occurs also in the Alps I dare not yet say for certain as I have seen no fertile specimens from these, nor sterile specimens that would allow a certain identification. However, *Omphalodiscus decussatus*, from which it in many cases may hardly be distinguished in sterile condition, especially when the specimens are small, and with which it has always been confused up to this date, occurs with certainty in the Alps as it has been found and identified there fructifying. I have myself seen fertile specimens of this *O. decussatus* from Asia Minor.

U. Lyngei belongs entirely in the natural section *Anthracinae*, and of the European species it seems to be most closely related to the more southern *U. leiocarpa*. It should, however, hardly be confused with this species on account of the characteristic thallus of *U. leiocarpa* which is areolated by fissures and not as a rule reticulated, or, if so, it is most distinct at the periphery (cf. Frey 1933 p. 400). In all probability the specimen mentioned by Du Rietz (1925 p. 8) from Lomfjorden in Northern Svalbard is *U. Lyngei* and not *U. leiocarpa*. The former is of rather common occurrence there but I never found *U. leiocarpa* in Svalbard and not in Greenland.

Neither is it to be confused with *U. cinerascens* as this species is characterized by a non reticulated surface, distinct polyphylly, and by warts on the lower surface arranged radially from the umbilicus (cf. Frey 1933 p. 378). *O. decussatus* may cause greater difficulties in regard to a differential diagnosis when one is dealing with sterile specimens, and that is unfortunately the rule, especially in southern material. One should pay special attention to the following points: *U. Lyngei*, thin thallus with a fine, prominent reticulum, lower surface unevenly and finely sooty, frequently with radial, soft folds about the umbilicus; *O. decussatus*: thick thallus, colour more or less pale grey to whitish from cortical taps, reticulum coarse and prominent towards the centre, towards the periphery passing into tubercles like in *G. corrugata*, small epithalline secondary lobes common. Lower surface almost always entirely soft-velvety black with or without

an indistinct fold structure at the umbilicus, frequently somewhat lacunose (otherwise see the descriptions p. 19 and p. 23). However, the apothecia of these two species are as different as day and night (cf. Pl. I) and the morphological transitions seen in the vegetative parts are one of the many instances in nature of similarity by convergence. An actual genetic transition between these two species seems to me quite inconceivable. *U. Lyngei* has on an average somewhat larger spores than *O. decussata.*

The original material of *G. discolor* Th. Fr. in Lich. Scand. I, 1871 p. 167 in Hb. Upsala is a mixture of typical *U. Lyngei* and typical *O. decussatus.*

The new species here described I dedicate with gratitude to my friend Dr. Bernt Lynge.

Umbilicaria microphylla Massal. Pl. I fig. 2.
Umbilicaria rigida (Du Rietz) Frey. Pl. IV fig. 2.
Umbilicaria subglabra Harm. Textfig. 1.

The species here mentioned all belong to the *Anthracinae* section, characterized i. a. by its simple spores. To this section belongs possibly also *Umbilicaria cinerascens* (Arn.) Frey, but that cannot be definitely settled, its apothecia being as yet unknown. It may as well be a *Gyrophora*, related to *G. polyphylla*, as maintained by Du Rietz (1925 p. 13).

The genus *Umbilicaria* also includes all the species of the *Lasalliae* section, characterized by their muriform spores and pustulate thallus, viz. the following 6 species:

Umbilicaria caucasica Lojka.
Umbilicaria glauca Stitz.
Umbilicaria membranacea Laur.
Umbilicaria pennsylvanica Hoffm. Pl. IV fig. 3.
Umbilicaria pustulata Hoffm. Pl. I fig. 3 and Pl. IV fig. 4.
Umbilicaria rubiginosa Pers.

Like in these species muriform spores are also found in the following three species:

Umbilicaria dichroa Nyl. Pl. IV fig. 5.
Umbilicaria haplocarpa Nyl.
Umbilicaria Krempelhuberi Müll. Arg.

Genus *Omphalodiscus* Schol. gen. nov.

Thallus foliaceus, mono- vel subpolyphyllus, substrato umbilico adfixus. Apothecia lecideina, plus minusve stipitata, marginata. Apothecia juvenilia columna centrali sterili prominenti instructa, hymenium ascogenum inter columnam et marginem apothecii evolutum. Columna interdum in aetate persistens, sed vulgo in fissuram centrali plus minusve ramosam et angulatam transiens. Hymenium ascogenum tum disciforme, inter fissuram et marginem apothecii evolutum, saepe hinc inde fissuris irregularibus secundariis angulatis interruptum.

According to the structure of the apothecia the following species belong to this genus:

Omphalodiscus decussatus (Vill.) Schol. emend., comb. nov. Textfig. 3; Pl. I fig. 4 and Pl. IV fig. 6. (*Lichen decussatus* Vill. in Hist. Plant. Dauphiné vol. III, 1789 p. 964, p. p.).

Thallus crassus, vulgo monophyllus, diam. 2—5 cm, superne grosse reticulatus, peripheriam versus minus distincte reticulatus, sed magis rugosus (ut in *G. corrugata*), superne cinereo-albidus, fere pruinosus, interdum magis obscure cinerascens, fusco-cinerascens, madefactus impellucidus inter rugas saepe distincte virescens. Lobi epithallini frequenter adsunt. Thallus in margine crassus, plus minusve recurvatus, imperforatus, sed plus minusve laciniatus. Thallus subtus pulchre nigrescens, saepe subrugosus, rarius centrum versus plicis crassis, rugosis, irregulariter radiatis instructus.

Apothecia rara, diam. 1—2 (—3) mm, ut in typo generis evoluta, papilla centrali sterili deinde in fissuram centralem transiente instructa, hymenium ascogenum inter papillam (fissuram) et marginem apothecii dispositum, saepe fissuris secundariis interruptum. Hymenium 90—120 μ, sporae octonae, simplices, rarius uniseptatae, 8—12 $\times$ 3—4 μ.

Typus: Spitsbergen, Advent Bay, "ved den gamle grube". Leg. B. Lynge August 25, 1926. Hb. Oslo. This type plant is illustrated in tab. IV fig. 6 of the present paper.

The thallus is 200—300 μ in thickness. The upper cortex 50—100 μ, built up of densely interlaced thick-walled hyphae, brownish in their upper part, and covered by an uneven, amorphous verrucose detritus, increasing in thickness towards the centre. The stratum gonidiale is 30—50 μ thick, compact and rather continuous, the gonidia are often arranged in distinctly vertical columns. The stratum medullare is composed of loosely

contexted, rather thin-walled hyphae. The lower cortex is 50—100 μ in thickness, composed of sclerenchymatic, densely contexted hyphae which are individually indistinct, and covered by an even stratum of very regular globular, dark-brown cells, forming the characteristic velvet-black under side of the thallus, just on account of their regularity. Along the margin the lower cortex often develops a small wall, giving the margin the appearance of being doubled.

Habitat: cliffs and boulders, in the Arctic distinctly nitrophilous, on bird stones and in bird-cliffs, frequently associated with other nitrophilous or relatively nitrophilous lichens, such as *Gyrophora arctica*, *Omphalodiscus Krascheninnikovii*, *Xanthoria candelaria*, *Physcia dubia*, *Parmelia infumata* a. o. In Central Europe nitrophily does not seem to be noticeable. In other words this is one of the many instances of relative nitrophily, the species being distinctly nitrophilous in the poor arctic regions but otherwise not distinctly nitrophilous. I have seen specimens from the following areas (a detailed list of localities will be published later): Novaya Zemlya common, Frans Josef Land, Svalbard common, N. E. Greenland common, West Greenland, Scandinavia rare, the Alps, Asia Minor.

U. Lyngei (cf. the differential diagnosis p. 21) belongs entirely to the species of the *Anthracinae* section whereas *O. decussatus* is far removed from these species, being in all parts nearly related to *O. Krascheninnikovii*. The latter is, however, clearly distinguished from *O. decussatus* by its light coloured, brown under surface, always ample fertility, and smaller size. In contrast to *O. Krascheninnikovii*, *O. decussatus* has never been found with rhizines.

Omphalodiscus Formosanus (Frey) Schol. comb. nov. (*Umbilicaria Formosana* Frey in Hedwigia. Bd. LXXI p. 115, 1931). This species should be compared with the *O. Krascheninnikovii* f. *rhizinosa* mentioned below.

Omphalodiscus Krascheninnikovii (Sav.) Schol. comb. nov. Text-fig. 2 and 4; Pl. IV fig. 7. (*Gyrophora Krascheninnikovii* Savicz in Bull. Jard. Imp. Bot. Pierre le Grand, vol. XIV, 1914 p. 117).

It appears from a study of the original material that this exceedingly characteristic species, which is closely related to

O. decussatus has been redescribed under other names at later dates. Synonyms are: *Gyrophora Hulténii* Du Rietz in Arkiv för Botanik, vol. XXII A. No. 13, 1929 p. 14, and my own *Gyrophora polaris* in Lynge and Scholander Skrifter om Svalbard og Ishavet Nr. 41, 1932 p. 57. Judging from the description, and a fragment which Dr. Frey has kindly sent me, *U. Formosana* Frey (Hedwigia Bd. LXXI, 1931 p. 115) may possibly also belong to this species. To judge from illustrations and description by Herre in Contr. from the U. S. Nat. Herb. Vol. 13, part 10, 1911 p. 316 it is quite clear that his *G. reticulata* cannot be *O. decussatus*, but in all probability it must be *O. Krascheninnikovii*. It is stated to be partly very common in the Sierra Nevada high mountains and it is also found in Colorado, thus being widely distributed, probably mostly so in western regions. In contrast to *O. decussatus* it is not always glabrous. Particularly some of the Kamtchatka specimens of Hultén are copiously hairy below, I have also seen a few hairy specimens from Svalbard and one from West Greenland. This hairy form might suitably be named *O. Krascheninnikovii* (Sav.) Schol. f. ***rhizinosa*** nov. f.: differt a f. typica subtus rhizinosa. *U. Formosana* Frey is also described as hairy below.

Omphalodiscus Ruebelianus (Du Rietz et Frey) Schol. comb. nov. Pl. I fig. 5. (*Gyrophora Ruebeliana* Du Rietz et Frey, Frey in Hedwigia LXIX 1929 p. 244).

Omphalodiscus virginis (Schaer.) Schol. comb. nov. Pl. I fig. 6. (*Umbilicaria virginis* Schaerer in Biblioth. universelle de Genève, t. 36, 1841 p. 153).

To judge from the description and figure of the apothecia of *O. virginis* var. *Meylani* Frey (1933 p. 318 and fig. 46 a, p. 319) this variety cannot be an *Omphalodiscus*, but must be a form of *Gyrophora cylindrica*, and for this purpose, viz. to describe a new variety or form of such a polymorphic species as *G. cylindrica* the material seems to me to be too scanty. In any case the matter should be reconsidered after the lines here proposed before the number of varieties or forms of *G. cylindrica* is further increased.

In addition to this *Decussatae* section of *Omphalodiscus* with simple spores we have the *Spodochroae* section with its more or less constant multilocular spores:

Omphalodiscus crustulosus (Ach.) Schol. comb. nov. Pl. II fig. 1. (*Gyrophora crustulosa* Acharius in Lich. Univ. 1810 p. 673).

All the copious material of the Scandinavian specimens of *O. crustulosus* which I have seen has typical *Omphalodiscus* apothecia as seen in Pl. II fig. 1. As already mentioned (p. 14) I have seen something in the line of an exception in some Central European specimens: Arn. Lich. Exsic. 1102. From the illustrations of var. *badiofusca* Frey (1933 p. 264, Fig. 36 c) and from a few specimens examined from "Alpen der Dauphinée" Migulae, Krypt. Exs. No. 268 and from "Savoische Alpen" idem No. 194 it appears that this is a typical *Gyrophora* not to be regarded as a variety of a species of *Omphalodiscus*. It seems to me that these amply fertile specimens are most closely related to *G. cinereorufescens* (Frey) Schol. and for this reason it is here listed as a variety of this species (cf. p. 28). Possibly this is a new species, but as I have seen too little material I will not now definitely express my opinion on this matter. It seems to me necessary that the Central-European forms of *O. crustulosus* must be subjected to a renewed revision along the lines proposed in this paper.

Omphalodiscus depressus (Frey) Schol. comb. nov. (*Umbilicaria depressa* Frey, 1933 p. 269).

Omphalodiscus spodochrous (Ach.) Schol. comb. nov. Pl. II fig. 2; Pl. IV fig. 8. (*Gyrophora spodochroa* Acharius in Meth. Lich. 1803 p. 108).

Genus *Gyrophora* (Ach.) emend. Schol.

Thallus foliaceus, mono- vel subpolyphyllus, ad substratum umbilico adfixus. Apothecia lecideina, stipitata. Hymenium ascogenum in plicis aequilatis (gyris) inclusum, quarum omnes rima media longitudinali hiant. Gyri concentrici, in gyros novos fissione dichotoma per rimam mediam se dividentes. Discus margine (±) distincto et continuo circumdatus, ex extremo margine gyri marginalis formatus. Apothecia excipulo communi continuoque instructus.

From the structure of the apothecia the following more or less distinct species belong to this genus:

Gyrophora arctica Ach. Pl. II fig. 3; Pl. V fig. 1.

?***Gyrophora cinerascens*** Arn. (sterilis, cf. p. 22).

Gyrophora corsicae (Frey) Schol. comb. nov. (*Umbilicaria corsicae* Frey in Hedwigia Bd. LXXI, 1931 p. 114). To judge from a small fragment kindly sent me by Dr. Frey this is a *Gyrophora*.

Gyrophora corrugata Arn.

Gyrophora intermedia (Frey) Schol. comb. nov. (*Umbilicaria intermedia* Frey, Zahlbruckner: Lichenes rariores exsiccati, N. 300.)

Gyrophora cylindrica (L.) Ach. Pl. II fig. 4, with varieties *Delisei* Despr., textfig. 5; Pl. V fig. 2 and *fimbriata* Ach., *denudata* Turn., *tornata* Ach. and *corrugatoides* (Frey) Schol. comb. nov. (*Umbilicaria cylindrica* Delise var. *corrugatoides* Frey, 1933 p. 334).

Gyrophora deusta (L.) Ach. Pl. II fig. 5.

Gyrophora Dillenii (Tuck.) Müll. Arg. Pl. II fig. 6.

Gyrophora erosa (Web.) Ach. Pl. V fig. 3.

Gyrophora esculenta Miyoshi. Pl. III fig. 1.

Gyrophora fuliginosa Havås (seen fertile in S. E. Greenland 1932, auth.).

Gyrophora hirsuta (Sw.) Ach. Pl. V fig. 4, with its varieties *papyria* Ach., *melanotricha* (Flot.) Schol. comb. nov. (*Umbilicaria hirsuta* Ach. var. *melanotricha* Flot. in 28. Jahresber. Schlesisch. Gesellschaft vaterl. Kultur 1850 p. 143); var. *pyrenaica* (Frey) Schol. comb. nov. (*Umbilicaria hirsuta* Ach. emend. Frey var. *pyrenaica* Frey, 1933 p. 296).

Gyrophora hyperborea Ach. Text fig. 8.

Gyrophora murina Ach.

Gyrophora phaea (Tuck.) Nyl.

Gyrophora polyphylla (L.) Funck. Pl. III fig. 2; Pl. V fig. 5.

Gyrophora proboscidea (L.) Ach. Textfig. 6; Pl. III fig. 3.

Gyrophora vellea (L.) Ach. Pl. V fig. 6.

The following species with more or less constantly occurring multilocular spores have *Gyrophora* apothecia:

Gyrophora angulata (Tuck.) Herre. The apothecia are described as having a thick persistent margin (cf. Tuckerman 1882 p. 88). Multilocular spores seem to be doubtful (cf. Frey 1931 p. 99). Most of the specimens which I have seen designated as *G. angulata* have been, as far as I can see, typical *Actinogyra polyrrhiza* (cf. p. 13).

Gyrophora calvescens Nyl.

Gyrophora caroliniana (Tuck.) Schol. comb. nov. (*Umbilicaria caroliniana* Tuck. in Proceed. Americ. Acad. Arts and Scienc., vol. VIII, 1877 p. 167).

Gyrophora cinereorufescens (Frey) Schol. comb. nov. (*Umbilicaria cinereorufescens* (Schaer.) Frey in Hedwigia, Bd. LXXI, 1931 p. 109).

Gyrophora cinereorufescens (Frey) Schol. var. *badiofusca* (Frey) Schol. comb. nov., ad interim (cf. p. 26) (*Umbilicaria crustulosa* Frey var. *badiofusca* Frey, 1933 p. 264).

Gyrophora semitensis (Tuck.) Schol. comb. nov. (*Umbilicaria semitensis* Tuck. Gener. Lich., 1872 p. 31).

Genus *Actinogyra* Schol. gen. nov.

Thallus foliaceus, mono- vel polyphyllus, ad substratum umbilico adfixus. Apothecia lecideina, pulvinata, estipitata. Hymenium ascogenum in plicis aequilatis (gyris) inclusum, quarum omnes rima media longitudinali hiant. Gyri supra thallus radiantes, in gyros novos furcatione apicum peripheric orum se dividentes; interdum insuper in gyris radiantibus fissiones longitudinales ut in genere praecedenti observantur. Apothecia subtus omnino vel pro maxima parte ad thallum affixa, excipulo margineque communi destituta.

I have only seen the following three species belonging to this genus:

Actinogyra Mühlenbergii (Ach.) Schol. comb. nov. Pl. III fig. 4; Pl. V fig. 7. (*Gyrophora Mühlenbergii* Acharius in Lichenogr. Univers., 1810 p. 227).

Actinogyra polyrrhiza (L.) Schol. comb. nov. Textfig. 10; Pl. III fig. 6; Pl. V fig. 8. (*Lichen polyrrhizos* Linnaeus in Spec. Plant., 1753 p. 1151).

Actinogyra polyrrhiza (L.) Schol. var. *luxurians* (Ach.) Schol. comb. nov. (*Gyrophora pellita* Ach. var. *luxurians* Acharius in Kgl. Vet. Akad. Nya Handl. 1808 p. 276).

Actinogyra pulvinaria (Sav.) Schol. comb. nov. Pl. III fig. 5. (*Gyrophora pulvinaria* Savicz in Bull. Jard. Imp. Bot. Pierre le Grand, vol. XIV, 1914 p. 117).

I wish to express my most cordial thanks to my friend Dr. phil. Bernt Lynge, Farmasøitisk Institutt, Oslo, for all help and fruitful suggestions during my work and for permitting me freely to make use of his extensive library.

Further I wish to tender my best thanks to Professor Dr. med. K. E. Schreiner, Anatomisk Institutt, Oslo, who has generously given me the opportunity of benefiting by the facilities of the laboratory of his institute. I am much indebted to Mr. Alf Søderholm, curator at the Anatomisk Institutt, Oslo, who has kindly placed the micro-photographical equipment of the institute at my disposal, and who has given me valuable advise during my photographical work.

In addition to the lichen collections in the Bot. Mus. in Oslo I have seen material from Professor Dr. phil. E. Du Rietz, Växtbiologiska Institutionen, Upsala; Dr. phil. E. Frey, Bern; Kungliga Riksmuseet, Stockhom, and Bergens Museum, to which scientists and directors of the institutes I wish to express my thanks.

The Botanical Museum of the University of Oslo, Sept. 1934.

Methods.

As it may possibly be of some interest to lichenologists I here allow myself to describe a very quick, good and safe micro-method without the use of time-wasting imbedding-media. The part of the lichen to be studied is moistened with absolute alcohol, then with water, and the piece is cut out with scissors or knife. It is placed, carefully orientated, between two pieces of Sambucus pith which are then enveloped in a strip of paper and tied together with twine by clove-hitch. It is placed in the microtome orientated in such a way that the slit with the object is perpendicular to the longitudinal direction of the knife, or at a somewhat acuter angle to this, the apex pointing away from us. The best knife to be used is a short, ordinary microtomeknife with a new Gilette blade fastened on it by a simple spring- or screw arrangement. The edge of the Gilette blade should not project more than a mm beyond that of the knife. This knife arrangement is attached to the sliding-block at very narrow angle to the direction of movement so that the edge of the Gilette blade slides (saws) very obliquely, at its

full length through the object when sectioning. Before sectioning 96 % alcohol is poured over the Sambucus pith with the object, which are kept wet with this all through the sectioning (cf. the celloidin method!). This is an important point which makes the knife do service three times as long as it otherwise would, and, furthermore, the sections may without difficulty be brought down to 10 μ in serial sections, and entire, simple sections may be brought down to 4 μ. The constant water content of the alcohol makes it possible all the time to control the degree of softness of the lichen preventing that it turns hard on drying, and, furthermore, the alcohol acts in oiling the knife. One should to great advantage place a binocular over the microtome, making it easier to follow the sectioning and to catch the delicate sections on the needle with a curved point, which has been dipped in absolute alcohol. Each section is immediately transferred to absolute alcohol to drive out the air. From absolute alcohol the sections are transferred to alcohols of lower percentages and then to any medium desired. Eventually adhering pith is easily removed in the lower alcohols. To give an example, I frequently transfer the sections through water to glycerin. When the glycerin sections are to be sealed they are heated on a plate and enclosed by a ring of warm Canada balsam which should be very thick when cold; the sections are then at once placed to cool. If the Canada balsam is so thin as it is commonly used it will run under the cover glass, replace the glycerin, and do irreparable damage.

Optics used for the photos in direct light, objective: Zeiss Planar 1:4,5 F′ 20 mm; in textfig. 7, Zeiss achromate 10 ×. For the sections Zeiss achromate 10 ×, in textfig. 3 idem 40 ×. As ocular in all cases a common Huygen's do., the strength of this and the length of the bellowoutpull varying according to requirement. All photographs have been taken on Agfa Chromo Isolar plates.

Material used for the text figures:

Fig. 1. *Umbilicaria subglabra* Harm. var. *pallens* Frey. French alps, Dauphiné, la Bernarde. Leg. Frey and Schmidt Aug. 10, 1932. Hb. Oslo.

» 2. *Omphalodiscus Krascheninnikovii* (Sav.) Schol. N.E. Greenland, Revet in Claveringfj. Leg. Scholander July 22, 1930. Hb. Oslo.

» 3. *Omphalodiscus decussatus* (Vill.) Schol. Spitsbergen, Advent Bay. Leg. Lynge Aug. 25, 1926. Hb. Oslo.

» 4. *Omphalodiscus Krascheninnikovii* (Sav.) Schol. N.E. Greenland, Revet in Claveringfj. Leg. Scholander July 22, 1930. Hb. Oslo.

Fig. 5. *Gyrophora cylindrica* (L.) Ach. var. *Delisei* Despr. Jan Mayen. Leg. Lid Aug. 2, 1930. Hb. Oslo.

» 6. *Gyrophora proboscidea* (L.) Ach. Norway, Galdhøpiggen. Leg. R. Jørgensen July 22, 1931. Hb. Oslo.

» 8. *Gyrophora hyperborea* Ach. Norway, Voss at Vetasjuvet. Leg. Lid Aug. 30, 1922. Hb. Oslo.

» 10. *Actinogyra polyrrhiza* (L.) Schol. Norway, Stavanger Amt at Rægefj. Leg. Havås Aug. 1905. Hb. Oslo.

Special Literature.

(For other literature cited, see the text).

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Zahlbruckner, A. 1927. Catalogus Lichenum Universalis. Bd. IV. Berlin.

— 1932. Ibidem Bd. VIII. Berlin.

Pl. I.

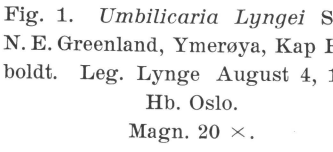


Fig. 1. *Umbilicaria Lyngei* Schol. N. E. Greenland, Ymerøya, Kap Humboldt. Leg. Lynge August 4, 1929. Hb. Oslo.
Magn. 20 ×.

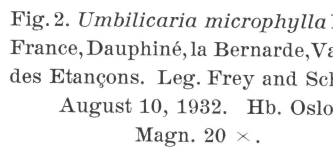


Fig. 2. *Umbilicaria microphylla* Mass. France, Dauphiné, la Bernarde, Vallons des Etançons. Leg. Frey and Schmidt August 10, 1932. Hb. Oslo.
Magn. 20 ×.

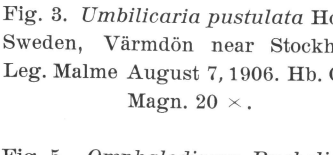


Fig. 3. *Umbilicaria pustulata* Hoffm. Sweden, Värmdön near Stockholm. Leg. Malme August 7, 1906. Hb. Oslo.
Magn. 20 ×.

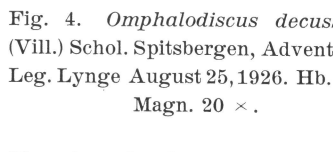


Fig. 4. *Omphalodiscus decussatus* (Vill.) Schol. Spitsbergen, Advent Bay. Leg. Lynge August 25, 1926. Hb. Oslo.
Magn. 20 ×.

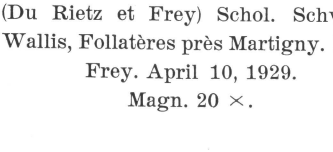


Fig. 5. *Omphalodiscus Ruebelianus* (Du Rietz et Frey) Schol. Schweiz, Wallis, Follatères près Martigny. Leg. Frey. April 10, 1929.
Magn. 20 ×.

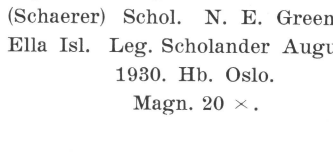


Fig. 6. *Omphalodiscus virginis* (Schaerer) Schol. N. E. Greenland, Ella Isl. Leg. Scholander August 8, 1930. Hb. Oslo.
Magn. 20 ×.

Pl. II.

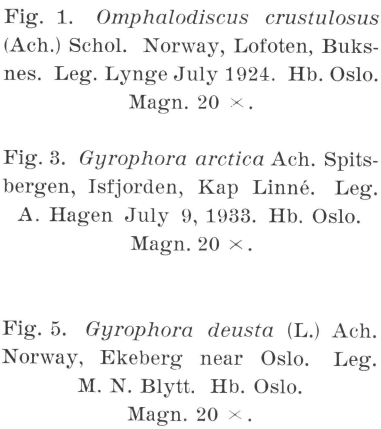


Fig. 1. *Omphalodiscus crustulosus* (Ach.) Schol. Norway, Lofoten, Buksnes. Leg. Lynge July 1924. Hb. Oslo. Magn. 20 ×.

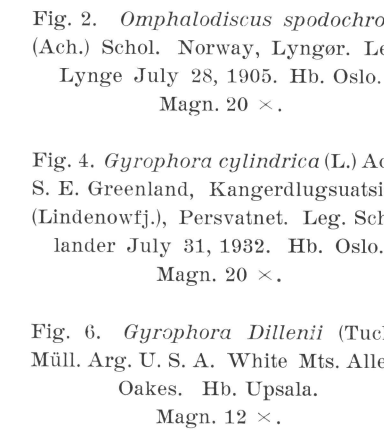


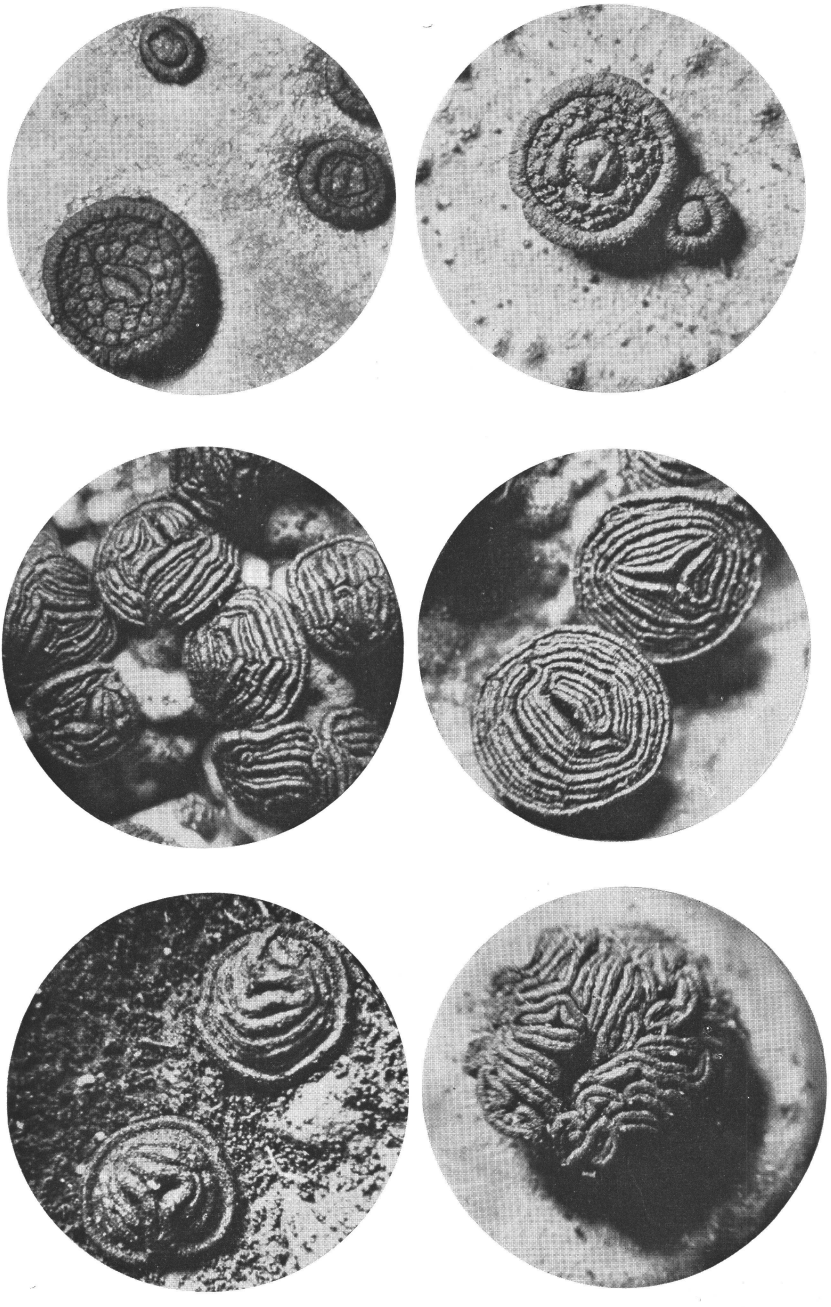
Fig. 2. *Omphalodiscus spodochrous* (Ach.) Schol. Norway, Lyngør. Leg. Lynge July 28, 1905. Hb. Oslo. Magn. 20 ×.

Fig. 3. *Gyrophora arctica* Ach. Spitsbergen, Isfjorden, Kap Linné. Leg. A. Hagen July 9, 1933. Hb. Oslo. Magn. 20 ×.

Fig. 4. *Gyrophora cylindrica* (L.) Ach. S. E. Greenland, Kangerdlugsuatsiak (Lindenowfj.), Persvatnet. Leg. Scholander July 31, 1932. Hb. Oslo. Magn. 20 ×.

Fig. 5. *Gyrophora deusta* (L.) Ach. Norway, Ekeberg near Oslo. Leg. M. N. Blytt. Hb. Oslo. Magn. 20 ×.

Fig. 6. *Gyrophora Dillenii* (Tuck.) Müll. Arg. U. S. A. White Mts. Allen, Oakes. Hb. Upsala. Magn. 12 ×.



Pl. III.

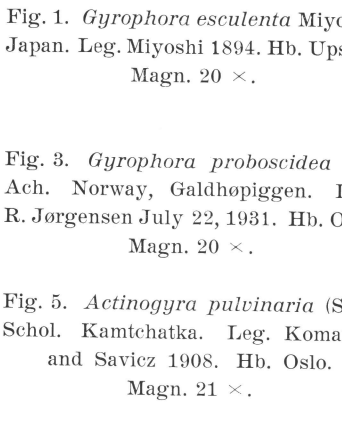


Fig. 1. *Gyrophora esculenta* Miyoshi. Japan. Leg. Miyoshi 1894. Hb. Upsala. Magn. 20 ×.

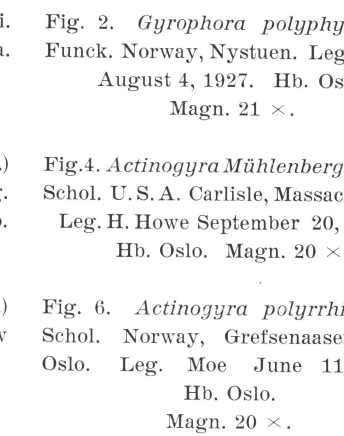


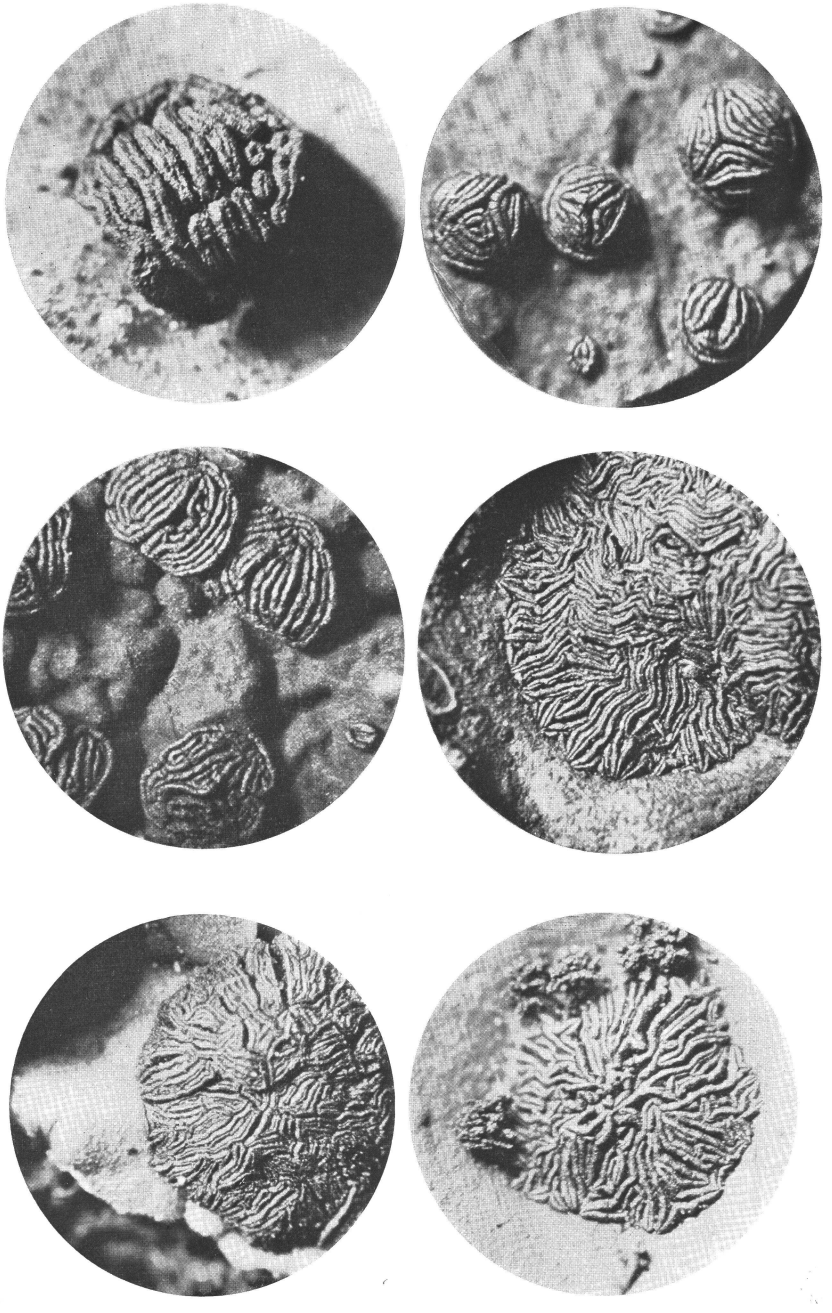
Fig. 2. *Gyrophora polyphylla* (L.) Funck. Norway, Nystuen. Leg. Lynge August 4, 1927. Hb. Oslo. Magn. 21 ×.

Fig. 3. *Gyrophora proboscidea* (L.) Ach. Norway, Galdhøpiggen. Leg. R. Jørgensen July 22, 1931. Hb. Oslo. Magn. 20 ×.

Fig. 4. *Actinogyra Mühlenbergii* (Ach.) Schol. U. S. A. Carlisle, Massachusetts. Leg. H. Howe September 20, 1905. Hb. Oslo. Magn. 20 ×.

Fig. 5. *Actinogyra pulvinaria* (Sav.) Schol. Kamtchatka. Leg. Komarow and Savicz 1908. Hb. Oslo. Magn. 21 ×.

Fig. 6. *Actinogyra polyrrhiza* (L.) Schol. Norway, Grefsenaasen near Oslo. Leg. Moe June 11, 1869. Hb. Oslo. Magn. 20 ×.



Pl. IV.

Fig. 1. *Umbilicaria Lyngei* Schol. N. E. Greenland, Kap Humboldt. Leg. Scholander August 3, 1930. Hb. Oslo. Magn. 25 ×.

Fig. 2. *Umbilicaria rigida* (Du Rietz) Frey. Norway, Knuthulstind. Leg. R. Jørgensen August 18, 1930. Hb. Oslo. Magn. 25 ×.

Fig. 3. *Umbilicaria pennsylvanica* Hoffm. U.S.A. Rhode Isl., Middletown. Leg. Blaine March 2, 1909. Hb. Oslo. Magn. 25 ×.

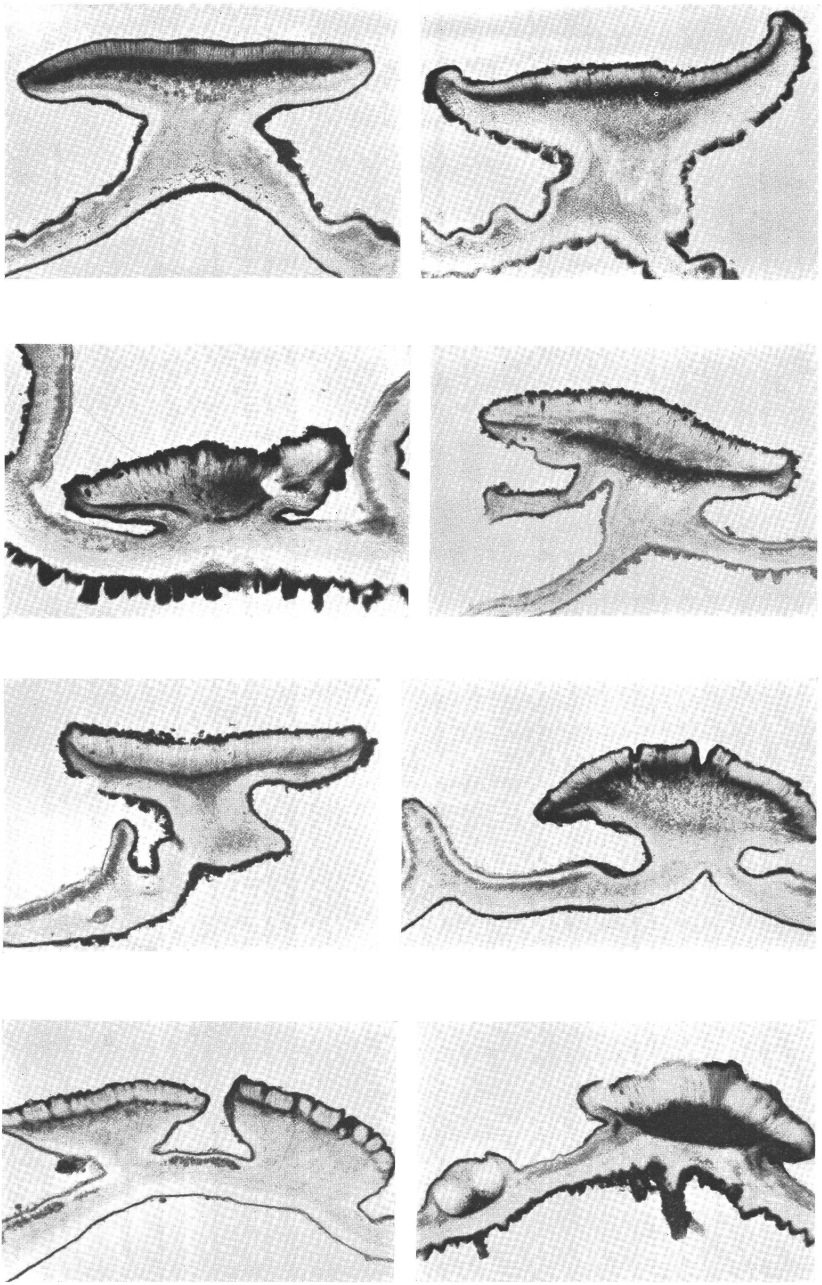
Fig. 4. *Umbilicaria pustulata* Hoffm. Sweden, Värmdön near Stockholm. Leg. Malme August 7, 1906. Hb. Oslo. Magn. 25 ×.

Fig. 5. *Umbilicaria dichroa* Nyl. Peru, Azangaro. June m. 1854. Hb. Oslo. Magn. 25 ×.

Fig. 6. *Omphalodiscus decussatus* (Vill.) Schol. Spitsbergen, Advent Bay, "ved den gamle grube". Leg. Lynge August 25, 1926. Hb. Oslo. Magn. 25 ×.

Fig. 7. *Omphalodiscus Krascheninnikovii* (Sav.) Schol. N. E. Greenland, Clavering fj. at Revet. Leg. Scholander July 22, 1930. Hb. Oslo. Magn. 25 ×.

Fig. 8. *Omphalodiscus spodochrous* (Ach.) Schol. Norway, Lyngør. Leg. Lynge July 28, 1905. Hb. Oslo. Magn. 25 ×.



Pl. V.

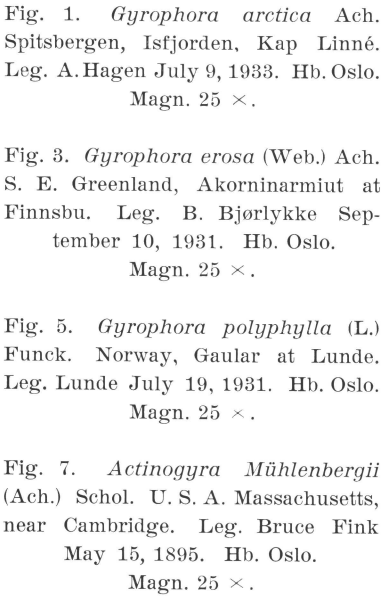


Fig. 1. *Gyrophora arctica* Ach. Spitsbergen, Isfjorden, Kap Linné. Leg. A. Hagen July 9, 1933. Hb. Oslo. Magn. 25 ×.

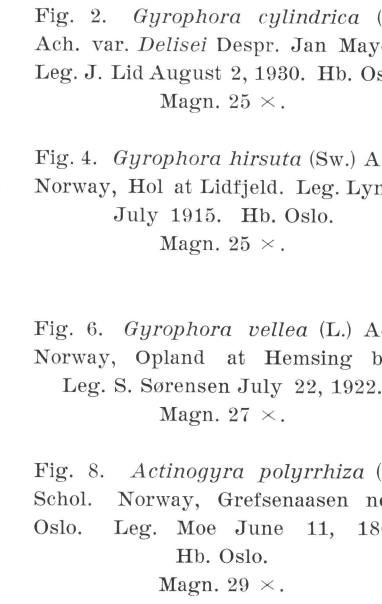


Fig. 2. *Gyrophora cylindrica* (L.) Ach. var. *Delisei* Despr. Jan Mayen. Leg. J. Lid August 2, 1930. Hb. Oslo. Magn. 25 ×.

Fig. 3. *Gyrophora erosa* (Web.) Ach. S. E. Greenland, Akorninarmiut at Finnsbu. Leg. B. Bjørlykke September 10, 1931. Hb. Oslo. Magn. 25 ×.

Fig. 4. *Gyrophora hirsuta* (Sw.) Ach. Norway, Hol at Lidfjeld. Leg. Lynge July 1915. Hb. Oslo. Magn. 25 ×.

Fig. 5. *Gyrophora polyphylla* (L.) Funck. Norway, Gaular at Lunde. Leg. Lunde July 19, 1931. Hb. Oslo. Magn. 25 ×.

Fig. 6. *Gyrophora vellea* (L.) Ach. Norway, Opland at Hemsing bro. Leg. S. Sørensen July 22, 1922. Magn. 27 ×.

Fig. 7. *Actinogyra Mühlenbergii* (Ach.) Schol. U. S. A. Massachusetts, near Cambridge. Leg. Bruce Fink May 15, 1895. Hb. Oslo. Magn. 25 ×.

Fig. 8. *Actinogyra polyrrhiza* (L.) Schol. Norway, Grefsenaasen near Oslo. Leg. Moe June 11, 1869. Hb. Oslo. Magn. 29 ×.