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STUDIES IN THE MORPHOLOGY OF DISCOMYCETES.

II. THE STRUCTURE AND DEVELOPMENT OF THE ASCOCARP.

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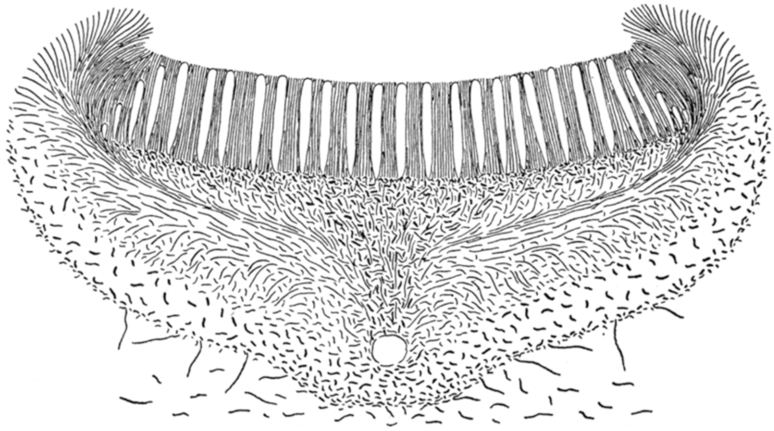
(With seven Text-figures.)

MORPHOLOGY in fungi is a science of the development of hyphal systems. In the ascocarp there are two principal systems, one of which is gametophytic and the other sporophytic. Attention has been given hitherto mainly to the sporophytic system and that of the gametophyte, which builds the ascocarp, is largely without developmental interpretation, although the mature structure has been investigated in a number of Discomycetes, notably by Durand (15) and Lagarde (19). In the present paper an attempt is made to describe the development of the gametophytic system and to relate on such lines the different forms of monaxial ascocarp.

The material for this study has been gathered in great part from the accounts which have already been given by other investigators, chiefly on operculate species; the facts have been confirmed for the commoner genera as *Ascobolus*, *Pyronema*, *Humaria*, etc.

SESSILE APOTHECIA.

In Text-fig. 1 the construction of a sessile apothecium is shown diagrammatically. The hyphae are represented by short lines the direction of which indicates the course of the main hyphae in the different tissues. The ascogenous hyphae are represented by short thick lines diverging from the ascogonium which is drawn as a circle near the base of the apothecium solely for reference; actually it is obliterated by the growth of the surrounding tissue at an early stage in development. Asci are drawn in successive stages of development at the margin of the hymenium to indicate the radial growth of the ascogenous hyphae, but no attempt has been made to show similarly their intercalary growth. The cortical pseudoparenchyma is shown by means of thick, well-spaced lines without special direction except at the margin, for the palisade arrangement is commonly lost in the mature tissue.

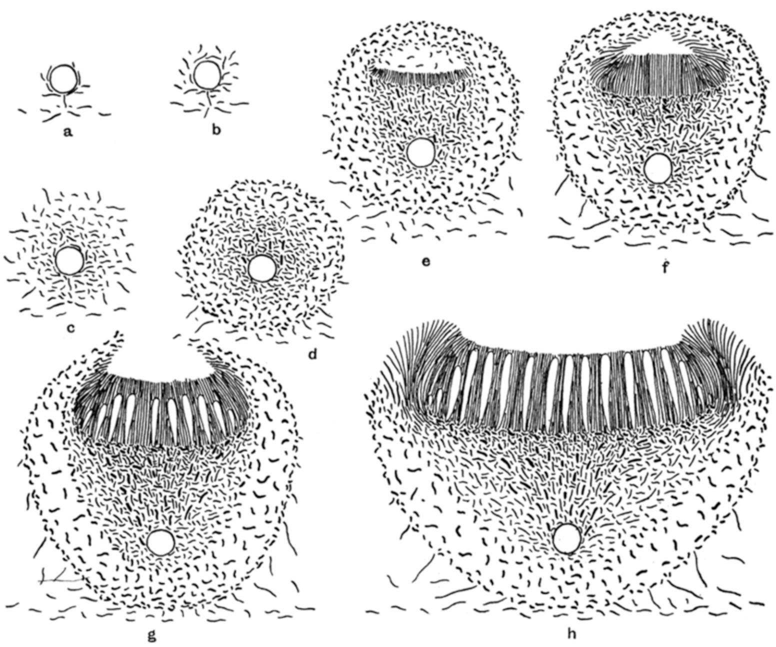


Text-fig. 1. Diagram of the construction of a sessile apothecium.

The construction will be obvious from the account of the marginal growth of apothecia. Mention should be made, however, of the secondary mycelium. It is composed of hyphae which grow from the underside of the apothecium, as excrescent cortical cells, into the substratum where they ramify as ordinary mycelial hyphae, 2–5 μ wide; to what extent they nourish the apothecium is not known. The secondary mycelium is restricted to the part of the apothecium in contact with the substratum, and if the apothecium is immersed it may be developed over the whole surface, *e.g.* the tomentum of *Sepultaria*. All structural transitions between secondary mycelial hyphae and "hairs" occur in the basal part of pilose apothecia.

The development of a sessile apothecium may follow one or other of two extreme courses, or it may take a middle course. It may be angiocarpic, the hymenium being formed within a mass of interwoven hyphae, called the primary sheath, or gymnocarpic, when the hymenium is superficial from the first. The middle, hemiangiocarpic, course can best be explained after a description of the two extremes.

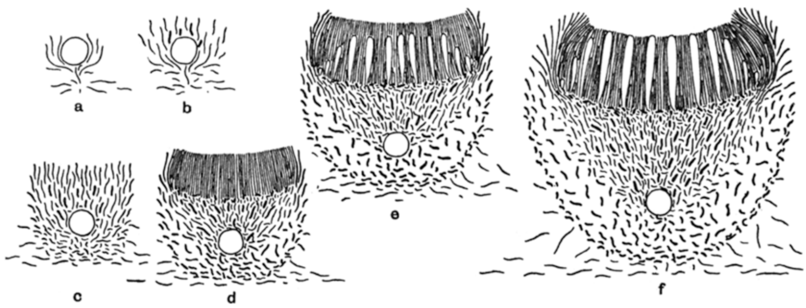
Angiocarpic development is shown diagrammatically in Text-fig. 2. The same notation is used; the ascogonium collapses about the time when the asci appear. In the first stage (*a*), sterile hyphae arise from the stalk cells of the archicarp or from adjacent mycelial hyphae and envelop the ascogonium in a loose weft, stage (*b*). The hyphae branch profusely, especially



Text-fig. 2. Diagram of the development of an angiocarpic apothecium.

to the inside, which suggests a sympodium, and the branches apparently grow in all directions so that a ball of interwoven hyphae with the ascogonium near the centre results, stage (*c*). Then tissue-differentiation begins, stage (*d*). The cells of the outer layers enlarge and often become rather thick-walled, forming a pseudoparenchymatous cortex, while the internal hyphae remain thin-walled, and continue to branch, so that the spaces which would be formed by the expansion of the cortex are filled. A mucilage cavity then forms in the upper part of the spherical mass internal to the cortex, stage (*e*). It originates partly by the stretching of the internal tissue but mainly by the dissolution of the internal hyphae. Numerous hyphae grow into the cavity as a palisade layer which spreads from the floor over the sides to the roof. Some hyphae are outgrowths from the cells lining the cavity, but others are said to originate from the neighbourhood of the ascogonium and to grow up with the ascogenous hyphae. The ascogenous hyphae are produced from the ascogonium after its envelopment and on reaching the floor of the cavity begin to form asci. The upgrowth of the palisade hyphae is soon arrested and they are transformed into paraphyses, which act marks the beginning of the hymenium, stage (*f*).

Subsequently the cortical layer overlying the mucilage cavity is ruptured by the expanding internal tissue, and about the same time the first asci are formed. The intercalary growth of the hymenium, due to the production of asci and paraphyses, presses the sides of the apothecium apart, exposing the disc, while the apothecium passes through a characteristic turbinate shape before becoming lenticular.



Text-fig. 3. Diagram of the development of a gymnocarpic apothecium.

Finally, in stage (*h*), a marginal growing-point is formed, and apparently from the hyphae which grew from the sides of the mucilage cavity and which, on exposure of the disc, form a sympodium: the outer laterals are converted into cortical hyphae and the inner ones into paraphyses.

Evidently primary and secondary parts can be distinguished in the angiocarpic apothecium. The primary part consists of the archicarp, the investing hyphae and the initial part of the hymenium and the primary period of development comprises all stages up to (*g*) (Text-fig. 2). The secondary part consists of all tissues derived from the marginal growing-point and the secondary period of development extends from the initiation of marginal growth to maturity.

Gymnocarpic development, shown in Text-fig. 3, is simple and direct compared with angiocarpic. The initial stages, (*a*) and (*b*), are identical, but the investing hyphae do not form a closed sheath; they continue to grow upward as a palisade layer which becomes better defined as new elements are added from below, as in stages (*c*) and (*d*). The thickness of the apothecium depends primarily on the extent of this upgrowth, and on its cessation, first in the centre, the distal parts of the hyphae mature into paraphyses. Thus the formation of the hymenium is started and continues centrifugally till maturity. About the same time the cells in the lower part of the primordium begin to enlarge: the process extends outward and upward to the margin, forming a pseudoparenchymatous cortex. The ascogenous hyphae arise about stage (*b*), and grow upward with the sterile hyphae; the formation of asci begins shortly after the appearance of the paraphyses, stages (*d*) and (*e*).

The formation of the hymenium marks the end of the primary period of development which is characterised here by the growth of the main hyphae of the primordium away from the substratum. The secondary period, as in angiocarpic development, is that of marginal growth, and the growing-point must originate likewise from the junction of cortex and hymenium, but in both cases the details are obscure.

In hemiangiocarpic development hyphae arch over the ascogonium, but they are of limited growth and do not form a closed sheath. On cessation of growth they are apparently modified into cortical hyphae and they branch mainly to the inside. The laterals appear to repeat the sympodium next the cortex, but those in the centre of the whole structure, overlying the ascogonium, grow upward for some time and branch monopodially, as in gymnocarpic development, before they are transformed into paraphyses. This sheaf of internal hyphae pushes the cortical hyphae aside and so displays the disc. The sympodium at the junction of cortex and hymenium then continues as the marginal growing-point.

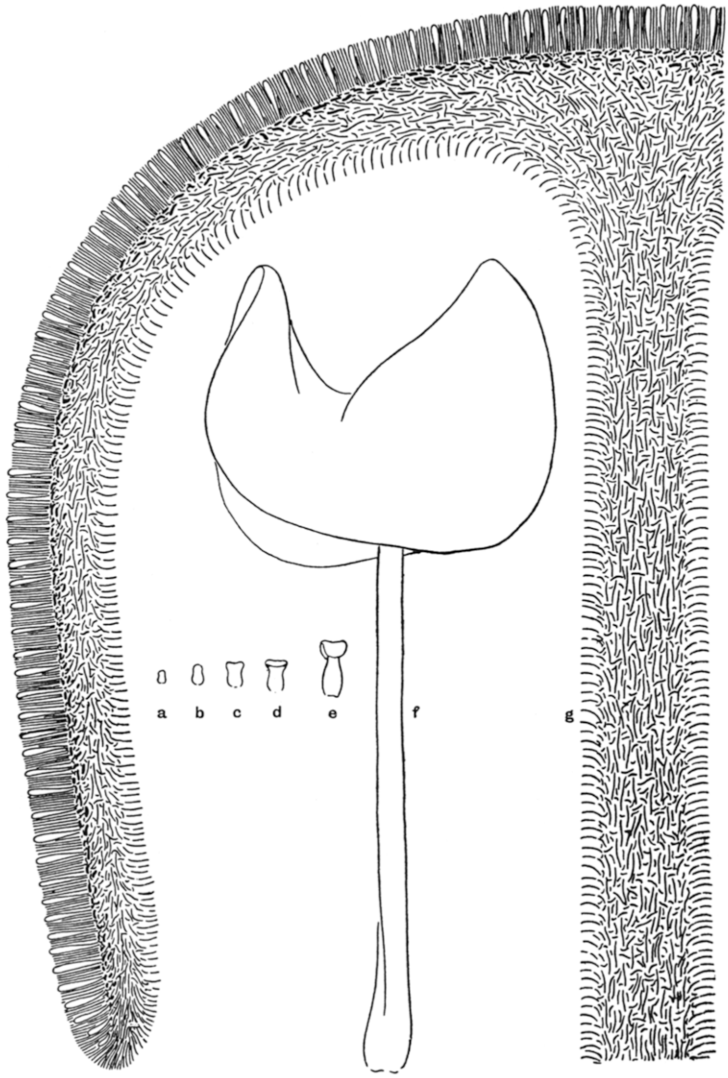
Of Operculeae with hemiangiocarpic apothecia may be cited *Cheilymenia stercorea* (Fraser (17)) and *Anthracobia melaloma*, *Ascophanus granuliformis* and probably *Peziza aurantia*, according to my observations: with angiocarpic apothecia may be cited *Coprobia granulata* (Blackman and Fraser (3)), *Ciliaria scutellata* (Brown (4)), *Ascophanus carneus* (Cutting (9)), *Ascobolus stercorarius* (Janczewski (18)), *A. carbonarius* and *A. Winteri* (Dodge (11)), *A. citrinus* (Schweizer (24)), *A. immersus* and probably *Saccobolus violascens* (Dangeard (10)), *Rhyparobius* (Dangeard (10)), (Barker (1)) and *Thelebolus* (Ramlow (22)): and with gymnocarpic apothecia, *Ascobolus magnificus* (Dodge (13)), *Pyronema confluens* (Claussen (6)), *Ascodesmis nigricans* (Claussen (5)) and perhaps *Rhizina inflata* (Fitzpatrick (16)), although in this fungus the apothecia are more like the stipitate form in that the ascogonia are produced in a gametophytic primordium at the end of a rhizomorph. It would appear—so perfect is selection—that the middle course is the one most frequently pursued, but the number of species which have been examined does not allow of definite statement.

Angiocarpic and gymnocarpic development have been strongly contrasted, but Dodge (12) has shown that the distinction cannot be of great moment in classification because both kinds may occur in a natural genus, *e.g. Ascobolus*. Indeed, the middle course shows that the distinction is one of degree and may depend on the extent of apical growth of the investing hyphae which may in turn be connected with the time of emergence of the ascogenous hyphae. Investigation of other species will doubtless solve the problem.

Stipitate apothecia.

The structure of part of a simple helvelloid ascocarp is shown diagrammatically in Text-fig. 4 (*g*). The apothecial part is built on the same plan as the sessile form. The medulla is composed of very closely interwoven hyphae, 3–5 μ wide, the origin of which can be traced from the proximal parts of the hyphae in the marginal growing-point. The cortical hyphae keep their palisade arrangement and form clavate rows of inflated cells, 10–20 μ wide, on the underside of the apothecium. Both medulla and cortex occur in the stem where they have the same character and are the only tissues; the two layers are continuous through the ascocarp. From Lagarde's account of the ascocarps of *Morchella*, *Helvella*, *Acetabula*, etc., it is plain that all stipitate apothecia of Operculeae are so constructed. In those with a lacunose or hollow stem the cortex is continuous over the whole surface and it extends also over the inside of the fertile region of morchelloid forms.

The development of the sterile system of hyphae in a stipitate apothecium has not yet been investigated in detail, but McCubbin (21) has described the general procedure in *Helvella elastica*. Text-fig. 4 (*a–e*), are successive stages in the development of the primordium and (*f*) represents a mature fruit-body drawn to the same scale. The ascocarp is evidently initiated by a shaft of hyphae growing away from the substratum. The shaft is comparable with that which invests the ascogonium in sessile apothecia but differs in the extent of upgrowth; it is of longer duration, so that a stem-region is laid down. On cessation of upgrowth the distal parts of the hyphae are transformed into paraphyses and, owing to the development of a marginal growing-point, the upper part of the primordium broadens into



Text-fig. 4. Diagram of the structure and development of the ascocarp of *Helvella elastica*: *a–f* × 2: *a–e* after McCubbin: *f* mature ascocarp.

a shallow cup. But at a very early stage intercalary growth of the hymenium becomes excessive; the sides of the apothecium are reflexed and the primordium acquires the helvelloid shape. McCubbin states that the ascogenous hyphae arise from ordinary sub-hymenial cells about the time when the apex of the primordium begins to expand, stage (*c*). However, Duff (14) considers certain "storage cells," which McCubbin describes in the sub-hymenium, to be ascogonia and believes that the apothecium is compound, like some of the Geoglossaceae. But the point has no bearing on the present purpose.

The noteworthy fact is the very early stage and hence the very small size of the primordium in which the parts of the mature ascocarp are defined. The hymenium begins to develop when the primordium is only 1·25 mm. high, stage (*c*), in which case the stem-region must already be formed, though it seems out of all proportion to the mature stem. As a matter of fact, this mode of development is characteristic of a great variety of fruit-bodies in both Ascomycetes and Basidiomycetes. It is the principle of the "toadstool-habit" in which the fruit-body rapidly attains full size and activity by the enlargement of the cells in certain motor-tissues laid down in relatively minute primordia. Development of such fruit-bodies takes place in two stages. There is firstly the period of tissue-formation when the hyphae grow and branch in a primordium, and secondly the period of expansion when the cells of the motor-tissues enlarge; expansion is usually accompanied with intercalary growth of the hymenium. Two-stage, or *indirect*, development has probably evolved by some alteration in the time-factor from the *direct* method in which cell-enlargement follows more or less closely on cell-formation in the growing-point. The direct method is illustrated by the basidiocarps of Clavariaceae and Polyporaceae in which apical growth continues until they have almost reached full length, in contrast to those of *Amanita*, *Coprinus* or Phalloidaceae. The direct method occurs in Discomycetes in the extension of the apothecium by marginal growth, but, apparently, the development of the stem is invariably indirect, unless it be in stipitate Ciboriaceae. But the point will be considered in connection with the Geoglossaceae.

In *H. elastica* the stem must elongate about fifty times its initial length during elevation of the apothecium, for it is about 1 mm. long when the hymenium begins to form and 4–6 cm. at maturity. The motor-tissue, as must be the case in all helvelloid and morchelloid ascocarps, for they have the same structure, is the cortex and not the medulla, as might be expected. Elongation is due in part to the lateral distension of the cells of the cortical hyphae, which are more or less perpendicular to the surface of the stem, but it must be due in part also to intercalary growth of the cortex after the stem-region has been laid down, because the increase in width of the cells, from 3–5 μ to 10–20 μ, does not account alone for the increase in length of the stem.

It should be mentioned that McCubbin describes a "veil" which encloses the primordium of *H. elastica* and is ruptured at an early stage, but it is questioned by Fitzpatrick (16) and it seems advisable to leave the matter for reinvestigation.

FORMS OF ASCOCARP.

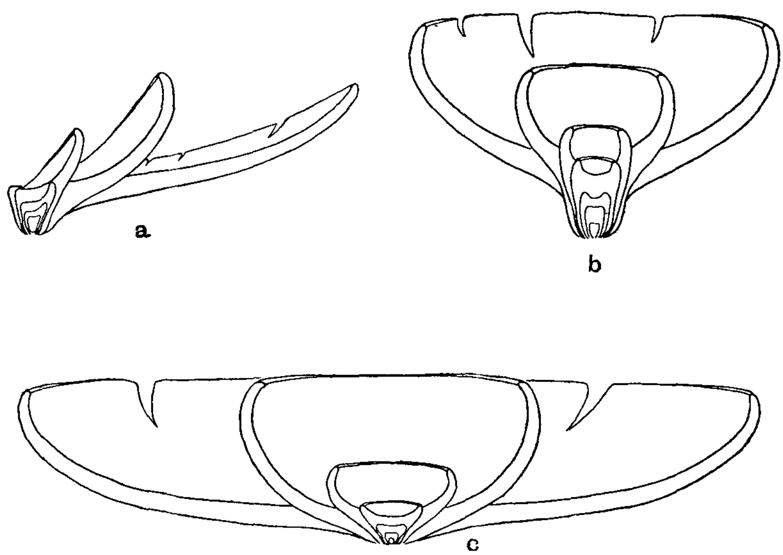
All monaxial ascocarps of Discomycetes can be classed either as stipitate or as sessile apothecia. In each class there are several more or less distinct forms, and, having described the main processes in the development of the ascocarp, the nature of these forms can now be explained.

The forms of sessile apothecium, in roughly descending order of complexity, are the cupular, the lenticular, the "turbinulate," the perithecioid, the "cleistocarpic" and the immarginate; they constitute a developmental series.

The distinction between cupular and lenticular forms is best explained by describing the transformation of a large apothecium during the secondary period of development. Successive stages in the development of the apothecium of *Peziza aurantia* are drawn in Text-fig. 5 (*c*), the youngest of which corresponds roughly with (*h*), Text-fig. 2, or (*f*), Text-fig. 3. The hymenium is at first plane but becomes more and more concave until it begins to flatten into a disc again towards maturity: the apothecium enlarges by marginal growth and by intercalary growth of the hymenium. The direction of the hyphae in the marginal growing-point is at first upward, or away from the substratum, but the margin is gradually incurved and the direction of the hyphae is altered by nearly 90° before reversal begins. The transformation is caused by the antagonistic tissue-pressures of the cortex and hymenium. The effect of the cortical pressure, due to the branching and inflation of the cortical cells, is to force the margin inward and that of the hymenium, due initially to the branching of the paraphyses and ascogenous hyphae, is to force the margin outward. If the two developed equally, the apothecium would be discoid throughout, but the cortical pressure at first exceeds that of the hymenium and only later, when the hymenial pressure is augmented by the intercalation of asci, can it overcome the resistance of the cortex and force the sides of the apothecium apart. The curvature of the sides indicates the balance between the two forces along that radius and the rate of flattening, which proceeds centrifugally, should indicate the rate of maturing of the hymenium, or the time required by the apothecium to come into action after taking up position: data on such points would be interesting.

The state of balanced tissue-pressures is revealed in the mature apothecium by a sudden drop in hymenial pressure through the simultaneous discharge of many asci; the sides of the apothecium jump inward as the hiss of discharge is heard and the spore-cloud appears immediately after over the hymenium. This exceedingly characteristic demonstration of the apothecial mechanism was first recorded by Haller in a letter to Linnaeus about 1750 (23).

If marginal growth continues for some time, the result is the large, relatively thin, cupular form of apothecium, 2–15 cm. wide, *e.g.* the last three stages in series (*c*), Text-fig. 5, which may be cupular, discoid or concave at maturity, according to the balance of tissue-pressures. Other things being equal, the



Text-fig. 5. Stages in the development of the ascocarp of *Peziza aurantia*, × 2: (*a*) of the auriculate form, (*b*) of the substipitate form, (*c*) of the sessile form.

convexity of the mature apothecium is a measure of its inefficiency, expressed as the ratio of sterile to sporogenous tissue. *Galactinia* and *Geopyxis* provide examples of persistently cupular forms, while *Discina* and *Rhizina* present the other extreme.

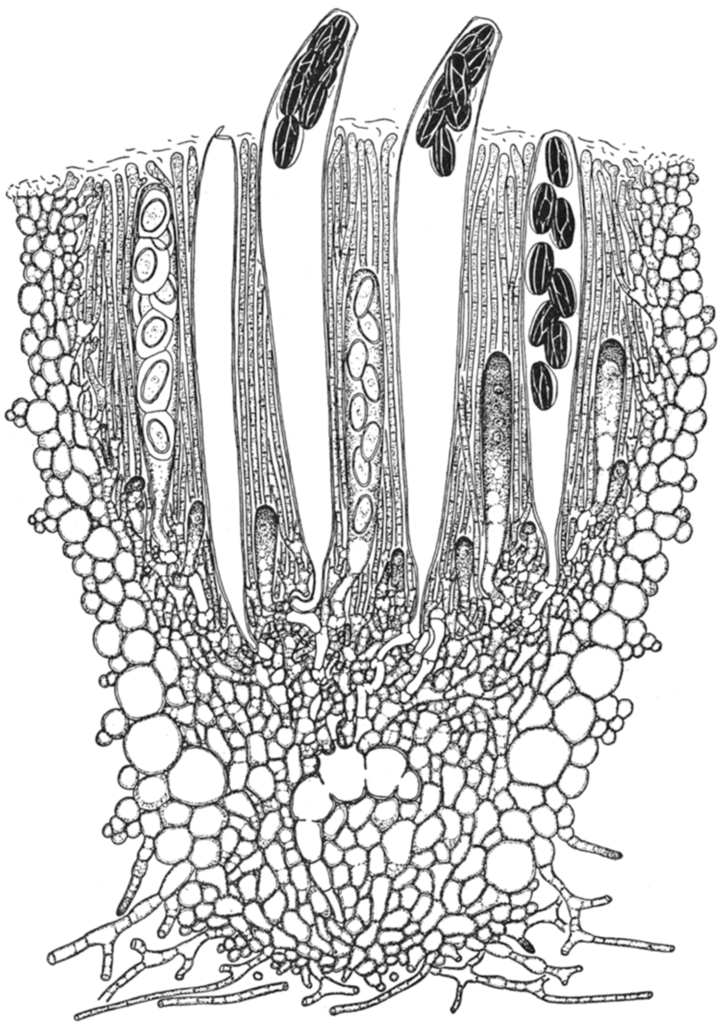
On the other hand, early cessation of marginal growth produces the small, relatively thick, lenticular form, 0·05–2 cm. wide, *e.g.* the first four stages of series (*c*). *Humaria* is the best example of a genus with lenticular apothecia.

A peculiar variety of the cupular form, in a sense intermediate between cupular and lenticular, is the auriculate, or spathulate. It is characterised by the cessation of marginal growth on one side of the apothecium at an early stage, so that further enlargement is more or less unilateral. In Text-fig. 5 a series of stages in the development of such a variety of *P. aurantia* is drawn, the sections being through the median plane; one-half of the apothecium is lenticular and the other is cupular. The auriculate variety shows perhaps even better than the hemispherical cups of cupular forms the precision with which development may be controlled, for in the beautifully symmetrical apothecia of *Otidea leporina*, and other species, marginal growth must decline regularly from one side to the other across the disc.

If an angiocarpic apothecium does not enter upon a secondary period of development, but remains structurally comparable with stage (*g*), Text-fig. 2, a very distinct form is produced for which the writer suggests the name *turbinulate*, in pursuance of Boudier's method of description. Turbinulate apothecia are characteristic of the angiocarpic Ascobolaceae already mentioned; a section of that of *A. stercorarius* is drawn in Text-fig. 6, though it is from a very diminutive specimen. They are small forms, 0·2–8 mm. wide, in which the part of the primary sheath overlying the hymenium is ruptured and further enlargement of the disc is due entirely to intercalary growth of the hymenium, mainly of ascogenous hyphae. They have hitherto been classed with small lenticular forms, which they may resemble in shape, but they have no marginal growth. However, there may be an abortive sprouting from the cortical cells at the margin and the cells of the outermost paraphyses may enlarge somewhat and suggest a disinclination to become cortical hyphae, *e.g. A. stercorarius*.

The perithecioid apothecium, 0·2–0·5 mm. wide, which the writer has described for *Neotiella Crozalsiana* (7), is similar to the turbinulate, but there is little intercalary growth of the hymenium; the sprouting of the cortical cells is more regular and forms a definite margin encircling a pore through which the asci dehisce.

In the same way the apothecia of *Thelebolus* and certain species of *Rhyparobius* can be explained. They may be called *cleistocarpic*—to coin another incongruity—for they have no more of a hymenium than the cleistocarps of Erysiphaceae and the condition of *Thelebolus* is almost exactly paralleled in *Sphaerotheca*. The apothecia of *Thelebolus* 0·1–0·3 mm. wide, are angiocarpic. The archicarp, according to Ramlow, consists of half a dozen cells, a central one of which is the ascogonium. Sterile hyphae envelop the archicarp in a primary sheath and the ascogonium develops directly into the one huge ascus in a mucilage cavity formed by the dissolution of the surrounding hyphae. The ascus eventually ruptures the sheath and dehisces. There are neither ascogenous hyphae nor paraphyses and the mature state corresponds to stage (*c*), Text-fig. 2. In those species of *Rhyparobius* with only two to four polysporous asci per apothecium development is similar, according to Dangeard,



Text-fig. 6. Median section of a diminutive apothecium of *Ascobolus stercorarius*. × 250.

but a few paraphyses may grow into the mucilage cavity and the asci are produced singly on short ascogenous hyphae; the apothecia correspond roughly with stage (*d*), Text-fig. 2. In others the paraphyses are more numerous and the ascogenous hyphae produce more than one ascus, and the best developed apothecia in the genus are turbinulate with a normal hymenium, *e.g.* the species examined by Barker.

The immarginate form, also of small size, 0·2–2 mm. wide, is characterised by the absence of a cortical margin to the hymenium. It occurs in the genera *Pyronema, Ascodesmis* and *Zukalina*, and is evidently a gymnocarpic apothecium without a secondary period of development. The structure of the mature apothecium of *P. confluens*, from Claussen's account, corresponds to a stage intermediate between (*c*) and (*d*), Text-fig. 3. The upgrowth of the sterile hyphae is soon arrested, their distal parts are transformed into paraphyses and the cells at the base of the apothecium enlarge to form a pseudoparenchyma. *Zukalina* is probably the same. But the organisation of the sterile tissue in *Ascodesmis nigricans*, from Claussen's account, is the simplest that has yet been described in Discomycetes. The apothecia mature in a state corresponding to stage (*b*), Text-fig. 3, or Text-fig. 2, if indeed there is any distinction at so early a period of development. The few sterile hyphae which envelop the ascogonia are transformed directly into paraphyses—about fifty per apothecium—and the ascogenous hyphae which are only a few cells long, produce a single ascus each. Dangeard (10), however, describes a pseudoparenchymatous base to the apothecium like that of *Pyronema*, and probably the extent of development varies just as in *Rhyparobius*.

The chief forms of stipitate apothecium in Operculeae are the cupular, the helvelloid and the morchelloid. Of the first it need only be said that it differs from the corresponding sessile form in the possession of a stalk, or a longer period of upgrowth, *e.g.* *Sarcoscypha, Acetabula*. The helvelloid form is characterised by the large amount of intercalary hymenial growth which begins so early in development that the apothecium never passes through a cupular stage. The sides of the apothecium are reflexed against the stem, to which they may be secondarily conjoint, and the lobings of the disc are caused by irregularities in growth: there are commonly two opposed regions of slight growth which gives the saddle-shape to many species of *Helvella*. The convolute bullate apothecia of *Gyromitra* and *Physomitra* are merely examples of excessive intercalary growth coupled with little or no marginal growth, and such an arrangement seems to provide an explanation of the morchelloid form, but the point will be discussed after the examination of the Geoglossaceae.

A complementary series can be recognised in Inoperculeae, though in miniature, on an apothecial scale of 0·01–2 cm. diameter, for they never reach the large size of operculate fruit-bodies.

There are elaborate stipitate apothecia in the Clavuleae, stipitate cupular forms in the Ciboriaceae, sessile cupular and lenticular forms in the Helotiaceae, Spisseae, etc., turbinulate forms in *Heterosphaeria* and probably most Patellariaceae, an immarginate form in *Ascocorticium*, and a medley of ill-defined apothecia in the Stictidaceae and Phacidiaceae which cannot be reviewed for lack of adequate description. Some develop on gymnocarpic lines, as *Geoglossum* and *Helotium*, others on angiocarpic lines, as *Microglossum*, *Bulgaria* and *Trichopeziza*, *Tapesia* and *Arachnopeziza*, according to Bayliss Elliott (2), and probably all of the "cartilaginous" group. What evolutionary principles apply in general to the one section of Discomycetes will clearly apply in general to the other, and attention will be confined, as hitherto, mainly to the better known Operculeae.

It need scarcely be mentioned that all transitions between the different forms of ascocarp occur, and not infrequently, so that only the more pronounced configurations can be named. In Text-fig. 5 (*b*) successive stages in the development of the substipitate form of *P. aurantia* are drawn; had the period of upgrowth been longer a stipitate apothecium, comparable in respect of gametophytic tissue with that of *Helvella*, would have resulted. Yet in Boudier's system of Discomycetes, which admittedly is the one attempt at a natural classification, the majority of families are distinguished by the form of the ascocarp. The effect of such a system of families, in the writer's opinion, is to classify the ascocarps of Discomycetes in a direction which cuts straight across their path of evolution. Certain series of Operculeae, which appear to be natural, will therefore be considered here.

Series of Operculeae.

Reference has already been made (7) to a most distinct humariaceous series characterised by the presence of carotin in the paraphyses. The series contains stipitate apothecia, *e.g.* *Sarcoscypha*, sessile cupular apothecia, *e.g.* *Peziza*, lenticular apothecia, *e.g.* *Humaria*, and the one species with perithecioid apothecia, *e.g.* *N. Crozalsiana*: turbinulate and immarginate apothecia apparently do not occur, though the former perhaps in *Lasiobolus*.

A second series of genera, *Helvella*, *Leptopodia*, *Cyathipodia*, *Macropodia* and *Acetabula*, can be distinguished by the grey colour of the hymenium, which may be due to a special pigment, the oval uniguttate spores, the gutta apparently derived from a single oleaginous centre, and the construction of the sterile tissue, according to Lagarde. It comprises helvelloid, and stipitate and sessile cupular, forms.

A third series, the Aleurieae of Boudier, distinguished by the presence of an amyloid substance in the ascus-wall, the purple or brown pigment in the paraphyses and the markedly pseudo-parenchymatous excipulum, comprises substipitate and sessile, cupular and lenticular forms. The series is interesting because the transitions occur separately in *Galactinia* and *Aleuria*, if not several times in each, and sessile cupular and lenticular forms occur in both *Plicaria* and *Pachyella*.

Another series, ranging from sessile cupular to lenticular forms, may possibly be distinguished by the pilose apothecium and by the absence of pigment in the paraphyses. It would include *Sepultaria, Lachnea, Trichophaea* and *Tricharia*, but they may only be unpigmented forms of the humariaceous series, cf. *Leucoscypha, Neotiella*.

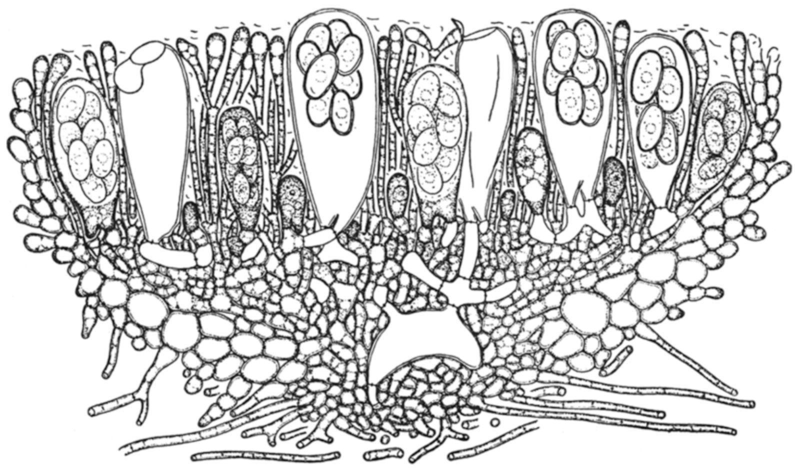
And finally the large composite genus, *Ascophanus*, may be mentioned. Some species are turbinulate, as *A. carneus*, and connect with *Rhyparobius* and thus with the cleistocarpic form in *Thelebolus*; the archicarp is similar in all three cases. *Rhyparobius* is separated from *Ascophanus* mainly by the squat form of the ascus and the multiplication of the octad, giving polysporous asci, but the distinction is largely one of opinion, for there is *A. sexdecimsporus*, while species of *Rhyparobius* may have only thirty-two spores per ascus, and *R. ascophanoides* Sacc. is synonymous with *A. rhyparobioides* Heim., according to Massee (20). There may also be a gymnocarpic series, for Dangeard finds that *A. ochraceus* has immarginate apothecia like *Pyronema*; they develop in the same way from a rosette of ascogonia, and in both genera the spores are colourless and eguttate. And yet other species are minute lenticular forms on hemiangiocarpic lines, of doubtful affinity, for example *A. granuliformis*, Text-fig. 7, which has been drawn for comparison with the minute turbinulate apothecium of *Ascobolus*. And if, moreover, to these illustrations be added Claussen's of *Pyronema*, an example is afforded from each mode of development of a sessile apothecium which can be considered to have matured at a correspondingly early stage.

Summary.

The chief processes in the development of the stipitate apothecium are upgrowth from the substratum, which defines the axis or stem, and marginal and intercalary hymenial growth which define the apothecium. The development of the stem is *indirect* in that cell-enlargement follows as a separate stage on cell formation. The tissue-pressures of cortex and hymenium are antagonistic and give rigidity to the apothecium. Likewise, in the sessile apothecium can be distinguished a primary period

of upgrowth, from initiation of the apothecium to the formation of the hymenium, and a secondary period of marginal and intercalary growth.

Helvelloid, cupular, lenticular, perithecioid and immarginate forms of ascocarp are interpreted developmentally, and two additional forms, described as *turbinulate* and *cleistocarpic*: both are angiocarpic sessile apothecia without a secondary period of development, the turbinulate with, and the cleistocarpic without, a definite hymenium. These forms are shown to constitute a developmental series.



Text-fig. 7. Median section of an apothecium of *Ascophanus granuliformis*. × 500.

Certain series of Operculeae which are considered to be natural are briefly described.

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A NEW SPECIES OF OIDIUM.

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(With Plate VII.)

ABOUT two years ago I was consulted in regard to a growth occurring in the sewer connecting a factory with the main sewer of a town. This growth occurred so rapidly and so freely that, after having been cleaned, the sewer in question became in a very short time almost blocked. This sewer was used for the purpose of conveying the factory effluent to the town sewer and was joined at a certain point by a side drain carrying a very small quantity of domestic sewage.

The growth above referred to always commenced just below the point at which the domestic sewage entered, and from this point onwards developed into a hard, gelatinous or tough leathery mass which ultimately blocked the sewer, and caused both the Firm and the town authorities a considerable amount of trouble.

The growth—for such it proved to be—consisted of a dark brown gelatinous mass, having the toughness of soft leather.