THE CLASSIFICATION OF LICHENS

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PART I

General discussion

When lichens were recognised as organisms distinct from algae or fungi they were arranged according to their external features into fruticose, foliose and crustaceous groups. Some lichens, in which the thallus was gelatinous when moist, were placed by some lichenologists(30) in a fourth group: the gelatinous lichens. This method was a useful one in the times prior to the elaboration of the compound microscope and enabled a large number of our common lichens to be discriminated. In the determination of lichens in the field it is of great service to-day, especially in regard to those lichens in which spore-producing bodies are seldom or never found, but the increased efficiency of the microscope and its manipulation in investigating the characters of the plant has caused the method to be almost entirely superseded by a more natural one in which all the characters are taken into account. Harmand's *Lichens de France* (1905–13), which unfortunately was never completed, followed this old method to a great extent, but is probably the last serious attempt to modify a moribund taxonomic system so as to make it accord with our increasing knowledge of the structure and life history of lichens. There was a time in the history of phanerogamic taxonomy when the external and vegetative characters were considered of primary importance, but complete emancipation from these views has now been largely achieved; internal and reproductive characters have been shown to be the most constant ones and their use is now held to be a leading principle in a natural classification. Complete emancipation from such ideas in lichen taxonomy is far from achieved, though it has been partially accomplished.

A lichen is generally considered to be a plant in which algal cells and fungal filaments are so intimately associated that an autonomous

organism is formed and this is able to live under conditions which are unfavourable or even fatal to one or both partners. During vegetable growth the partners are of similar importance to the organism, the algal cells obtain the carbonaceous material whilst the fungal filaments obtain water and the inorganic salts dissolved in it. In vegetative reproduction the partners are again of similar importance, algal cells being wrapped round by fungal filaments so as to produce a soredium. When reproduction is effected by means of spores the process is controlled by the fungal partner, the subsidiary rôle of the algal partner being to help in the supply of food and the environment necessary for the formation of the spore-producing body. The spore essentially belongs to the fungal partner but is usually so modified that it can only develop into an autonomous plant when the appropriate alga is supplied and then it forms a plant similar to the parent lichen.

This view of the lichen follows, in a general way, the dual hypothesis propounded by Schwendener (31) and modified by later lichenologists. Other views, such as those of Church (4), Elenkin (9) and Danilov (7), Moreau (24), Fink (10) and McWhorter (23), have not received any general support from lichenologists (28, 32*c*, 33).

In accordance with these views of lichen organisation a natural classification must take account of both symbionts but, as the sexual and asexual methods of reproduction are chiefly concerned with the formation of the fungal partner, the characters of the latter should be considered of greater importance than the nature of the algal one. The method of formation of the thecium, its shape and the production and septation of the spore are now considered of greater importance than the algal symbiont or the form which the vegetative thallus assumes. The probable phylogenetic history must also be co-ordinated with any attempt at classification. As I have written previously (1912), "a system of classification should take into account not only the present structure of the plants involved, but also their evolutionary history, interpreting the former in terms of the latter. This is a complicated business in a composite group such as the lichens, for even if the ancestors of the (fungal) symbionts have not disappeared, the modifications induced by their mutualism may have been so great that it is now almost impossible to trace them" (35*a*).

Acharius (1), as early as 1803, made use of the apothecium in his classification, whilst Nylander (27) in 1854 and 1858 used both thalline and thecial characters in his complicated scheme. He almost entirely neglected the spore characters and, despite the great service rendered

by him to lichenology, his scheme has few sympathisers to-day. His system is of interest to British lichenologists as it was followed by Leighton (17*b*) and Crombie (6) in their works on British lichens. It is only in recent years that the shackles of this slavish attachment to Nylanderian conceptions have been broken by British lichenologists (32*a*). The importance he attached to the spermogones and spermatia is not warranted by the present-day knowledge of these structures, and their occurrence is too uncertain and limited for their characters to be considered important for taxonomic purposes. If one considers them as male gametangia and gametes, which are sometimes functional though usually functionless, they have a certain value, especially in doubtful cases of affinity, but they are too frequently absent in many lichens to be of general taxonomic value. On the theory that they are pycnidia and pycnidiospores their value is lessened when one considers the variability of such accessory asexual structures in the fungi. Nylander's work on the spermogonia was supplemented in this country by that of Lindsay (20), but, as Lorrain Smith remarks ((32*c*) p. 205), "in many instances he must have been dealing with species of the 'Fungi imperfecti' that were growing in association with the scattered granules of crustaceous lichens." This proneness to inaccuracy when dealing with spermogonia seriously discounts their use in a general scheme of classification.

Leighton, in 1851, was one of the first lichenologists to pay particular attention to the spore, as in his account of the British angiocarpous lichens (17*a*). A little later Massalongo and Koerber (16), among continental lichenologists, evoked a large amount of hostile criticism by using the spore as a generic distinction. They were followed by Mudd, who in his *Manual of British Lichens* (25), anticipated many of the generic names which are in general use to-day.

The classification proposed by Müller-Argau (26) in 1862, and the important contributions of Reinke (30)[1] in 1894–6 made some advances towards the development of a natural system of classification of lichens, but the most successful attempts have been made by Zahlbruckner whose system has, to a large extent, been followed by British lichenologists. It is based on all the characters of the dual plant though the thecia and the spores contained in them have a dominating influence. Instead of the old divisions founded upon the

[1] Reinke's treatment of the subject was far superior to that of Müller-Argau. The progress which has been made towards a natural scheme of classification is largely due to his influence.

fruticose or foliose or crustaceous character of the thallus a sounder classification has been gradually evolved and Zahlbruckner has embodied most of the advances made in his taxonomic scheme.

The few lichens, in which the spores are borne on basidia, form the sub-class Basidiolichens (Hymenolichens), whilst the great majority of lichens, in which the spores are produced in asci, constitute the sub-class Ascolichens. The latter are divided into two groups: (1) Gymnocarpeae, with a thecium (apothecium) exposed at maturity, and (2) Pyrenocarpeae, with a thecium (perithecium) in which the hymenium is not exposed or communicates with the exterior by a small apical pore only. The first group is a large one and, as it includes lichens with three types of apothecia, three groups, Coniocarpineae, Graphidineae and Cyclocarpineae, are recognised. In the first group the apothecia are usually stalked and, at maturity, the spores leave the asci and form a sporal mass (mazedium) on the surface. In the second the apothecia are elongated or with a disc more or less slit-like. In Cyclocarpineae the apothecium has an open orbicular ± disc at maturity. These groups may be considered as analogous to orders in other groups of Thallophyta but not as exactly corresponding. The arrangement of lichens in them does not necessarily imply that all the members of a particular order have been derived from a common ancestor. The usual inferences from the use of the term "order" cannot be made owing to the probability that there have been many starting-points of consortia. Fungi enter into symbiotic union with many plants of different phyla, not only with algae, but also with liverworts, ferns and flowering plants, and, in some cases, the union is an obligate one(29). On Mendelian principles it is difficult to group lichens at all, the consortium and its origin being so difficult to interpret. In the familiar cases of orchids and mycorrhizas the origin of the consortium was probably due to a mild parasitism of the fungus on the higher plant(29), but in the lichen the origin is to be sought for in the close association of two independent plants of similar status. How this has resulted in the obligate symbiosis of a lichen plant and how the factors for producing the consortium have been impressed in the fungal spore are questions of great interest to students of heredity but, in the present state of our knowledge, need not necessarily concern the systematist. The fact that so many plants are able to enter into a temporary or permanent symbiosis with fungi does, however, show that a polyphyletic theory of the origin of lichens is quite sound. It may, perhaps, be possible, when the conditions governing germina-

tion are better understood and sufficient skill in manipulation of cultures obtained, to produce an entirely new lichen by the synthesis of an alga and a fungus. So far as is known a completely new synthesis has not been accomplished between a fungus and another plant in the numerous experiments on mycorrhizas. Bachmann has recently given an account of the establishment of mutualistic relations between a foreign fungus and the algal cells in the thallus (podetial) of a *Cladonia*. The algal cells multiplied to a great extent, the fungal hyphae were stimulated and a gall-like body was formed (2).

The probability that there have been many independent origins of the consortia, together with the relationship of the spore to the fungal constituent, has led some botanists to discard lichens as a class, and some attempts have been made to relegate them to appropriate positions amongst the fungi. Lichenologists are not prepared to admit this general subordination. The mutualistic relations between the fungus and the alga result in what is usually a complex and entirely different type of plant, whose life depends as much on the alga as the fungus, except during the formation of the thecium. In this new plant, evolutionary development has occurred. Many lichens are also partially or altogether dependent for their continuance on their vegetative methods of reproduction, and in these the two symbionts are of similar importance.

An order of lichens then, is merely a group in which families sufficiently similar can be arranged together. Lichenologists accept the thecia as the taxonomic bases of these "orders," which are mostly considered as polyphyletic. When the fungal constituents of two lichens (containing the same alga) are distinctly different, one can generally assume that two independent associations of alga and fungus have originated the consortia. It must not be overlooked, however, that variation and evolution may go on in the fungal partner after symbiotic union has been established. The likeness between the fungal symbiont of a lichen and a free-living fungus of the present day does not necessarily mean that the latter is the representative of the former, since the resemblance may be due to convergence.

When the algal constituents of two lichens (containing the same fungus) are different, it is often assumed that the consortia have had quite independent origins from the association of free-living algae and fungi. This may not be exactly correct, since there is a possibility that the germinating spore of the first lichen may have been able to enter into partnership with another alga so as to produce the second lichen.

The Cyclocarpineae are a large group which has been rendered less cumbersome by some lichenologists who have followed Reinke (30) in taking away from it those lichens which have Cyanophyceous algae as their algal symbiont, and putting these under a separate group Cyanophila. This group has a thallus which is usually more or less gelatinous owing to the nature of the algal symbiont. It includes a few plants with green algal cells, but otherwise so agreeing in general characters with species containing the usual blue-green algae as to suggest a similar phylogenetic origin, at any rate in regard to the species compared. By the adoption of this method the algal symbiont seems to have a taxonomic importance similar to that of the fungal one and a modification will be proposed, later on, which will divide Cyclocarpineae into five secondary groups. It may, however, be mentioned here that Zahlbruckner seems to recognise the group Cyanophila, in a partial way, by the manner in which he arranges the families belonging to the Cyclocarpineae. The families with blue-green algae are sandwiched between two lots of families with algal cells belonging to Chlorophyceae. Of these three lots the first one consists largely of families with primitive or homoiomerous thallus, then follow the families with blue-green algae, whilst the last lot consists of families in which the thallus is usually heteromerous. It may also be noted that the Cyanophyceous lichen families are arranged so that those with heteromerous thallus follow those with homoiomerous.

The chlorophyceous lichens included in the Cladoniaceae have two kinds of thallus as, in addition to the ordinary one, they have a more or less erect podetium with a structure which is usually radiate. The podetium, in most cases, is usually taken to represent a development of an apothecial stalk into which algae have extended. Wainio believes that the members of Cladoniaceae had a monophyletic origin and Lorrain Smith agrees ((32c) p. 293) that the "family is monophyletic in origin, though many subordinate phyla appear later[1]." Though it is not difficult to derive them from some form of *Lecidea* or *Biatora* ((32c) p. 293), it is probable that they form a group quite distinct from any other. The amount of variation they exhibit indicates the antiquity of the group, and even if *Lecidea* and *Cladonia* had a common ancestor, the evolution of their derived members has proceeded along divergent lines. Cladoniaceae has long been recognised as a group distinct from others: so long ago as 1780

[1] It is probable that these subordinate phyla are parallel developments and that "Cladoniaceae" has had three originating points, see p. 31.

Weber gave *Cladonia* as one of the 18 genera amongst which he distributed lichens, whilst Müller-Argau in 1862 recognised the *Cladonia* group (Capitularieae) as one of the three groups in his Eulichens.

On account of these considerations and others which will be mentioned later, it is proposed to divide Ascolichens as follows. The Pyrenocarpeae, Coniocarpineae and Graphidineae constitute the orders Pyrenocarpales, Coniocarpales and Graphidales respectively. The group Cyclocarpineae is such a large and varied one that it is more convenient to divide it into smaller groups, which may be considered as follows:

(1) Ectolechiales. Apothecia unstalked and of simple structure; thallus primitive and usually homoiomerous; algal cells belonging to Chlorophyceae.

(2) Collemales. Apothecia unstalked; thallus homoiomerous, usually more or less gelatinous; algal cells belonging to Cyanophyceae.

(3) Peltigerales. Apothecia unstalked; thallus heteromerous; algal cells normally belonging to Cyanophyceae.

(4) Parmeliales. Apothecia unstalked (or almost so); thallus heteromerous; algal cells belonging to Chlorophyceae.

(5) Cladoniales. Thallus heteromerous and of two kinds, the ordinary or primary and the podetial or secondary; algal cells belonging to Chlorophyceae. The podetial thallus is usually more or less erect, often has a radiate structure and, on it, the apothecia are borne.

Reinke's Cyanophila(30) includes Collemales and Peltigerales, Ectolechiales consist of those lichens arranged by Zahlbruckner before the cyanophyceous ones whilst Parmeliales and Cladoniales follow them.

It must again be noted that the division of Cyclocarpineae into five groups does not necessarily imply a separate monophyletic origin for each group, though such a desirable objective is brought appreciably nearer. The five groups must be regarded as convenient for placing together families possessing similar characters.

Ectolechiales are certainly a primitive group in regard to the thallus but the possession of a homoiomerous thallus cannot be taken as a rigid character for purposes of classification. Some Ectolechiale families may possess members in which the algal cells have become arranged in a definite layer whilst some members of the Parmeliale group may remain in a primitive thalline condition. From the Ectolechiale families the Parmeliale families were probably

derived, and good reasons may be advanced for including many members of the Ectolechiales as primitive members of Parmeliale families.

Collemales may be a primitive group, or they may have been derived from the Ectolechiales by the substitution of a cyanophyceous alga for a chlorophyceous one. That they have not advanced to stages higher than a foliose one may be due to a smaller capacity for advancement when the algal component belongs to the simpler alga or, on the other hand, may be due to their later development. If the former view is taken the taxonomic value of their homoiomerous thallus is considerably increased, especially if the Peltigerales are regarded as derivatives from the Parmeliales. Then the Collemales may be considered to be a primitive group in which the thallus containing blue-green algae does not usually advance beyond the homoiomerous condition.

Peltigerales may be considered as advances from the Collemales or as derivatives from Parmeliales. The similarity of certain genera (or subgenera, *section* of many lichenologists) containing different algal cells lends some support to the latter view. For example, in *Lobarina scrobiculata* the algal cells are blue-green, whilst in the similar plant *Lobaria* (*Ricasolia*) *laetevirens* they are bright green. Lichenologists are in general agreement in regard to the close affinity between these two plants. If one assumes the correctness of this view with its phylogenetic implications, *Lobaria* (*Ricasolia*) *laetevirens* may be considered as near to the ancestral form whilst *Lobarina scrobiculata* has been derived from it, owing to the germinating ascospore of the ancestral form entering into mutualistic relations with a blue-green alga. On the other hand, the *Lobaria* may have originated from the *Lobarina*, by the substitution of green for blue-green algal cells[1]. In any case the group, as it exists to-day, is a convenient one in which to place the families Peltigeraceae, Stictaceae and Pannariaceae.

Parmeliales contain the lichens with the greatest capacity for thalline advancement. The names Lecideales and Lecanorales have been formerly employed, in part, for them, but not in the sense in which Parmeliales is here used. These names (Lecideales and Lecanorales) implied a great taxonomic value to the absence or presence of a thalline margin to the apothecium. As this character is not used in the separation of Parmeliales from the other Cyclocarpineae, neither name is applicable to this group.

These five groups of Cyclocarpineae may be considered as sub-

[1] Further examples of possible substitution are given on pp. 16–17.

orders or as orders. The chief objection to the use of the latter term (in addition to the phylogenetic implication previously mentioned) is that thalline characters, as well as thecial ones, are used as taxonomic bases, so that these "orders" are not commensurate with Pyrenocarpales, Coniocarpales and Graphidales in which thecial characters form the main bases of classification. As a matter of convenience their consideration as orders is justifiable.

In the further separation into families the taxonomic importance of the apothecia and the spores are again emphasised by Zahlbruckner. As regards the importance attached to spore characters the most striking example is afforded by the treatment of the present-day genera of *Teloschistes*, *Xanthoria*, *Caloplaca* (*Placodium* and *Callopisma*), *Blastenia*, *Anaptychia*, *Physcia*, *Rinodina* and *Buellia*. In many lichenological works the thalline characters of these plants largely determine their positions. The fruticose *Teloschistes*, the more or less fruticose *Anaptychia* and the foliose *Xanthoria* were included together under the foliose *Physcia*. Because their thalli were ± crustaceous *Caloplaca*, *Blastenia* and *Rinodina* were put under *Lecanora*, whilst *Buellia* was placed with *Lecidea*. In these lichens Zahlbruckner seems to consider the colour and septation of the spore as of great importance. Those having colourless and polarilocular spores are placed in the neighbouring families of Teloschistaceae (Theloschistaceae) and Caloplacaceae, the former containing the fruticose *Teloschistes* and *Lethariopsis*, and the foliose *Xanthoria*, whilst the latter contains the ± crustaceous *Caloplaca* and *Blastenia*[1]. Those having one-septate and brown spores constitute the allied families Physciaceae and Buelliaceae, the former containing the fruticose or foliose *Anaptychia*, *Physcia* and *Pyxine*, whilst the latter contains the crustaceous *Rinodina* and *Buellia*.

This consideration of the apothecium and its contained spores as of great importance seems to be in accordance with the habits of crustaceous lichens. In many of these the thallus is either evanescent or poorly developed, and in many others in which a thallus is normally present, there are varieties or forms in which the thalli are so poorly developed that they render no aid to their identification. This is especially the case with lichens occurring in the arctic or alpine regions, the thallus often being so scanty that the characters of the apothecium form the only means of determination. "Some lichens

[1] The inclusion of the simple-spored *Protoblastenia* and the 3–many-septate-spored *Bombyliospora* in the family Caloplacaceae, shows that he does not consider the septation of the spore as of paramount importance.

...living under arctic conditions of life...are reduced to hardly anything, some apothecia and scattered thin areolae (21). There are also innumerable cases of lichens, especially crustaceous ones, in which the thalline characters fluctuate to a considerable extent, the only constant characters being those of the apothecium and spore. Lichenologists therefore rely largely on the size, colour, number and septation of the spores in their determinations and it seems quite justifiable to attach importance to these characters for taxonomic purposes. This reliance for determination purposes on spore characters does not imply that they should override all others when taxonomic questions are considered, but it certainly suggests that much consideration should be given to them. This was recognised by Mudd, so long ago as 1862, when he wrote "of all organs furnished by a given group of plants, none offer so many real, constant, and physiological characters as the spores of the Lichens, for the formation of a simple and natural classification" (25).

Just as changes have occurred in other characters, the colour and septation of the spore may have changed during the phylogenetic development of a particular group, so that the sporal characters must be considered in conjunction with others. The view that septation changes in the spore have been frequent after the consortium has originated, is not favoured when we consider that the majority of the highly developed lichens have simple spores. Although the colour and septation of the spore are two of the most constant characters in lichens, they are subject to variation in some genera and even in some species. In Rhizocarpon the spore is colourless in some species and dark in others. In *Buellia* a dark-coloured spore is a generic character but there are some species (e.g. *B. colludens*) in which the spore is colourless up to, or almost up to, maturity. Inconstancy is also shown in the septation of the spore. *Rinodina* has dark 1-septate spores but *R. conradi* appears to be 3-septate owing to the partial development of two extra septa. A similar thing occurs in *Callopisma tetrastichum*, the spores of which, apart from their apparent 3-septate character, are very similar to the colourless polarilocular spores of the allied *C. ochraceum*. In *Rinodina diplinthia*, which is otherwise very similar to *R. conradi*, the spores are often described as becoming more or less muriform. *Biatorina* (with 1-septate colourless spores) is not always easy to distinguish from *Bilimbia* (*Weitenwebera*), in which the spores are also colourless but 3- or more-septate. An extra septum may be developed in the spores of some Biatorinas whilst some species of

Bilimbia do not show more than one septum except when full development has occurred. Some species of *Biatorina* also appear to belong to *Lecidea* (with unseptate spores) as a septum is not formed till the spores are completely mature. The appearance of longitudinal divisions in transversely-septate spores so as to give rise to muriform spores is inconstant in some cases (e.g. species of *Rhizocarpon*), many apothecia having spores with transverse septa only; full development so as to give rise to muriform spores only occur in some of the apothecia. On the other hand, an extra oblique or longitudinal septum occasionally occurs in species (e.g. *Thelidium cataractarum*) which are considered to have spores which are merely transversely 3-septate. In the same plant some perithecia may contain spores which are merely 1-septate or even unseptate. Many of these irregularities can be shown to be more apparent than real. In *Rinodina conradi* and *Callopisma tetrastichum* the 3-septate appearance of the spore may be considered as due to the constriction of the lumina, whilst some other irregularities are due to incomplete development. A sufficient number of real irregularities occur to show that one or more extra divisions may be formed. This is especially the case with spores having three or more septa, one or more extra longitudinal divisions frequently occurring. The easy nature of the passage from spores with many transverse septa to spores which are more or less muriform, suggests that it is unnecessary to attach much taxonomic value to such additional septation. It may be sufficient to put the species possessing longitudinal as well as transverse division into a different genus from those with transverse septation only, but it seems of doubtful value for placing them in different families.

It should also be noted that Zahlbruckner's classification sometimes cuts across the old line of demarcation between lecanorine and lecideine apothecia, as in Buelliaceae he includes the lecanorine *Rinodina* and the lecideine *Buellia*. In Caloplacaceae the species having a thalline margin to their apothecium are placed in *Caloplaca*, whilst those without are put in *Blastenia*. The presence or absence of a thalline margin to the apothecium does not deserve to have such a weighty significance attached to it as is done by some lichenologists, who, on this account, place in a particular family genera with various sporal characters. Zahlbruckner himself, in his families Lecanoraceae and Lecideaceae, seems to attach great importance to the presence or absence of a thalline margin. The apothecium has a thalline margin in his family Lecanoraceae which includes the simple-spored genera of *Lecanora*, *Harpidium* and *Ochrolechia* with the

septate-spored genera of *Lecania*, *Icmadophila*, *Haematomma*, *Phlyctis*, etc. His family Lecideaceae has the apothecium without a thalline margin and contains the simple-spored *Lecidea*, the uniseptate-spored *Catillaria* (*Biatorina*), the polyseptate-spored *Bacidia* (including *Bilimbia*) and the muriseptate-spored *Rhizocarpon*. In the same family Lorrain Smith (32*a*) also includes *Buellia* with brown, 1-septate spores. Zahlbruckner recognises that the latter genus is better placed with *Rinodina* which merely differs in the possession of a thalline margin by the apothecium. He also follows in the wake of others in attaching little significance to the thalline margin in the families Caloplacaceae or Physciaceae, as he includes in them lichens with (e.g. *Physcia*), or without (e.g. *Pyxine*), a thalline margin to the apothecium. A similar course in regard to the presence or absence of a thalline margin is adopted by Lorrain Smith (32*b*) for *Caloplaca* and *Blastenia*, all the species, whether they possess a thalline margin or not, being put under *Placodium*. Lichenologists often meet with great difficulty in deciding whether a thalline margin is present or absent, and have gradually realised that algal cells are present, around or under the apothecium, in many lichens which otherwise appear to have a lecideoid apothecium. In consequence of this difficulty there are diverse views in regard to the genus in which some species should be placed, e.g. *Lecania* or *Biatorina cyrtella*, *Rinodina* or *Buellia discolor*, *Lecanora* or *Lecidea coarctata*. A further argument against attaching too much importance to the thalline margin is that some species, which normally have a thalline margin to the apothecia, have varieties or states in which a thalline margin is absent, or, if present at first, quickly becomes obliterated, e.g. *Lecania erysibe*, *Lecanora sarcopisioides*, *L. sulphurea*, *L. polytropa*. The number of such cases is so great that one cannot attach such great importance to the method of emergence of the apothecial body, or to the occurrence of algae in its margin, as the old taxonomic systems demand. The difference is usually significant enough to warrant a generic separation as between *Lecanora* and *Lecidea*, *Lecania* and *Biatorina*, or *Rinodina* and *Buellia*, but not sufficient by itself to form the basis on which a family is founded. As stated previously in 1922 (35*d*), "too much importance may be assigned to the systematic value of the distinction between lecideine and lecanorine apothecia...and an extension of the principle which includes *Blastenia* with *Placodium*, and *Buellia* with *Rinodina*, seems justifiable."

In regard to the crustaceous members of Lorrain Smith's

Teloschistaceae (put under Caloplacaceae by Zahlbruckner), attempts to apportion them to genera with or without a thalline margin lead to much confusion. When both the thallus and apothecium are yellow the concolorous margin may belong to either, and there is so much uncertainty in deciding as to the presence or absence of algal cells, around or immediately under the apothecium, that it seems advisable to place all those which possess yellowish apothecia under one genus. This course was practically adopted by Lorrain Smith (32*b*) when she used *Placodium*, though this was used in a wider sense still, including the radiately-lobed species as well as the truly crustaceous ones[1]. Malme adopts a similar course but uses *Callopisma* instead of *Placodium* as the generic name (22). For many years *Callopisma* has been used by me for all the truly crustaceous species (as in (35 *e*)). When *Blastenia* is used as the generic name for those without thalline margins there is much divergence in the nomenclature, e.g. both *citrinum* and *phloginum* are put in the *Callopisma* section (or its equivalent) by Lorrain Smith and Zahlbruckner, whilst Lesdain puts them under *Blastenia* (18). The difficulty of deciding whether the margin is a thalline or proper one when these are concolorous, is often so great that it counterbalances the convenience of reducing the size of the genus *Callopisma*.

Zahlbruckner further emphasises the taxonomic importance of the sporal reproductive bodies in another way. His family Acarosporaceae is founded chiefly on the presence of many spores in the ascus. The spores, with the possible exception of *Maronea*, are simple. The apothecium of *Acarospora* may be regarded as possessing a thalline margin whilst in *Biatorella* a thalline margin is never present. *Glypholechia* is more or less foliose whilst the other members are crustaceous or, at most, squamulose. Some lichens with polyspored asci are not included under Acarosporaceae because their structure in other respects suggests a different phylogenetic relationship. This applies to the foliose *Anzia* which was included by Reinke in this family.

Zahlbruckner therefore takes account of all the characters and considers the probable phylogeny in his attempts to found a natural classification, but is not altogether consistent in his methods. There seems to be no real reason why the method of treatment adopted for Teloschistaceae, Caloplacaceae, Physciaceae and Buelliaceae should not be extended in regard to other lichens. For family characters

[1] These are placed under the sub-genera *Callopisma*, with a thalline margin, and *Blastenia*, without a thalline margin.

the structure of the spore is considered to be important, the presence or absence of a thalline margin to the apothecium is disregarded and the thalline characters are treated as of secondary importance. The phylogeny of lichens is rather obscure but the phylogenetic relationship of most of the genera included in these four families seems fairly clear, whilst in his families Lecanoraceae and Lecideaceae some genera (see pp. 11–12), which seem to have little phylogenetic connection, are included. If a family containing both septate and unseptate spores has any phylogenetic significance, we must consider that its members have had additional septa developed in the spores during the course of descent from a common ancestor possessing a lecideine or lecanorine (as the case may be) apothecium and simple spores. Ontogeny indicates that this was how septation originated, but does not necessarily suggest that the process occurred after the fungus took on a partnership with the alga. In fact, the widespread occurrence of septation in pure fungi, and the presence of simple spores in many highly developed lichens, indicates otherwise, unless one assumes that the septate-spored fungi have originated since the establishment of most lichen consortia. In the suggested re-arrangement the fungal partner is generally regarded as having had a simple or septate (as the case may be) spore, the lecideine apothecium is considered as primitive, and the usual course of evolution was in the extension of the algae into the margin, or in the formation of an additional margin in which algae were present. As Lorrain Smith says (32*c*) p. 298), "the marginate apothecium has appeared once and again.... *Lecanora* must have originated when the crustaceous lecideine thallus was already well established. Its affinity is with *Lecidea* and not with any fungus: where the thallus is evanescent or scanty, its lack is due to retrogressive rather than to primitive characters."

The following table arranges some of the common genera according to their spore-characters and indicates that there are groups which are more or less parallel to the four families mentioned above.

The table shows that in this particular order of lichens (Parmeliales) those with 1-septate and colourless spores form a series almost parallel to those formed by Teloschistaceae and Caloplacaceae or by Physciaceae and Buelliaceae. This series includes the fruticose *Ramalina*, the squamose *Solenopsora* (*Placolecania* or *Diphratora*), the squamulose *Thalloidima* and the crustaceous *Lecania* and *Biatorina*, *Lecania* having a thalline margin to the apothecium whilst *Biatorina* has not. There does not seem to be any reason (if

Tabular arrangement of some genera of lichens (Parmeliales) so as to show how different types of spore are found in different types of thallus.

Spores are usually 8 in the ascus	Thallus is fruticose and apothecia have a thalline margin in	Thallus is foliose and apothecia have a thalline margin in	Thallus is squamose or squamulose: Apothecia with thalline margin in	Thallus is squamose or squamulose: Apothecia without thalline margin in	Thallus is crustaceous: Apothecia with thalline margin in	Thallus is crustaceous: Apothecia without thalline margin in
Colourless and polarilocular in	Teloschistes Lethariopsis	Xanthoria	Placodium (Gasparrinia)		Callopisma	Blastenia
	Teloschistaceae		Caloplacaceae			
Dark and 1-septate in	Anaptychia	Physcia Pyxine (with lecideoid apothecia)	Placothallia (=Dimelaena)	Diploicia	Rinodina	Buellia
	Physciaceae		Buelliaceae			
Colourless and 1-septate in	Ramalina		Solenopsora (=Placolecania) Callopis Trichoplacia (2-septate)	Thalloidima	Lecania Icmadophila	Biatorina Catillaria Megalospora Microphiale
Colourless and simple in	Usnea Letharia Evernia and Cetraria Alectoria Dactylina Dufourea	Parmelia Parmeliopsis Everniopsis Platysma Nephromiopsis Heterodea	Squamaria	Psora Phyllopsora	Lecanora Ochrolechia Aspicilia Jonaspis Harpidium (thallus homoiomerous)	Lecidea Orphniospora (spores brown) Mycoblastus
Colourless or dark, 3- or more-septate to muriform in	Oropogon (muriform spores)	Psorella (spore 3–15-septate and apothecia lecideoid) Megalospora (0–3-septate and acicular spores)	Physcidia (many-septate spores)	Toninia (3- or more-septate spores)	Haematomma (3–many-septate) Myxodictyon (muriform)	Bilimbia Bacidia Bombyliospora Rhizocarpon (muriform spores)

the principle of including *Callopisma* and *Blastenia* in the family Caloplacaceae, or *Rinodina* and *Buellia* in the family Buelliaceae is sound, as it seems to be) for placing *Lecania* and *Biatorina* in different families. Their relationship is so close that some species (e.g. *Biatorina cyrtella*) are placed in *Biatorina* by some authors and in *Lecania* by others. These two genera and their near allies may then be grouped together in a family called Lecaniaceae. The squamose *Solenopsora* may be included with them but the fruticose *Ramalina* seems sufficiently distinct to form a family of its own. The two lichens formerly known as *Biatorina lutea* and *B. diluta* (32*a*) seem similar to other Biatorinas in their reproductive characters, but differ in having *Trentepohlia* as their algal symbiont. On this account they have been placed by Zahlbruckner under the genus *Microphiale* and included in the family Gyalectaceae. When the reproductive characters are considered as of primary importance *Microphiale* must be placed in the same family as *Biatorina*. This arrangement implies that *Microphiale* has been derived from *Biatorina* by the substitution of a red algal symbiont for the more usual green one. That this is quite a probable method of evolution is shown by the consideration of some other cases where one algal symbiont is more or less replaced by another. The standard cases of this partial replacement (or addition) are those which occur in *Lecanora granatina* (11*b*) and *Solorina* (with green algal cells). In some species of *Solorina* groups of blue-green algae are scattered in the lower part of the thallus, or in special squamules, whilst in *S. crocea* they form a fairly continuous stratum below the layer of the ordinary green algal cells. According to Forssell (11) a similar thing occurs in *Psoroma hypnorum*. The squamules formed are very similar to those of *Pannaria pezizoides* (with blue-green algal cells) and this suggests that the latter may be a substitution product of the *Psoroma*. The taxonomic treatment of many other lichens shows that the inclusion of genera having two different algal symbionts in the same family breaks no canon of lichenological classification. *Sticta* and *Stictina* are often included in the same genus (*Sticta*) though they differ in the algal constituent. *Lobaria*, in its broad sense, includes species with green algae (in *Lobaria* and *Ricasolia*) or with blue-green (in *Lobarina*). *Arthonia*, of many authors, includes species which possess green algal cells instead of the more usual *Trentepohlia*. In the family Byssolomaceae (*sec.* Zahlbrückner) *Byssoloma* and *Amphischizonia* have green algal cells, whilst *Asteristion* contains *Trentepohlia*. The family Thelotremaceae (*sec.* A. L. Smith (32*b*)) also includes genera with these two kinds of

algal cells. That substitution of the algal cells is possible is also implied by the casual invasion of foreign algae, as in *Lecidea uliginosa*, though it is doubtful whether any benefit results from their inclusion in any examples which have been investigated. *L. uliginosa* is often very abundant on peaty ground and, occasionally, blue-green algae occur in the thallus along with the ordinary green ones. A similar phenomenon has been noted in other lichens.

The probability that these foreign algae give no benefit to the lichen, or, at any rate, do not enter into relationship with the hyphae, does not invalidate the possibility of substitution being an evolutionary method. At an early period in the history of the lichen, the relationship between the alga and fungus may have been less definitely fixed, and the invading alga may have become the paramount algal partner, or may even have entirely replaced the original one. In the simple-spored group, *Jonaspis* differs from *Aspicilia* in having reddish algal cells instead of green. It has been placed, on this account, in the family Gyalectaceae by Zahlbruckner but, apart from its algal symbiont, has no relationship with *Gyalecta*, and from the considerations advanced above should rather be regarded as an aberrant *Aspicilia*. The table on p. 15 shows that there are two other series, which are more or less parallel to those accepted by Zahlbruckner. In one of these series the spores are simple and in the other they are 3- or more-septate.

The simple-spored group includes such a large number of genera that it seems advisable for several families to be formed from it. *Usnea*, on account of its solid axis, almost merits a family to itself, but *Letharia* is sometimes more or less intermediate in this respect so as to link it to *Alectoria* with a "webbed" axis. When *Ramalina* and *Oropogon* are excluded, the family Usneaceae (of Zahlbruckner) can be accepted as conforming to the sporal requirements though *Thamnolia* (*Cerania*), *Siphula* and *Endocena* remain doubtful members, since their apothecia are unknown. The family Parmeliaceae (*sec.* Zahlbruckner) has two genera (*Megalospora* and *Physcidia*) attributed to it, which on account of spore-characters are better omitted. *Candelaria*, despite the many-spored ascus and the absence of parietin, appears to be phylogenetically related to *Caloplaca* (*Placodium*) and should be transferred to Caloplacaceae. Its spores, though simple, often simulate the polarilocular spores of other members of the family. The families Lecanoraceae and Lecideaceae require emendation, the septate-spored genera being omitted. *Candelariella*, for reasons similar to those advanced above in regard

to the inclusion of *Candelaria*, should be put under Caloplacaceae (see p. 21).

The following represents the proposed arrangement when the reproductive characters have sufficient importance assigned to them. Where the relations between the genera are better shown by means of a key, one is usually given.

Class *LICHENS*

Sub-class HYMENOLICHENS (BASIDIOLICHENS)

Order I. CORALES. *Cora, Dictyonema, Corella*

Sub-class ASCOLICHENS

Orders II. PYRENOCARPALES	III. CONIOCARPALES
IV. GRAPHIDALES	V. COLLEMALES
VI. PELTIGERALES	VII. ECTOLECHIALES
VIII. CLADONIALES	IX. PARMELIALES

In this arrangement the orders which are, generally speaking, the more highly developed, are placed last, but in their further consideration it will be more convenient to treat them in the inverse order. The diagnoses of these orders have been given previously (p. 7).

Order PARMELIALES

Family TELOSCHISTACEAE

Characters as defined by Zahlbruckner (36), except that the ascus should be given as usually 8-spored and the spores as usually polarilocular.

Thallus fruticose.

Medulla of loose tissue	*Teloschistes*
Medulla of closely-packed hyphae	*Lethariopsis*
Thallus ± foliose; horizontal or partly ascending ...	*Xanthoria*

Teloschistes includes some species in which the spores have a similar structure to the rest, but extra lumina have been developed, so that the spore appears to be 3-septate. These have been placed by Zahlbruckner under the sub-genus *Niorma*. Their spores differ from those of the typical *Teloschistes* in a similar way as those of *Callopisma tetrastichum* differ from those of *C. ochraceum*.

Family CALOPLACACEAE

Characters as given by Zahlbruckner (36).

Ascus 8-spored. Thallus and apothecia usually K + purple

Thallus squamulose (usually placodioid) ...	*Placodium*
Thallus entirely crustaceous	
Apothecia normally yellowish or reddish ...	*Callopisma*
Apothecia dark-coloured, K –	*Pyrenodesmia*

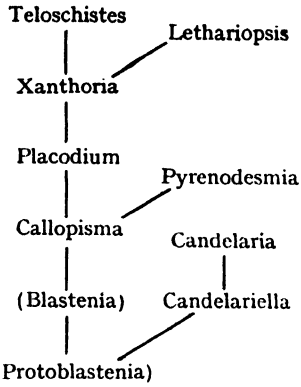
Ascus many-spored. Thallus and apothecia K –

Thallus squamulose	*Candelaria*
Thallus crustaceous	*Candelariella*

Placodium is used here in the same way as Lorrain Smith uses *Euplacodium*. Like so many other names of lichen genera it owes its name to vegetative characters. It was first used to denote those lichens having a radiate-squamulose (placodioid) thallus and included some plants in which the spores were not polarilocular. In consequence it has been rejected by some lichenologists, whilst some use it for the placodioid lichens with simple spores. *Amphiloma* and *Gasparrinia* are substituted for it by some authors, whilst others extend its range, so as to include the polarilocular-spored lichens with an entirely crustaceous thallus. Zahlbruckner (36) and Malme (22) use *Caloplaca* and *Callopisma* respectively, in the last-mentioned way. Questions of priority are difficult to settle in such cases but *Placodium* is such a suitable name that its disuse should be deprecated. Its extension to the species which are not squamulose-radiate cannot, however, be justified on account of the appropriateness of the name.

Callopisma includes the sub-genera *Callopisma* and *Blastenia* of Lorrain Smith (32*b*) for reasons previously given (*vide supra*, p. 13). It includes *Protoblastenia* and *Blastenia* of Zahlbruckner (36) as well as those species of *Caloplaca* in which the thallus is entirely crustaceous. *Protoblastenia rupestris* (Scop.) Zahl. is *Placodium rupestre* B. and R., and is similar to some of the other species of *Callopisma* except in regard to its simple spores. Its inclusion in *Callopisma* is analogous to Zahlbruckner's inclusion of the simple-spored *Lecanora fulgens* Ach. in *Caloplaca* (= *Placodium*). *Lecidea immersa* (Web.) Ach. is put by Zahlbruckner with *Protoblastenia* but seems better kept under *Lecidea*. The reddish or yellowish colour of the apothecium is such a pronounced character in *Callopisma* that the segregation of *Pyrenodesmia*, to contain the species with dark apothecia, seems justifiable, though the old apothecia in some undoubted species of *Callopisma* may become darker. Some parietin is present in *P. variabilis* Krb., but it is absent or doubtful in other species.

Candelaria concolor is placed by Zahlbruckner and Lorrain Smith in the Parmeliaceae, but its affinities seem to be with *Placodium* (see p. 17) or with *Xanthoria lychnea*, states of which it "closely resembles and with which it has been often confounded" ((6) p. 368). The genus *Candelaria* should include *Lecanora crenata* Nyl., as this also has its thallus devoid of parietin and its ascus many-spored, though its thallus is more placodioid than that of *C. concolor*. The inclusion of both *concolor* and *crenata* in the same genus can be justified by the consideration of *Lecanora elegans* Ach. and *L. lobulata*



Somm.[1] These two plants differ in thalline characters, more than *Candelaria concolor* differs from *C. crenata*, yet they are included in the same genus by most lichenologists. They are placed as *Placodium elegans* and *P. lobulatum* by Lorrain Smith and as *Caloplaca elegans* and *C. lobulatum* by Zahlbruckner. The close likeness which *Candelaria concolor* exhibits to states of *Xanthoria lychnea* is due to parallel development of the thallus in their ancestral forms of *Candelariella* and *Callopisma* respectively.

The presence of parietin is such a normal feature of the family that it may almost be considered as one of its important characters. In the otherwise abnormal genera, *Candelaria* and *Candelariella*, it is always absent. It is absent in *Placodium medians* Nyl., and its absence may be the reason why Lorrain Smith has named this *Candelariella medians*. This species is very similar to *P. murorum* except in its lack of parietin. If *Candelariella* is allowed to include placodioid species there seems to be no reason why it should be segregated from *Candelaria*. Both genera lack parietin and have many spores in the ascus. *Candelaria* is squamulose whilst *Cande-*

[1] Lynge, in his recently published *Lich. Nov. Zemlaya*, has rejected this name and substituted *Caloplaca marina*.

lariella is truly crustaceous in its common and original species, *C. vitellina*. If it is desirable to separate the 8-spored species without parietin from *Placodium* and *Callopisma*, *Candelariella* may be extended to include those which are crustaceous, whilst a similar course may be followed for *Candelaria* in regard to the squamulose species. This does not seem desirable and *Candelariella* should be restricted to crustaceous species containing many spores in the ascus. When used in this restricted sense it occupies a similar position to *Callopisma* as *Candelaria* does to *Placodium*. It seems better to retain the name *Placodium medians*, to put *Lecanora crenata* Nyl. under *Candelaria* and *L. epixantha* Nyl. under *Callopisma*. The absence of parietin is to be noted in other plants placed under *Placodium* and *Callopisma*. It is absent in the apothecia of *C. refellens* and in the thallus of several other species.

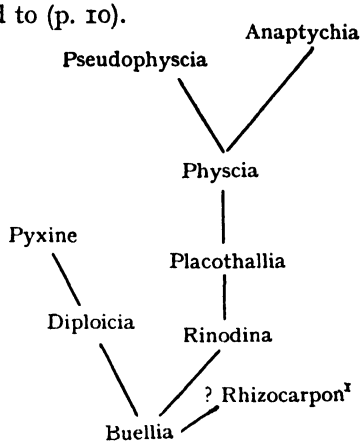
Both Smith and Zahlbruckner recognise the relationship of *Candelariella* to Caloplacaceae though the latter puts the genus in the Lecanoraceae. He, however, says that its inclusion with Lecanora is doubtful, as it "zeigt zweifellos Beziehungen zur Gattung *Caloplaca* und ist entweder der Ausgangpunkt der letzteren oder eine reduzierte Form derselben. Ein Zusammenfassen der Gattung, lediglich nach der Sporenform, mit *Lecanora* oder *Lecania*, von welchen sie einzeln genommen allerdings durch geringe, in ihrer Gesamtheit jedoch bemerkenswerte Merkmale abweicht, würde den phylogenetischen Verhältnissen kaum entsprechen" ((36) p. 207). Lorrain Smith also states that "there is also affinity with the genus *Candelaria*" (32*b*).

The two polar loculi are usually evident in the spore but are sometimes absent or indistinct, as in *Placodium fulgens*, *Callopisma nivale*, and *C. rupestre* (*Protoblastenia r.*). A 1-septate appearance may be shown in the spores of *C. luteo-album* and *C. nivale*, whilst *C. tetrastichum* has the spore-contents so arranged as to give a 3-septate appearance. *C. cerinellum* often has more than eight spores in the ascus, but, like the other exceptions, should be considered as a variant within the genus.

Family Physciaceae

Thallus fruticose, foliose, or crustaceous, heteromerous, with or without rhizinae, with green algal cells. Apothecia orbicular, immersed or sessile, lecideine or lecanorine; paraphyses simple or little branched. Spores usually eight in the ascus, brown, 1-septate, occasionally with further transverse or longitudinal septa; spore-wall usually thick. This family includes Zahlbruckner's Buelliaceae.

There seem to be sufficient grounds for recognising Hue's *Pseudophyscia* (15) as a genus. The fibrous structure of its upper cortex separates it from the plectenchymatous *Physcia*, with which it agrees in the horizontal arrangement of its lobes. It agrees with *Anaptychia* (*sensu stricto*) in the fibrous character of the upper cortex, but its lobes are neither ascending not fruticose. The inclusion of *Pyxine* has been commented on earlier (p. 12) as an example of the inclusion of lichens with lecideine apothecia in the same family as those with lecanorine. *Placothallia* and *Diploicia* are allowed generic rank. In *Rinodina insperata* the polarilocular character of the spore is very evident and emphasises the close relationship of this family with Teloschistaceae and Caloplacaceae. The tendency of *R. conradi* and *R. diplinthia* to form additional septa in their spores has been previously alluded to (p. 10).



Apothecia lecanorine.
- Thallus foliose or fruticose.
  - Cortical hyphae parallel to the surface of the thallus ... ... *Physcia*
  - Cortical hyphae perpendicular to the surface of thallus.
    - Thallus fruticose or sub-fruticose ... *Anaptychia*
    - Thallus horizontal ... ... *Pseudophyscia*
- Thallus placodioid ... ... *Placothallia* (*Dimelaena*)
- Thallus crustaceous ... ... *Rinodina*

Apothecia lecideine.
- Thallus foliose ... ... *Pyxine*
- Thallus placodioid or squamulose ... ... *Diploicia*
- Thallus crustaceous ... ... *Buellia*

[1] See page 29.

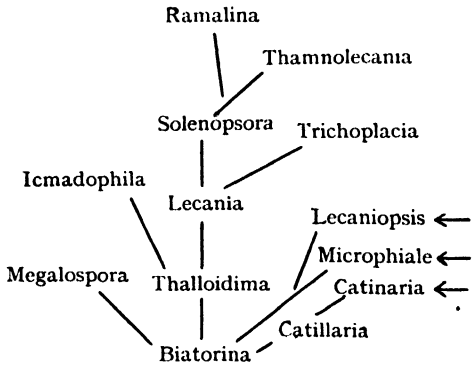
Family RAMALINACEAE

Thallus fruticose with radiate structure and algal cells belonging to Chlorophyceae, medulla webbed, cortical hyphae chiefly arranged longitudinally. Apothecia terminal or lateral, marginate; spores eight in the ascus, colourless, 1-septate.

Ramalina is usually placed with Usneaceae, but is separated from it because of its septate spores.

Family LECANIACEAE

Thallus crustaceous, sometimes placodioid or ± squamulose, corticate or non-corticate above, attached by hyphae to the substratum, with heteromerous structure and green algal cells, exceptionally orange or reddish. Apothecia usually superficial and sessile, with or without a thalline margin; spores eight or fewer in the ascus (exceptionally more), colourless, 1-septate, occasionally with three septa.



Apothecium with a thalline margin.

Thallus with a dwarf fruticose habit	*Thamnolecania*
Thallus placodioid or squamulose	*Solenopsora*
Thallus crustaceous.	
Apothecium often somewhat stalked; spores ellipsoid and spermatia pleurogenous ...	*Icmadophila*
Apothecium sessile; spores fusiform; spermatia acrogenous	*Lecania*

Apothecium without a thalline margin.

Algal cells orange or yellowish.	
Algal cells *Trentepohlia*. On bark or mosses	*Microphiale*
Algal cells *Phycopeltis*. On leaves	*Lecaniopsis*

The arrows in the diagram indicate that a trentepohlioid alga has displaced the original one.

Algal cells green.
Thallus ± squamulose ... ... *Thalloidima*
Thallus crustaceous.
Spores large (over 40μ long) with thick walls; spermatia pleurogenous ... ... *Megalospora*
Spores under 30μ with thin walls; spermatia acrogenous.
Apothecium dark; hypothecium usually dark ... ... *Catillaria*
Apothecium and hypothecium pale or bright coloured ... ... *Biatorina*

Thamnolecania, which is given as a sub-genus by Zahlbruckner (36), has a dwarf fruticose habit and partly links up the family to Ramalinaceae. *Solenospora* (*Placodium candicans* Dub., etc.) is synonymous with *Diphratora* and *Placolecania*. The presence of 16 or more spores in the ascus of *Lecania syringea* is too occasional an occurrence to justify its separation from the other *Lecania* species with 1–3-septate spores. *L. vallata* (*Stir.*) Müll., if placed in this genus, is an aberrant member, as its spores are 8- or more-celled.

Callopis, which is given by Zahlbruckner as a sub-genus of *Physcidia*, may belong to this family but the structure of its spore is doubtful. It is 2-celled and possibly polarilocular. If the latter is the case it is allied to *Placodium*. In any case the broadly-fusiform and 2-celled spore separates the plant from *Physcidia*, with acicular and many-septate spores.

Trichoplacia with 2-septate spores and a squamulose thallus having rhizoids beneath, whilst algal cells are present beneath the apothecium, seems near to *Solenospora* (*Placolecania*), though it is placed as a doubtful member of Phyllopsoraceae by Zahlbruckner and considered to be a fungus by Müller ((36) p. 94).

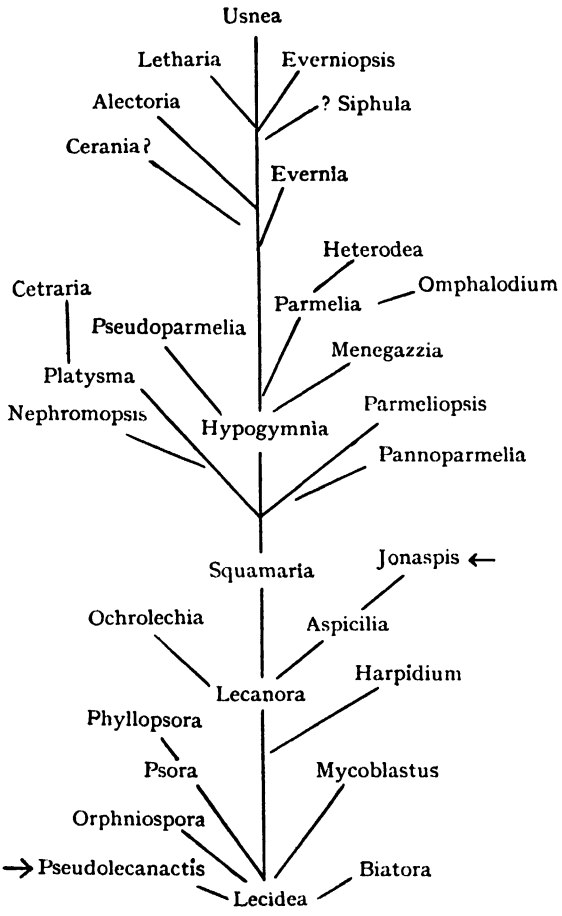
Lecaniopsis is included in Gyalectaceae by Zahlbruckner but it differs from some Biatorinas and *Microphiale* by algal characters only.

Family USNEACEAE

Characters as given in Zahlbruckner except that "sporen... zweizellig oder mauerartig-vielzellig," should be omitted. *Ramalina* with 1-septate spores is placed in Ramalinaceae whilst *Oropogon*, with muriform spores, is put under Bacidiaceae. The other genera, *Usnea*, *Letharia*, *Alectoria*, *Evernia*, *Everniopsis*, *Dactylina*, *Dufourea*, *Thamnolia* (*Cerania*), *Siphula* and *Endocena*, may be included in the family, though the three last named are doubtful members, since

their apothecia are unknown or doubtful. Massalongo and Th. Fries considered *Cerania* to have apothecia similar to *Cladonia* and therefore it has been placed in Cladoniaceae by some authors. Harmand (13) and Crombie (6) place *Cerania* and *Siphula* together as a family (tribe) of their own. The descriptions of the apothecia remain unconfirmed, and therefore *Cerania* is included with *Siphula* and *Endocena* in Usneaceae, but as of doubtful place.

The spermatia in *Usnea* and *Dufourea* are acrogenous, whilst in the other genera of Usneaceae they are pleurogenous or unknown. There is a possibility that these two genera have evolved from *Parmeliopsis*. In that case they would constitute the family Usneaceae, the remaining genera forming another family.



Family PARMELIACEAE

Characters as given by Zahlbruckner (36) or Smith (32*b*). *Candelaria*, *Megalospora* and *Physcidia* are included in this family by Zahlbruckner. Reasons for the omission of *Candelaria* have already been given (*vide supra*). *Megalospora* and *Physcidia* should be excluded on account of their septate and acicular spores.

Cetraria and *Platysma* are closely akin, otherwise the radiate structure and habit of the former is nearer to Usneaceae. The subgenera *Hypogymnia*, *Menegazzia* and *Omphalodium* of *Parmelia* may be allowed generic rank as they are sufficiently distinct from the other members of this large genus.

The genera of Parmeliaceae are as follow: *Hypogymnia*, *Menegazzia*, *Omphalodium*, *Parmelia*, *Pseudoparmelia*, *Parmeliopsis*, *Pannoparmelia*, *Cetraria*, *Platysma*, *Nephromopsis* and *Heterodea*.

Anzia, with many spores in the ascus, is included in this family by Zahlbruckner, but Reinke puts it with the Acarosporaceae. *Pannoparmelia*, placed under it as a sub-genus, should retain the generic rank which Darbishire gave to it.

Family LECANORACEAE

Characters as given by Lorrain Smith (32*b*) except that the last sentence should read as follows: spores usually 8, rarely more in the ascus, colourless, simple.

Harpidium is placed here by Zahlbruckner. Its spores are simple and it conforms in many other respects, but its pseudoparenchymatous homoiomerous thallus is different from any other member of the family. Reasons for limiting the family are given previously. *Jonaspis* is included for reasons mentioned on p. 17.

Thallus homoiomerous ... ... *Harpidium*
Thallus heteromerous.
  Thallus squamulose ... ... *Squamaria*
  Thallus crustaceous or almost so.
    Apothecia immersed at first and often remaining so.
      Algal cells green ... ... *Aspicilia*
      Algal cells reddish or yellow ... ... *Jonaspis*
    Apothecia superficial, or almost so, from the beginning.
      Spores very large with thick epispore ... *Ochrolechia*
      Spores smaller (less than 40μ) ... ... *Lecanora*

Family LECIDEACEAE

Thallus crustaceous, occasionally squamulose, sometimes evanescent, heteromerous, not rhizinose below; algal cells green. Apothecia circular, discoid or patellate, without a thalline margin: spores usually eight in the ascus, simple and usually colourless.

Spores 1–3-nae, large (over 50μ) with thick walls	*Mycoblastus*
Spores usually eight, smaller (under 40μ) with thin walls.	
Spores brown, small, more or less spherical ...	*Orphniospora*
Spores normally colourless.	
Thallus almost foliose	*Phyllopsora*
Thallus squamulose	*Psora*
Thallus crustaceous.	
Apothecia dark; hypothecium often dark...	*Lecidea*
Apothecia pale or coloured; hypothecium often pale	*Biatora*

Phyllopsora sometimes differs from other members of the family in its possession of rhizinae.

Uncertainty sometimes occurs as to whether a species should be put in *Biatora* or *Lecidea* but this slight confusion is compensated for in the reduction of the inconveniently large genus *Lecidea*.

Müller-Argau ((26) p. 351) gives good reasons for rejecting the genera founded on the colour of the apothecium. Mudd also is against the use of *Biatora* as a genus. He says(25) (p. 192), "I see no permanent and definite characteristic distinction between... *Biatora* and *Lecidea*....The colour of the apothecium in many instances furnishes a prominent specific character, but it is too variable and too liable to be changed by atmospheric influence to be admitted as a generic guide. The degree of solidity or compactness of the hypothecia, and their different shades of colour, are also too fine and delicate points for generic purposes in the present tribe." These expressions of opinion can easily be justified by examples, but for determinative purposes it is very convenient to have *Biatora* separated from *Lecidea*.

Family BACIDIACEAE

Thallus usually crustaceous, occasionally squamose, rarely cylindrical, sometimes evanescent, heteromerous, neither corticate nor rhizinose below; algal cells green. Apothecia circular, discoid or patellate, with or without a thalline margin: spores usually eight in

the ascus, usually colourless, with three or more transverse septa, sometimes with longitudinal septa also.

Thallus cylindrical. Spores 1-nae, large and muriform ... ... *Oropogon*
Thallus foliose or squamose or squamulose.
  Thallus foliose. Apothecia pseudobiatorine and spores acicular, 3-septate ... ... *Megalospora*
  Thallus somewhat foliose or squamose.
    Apothecia lecanorine. Spores acicular, many-septate ... ... *Physcidia*
    Apothecia lecideine. Spores 3–15-septate ... *Psorella*
  Thallus squamulose. Apothecia lecideoid and spores 3- or more-septate ... ... *Toninia*
Thallus crustaceous (not or very little squamulose)
  Algae cells orange or reddish ... ... *Lecanactis*
  Algae cells green.
    Apothecia coloured and with thalline margin; hypothecium pale.
      Thallus usually corticate. Spores 8-nae, colourless, 3- or more-septate ... ... *Haematomma*
      Thallus not corticate. Spores 1-nae, muriform ... ... *Myxodictyon*
    Apothecia without thalline margin, coloured or dark. Spores usually eight.
      Spores with transverse septa only, usually colourless.
        Spores 3- or more-septate, fusiform, colourless ... ... *Bilimbia*
        Spores pluriseptate, elongate-acicular, colourless ... ... *Bacidia*
        Spores 5–10-septate, very large, often 1-nae ... ... *Bombyliospora*
        Spores 3-septate, brown. Parasitic ... *Leciographa*
      Spores muriform, colourless or brown.
        Spores usually 8-nae and halonate; paraphyses branched ... ... *Rhizocarpon*
        Spores usually 1-nae, not halonate; paraphyses unbranched ... ... *Lopadium*

Oropogon is similar to *Alectoria* and is often placed in Usneaceae. Its position depends upon its origin. If the septa have developed in the spore since the fungus took on a partnership with the alga, its affinity is with *Alectoria*. If the spores of the original fungal partner

were septate, *Oropogon* is allied to *Myxodictyon*. The large muriform and sometimes brown spore which is single in the ascus suggests affinity with *Myxodictyon*, but there are no certain links, in regard to thalline development, connecting the two genera.

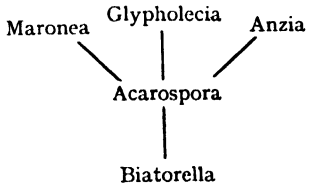
Megalospora, because of its acicular spores which may become 3-septate, is transferred from Parmeliaceae.

Psorella is like a foliose or squamose *Bilimbia* or *Bacidia* and may differ from other members of the family in possessing rhizinae. Zahlbruckner placed it in the family Phyllopsoraceae with *Phyllopsora* and the doubtful *Trichoplacia*. *Phyllopsora*, as its name implies, is similar to a foliose *Psora* and is here included in Lecideaceae, whilst *Trichoplacia* is here regarded as akin to *Solenopsora*. The family Phyllopsoraceae therefore disappears, the three genera which constituted it being distributed to three different families.

Some species of *Rhizocarpon* appear to be related to *Buellia*. *R. alboatrum* is usually quite distinct from *B. myriocarpa*, but occasionally there is some difficulty in distinguishing them. In both the paraphyses are capitate and dark-tipped. The spores become dark in both plants, but in the former become muriform, whereas in the latter the septation does not proceed further than the development of one transverse septum. In the formation of the spores *R. alboatrum* partially "recapitulates" the mature *B. myriocarpa*. The spores are 1-septate, become dark, and then extra transverse and longitudinal divisions occur. In *R. oederi* the septation seldom proceeds further than the development of two additional transverse septa. There are some reasons for regarding both *Rhizocarpon* and *Bilimbia* as mixed, i.e. as having species relegated to them which have had an origin different from the others.

Family Acarosporaceae

Characters as given by Zahlbruckner. He includes *Thelocarpon* but this seems to be better placed in a family of its own (Thelocarpaceae) amongst the Pyrenocarpales, a course followed by Lorrain Smith (32*a*), on account of its perithecium. *Maronea* may



have a septum developed in the spore, but otherwise agrees with the other genera (simple-spored) of the family.

Anzia has a many-spored ascus, but is excluded from the family by Zahlbruckner and placed in Parmeliaceae. Its affinities seem to be nearer to Acarosporaceae, in which it was placed by Reinke (30).

Family PERTUSARIACEAE

Characters and genera as given by Zahlbruckner. *Perforaria* has the disc so little exposed that the thecium is almost a perithecium. *Varicellaria* has the spore 1-septate but, in other respects, is so much like a *Pertusaria* that a phylogenetic connection is probable.

Family GYROPHORACEAE

Characters as given by Zahlbruckner (36) p. 209). This seems like a natural family but there are many deviations from what may be considered as a typical member. Most species of *Gyrophora* have a dark foliose thallus attached by a central hold-fast, furrowed apothecia (gyrose) and 8-nae, simple and colourless spores. Even in the genus *Gyrophora* there is considerable diversity. Some species (e.g. *G. cylindrica*) have a divided or lobed thallus attached by rhizinae to the substratum, and in some others (e.g. *G. leiocarpa*) the apothecium is not furrowed. The other genera of the family agree with the typical Gyrophoras in general appearance and in their manner of attachment but the spores are septate. They are 1-septate and colourless in *Charcotia*, 1-septate and brown in *Dermatiscum* and muriform in *Umbilicaria*, the latter also having fewer spores in the ascus. The apothecial disc is usually plane except in *Gyrophora*. The only distinguishing characters common to all the genera are vegetative ones (which are possessed by *Dermatocarpon miniatum*) and it is possible that their apparent relationship is due to convergence, rather than to phylogenetic connection.

Family THELOTREMACEAE

Characters as given by Lorrain Smith (32*b*) p. 378). The two families Thelotremaceae and Diploschistaceae scarcely differ except that the latter has green algal cells. The relative positions of these families to others, as given by Zahlbruckner (36), indicate their affinity with the Ectolechiales. The thallus is usually primitive and sometimes homoiomerous but is heteromerous in the higher-evolved members, so that the family may be considered as a low member of the Parmeliales.

Phlyctis, *Phlyctella*, and *Phlyctidia*, though placed by Zahlbruckner in Lecanoraceae, show better kinship with this family, in which *Phlyctis* is placed by Lorrain Smith.

Conotrema has such peculiar spores that its inclusion in the family is doubtful.

Order CLADONIALES

Characters as given on pp. 6 and 7, or as defined by Lorrain Smith for Cladoniaceae ((32*b*) p. 402). This order may be arranged in three families: (1) Cladoniaceae, with simple spores; (2) Stereocaulonaceae, with spores 3- or more-septate; and (3) Gomphillaceae, consisting of the monotypic genus *Gomphillus*, which differs in so many respects from the members of the other families that it is best placed in a family of its own.

This order is sometimes considered to be of monophyletic origin, in which there have been "changes in form and septation (of the spore) not commensurate with thalline advance" as "in *Gomphillus*, with primitive thallus and podetium, the spores are long and narrow with about 100 divisions" ((32*c*) p. 293). The three families, however, may have had distinct origins, and the similarity in podetial development may be due to convergence.

Family CLADONIACEAE

The spores are usually simple but occasionally 1- or more-septa are developed in *Pycnothelia*, *Thysanothecium* and *Baeomyces*. In some species of *Baeomyces* the podetium originates in the same way as an apothecial stalk whilst in others it is formed by the extension upwards of the primary granule. The latter method of podetial development also occurs in *Pilophorus*.

Podetia usually well developed and often widening upwards.
- Primary thallus squamulose and ± persistent; podetia often scyphiferous ... ... *Cladonia*
- Primary thallus evanescent or obsolete. Podetia rarely scyphiferous.
  - Podetia perforated by many pores ... *Clathrina*
  - Podetia not perforated ... ... *Cladina*
- Primary thallus crustaceous and persistent; podetia short and not scyphiferous ... ... *Pycnothelia*

Podetia short and not widening upwards.
- Podetia clothed with granules or squamules *Pilophorus*
- Podetia not clothed with granules or squamules.
  - Primary thallus foliose with marginal podetia *Gymnoderma*

Primary thallus crustacco-granulose or squamulose with superficial podetia ...	*Baeomyces*
Primary thallus lobed and leaf-like above	*Thysanothecium*

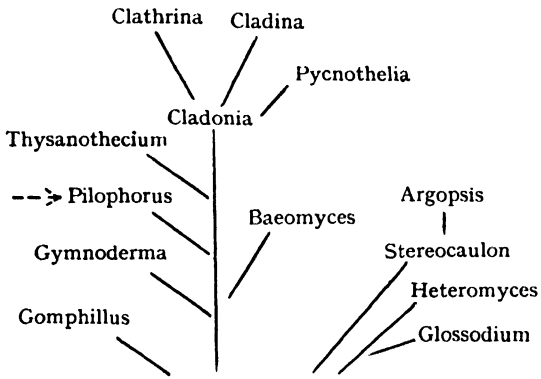
Family STEREOCAULONACEAE

Podetia usually well developed, solid, clothed with granules or squamules.

Spores elongate, 3- to many-septate ...	*Stereocaulon*
Spores muriform	*Argopis*

Podetia short, ± hollow and naked. Spores 1–3-septate.

Primary thallus foliose. Spores cylindrical	*Heteromyces*
Primary thallus crustaceous. Podetia widened above with apothecia on one side. Spores fusiform	*Glossodium*



Family GOMPHILLACEAE

Gomphillus, the only member of the family, has a superficial and naked podetium bearing 1–5 apothecia at the apex. In many other respects it differs from other members of the Cladoniales. Its thallus is a thin gelatinised membranous crust and homoiomerous. Its spores are remarkable for their long filiform and many-celled (up to 100) character. Despite the homoiomerous thallus, the presence of podetia justify its inclusion in the *Cladonia* group.

Order ECTOLECHIALES

In this order the thallus is primitive (usually homoiomerous) and the apothecial wall is absent or poorly developed. It includes the families Ectolechiaceae, Byssolomaceae, Coenogoniaceae, and Chrysothricaceae. Ectolechiaceae has many-septate or muriform

spores. The genera *Asterothyrium, Gonolecania, Byssolecania* and *Actinoplaca* have spores which are 1–2-septate, and a separate family, Asterothyriaceae, may be formed to receive them. The family Gyalectaceae (characters as given by Lorrain Smith) is also better included in the Ectolechiales. Zahlbruckner includes in the family the simple-spored *Jonaspis* and the 1-septate-spored *Microphiale* and *Lecaniopsis*. The relations of these have been previously indicated (*vide supra*, pp. 16, 17, 23, 24, 26). *Ramonia* is of doubtful position. The following key shows the relationships of the members remaining in Gyalectaceae:

Thallus with Scytonema algae	*Petractis*
Thallus with Phycopeltis algae	*Semigyalecta*
Thallus with Trentepohlia algae.	
Ascus with 12 or more 3- or more-septate spores	*Pachyphiale*
Ascus with 8 or fewer spores.	
Apothecium and hypothecium dark	*Sagiolechia*
Apothecia coloured or pale	*Gyalecta*

Order PELTIGERALES

This order contains the families Peltigeraceae, Stictaceae and Pannariaceae (*vide supra*, pp. 7, 8).

The characters of these families, as arranged by Zahlbruckner and Lorrain Smith, are generally accepted. Zahlbruckner includes plants having blue-green algae in the genus *Nephroma*. It seems preferable to keep *Nephroma* for those plants possessing green algae in their thalli, and to put those possessing *Nostoc* in *Nephromium*, which Zahlbruckner uses in a sub-generic manner. A similar re-arrangement, or rather a return to the Nylanderian arrangement, also seems preferable in regard to *Sticta* and *Stictina*, or *Lobaria* and *Lobarina*, for exactly the same reason. Lorrain Smith is not consistent when she accepts *Nephroma* and *Nephromium* as two genera because of the different alga present in the thallus, but includes *Stictina* with *Sticta* and *Lobarina* with *Lobaria*. In a similar way, Nylander, who was followed by many other lichenologists, used *Peltidea* and *Peltigera*, the former containing those species of *Peltigera* (*sensu lato*) in which the algal layer of the thallus was green, whilst *Peltigera* was reserved for the cephalodiiferous species with a blue-green algal layer. These names were in vogue for many years but, as the Acharian name of *Peltidea* was used as a synonym of *Peltigera* (*sensu lato*), it is difficult to reconcile them with the Vienna

rules unless *Peltidea*, as used by Nylander, is accepted as a *nomen conservandum*. The following tabular arrangement shows how Nylander named the genera:

Thallus with green algae	Nephroma	Sticta	Lobaria	Peltidea
Thallus with blue-green algae	Nephromium	Stictina	Lobarina	Peltigera

The position of *Placynthium* also requires to be rendered more definite. Lorrain Smith ((32a) p. 31), "on account of the homoiomerous thallus," places it in the family Ephebaceae whilst Zahlbruckner(36) retains it in Pannariaceae. The thallus is not quite homoiomerous and, in many respects, approaches closely to that of the genus *Parmeliella* (*Pannularia* of Nylander). Nylander actually included our common British species in the genus *Pannularia* as *P. nigrum*. The spores are 1- or more-septate, whilst in most of the genera included by Zahlbruckner in Pannariaceae (*Psoroma, Psoromaria, Pannaria, Parmeliella, Erioderma, Coccocarpia, Lepidocollema, Lepidoleptogium*) they are simple. Apart from this septation of the spore, the genus *Placynthium* (as well as the genus *Massalongia*) is better retained in the Pannariaceae. The common British member of the genus, *Placynthium nigrum* Gray(12), varies very much in the septation of the spores. These are usually 1-septate, but in some apothecia (otherwise seemingly well developed) they are mostly simple, whilst other apothecia, on the same rock, possess 3-septate spores.

Hydrothyria is put with Pannariaceae(36) but it seems more at home with *Peltigera*.

Order COLLEMALES

This order (*vide supra*, p. 7) contains the families Heppiaceae, Collemaceae, Physmaceae (to include the genera parallel to those of Collemaceae, but with simple spores), Lichinaceae, Ephebaceae and Pyrenopsidaceae. As algal characters are largely used for the arrangement into families, some slight alterations (other than the one indicated above) may be necessary. The species with definite perithecia should be relegated to the Pyrenocarpales. *Latzelia*, because of its muriform spores, is more probably derived from *Collema*, even though its thallus is not (or only very slightly) gelatinous, and contains algal cells like those of *Heppia*.

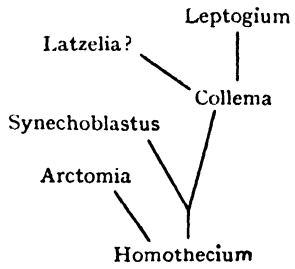
The changes chiefly involve the families Collemaceae and Physmaceae, which are therefore given in more detail.

Family COLLEMACEAE

Thallus gelatinous when moist, homoiomerous, usually ± foliose, corticated or non-corticated, with or without rhizinae, with blue-green algal cells single or moniliform. Apothecia ± open, with or without thalline margin, immersed or sessile; spores septate, often muriform. Spermogonia with pleurogenous or acrogenous spermatia.

The characters and the genera are similar to those given by Lorrain Smith ((32*b*) p. 46) or by Zahlbruckner ((36) p. 164), except that the genera with definitely closed apothecia, or with simple spores, are excluded. Lorrain Smith is followed in the allowance of generic rank to *Synechoblastus* (including *Collemodiopsis*).

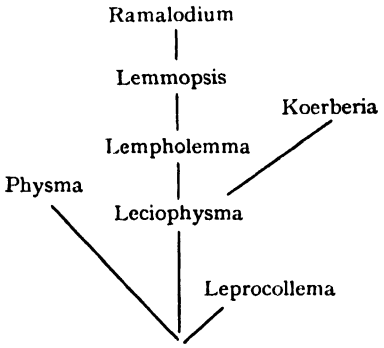
On account of the pseudoparenchymatous nature of the thallus or its cortical portion, the family Leptogiaceae has been separated. Mudd's diagnosis ((25) p. 20) is as follows: "Thallus coriaceous,



membranaceous, foliaceous or caulescent, variously lobed and laciniated, rigid when dry, gelatinous and somewhat turgid when wet; epithallus distinctly cellular; gonidiac granules simple or moniliform-coherent. Apothecia scutelliform or patellaeform." Good reasons may be advanced for the retention of this family but the general evidence is against it. The presence of pseudoparenchyma is not a clear-cut character, as in *Synechoblastus nigrescens* Anzi. (*Collema n.* Ach.) and *S. rupestris* A. L. Sm. (*C. flaccidum* Ach.), pseudoparenchyma is absent except in the thallus near the apothecia. There also seems to be a parallel development of pseudoparenchyma in the simple-spored genera placed here in Physmaceae. Just as *Collema* advances in thalline structure to *Leptogium*, so *Lemphollemma* (with simple spores and non-corticated thallus) advances, through some species with pseudoparenchyma near the apothecia, to *Lemmopsis* (with simple spores and corticated thallus).

Family PHYSMACEAE

Thallus ± gelatinous when moist, crustaceous or foliaceous or minutely fruticose, corticated or non-corticated, with or without rhizinae, with blue-green algal cells. Apothecia ± open, sometimes apparently almost closed, usually with thalline margin, mostly innate; spores simple. Spermogonia with pleurogenous or acrogenous spermatia.



Spores spherical or ± ellipsoidal, straight.

Thallus crustaceous, scarcely gelatinous. Apothecia biatorine ... ... *Leprocollema*

Thallus ± fruticose ... ... *Ramalodium*

Thallus usually small-lobed, foliose or fruticulose, gelatinous.

Thallus corticated ... ... *Lemmopsis*

Thallus not corticated.

Apothecia lecanorine.

Spores thick-walled or with epispore ... *Physma*

Spores thin-walled. Thallus usually smaller and more appressed ... ... *Lempholemma*

Apothecia lecideine ... ... *Leciophysma*

Spores acicular and contorted ... ... *Koerberia*

THE CLASSIFICATION OF LICHENS

PART II

THE genera which have been previously arranged into families contain the most highly developed of all the lichens in regard to thalline characters. They show various series of advances from a primitive to a complicated thalline structure. The orders Graphidales, Coniocarpales and Pyrenocarpales do not generally exhibit such diversity, and it is probably safe to assume that their consortia have been evolved, on the whole, at later periods. Before dealing with these orders further, it will be useful to repeat and place in more concise forms some of the conclusions arrived at in Part I.

(1) Every lichen species has not been formed by a separate symbiosis between a free-living fungus and alga. In a lichen formed from an original symbiosis, variation has gone on and a number of species may have been evolved. In some cases the number of derived species may have been so great, and their differentiation of sufficient magnitude, to justify the creation of genera or even families.

(2) The fungal characters are of more taxonomic importance than the algal. In sexual or asexual reproduction the cells directly concerned are of fungal origin, the function of the algal cells being nutritive.

(3) Variation and evolution are usually greater in external than in internal characters. The most constant characters are fungal; the internal characters of the apothecium, especially the spores, being those least liable to modification and selective influences by environment. There is a greater probability for a foliose thallus to be evolved from a crustaceous one than for a change of similar magnitude to occur in the spore.

(4) The presence of a simple spore in many of the fruticose and foliose lichens shows the persistence of such a character during the ages in which the thallus has been developed. The rarity of many-septate spores in the lichens, with highly-developed thalli, indicates that the origin of lichens with such spores is, generally speaking, more recent than the origin of simple-spored lichens.

(5) That mycologists do not lay great stress on the septation of the spore, for family characters, is not a strong argument against lichenologists doing so, since the fungus (in its original form) was in existence before symbiosis occurred. The formation of the thallus is a post-symbiotic development. The spore may have altered since symbiosis occurred but there is much probability that it has often remained fairly constant. The possibility of post-symbiotic change in the spore, however, shows the need of caution in excluding a particular genus from a family on account of spore-division only.

(6) Lichens with green algal cells have the greatest capacity for thalline development. This is generally better in corticicolous than in saxicolous lichens, though exceptional development may occur in nitrophilous habitats. The thallus, though often more immersed in calcareous rock, is usually better developed than that of a lichen on siliceous rock, especially when the latter is hard. Terricolous lichens, owing to their insecurity of tenure, are often little developed.

(7) Paraphyses are fairly constant and must be considered in lichen taxonomy. Their disappearance, coherence, colour and degree of swelling at the apices, and intrusion of algae among them, do not seem to be of great significance for family characters.

(8) The symbiotic relationship, and also to some extent the habitat, affects the algal cells. The appearance presented by the algal cells in the thallus is often very different from that presented by the free-living alga. In consequence there is some confusion and conflict of opinion as to the name given to the algal symbiont. This difficulty is often avoided in the text by simply giving the colour of the algal cells. There is much uncertainty as to the exact relationship of *Trentepohlia* with the allied algae (*Phyllactidium*, etc.) found in epiphyllous lichens.

(9) So much uncertainty exists as to the exact relationship of the fungal symbiont that definite naming has been avoided.

(10) Substitution of one alga for another has probably occurred in some cases.

(11) Spermogonia and spermatia are too uncertain, both in nature and occurrence, to be held of great taxonomic importance.

Order GRAPHIDALES

As Lorrain Smith (32c p. 278) writes: "there is ample evidence of polyphyletic descent in the series." A natural classification should attempt to arrange those having a common origin in the same group, and the arrangement into families, as given by Zahlbruckner, requires some alteration. Due importance is usually attached to the apothecium and the spore except in the family Graphidaceae. In Roccellaceae and Dirinaceae the ascus contains 8 septate spores and the thallus has *Trentepohlia* algae. Chiodectonaceae is similar in these respects except that the ascus may contain fewer spores and that *Heterothallus* or *Phyllactidium* is occasionally present in the thallus instead of *Trentepohlia*. In Arthoniaceae the spores are also 8 in the ascus and septate but the thallus in two genera (*Allarthonia* and *Allarthothelium*) contains green algal cells. In Lecanactaceae the spores are septate[1], 8 or less in the ascus, and the algal cells are *Trentepohlia*. This family is not included in this group by Zahlbruckner, though he acknowledges its relationship as follows: "die verwandtschaftlichen Beziehungen der *Lecanactidaceae* zu den *Graphaceae* sind sehr nahe; die Selbständigkeit der Familie innerhalb der *Cyclocarpineae* würde von Wainio begründet" (36 p. 131). Lorrain Smith includes it with the group and, if the family is retained, is certainly justified in doing so when *Platygrapha* (*Schismatomma*) is considered as one of its genera, as is done by both Zahlbruckner and herself. When the lirelloid members of *Schismatomma* are distributed in their respective positions amongst the Graphidales there seems little reason for retaining the family. *Pseudolecanactis* and *Catinaria* may be considered as derived from *Lecidea* and *Catillaria* respectively, by the substitution of *Trentepohlia* for a protococcoid alga in the thallus, whilst *Lecanactis* and some *Schismatommae* may be substitution products of *Bilimbia* and *Bacidia*. *Melampydium* is not described in the same way by different lichenologists but seems near to *Rhizocarpon* with *Trentepohlia* for its algal symbiont.

The five families given by Zahlbruckner are primarily dependent on apothecial characters, except in Roccellaceae, which is distinguished from the others owing to the fruticose habit of its members. Arthoniaceae is distinguished from the other families with a crustaceous thallus by the immarginate apothecia; Dirinaceae and Graphidaceae have marginate apothecia, the thallus being corticate

[1] *Pseudolecanactis*, with simple spores, is included in the family by Zahlbruckner.

or non-corticate respectively; whilst Chiodectonaceae has the apothecia aggregated in special portions (stromata or pseudostromata) of the thallus. However convenient this method of classification may be from a collector's point of view (since it provides him with an easy way of arranging his plants so as to determine them readily), it is too artificial unless other characters are in conformity with it. There is no more reason for placing all the fruticose plants, simply because they are fruticose, in one family than there is for putting in a special family all the woody plants belonging to the Rosaceae or Papilionaceae, or for creating a special family for *Cytisus*, *Robinia* and other arborescent Papilionaceae. Again, the formation of the family Chiodectonaceae, on account of the aggregation of the apothecia, is no more justifiable than the creation of a special family to receive *Trifolium* from Papilionaceae and *Poterium* from Rosaceae. It is a method which is not adopted in other orders of lichens except in the Pyrenocarpales. Even in the Graphidales it is not adopted in regard to *Synarthonia*, a stromatoid *Arthonia*, which is allowed to remain in the Arthoniaceae. The aggregation of the apothecia has occurred independently in various genera, and the various members of Chiodectonaceae should be distributed amongst the other families, in accordance with their probable derivation. During the aggregation the apothecial margin is likely to become less prominent, or entirely disappear, but in some cases (e.g. *Glyphis*, *Sarcographa*, *Sarcographina*) it remains permanent. In the table on p. 41 the presence or absence of a margin is neglected and the arrangement shows that Chiodectonaceae is a variable group in regard to septation, colour and cell-shape of spores and paraphyses, also that its various genera agree, in these respects, with genera belonging to other families of Graphidaceae. This agreement generally extends to other characters as well. Three members are without definite parallel representatives. *Rotularia* may be a derivative of *Mazosia*, *Enterostigma* of *Sclerographis* with longitudinal septa added in the spore, and the only genus without a known representative ± parallel to it is *Enterodictyon*. The spore-cells of this approach those of the *Opegrapha* group, but the simple and free paraphyses indicate a relationship to *Graphis*.

In the Graphidaceae of Zahlbruckner there are three groups: (1) the main group in which the spores are septate, up to 8 in the ascus and the thallus contains trentepohlioid algae; (2) a small group in which the spores are simple, or almost so, and many in the ascus; (3) a group in which the ascus contains 8 (or less) simple (occasionally

Genera of Chiodectonaceae compared with parallel genera of Graphidales with single apothecia.

Apothecia grouped (Chiodecton-aceae)	Apothecium single	Spores				Paraphyses	Algal symbiont
		Septation	Colour	Shape of cells	No. in ascus		
Glyphis	Graphis	3–11 transverse	o	±lens-shaped	4–8	Simple and free	Trentepohlia
Pycnographa	Micrographa	1 transverse	o to brownish	Unequal	8	Simple and free	Phyllactidium
Chiodecton	Opegrapha	Many transverse	o	±cylindrical	8	Branched and anastomosing	Trentepohlia
Rotularia	—	Many transverse	o	,,	8	Branched and anastomosing	Heterothallus
Mazosia	Fouragea	Many transverse	o	,,	4–8	Branched and anastomosing	Phyllactidium
Sarcographa	Phaeographis	Many transverse	Dark	±lens-shaped	–8	Simple and free	Trentepohlia
Sclerophyton	Sclerographis	Many transverse	Dark	±cylindrical	–8	Branched and anastomosing	,,
Medusulina	Graphina	Muriform	o	±rounded	1–8	Simple and free	,,
Enterodictyon	—	,,	o	±cubic	–8	,,	,,
Sarcographina	Phaeographina	,,	Dark	±rounded	1–8	,,	,,
Minksia	Dictyographa	,,	o	±cylindrical	1–8	Branched and anastomosing	,,
Enterostigma	—	,,	Dark	,,	–8	Branched and anastomosing	,,

1-septate) spores, and the thallus usually possesses green algal cells. The last group corresponds more-or-less to Xylographidaceae in Mudd's *Manual* and to Reinke's Xylographacei, though in these groups the sporal characters were not considered as diagnostic, so that the name of Xylographaceae may be used for it. The second group corresponds to the family Acarosporaceae of the Parmeliales and may be called, after one of its members, Graphinellaceae. The main group cannot be considered as a simple group as two kinds of spore-cells are shown and the paraphyses are different. In one of these smaller groups the cells of the spore are cylindrical or cubic and the asci are accompanied by branched and anastomosing paraphyses; in the other the spore-cells are lens-shaped or rounded with thick walls and the paraphyses are simple and free. The table on p. 43 shows the main characters of the members of Zahlbruckner's Graphidaceae inclusive of the lirelliform members of Roccellaceae. The algal cells are *Trentepohlia* unless otherwise stated[1].

The group to which *Graphis* belongs has spores with lens-shaped or rounded cells, usually three or more in number, and having thick walls[2]; the paraphyses are simple and free and the hypothecium is colourless or almost so. The name of Graphidaceae is restricted to this group. The *Opegrapha* group has spores with more-or-less cylindrical cells, usually three or more in number, and having thin walls; the paraphyses are branched and anastomosing, the hypothecium is often dark and the apothecia are usually more superficially situated. This group constitutes the emended family Opegraphaceae. *Melaspilea*, *Micrographa* and the stromoid *Pycnographa* form a group, which may be an offshoot from the line which gave rise to the Graphidaceae, or may have an independent origin. The group is however sufficiently distinct to form the separate family of Melaspileaceae.

Family ROCCELLACEAE

The relations of the members of this family, as given by Zahlbruckner, are shown in the table on page 44.

There are three members with lirelliform apothecia in which a thalline margin is absent. *Ingaderia* and *Reinkella* agree almost exactly with *Opegrapha* except for their fruticose habit. *Roccellographa*, even though it has an immersed apothecium, also seems to

[1] The usual interpretation of the green algal cells as *Palmella* has been followed.

[2] These characters are also considered to be of taxonomic importance in the Pyrenocarpales. See p. 51.

Comparative table of Graphidaceae (*sec.* Zahlbruckner and inclusive of lirelliform Roccellaceae).
Thallus crustaceous and algal cells Trentepohlia unless otherwise stated.
Spores 8 in ascus.

Spore				Paraphyses and any other special characters	
Septation	Colour	Cell-shape	Hypothecium		
Parallel	o	±lens-shaped	Pale	Simple and free	Graphis
,,	o	,,	,,	Simple and free with clavate and verrucose apices	Acanthographis
,,	Dark	,,	,,	Simple	Phaeographis
Muriform	o	,,	,,	,,	Graphina
,,	o	,,	,,	Simple with clavate and verrucose apices	Acanthographina
,,	Dark	,,	,,	Simple	Phaeographina
,,	,,	,,	Brownish	Loose and relatively thick. Algal cells Palmella?	Xyloschistes
,,	o	±lens-shaped to cubic	Pale	Branched and anastomosing	Helminthocarpon
Parallel	o	±cylindrical	Dark or pale	,, ,,	Opegrapha
,, 3–9	o	,,	Pale	Branched and anastomosing. Alga Phyllactidium	Fouragea
,, 3–8	o	,,	,,	Branched and anastomosing. Algal cells Palmella	Aulaxina
,, 7–8	o	,,	Dark	Branched. Thallus fruticose	Ingaderia
,, (7)	o	,,	,,	Branched and coherent. Thallus fruticose	Reinkella
,, 3	Dark	,,	Pale	—	Gymnographis
,, (5–7)	,,	,,	Dark or pale	Branched and anastomosing	Sclerographis
,, (5–7)	,,	,,	Pale	Branched and anastomosing. Apothecia immersed	Roccellographa
Muriform	o	,,	,,	Branched and anastomosing	Dictyographa
Parallel 3	o	—	Dark	Branched and anastomosing. Palmella. Compound hymenium	Diplogramma
,, 1	o	Unequal	—	Simple and free. Alga Phyllactidium	Micrographa
,, 1 (–3)	Dark	±cylindrical	Dark or pale	Simple and free	Melaspilea
,, 1	,,	Unequal	Dark (pale)	Branched and coherent. Algal cells Palmella	Encephalographa
Simple	o	Ellipsoidal	Dark	Branched and coherent. Algal cells Palmella	Lithographa
,,	o	,,	Pale	Simple and free. Algal cells green	Xylographa
,,	o	,,	Dark	Compound hymenium. Algal cells Palmella	Ptychographa

Comparative table of Roccellaceae (*sec.* Zahlbruckner).

Thallus fruticose (except in Roccellina where it is crustaceous) with Trentepohlia.

Ascus with 8 parallel- and transversely-septate spores. Paraphyses branched.

Spore			Apothecium				
Septa	Colour	Shape	Position	Shape	Margin	Hypothecium	
7–8	o	Fusiform	Sessile	Lirelliform	Proper	Dark	Ingaderia
3	o	,,	±elevated	Rounded	Thalline	,,	Dendrographa
3	o	—	Sessile	,,	Proper	,,	Roccellaria
2, median cell small	Brownish	Oval	Adnate	,,	Thalline	Pale	Darbishirella
5–7	,,	—	Immersed	Lirelliform	Proper	Colourless	Roccellographa
–7	o	Cylindrical	Sessile	,,	,,	Dark	Reinkella
3	o	Fusiform	,,	Rounded	Thalline	,,	Roccellina
3–	o	—	,,	,,	Proper or thalline	,,	Roccella
3	o	Fusiform	±sessile	,,	±thalline	Pale	Combea
3	o	,,	±elevated	,,	Thalline	,,	Pentagenella
3	Brownish	,,	±sessile	Rounded and ±lobed	,,	Dark	Schizopelte
3	,,	Cylindrical	Shortly stalked	Rounded and ±lobed	,,	,,	Simonyella

In Ingaderia, Dendrographa, Roccellaria and Darbishirella the hyphae are parallel to the surface of the thallus, whilst in the others they are transverse.

have been derived from *Opegrapha* through *Sclerographis*. These three genera may then be considered as fruticose members of Opegraphaceae. After these have been removed from Roccellaceae the remaining genera have rounded apothecia and there seems little reason for retaining the emended family amongst the Graphidales.

Family Dirinaceae

Characters and genera as given by Zahlbruckner. *Cyclographa* differs from *Dirina* and *Dirinastrum*, the other two genera belonging to this family, in having the paraphyses branched and coherent instead of simple and free. The roundish apothecia, which are usually provided with a thalline margin, and the corticate nature of the thallus, indicate the near relationship of this family to the Parmeliales.

Family Arthoniaceae

In this family the immarginate apothecium is taken as a critical character. However useful it may be for determinative purposes, it cannot, by itself, be regarded as a critical taxonomic character. In many genera (e.g. *Lecidea*) belonging to the Parmeliales, the presence or absence of a proper margin to the apothecium is disregarded. Even in the Graphidales some species belonging to other families have forms in which the proper margin is absent, e.g. *Opegrapha herpetica* form *arthonoidea*, *O. atra* var. *arthonoidea*, forms of *O. varia* and *O. siderella*. The immarginate apothecium is, however, found in conjunction with other characters which are rare or absent in other families, so that Arthoniaceae may be considered as a fairly natural group. The asci are usually short and pyriform, the paraphyses are usually branched and closely coherent and the spore is often unequally celled. The latter character is not shown in all the species and is occasionally found in members of other families, e.g. *Encephalographa*, *Micrographa*, *Darbishirella*, *Pycnographa* and some species of *Opegrapha*.

The characters and genera are as given by Zahlbruckner.

Comparative table of Arthoniaceae

		Algal cells present in thallus		
		Palmella	Trentepohlia	Phyllactidium
Spore with parallel septa	Apothecium single	Allarthonia	Arthonia	Arthoniopsis
	Apothecia grouped	—	Synarthonia	—
Spore muriform	Apothecium single	Allarthothelium	Arthothelium	Trichophyma

Family XYLOGRAPHACEAE

Thallus crustaceous, non-corticate, fastened to the substratum by hyphae, epi- or hypo-phlocodal, with green algal cells ("*Palmella*"). Apothecia oblong or ovoid or more-or-less angular, simple or branched, sessile or erumpent, marginate; ascus more-or-less clavate, with 4–8 simple (or 1-septate), colourless (or dark) spores.

Encephalographa is peculiar in some respects, such as the 1-septate brown spores with unequal cells. It is almost distinct enough to form a separate family, though it is possibly derived from *Lithographa.*

Spores simple, colourless and ellipsoidal.	
Apothecium with simple hymenium.	
Hypothecium dark	*Lithographa*
Hypothecium pale	*Xylographa*
Apothecium with 2–4 parallel hymenia ...	*Ptychographa*
Spores 1-septate and brown. Apothecia usually grouped	*Encephalographa*

Family MELASPILEACEAE

Thallus crustaceous, non-corticate, fastened to the substratum by hyphae, epi- or hypo-phloeodal, with trentepohlioid algal cells. Apothecia lirelliform or roundish, single or congregate, marginate; paraphyses simple and free; ascus more-or-less clavate with 8 (or fewer) 1-septate (occasionally 3-septate), colourless or dark spores.

There is a possibility that this group has been derived from *Xylographa* and that from the same evolutionary line the family Graphidaceae (in its restricted sense) has been derived.

Algal cells *Trentepohlia.* Spores becoming darker ...	*Melaspilea*
Algal cells *Phyllactidium.*	
Apothecia in stromata	*Pycnographa*
Apothecia not in stromata	*Micrographa*

Family OPEGRAPHACEAE

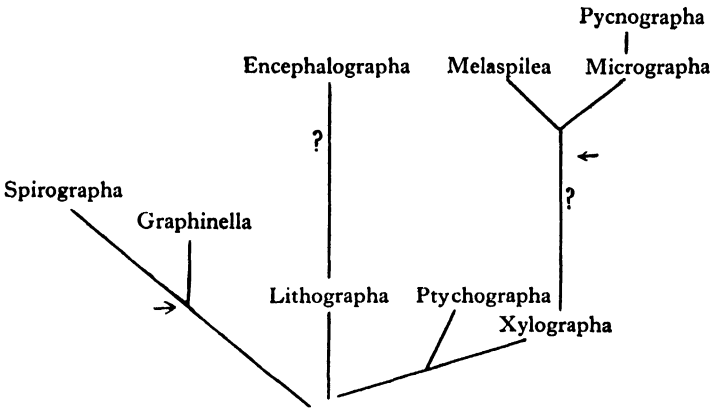
Thallus crustaceous, rarely fruticose, usually with trentepohlioid algal cells. Apothecia usually lirelliform, simple or branched, sessile and often more-or-less superficial (exceptionally immersed), single or congregate or in stromata. Ascus more-or-less clavate, 8- or fewer-spored. Paraphyses branched and anastomosing. Spores usually colourless, with 3 or more parallel transverse septa, or muriform; cells more-or-less cylindrical with thin walls.

Spores transversely (3–9)-septate.
Algal cells *Trentepohlia.*
Thallus fruticose.
Hyphae parallel to surface.
Hypothecium dark. Spores colourless.
Soredia absent ... ... *Ingaderia*
Hyphae perpendicular to surface.
Apothecia sessile. Hypothecium dark.
Spores colourless. Soredia present ... *Reinkella*
Apothecia immersed. Hypothecium pale.
Spores dark. Soredia absent ... ... *Roccellographa*
Thallus crustaceous.
Spores 3-septate brown. Hypothecium pale. Apothecia immersed ... ... *Gymnographa*
Spores 3- or more-septate. Apothecia usually superficial.
Spores colourless.
Apothecia not in stromata ... ... *Opegrapha*
Apothecia in stromata.
Hypothecium pale ... ... *Enterographa*
Hypothecium dark ... ... *Chiodecton*
Spores dark.
Apothecia not in stromata ... ... *Sclerographis*
Apothecia in stromata ... ... *Sclerophyton*
Algal cells *Phyllactidium* (or *Heterothallus*). Spores colourless.
Apothecia not in stromata ... ... *Fouragea*
Apothecia in stromata.
Algal cells *Phyllactidium* ... ... *Mazosia*
Algal cells *Heterothallus* ... ... *Rotularia*
Algal cells "*Palmella.*" Spores colourless.
Spores 3–8-septate. Hypothecium pale. Hymenium simple ... ... *Aulaxina*
Spores 3-septate. Hypothecium dark. Hymenium compound ... ... *Diplogramma*
Spores muriform. Algal cells *Trentepohlia.*
Apothecia not in stromata ... ... *Dictyographa*
Apothecia in stromata.
Spores colourless ... ... *Minksia*
Spores dark ... ... *Enterostigma*

Family Graphidaceae

Thallus crustaceous, cortex absent or amorphous, epi- or hypophloeodal, fastened to the substratum by hyphae, with *Trentepohlia*

or rarely *Palmella*. Apothecia usually more or less immersed, lirelliform or roundish, simple or branched, single or aggregate, usually marginate. Ascus ± clavate, with 8 or fewer spores. Paraphyses simple and free. Hypothecium usually colourless or pale. Spores colourless or brown, with 3 or more parallel transverse septa or muriform; cells short, lens-shaped or rounded with thick walls.

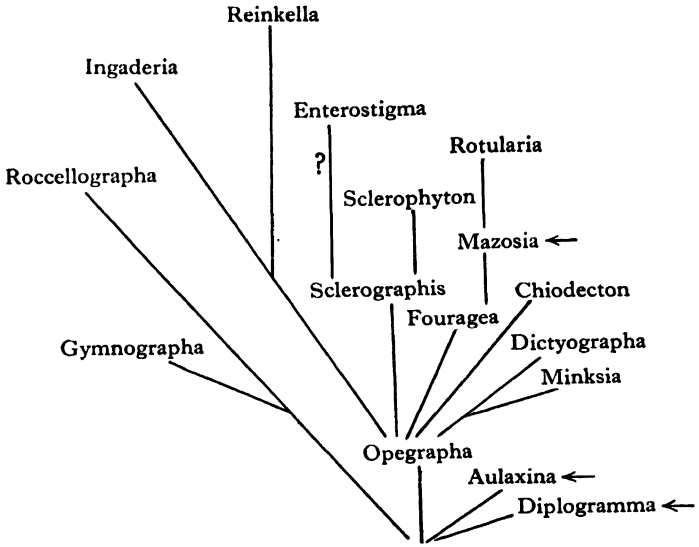


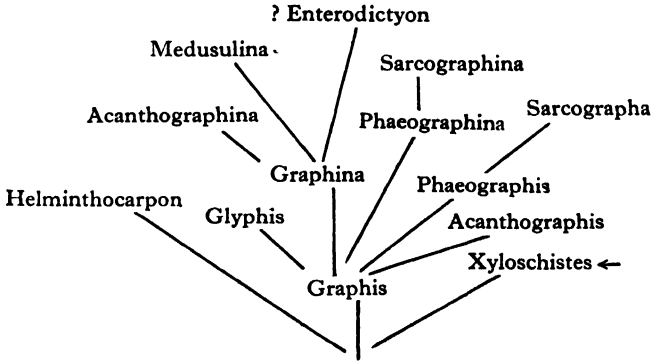
Helminthocarpon is a rather peculiar genus. The branched and coherent paraphyses link it to Opegraphaceae, but the shape of the spore-cell is a more important taxonomic character, and this is nearer to that of Graphidaceae. The volva-like thalline margin is also peculiar. The stromoid *Enterodictyon* has the spore-cells more cubic and with thinner walls, but its paraphyses are simple and free. There is no known member of Opegraphaceae parallel to it and, on the whole, it agrees better with Graphidaceae, though its derivation is doubtful.

Spores transversely (3–19)-septate.
  Spores colourless.
    Paraphyses clavate and warted at apices *Acanthographis*
    Paraphyses little clavate and smooth at apices.
      Apothecia not in stromata ... ... *Graphis*
      Apothecia in stromata ... ... *Glyphis*
  Spores brown or dark.
    Apothecia not in stromata ... ... *Phaeographis*
    Apothecia in stromata ... ... *Sarcographa*
Spores muriform.
  Spores colourless. Paraphyses simple and free.
    Paraphyses clavate and warted at apices *Acanthographina*

Paraphyses little clavate and smooth at apices.

Apothecia not in stromata	*Graphina*
Apothecia in stromata.	
Spore-cells lens-shaped with thick walls	*Medusulina*
Spore-cells ± cubic with thinner walls	*Enterodictyon*
Spores colourless. Paraphyses branched and coherent	*Helminthocarpon*
Spores dark. Hypothecium brownish. Algal cells green	*Xyloschistes*
Spores brown. Algal cells *Trentepohlia*.	
Apothecia not in stromata	*Phaeographina*
Apothecia in stromata	*Sarcographina*





Family GRAPHINELLACEAE

Thallus crustaceous, non-corticate, fastened to the substratum by hyphae, with *Trentepohlia* algal cells. Apothecia lirelliform, single, superficial or immersed. Ascus many-spored. Spores colourless, simple or indistinctly 1-septate and usually elongate.

Paraphyses branched and anastomosing	*Spirographa*
Paraphyses simple and free	*Graphinella*

Order CONIOCARPALES

The families and genera given by Zahlbruckner are provisionally accepted, though there are some indications that a revision of the order, in which greater importance is given to sporal characters, is desirable. *Tylophorella*, with its many-spored ascus, seems comparable to *Acarospora* of the Parmeliales and to *Graphinella* in the Graphidales. The family Cypheliaceae, which differs chiefly from the family Calicaceae in the absence of an apothecial stalk is not used by Lorrain Smith (32*b*). In some of the genera placed in Calicaceae the apothecia are sessile or almost so (*Sphinctrina*, *Pyrgidium*), whilst in some (*Pyrgillus*, *Tylophoron*) placed in Cypheliaceae the apothecia are more-or-less elevated. The length of the apothecial stalk is a variable quantity in the species in which it is usually present, and scarcely warrants having such taxonomic importance attached to it.

Order PYRENOCARPALES

The classification into families is again largely influenced by its convenience to the collector and determinator. From this point of view it is a successful one, as it renders a pyrenocarpous lichen easy to place in its particular group. This influence has, however, been somewhat detrimental to a natural classification and has tended to exaggerate the importance of thalline and other characters easily seen by the naked eye, or with the aid of a lens.

The development of a foliose thallus is chiefly shown in those Pyrenocarpales with green algal cells. It is considered as the critical character on which the family Dermatocarpaceae is founded, whilst the fruticose habit distinguishes the family Pyrenothamniaceae. These two "families" are varied in regard to spores and paraphyses; they do not form natural groups, and it seems probable that the

genera composing them have originated independently from genera with crustaceous thallus and corresponding thecial characters. In some cases the genera are of comparatively recent creation: thus *Agonimia* was founded in 1909 to receive the more-or-less foliose species of *Polyblastia*, whilst *Nylanderiella* was created as late as 1914. The only British representative of *Agonimia* is still given as *Polyblastia tristicula* in the standard Monograph of British Lichens. It was found by Admiral Jones in 1864 at Aviemore and that was the only British record till it was discovered in Somerset in 1917. All the characters agree with *Polyblastia* and its foliose nature is often little more pronounced than in some specimens of *Bilimbia sabuletorum*, so that even its generic segregation is doubtful, whilst its relegation to another family is unwarranted. The table on p. 52 shows the relationships of the genera placed in Dermatocarpaceae and Pyrenothamniaceae, with those placed in Verrucariaceae. It indicates that the foliose and fruticose genera should be regarded as derived from various sources and that the retention of the families Dermatocarpaceae and Pyrenothamniaceae is phylogenetically unsound.

The spores in species of *Verrucaria* are remarkably constant in regard to their simple character, and the same statement holds good for other genera with simple spores. The unicellular character of the spore can therefore be taken as of considerable systematic value. There is much less constancy in the septate spores. In the genus *Thelidium* one and the same species may show what appear to be mature spores with different septation, some 1-septate, others 3-septate, whilst occasionally a longitudinal septum connects two of the transverse septa. The continued division, so that the spore becomes muriform, is shown in the subdivision *Thelidioides* (37) of *Polyblastia*. Some spores in the ascus of one and the same perithecium are 1-septate, some 3-septate, in others further transverse septa occur, whilst, finally, oblique or longitudinal septa appear and the spore becomes muriform. These changes may, of course, be recapitulations of the fungal ancestor antecedent to its symbiosis with the algae. Whether antecedent or not, the gradual transition from one to further septa in different Pyrenocarpales implies that such septation must be used cautiously, even for generic distinction.

The shape of the sporal chambers seems to be of greater value than their number. Most Pyrenocarpales have cylindrical or cubic cells with thin walls, but some genera possess lens-shaped or ± rounded cells with thick walls. This difference is used for generic distinction

Comparative table of Pyrenocarpales with green algae and simple apothecia with apical ostioles.

Spore								
Septa	Colour	Shape	No. in ascus	Paraphyses	Hymenial algae	Crustaceous	Foliose	Fruticose
None	o	±ellipsoid	8 (–16)	Mucilaginous and disappearing	o	Verrucaria	Dermatocarpon	—
,,	o	Vermiform	8	Mucilaginous and disappearing	o	Sarcopyrenia	—	—
,,	o	±ellipsoid	Many	Mucilaginous and disappearing	o	Trimmatothele	—	—
,,	o	,,	1	Branched	Present	Thelenidia	—	—
,,	o or brownish	,,	4–8	,,	o	Thrombium	Anapyrenium	—
1–3	o	,,	8	Mucilaginous and disappearing	o	Thelidium	Placidiopsis	Nylanderiella
1–3	Brown	,,	8	Mucilaginous and disappearing	o	—	Heterocarpon	—
1	,,	,,	8	Simple with mucilaginous walls	o	Thelidiopsis	—	—
5–7	o or brownish	Elongate	6–8	Mucilaginous and disappearing	o	—	Normandina	—
3	o	Fusiform	8	Branched	o	Geisleria	—	—
Many	o	Acicular	4–8	Unbranched	o	Gongylia	—	—
Muriform	o or dark	±ellipsoid	1–8	Mucilaginous and disappearing	o	Polyblastia	Agonimia	Pyrenothamnia
,,	,,	,,	1–8	Mucilaginous and disappearing	Present	Staurothele	Endocarpon	—
,,	o	,,	2–8	Branched	o	Microglaena	Psoroglaena	—
,,	o or pale	±fusiform	4–6	Simple and ±free	o	Aspidothelium *	—	—
Many	o	Fusiform	—	Branched and coherent	o	Aspidopyrenium *	—	—

* Perithecium widening to form a shield round the ostiole.

and, in conjunction with other characters, must be considered for the grouping into families. The paraphysial characters are also fairly constant in certain groups and due consideration must also be given to them. The paraphyses sometimes become mucilaginous and disappear, but this character appears to have been evolved independently in several families and even in different genera. The darkening of the spore and the expansion of the apothecial apex to form a shield have also occurred independently in different consortia. The formation of stiff hairs on the perithecium of *Stereochlamys* and *Trichothelium* is probably a case of convergence, though there is a slight possibility that both genera were derived from the same ancestral form possessing a bristly perithecium. In both the ascus has 8 colourless spores, hymenial algae are absent and the paraphyses are simple. *Trichothelium* occurs on leaves on living trees, the alga is *Phyllactidium*, the spores are many-septate and it is probably evolved from *Phylloporina*. *Stercochlamys* occurs on bark, the alga is *Trentepohlia*, the spores are muriform and it seems allied to *Pyrenula*.

Algal cells are present in the hymenium of *Staurothele*, *Endocarpon* and *Thelenidia*, but their occurrence is of little phylogenetic significance as their intrusion seems to have been quite independent in the first and last of these genera.

The following tables show the characters of the genera placed in the Pyrenocarpales. Some genera, as *Coriscium* and *Cocciscia*, are omitted because of the unknown, or doubtful, nature of some of the characters.

Comparative tables of Pyrenocarpales

Table I. Spores simple. No stromoid representatives.

Spore					Thallus	
Colour	Shape	No. in ascus	Paraphyses	Alga	Crustaceous	±foliose
o	±ellipsoid	8	Disappearing	Green	Verrucaria	Dermatocarpon
o	Vermiform	8	,,	,,	Sarcopyrenia	—
o	Elongate	8	±disappearing	Prasiola	Mastodia	—
o	±ellipsoid	Many	Disappearing	Green	Trimmatothele	—
o	,,	,,	Simple and free	Dactylococcus	—	Placothelium
o	,,	6–8	Almost simple	Trentepohlia	Coccotrema	—
o	Elongate	6–8	Delicate and short	Nostoc	Hassea	—
o	±ellipsoid	8	Branched	,,	Rhabdospora	—
o	,,	–8	±branched	Scytonema	Rhodothrix	—
o	,,	1	Branched (hym. algae)	Green	Thelenidia	—
o	,,	4–8	±branched	,,	Thrombium	—
Brown	,,	4–8	,,	,,	,,	Anapyrenium
o	,,	8	±branched and anastomosing	Trentepohlia	—	Lepolichen
o	,,	2–4	Branched and anastomosing	,,	Monoblastia	—
Dark	,,	8	Branched and anastomosing	Phyllactidium	Haplopyrenula	—

Table II.

Spores transversely septate. No stromoid representatives.

Spore							Thallus	
Septa	Colour	No. in ascus	Shape	Cell-form	Paraphyses	Algal cells	Crustaceous	±foliose or fruticose
1	o	8	Fusiform	±cylindrical	Disappearing	Scytonema or Sirosiphon	Eolichen	—
3	Brown	4	±ellipsoid	,,	,,	Nostoc	—	Pyrenidium (fr.)
1–3	o	8	,,	,,	,,	Green	Thelidium	Placidiopsis
1	o	–8	,,	,,	±disappearing	,,	—	Nylanderiella (fr.)
1–3	Brown	8	,,	,,	Disappearing	,,	—	Heterocarpon
1	Dark	8	,,	,,	Simple with slimy walls	,,	Thelidiopsis	—
5–7	o (brown)	6–8	Elongate	,,	Disappearing	,,	—	Normandina
1(–5)	Brown	4–8	±ellipsoid	,,	Branched and anastomosing	Trentepohlia	Microthelia	—
1–3	,,	8	,,	,,	Branched and anastomosing	Phyllactidium	Microtheliopsis	—
1	o	8	,,	,,	Branched and entangled	Trentepohlia	Acrocordia	—
3	o	8	,,	,,	Branched	Green	Geisleria	—
1	o	8	,,	,,	±branched	Xanthocapsa	Xanthopyrenia	—
1	o	Many	Cylindrical	,,	,,	Green	Epigloea	—
(0)–3	o	,,	±ellipsoid	,,	Simple	Trentepohlia	Thelopsis	—
(0)–more	o or brown	4–many	,,	,,	—	Green and colonial	Moriola and Spheconisca	—
Many	o	4–8	Acicular	,,	Simple	Green	Gongylia	—
,,	o	8	Fusiform	±lens-shaped	Branched and coherent	,,	Aspidopyrenium (perithecium shield-forming)	—

Table III.

Spores transversely septate. Stromoid representatives sometimes present. Thallus crustaceous except in Strigula.

Spore										
Septa	Colour	No. in ascus	Shape	Cell-form	Paraphyses	Alga	Apothecium single	Apothecia stromoid or compound	Apothecia oblique or with oblique mouth	Apothecia radiate and ±stromoid
1–5	o	–8	±ellipsoid	±cylindrical	Branched and anastomosing or o	Trentepohlia	Arthopyrenia	Tomasiella	Pleurotrema	—
1–5	o	8	,,	,,	Branched and anastomosing or o	Phyllactidium or Heterothallus	Raciborskiella	—	—	—
3–many	o	–8	Elongate	,,	Branched and anastomosing or o	Trentepohlia	Pseudosagedia	Athrismidium	Pleurotrema (p.p.)	—
3–many	o	4–8	Acicular	,,	Branched and anastomosing or o	,,	Leptorhaphis	Celothelium	Pleurotrema (p.p.)	—
Many	o	4–8	,,	,,	Simple and free	,,	Belonia	—	—	—
,,	o	8	,,	,,	Disappearing	Phycopeltis	Phylloblastia	—	—	—
,,	Brown	8	Elongate	,,	Simple and free	Trentepohlia	Blastodesmia	—	—	—
(1)–5–	o	6–8	,,	,,	,,	,,	Porina	—	—	Lithothelium
,,	o	8	,,	,,	,,	Phyllactidium or Heterothallus	Phylloporina	—	—	—
Many	o	8	,,	,,	,,	Phyllactidium	Trichothelium	—	—	—
1	o–brown	8	Unequal	,,	Simple or branched	Trentepohlia	—	Asteroporum	—	—
3–5	,,	8	Elongate	,,	±branched and coherent or o	,,	—	Mycoporellum	—	—
(1)–5–	Brown	8	Fusiform	Lensiform	Simple and free	,,	Pyrenula	Melanotheca	—	—
3–5–	,,	–8	±fusiform	,,	Branched and anastomosing	,,	—	,,	Parathelium	Pyrenastrum
3	o–brown	8	Fusiform	,,	Absent	Phycopeltis	Micropyrenula	—	—	—
3–5–	o	–8	±fusiform	,,	Branched and anastomosing	Trentepohlia	Pseudopyrenula	Trypethelium	Plagiotrema	Astrothelium
1–3	o	8	Elongate	±cylindrical	Simple and free	Phyllactidium or Heterothallus	Strigula*	—	—	—

* In Strigula the thallus is radiately-lobed at the margin.

Table IV.

Spores muriform. Stromoid representatives sometimes present.

Spore									
Colour	No. in ascus	Cell-form	Paraphyses	Algal cells	Apothecium single. Thallus crustaceous	Apothecium single. Thallus foliose or fruticose	Apothecia stromoid or compound	Apothecia oblique or with oblique mouth	Apothecia radiate and ±stromoid
o or dark	1–8	±cylindrical	Disappearing	Green	Polyblastia	Agonimia	—	—	—
o or dark	1–8	,,	Disappearing (hym. algae)	,,	Staurothele	Endocarpon	—	—	—
Brown	1–8	,,	Disappearing	,,	—	Pyrenothamnia (fruticose)	—	—	—
o	2–8	,,	Branched	,,	Microglaena (p.p.)	—	—	—	—
Brown	2–8	,,	,,	,,	Microglaena (p.p.)	Psoroglaena	—	—	—
Dark	8	,,	,,	Scytonema	Pyrenothrix	—	—	—	—
o	1–8	±cylindrical or cubic	Branched and anastomosing	Trentepohlia	Polyblastiopsis	—	Laurera	Campylothelium	—
Brown	1–8	±cylindrical	Branched and anastomosing	,,	—	—	Bottaria (p.p.)	Pleurotheliopsis	Parmentaria
or brown	6–8	±cubic	Branched and coherent or o	,,	—	—	Mycoporum	—	—
o	–8	±cylindrical or cubic	Simple and free	,,	Clathroporina	—	—	—	Cryptothelium (p.p.)
Brown	1–8	±cylindrical	,,	,,	—	—	Bottaria (p.p.)	—	Cryptothelium (p.p.)
o	4–8	Cubic	,,	Phyllactidium	Phyllobathelium	—	—	—	—
Brown	1–8	Lensiform	,,	Trentepohlia	Anthracothecium	—	—	—	—
o	8	±cylindrical	,,	,,	Stereochlamys*	—	—	—	—
o or pale	4–6	±cubic	,,	Green	Aspidothelium†	—	—	—	—

* Stiff hairs on upper part of perithecium.

† Perithecium expanding to form a shield around the ostiole.

The stromoid pyrenocarpous lichens are often grouped together under a distinct family, though Wainio distributed them as sub-genera under the corresponding genera of Pyrenulaceae. Zahlbruckner rejects the method of Wainio, but gives insufficient reasons for grouping them under the special family Trypetheliaceae. As with Chiodectonaceae amongst the Graphidales, they are here recognised as constituting different genera, and placed in their appropriate positions in other families. It may also be noted that stromata or pseudostromata are met with in some of the species placed by Zahlbruckner in Astrotheliaceae, whilst the perithecia are compound in Mycoporaceae and often congregate in plants belonging to genera placed in Pyrenulaceae, e.g. species of *Arthopyrenia*, *Leptorhaphis*, *Pseudopyrenula*, *Anthracothecium*. In those included in the special family Trypetheliaceae, *Tomasiella* is a stromoid genus corresponding to *Arthopyrenia*, *Athrismidium* (used as a sub-genus) to *Pseudosagedia* (sub-genus of *Arthopyrenia*), *Celothelium* to *Leptorhaphis*, *Melanotheca* to *Pyrenula*, *Trypethelium* to *Pseudopyrenula* and *Laurera* to *Polyblastiopsis*. *Bottaria* seems to correspond to a compound *Pleurotheliopsis* with a vertical mouth. The corticate nature of the upper part of the thallus suggests that it may have developed from a lichen with green algae, but the only one it could directly develop from is *Microglaena*, and in this the cortex is doubtful. Another possibility is that it comes from *Laurera*, but the varying character of the paraphyses indicates that it is a mixed genus.

The family Strigulaceae is founded largely on habitat. Most of the genera are epiphyllous and contain a trentepohlioid alga other than *Trentepohlia*. The apothecia are always single and vertical with straight ostiole, but the sporal and paraphysial characters are too varied for the genera to be considered as a phylogenetic group. The family is a useful one for determinative purposes but, on phylogenetic grounds, the genera appear to be better distributed as derivatives of genera belonging to other families. Except for the alga and habitat, *Microtheliopsis* corresponds to *Microthelia*, *Phylloporina* to *Porina*, *Phyllobathelium* to *Clathroporina*, *Raciborskiella* to *Pseudosagedia*, and *Haplopyrenula* to *Monoblastia*. *Micropyrenula* is similar to *Pyrenula* and *Phylloblastia* to *Belonia*, though paraphyses are absent or disappear in the epiphyllous plants. *Trichothelium* is like *Phylloporina* but possesses hairs on the perithecium, whilst *Strigula* itself is also like a *Phylloporina*, which forms definite circular patches with a radiate margin.

Family MORIOLACEAE

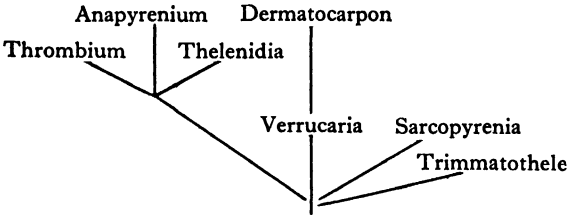
Characters and genera as given by Zahlbruckner ((36) p. 64). *Baeotitthis*, given as a section or sub-genus of Spheconisca, may be given generic rank because of its many-spored ascus and its simple or indistinctly septate spores.

Family EPIGLOEACEAE

Characters and genus as in Zahlbruckner ((36) p. 65).

Family VERRUCARIACEAE

Thallus crustaceous or foliose, non-corticate when crustaceous, but usually corticate when foliose, with green algal cells. Perithecia simple, immersed or superficial, entire or dimidiate, with an apical pore. Ascus with 1–8, occasionally 16 spores. Paraphyses soon becoming mucilaginous and disappearing or more-or-less persistent. Spores simple, colourless or sometimes brown.



Paraphyses soon becoming mucilaginous and disappearing.

Spores vermiform and clavate at ends ...	*Sarcopyrenia*
Spores ± ellipsoid and not clavate at ends.	
Thallus crustaceous	*Verrucaria*
Thallus ± foliose	*Dermatocarpon*

Paraphyses persisting and usually branched.

Thallus crustaceous.	
Hymenial algae present	*Thelenidia*
Hymenial algae absent	*Thrombium*
Thallus foliose	*Anapyrenium*

Family MONOBLASTIACEAE

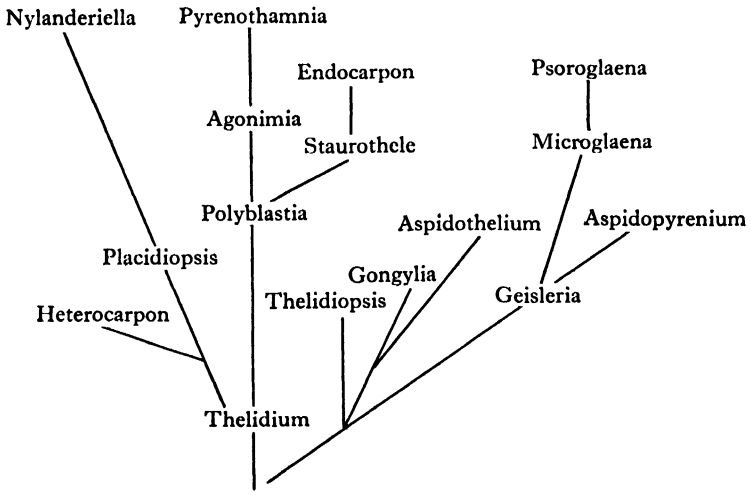
Thallus crustaceous or foliose with *Trentepohlia* or allied alga (*Phyllactidium* in *Haplopyrenula*). Perithecia simple, with an apical pore; ascus with 2–8 simple spores.

This family includes *Coccotrema* and *Monoblastia* from "Pyrenulaceae," *Haplopyrenula* from "Strigulaceae" and *Lepolichen*, the single representative of "Phyllopyreniaceae."

Thallus foliose ... ... *Lepolichen*
Thallus crustaceous.
Paraphyses branched and entangled.
Algal cells *Trentepohlia* ... ... *Monoblastia*
Algal cells *Phyllactidium* ... ... *Haplopyrenula*
Paraphyses simple and free ... ... *Coccotrema*

Family THELIDIACEAE

Thallus crustaceous or foliose, rarely fruticose, non-corticate when crustaceous, but usually corticate when foliose or fruticose. Algal cells green. Perithecia simple, immersed or superficial, entire or dimidiate, with an apical ostiole. Paraphyses soon becoming mucilaginous and disappearing, or more-or-less persistent. Spores transversely septate or muriform, colourless or dark.



Paraphyses soon becoming mucilaginous and disappearing.
Spores 1–3-septate (5–7-septate in *Normandina*).
Thallus crustaceous. Spores colourless ... *Thelidium*
Thallus foliose.
Spores 5–7-septate, elongate ... ... *Normandina*
Spores 1–3-septate, ± ellipsoid.
Spores colourless ... ... *Placidiopsis*
Spores brown ... ... *Heterocarpon*
Thallus fruticose. Spores colourless ... *Nylanderiella*

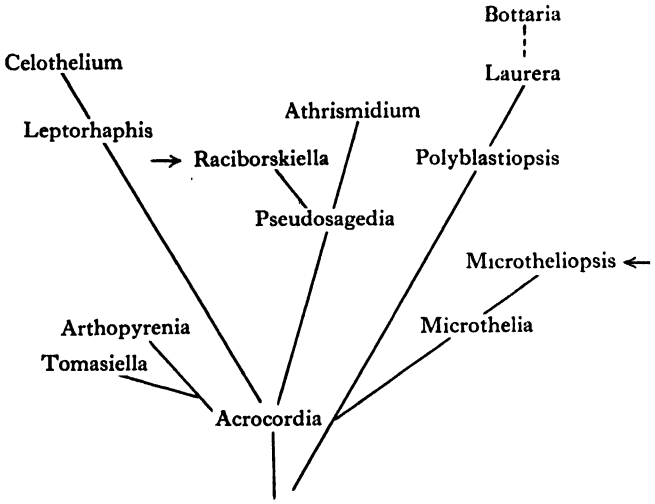
Spores muriform.
Hymenial algae absent.
Thallus crustaceous ... ... *Polyblastia*
Thallus more-or-less foliose ... ... *Agonimia*
Thallus more-or-less fruticose ... ... *Pyrenothamnia*
Hymenial algae present.
Thallus crustaceous ... ... *Staurothele*
Thallus more-or-less foliose ... ... *Endocarpon*
Paraphyses remaining. Hymenial algae absent.
Spores 1-septate and dark ... ... *Thelidiopsis*
Spores 3- or more-septate, colourless, fusiform.
Perithecia expanded above into a shield ... *Aspidopyrenium*
Perithecia immersed ... ... *Geisleria*
Spores acicular with many (14–19) septa ... *Gongylia*
Spores muriform (eventually).
Perithecium expanded above into a shield *Aspidothelium*
Perithecium immersed or free but not expanded.
Thallus crustaceous. Spores often brownish ... ... *Microglaena*
Thallus ± foliose. Spores colourless ... *Psoroglaena*

Family ARTHOPYRENIACEAE

Thallus crustaceous, non-corticate or rarely ± corticate above, without rhizinae, with *Trentepohlia* or allied alga. Perithecia simple or rarely grouped in a stroma, sessile or immersed, vertically placed with apical ostiole. Asci ovate or cylindrical, 1–8-spored. Paraphyses branched and more-or-less entangled, sometimes disappearing. Spores 1–many-septate or muriform, usually colourless but sometimes brown; cells cylindrical or cubical with thin walls.

Spores ± ellipsoid (occasionally acicular), 1–many-septate, colourless.
Spores 1-septate, broad. Asci elongate. Paraphyses branched and entangled ... ... *Acrocordia*
Spores 1–3–(5)-septate, longly-ellipsoid. Paraphyses often disappearing.
Perithecia not in stromata ... ... *Arthopyrenia*
Perithecia in stromata ... ... *Tomasellia*
Spores 3–9-septate, elongate or fusiform. Paraphyses branched and entangled.
Perithecia not in stromata.

Algal cells *Trentepohlia* ... ... *Pseudosagedia*
Algal cells *Phyllactidium* or *Heterothallus* *Raciborskiella*
Perithecia in stromata ... ... *Athrismidium*
Spores 1–many-septate, acicular. Paraphyses branched and entangled.



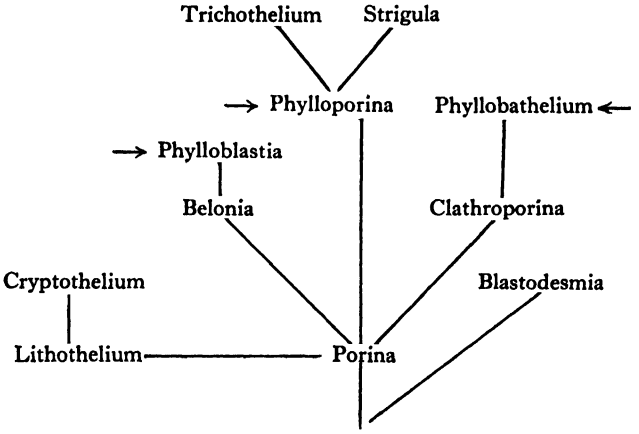
Perithecia simple ... ... *Leptorhaphis*
Perithecia in stromata ... ... *Celothelium*
Spores ovate or elongate-fusiform, brown, 1–3–(5)-septate.
Algal cells *Trentepohlia* ... ... *Microthelia*
Algal cells *Phyllactidium* ... ... *Microtheliopsis*
Spores muriform, colourless or brown.
Perithecia simple. Spores colourless ... *Polyblastiopsis*
Perithecia in stromata.
Spores colourless ... ... *Laurera*
Spores brown ... ... *Bottaria*

Family PORINACEAE

Thallus crustaceous, non-corticate, without rhizinae, with *Trentepohlia* or allied algal cells. Perithecia single (in known representatives), sessile or immersed, vertically placed and with apical ostiole. Paraphyses simple and free, usually persisting. Ascus usually elongate with 8 or fewer spores (in *Thelopsis*[1] many-spored). Spores 1–many-septate or muriform, usually colourless but occasionally brown; cells cylindrical or cubical with thin walls.

[1] See p. 67.

Ascus with many (0)–1–3-septate spores ... *Thelopsis*[1]
Ascus with 8 or fewer spores.
Spores 1–many-septate, colourless.
Asci and paraphyses persisting. Spores elongate.
Algal cells *Trentepohlia* ... ... *Porina*
Alga *Phyllactidium* (or *Heterothallus*) Epiphyllous
Perithecium naked.
Thallus indefinite ... ... *Phylloporina*
Thallus of definite spots with radiate margin ... ... *Strigula*
Perithecium with stiff hairs on it ... *Trichothelium*



Asci or paraphyses becoming ± slimy. Spores many-septate, acicular.
Alga *Trentepohlia*. Ascus becoming slimy *Belonia*
Alga *Phycopeltis*. Paraphyses becoming slimy ... ... *Phylloblastia*
Spores 1–many-septate, brown ... ... *Blastodesmia*
Spores muriform, colourless.
Algal cells *Trentepohlia* ... ... *Clathroporina*
Algal cells *Phyllactidium* ... ... *Phyllobathelium*

Family PYRENULACEAE

Thallus crustaceous, non-corticate, or rarely ± corticate above, without rhizinae, with *Trentepohlia* or allied alga. Perithecia simple or aggregate or in stromata, vertically placed and with apical ostiole. Ascus 1–8-spored. Paraphyses usually simple, free and persisting.

[1] See p. 67.

Spores 1–many-septate to muriform, colourless or brown; cells lens-shaped, rounded or angular, with thick walls.

Paraphyses simple and free.

Spores 1–more-septate, often 3-septate and fusiform.

Algal cells *Trentepohlia*. Spores brown.

Perithecia in stromata ... ... *Melanotheca*

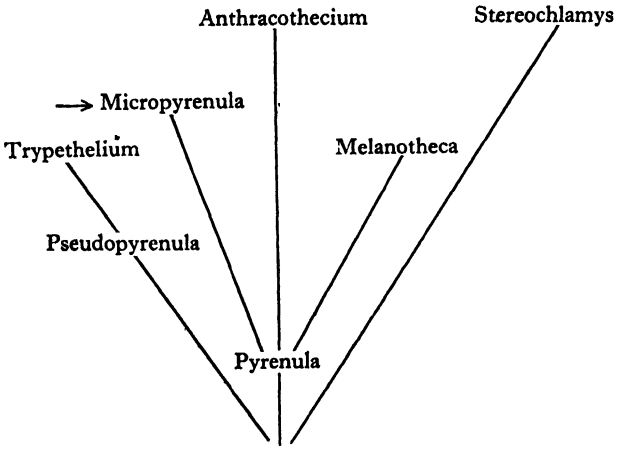
Perithecia not in stromata ... ... *Pyrenula*

Algal cells *Phycopeltis*. Spores colourless to brownish ... ... *Micropyrenula*

Spores muriform.

Perithecium naked. Spores dark ... ... *Anthracothecium*

Perithecium beset with stiff hairs. Spores colourless ... ... *Stereochlamys*



Paraphyses branched and ± entangled. Spores 3–many-celled, colourless.

Perithecia simple or congregate but not in stromata ... ... *Pseudopyrenula*

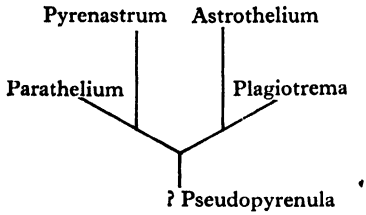
Perithecia in stromata ... ... *Trypethelium*

Family Astrotheliaceae

One of the important characters of this family is the more-or-less radiate arrangement of the perithecia. This is usually associated with other characters and may therefore be considered important, but otherwise does not deserve to have much taxonomic value given to it. Amongst the Graphidales the radiate arrangement is not considered to be generically important, or even, in some cases, specifically important. In both *Opegrapha* and *Graphis* there are some species,

in which the apothecia are free from one another, and others in which they are radiately arranged. *Opegrapha vulgata* has a variety *siderella*[1], with the apothecia in radio-stellate groups, whilst *Graphis scripta* and *G. elegans* also have forms or varieties in which the apothecia are stellately arranged.

In Astrotheliaceae the radiate grouping of the perithecia is associated with other characters. The perithecia are often oblique and united in stromata, and the elongated ostioles usually coalesce so as to form an elongated common canal. The association of these characters justify the formation of one or more groups. The varying nature of the spores and paraphyses in the genera listed under



"Astrotheliaceae" does not indicate any single origin. The spore-cells may be either cylindrical, as in *Lithothelium*, or lens-shaped, as in *Astrothelium*, whilst the paraphyses are simple in the former and branched in the latter. In the allied family Paratheliaceae the perithecia are neither radiately arranged nor united in stromata, but are either oblique or open by elongated and oblique canals. Here again, an artificial grouping is indicated by the varying nature of the spores and paraphyses. There are three distinct origins for these two "families," the probable origins being from the lines which gave rise to *Pseudopyrenula*, *Polyblastiopsis* and *Porina* respectively. Accordingly the genera are distributed amongst three families: Astrotheliaceae (emended), Pleurotremaceae and Cryptotheliaceae. The emended family Astrotheliaceae is limited to four genera, two of which were placed by Zahlbruckner in it, whilst the other two were put in "Paratheliaceae."

The characters of the emended family are as follows:

Thallus crustaceous, non-corticate or somewhat corticate above, with *Trentepohlia*. Perithecia single or in stromata, sometimes radiately grouped, obliquely or vertically placed with ostioles oblique or lateral; ostioles elongated and sometimes coalescent into a common

[1] This may be given specific rank as *O. siderella* because of the short spermatia: in that case, *O. siderella* itself has a var. *subsiderella* in which the apothecia are not radio-stellate.

canal. Paraphyses branched and entangled or coherent. Spores 2–many-septate with ± lens-shaped, or rounded cells, with thick walls. Spores colourless.

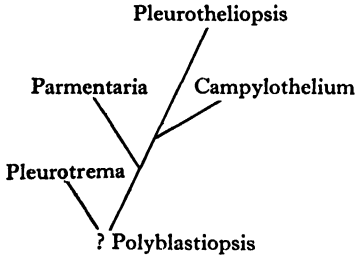
Perithecia single	*Plagiotrema*
Perithecia radiate and in a stroma	*Astrothelium*

Spores brown.

Perithecia single	*Parathelium*
Perithecia ± united or in a stroma	*Pyrenastrum*

Family PLEUROTREMACEAE

Characters as given in the former family except that the spores are 1–many-septate to muriform, with ± cylindrical cells having thin walls.



The following belong to this group: *Pleurotrema* with 1–many-septate spores, *Campylothelium* and *Pleurotheliopsis* with simple perithecia and muriform spores, and *Parmentaria*, a stromoid genus with muriform and brown spores. The definite positions of some of the muriform-spored genera in this family is somewhat indecisive till a conclusive analysis of their spore-cells is reached.

Family CRYPTOTHELIACEAE

Characters as in Astrotheliaceae except that the paraphyses are simple and free, or almost so, and that the spore-cells are more-or-less cylindrical. The two genera placed here are stromoid. *Lithothelium* has 3-septate and colourless spores whilst in *Cryptothelium* they are muriform and colourless.

Family MYCOPORACEAE

When the doubtful lichen *Asteroporum* is excluded, the characters and genera given by Zahlbruckner (36) pp. 92–3) can be accepted.

Family XANTHOPYRENIACEAE

The critical character is the presence of *Xanthocapsa* as the algal symbiont. *Xanthopyrenia*, the only known representative, has simple perithecia, 1-septate, colourless spores and a crustaceous homoiomerous thallus.

Family PYRENOTRICHACEAE

The critical character is that the byssaceous thallus has *Scytonema* algae. The family contains two genera which agree fairly well in the characters of the perithecia except that *Rhodothrix* has 1-septate and *Pyrenothrix* muriform spores.

Family MASTODIACEAE

The critical character is the occurrence of *Prasiola* as the algal constituent. *Mastodia*, the only known representative, has simple perithecia, colourless and simple spores, whilst the thallus is homoiomerous.

Family PYRENIDIACEAE

This is admittedly a family of doubtful value and is only provisional. In it are placed most of the pyrenocarpous lichens having blue-green algal symbionts.

Pyrenidium has a brownish 3-septate spore, the structure of the supposed thallus is similar to one of the fruticulose *Leptogia*, and the perithecia may belong to a parasitic fungus. The other two corticate lichens placed in this group are *Cocciscia* and *Coriscium*, and the thecia of the latter are unknown. *Rhabdospora*, *Hassea*, *Placothelium* and *Eolichen* have the thallus non-corticate; the first two have simple spores whilst the latter has 1-septate spores and its lichen nature is not well established. *Placothelium* has *Dactylococcus* algae and the ascus contains many small spores[1]. *Obryzum*, which is placed in this family by Lorrain Smith, has no thallus, and is not admitted to be a lichen by most lichenologists. *Lophothelium*, which is doubtfully included by Zahlbruckner, has recently been re-examined by Lorrain Smith, who considers that the blue-green algae were merely associates, and that it is a fungus (*Discothecium*) parasitic on the squamules of *Stereocaulon condensatum* ((32 *a*) p. 384).

Family CRYPTOTHECIACEAE

Characters and genera as given by Lorrain Smith (32 *e*).

Family THELOCARPACEAE

Thelocarpon was doubtfully placed by Reinke (30) in the family Acarosporaceae and Zahlbruckner has accepted that arrangement. Lorrain Smith rejects that interpretation and insists on placing it in a separate family ((32 *a*) p. 377). The absence of a horizontal thallus may justify this separation but, apart from the thalline character,

[1] See p. 67.

there seems no reason why the crustaceous *Trimmatothele* should not be included in the same family. Other pyrenocarpous lichens with the ascus many-spored are *Placothelium, Thelopsis, Epigloea* and *Baeotitthis*. In *Placothelium* and *Thelopsis* the algal constituents are respectively *Dactylococcus* and *Trentepohlia*, whereas in *Thelocarpon* they are distinctly protoccoid. *Placothelium* has been put in the family Pyrenidiaceae, a family of doubtful value, and its affinities are uncertain. *Thelopsis* is included in Porinaceae, though its position there is questionable. A provisional arrangement of these two genera with *Thelocarpon* and *Trimmatothele* may be less artificial than the arrangement previously adopted. *Epigloea* is given a family of its own whilst *Baeotitthis* seems more nearly akin to Moriolaceae.

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