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ORIGIN AND DEVELOPMENT OF THE PYCNIDIUM

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(WITH PLATES XVII–XXII)

Introduction

The Ascomycetes have been the subject of repeated investigations, especially in regard to the morphology of the perithecium and the cytology and sexuality of the ascigerous stage. The conidial stages, placed in the Fungi Imperfecti in the absence of knowledge of their ascigerous stages, of necessity are classified on a basis of the morphology of the conidia-bearing structures. For this reason, and because the pycnidia are said sometimes to develop directly into perithecia, extension of our knowledge of the morphology of such conidiiferous structures as the pycnidium and the acervulus is highly desirable.

The references in literature to the development of the pycnidium are, for the most part, merely incidental, and studies directly devoted to the subject are few. As early as 1876 BAUKE (5) described what he considered as 3 methods of pycnidial development, without giving names to them. In 1884, however, DEBARY (9) distinguished 2 main methods of development, which he designated as "symphogenous" and "meristogenous": "symphogenous" when the pycnidial primordium arises through the interweaving of young hyphal branches to form a network that is at first loosely woven, but later becomes compact and knotlike;

"meristogenous" when the primordium arises from a single hyphal cell or a group of adjacent cells of a single hypha by continued cross and longitudinal division. In the latter, branches from neighboring cells or from the mass itself may share. A number of variations of these 2 methods have been described. Classification of the pycnidial developments described by BAUKE according to the methods distinguished by DEBARY places *Cucurbitaria* as meristogenous, *Diplodia* as symphogenous, and *Pleospora polytricha* as a combination of the two.

ZOPF (52) in 1890 mentioned 3 types of pycnidial development: "Hyphenfrucht," "Gewebefrucht," and "Knäuelfrucht." The "Hyphenfrucht" comprises those in which development proceeds from a single hyphal cell which by dividing and swelling forms a quadrant, from which with the aid of 2 or 3 neighboring cells a primordium is formed. By "Gewebefrucht" is designated those instances in which a tissue mass is formed. This mass may develop in either of 2 ways: by neighboring cells of a hypha becoming septate, swelling, dividing, becoming more rounded, while short dividing hyphae either from the mass or from neighboring cells of the hypha share in the formation; or in a like manner it may be formed from cells of 2 or more contiguous hyphae. The "Knäuelfrucht" develops a primordium from 1 or more short hyphal branches which coil spirally, branch, and interweave into a knot which later develops into the pycnidium. The "Hyphenfrucht" and "Gewebefrucht" are clearly variations of the meristogenous method of development of DEBARY. The other, "Knäuelfrucht," is symphogenous.

In addition to these should be mentioned the "sporopycnidium" of VON TAVEL (46), referred to also by PLANCHON (29) and SCHNEGG (33). This pycnidium arises meristogenously, according to VON TAVEL, representing the most extreme case of meristogenous development. A single spore in the presence of abundant food germinates and grows a short mycelium; then by division and growth becomes a pycnidium. REDDICK (31) notes that pycnosclerotia may be found in *Guignardia*. These bodies arise as pycnidia, produce pycnidiospores, and later function as perithecia, producing asci and ascospores.

Although in many instances the fungi were not studied primarily as to their pycnidial development, and such information as was collected regarding this was incidental, according to the figures and descriptions given the following belong to the meristogenous group of DeBary: *Pleospora* (Gibelli and Griffini 17; Bauke 5), *Cucurbitaria* (Eidam 14; Bauke 5), *Pycnis* (Brefeld 6), *Fumago* (Tulasne 43; Zopf 53; Schostakowitsch 34), *Sphaeronaema* (Halsted and Fairchild 18), pycnidium with *Teichospora* (Nichols 27), *Phyllosticta* with *Alternaria* (Planchon 29), *Sphaeropsis* and *Coniothyrium* (Potebnia 30), *Chaetophoma* (Arnaud 3), *Phoma* (Reddick 31; Mercer 26; Schnegg 33), *Endothia* (Anderson 1). As symphogenous may be classed: *Cicinnobolus* (DeBary 8), *Fumago* (Tulasne 43; Zopf 52); *Diplodia* (Bauke 5; Van der Bijl 44), *Graphiola* (Fischer 15), *Cystispora* (von Tavel 46), *Hendersonia* (Voges 45; Wolf 51), pycnidium with *Sphaerella* (Higgins 21), *Sphaeropsis* (Hesler 19), *Septoria* (Levin 25). A few of the species have both types of development.

The present investigation is an endeavor to extend our knowledge of the very early stages in the development of the pycnidium and kindred structures.

Methods

For the present study, the fungi were either isolated from their hosts or cultures were procured from various sources as noted. Corn meal agar (35) was used because it gave an abundant growth, and its transparency facilitated the study of even the youngest stages. Other media were used in a few instances for comparison. Cultures for study were grown in Petri dishes, at room temperature (15–37° C.). Transfers were made by lifting hyphae or spores from pure cultures to the poured agar in Petri dishes. Drop cultures of melted agar were made by the use of sterile pipettes. In some cases the drop of agar was inoculated with spores as for dilution plating. In others, each drop was inoculated by transfer. These drop cultures served well for study of early stages of development, but seldom produced mature conidiiferous structures.

Disks of agar containing young pycnidia were removed from Petri dish cultures, placed on cover glasses, and inverted on

Van Tieghem rings in order to follow further the development of the pycnidia. Growth in Petri dishes was observed periodically, the intervals depending upon the rate of growth of the organism. Pycnidia of each species were kept under observation during their entire period of early development. For close detailed study and for drawing, mounts were made by removing from Petri dish cultures small squares of agar containing pycnidia in various stages of development, mounting them either in water for immediate study, or in glycerine for later study. Material from test tube cultures was teased out and studied for comparison and verification of many points.

Following the usage of earlier writers, DEBARY (9), BAUKE (5), ZOPF (52), and VON TAVEL (46), the word primordium is used throughout this paper to designate a group of cells that have become so differentiated that it is clearly evident that from them a pycnidial or similar structure will arise.

Genera and species studied

PHOMA (Fries) Desmazières

Phoma herbarum West; isolated from its host, *Polygonum hydropiper* L., at Urbana, Illinois, July 8, 1916.

Pycnidia are produced in cultures in moderate abundance. All stages of development, from the mature pycnidia on older mycelium to beginning stages on the younger mycelium, can be observed even in a small sector of a Petri dish culture. Development proceeds typically from a single cell of a hypha. This cell divides both transversely and diagonally (fig. 1) into a few cells which swell and enlarge. These cells by continued swelling and dividing form an irregular mass with very few or no hyphal branches. This mass shows distinctly its origin from a single hypha (figs. 1–3). As the mass continues to enlarge, one side protrudes slightly as a short rostrum which becomes lighter in color (fig. 4). This is the primordium which later becomes a pear-shaped pycnidium with an ostiole from which spores are discharged (fig. 5). The development is a typically simple meristogenous one.

Phoma pirina (Fries) Cooke; isolated at Urbana, Illinois, May 10, 1916, from dead twigs of *Pyrus communis* L. from Savoy, Illinois.

This fungus produces abundant small pycnidia 60–120 μ in diameter, at first closed but later with an ostiole 20–30 μ wide. The spores vary in size from 5×3 to 10×4 μ. A few cells of the hypha swell, divide both crosswise and diagonally, swell, and divide again (figs. 6, 7). This small mass continues to enlarge by cell division, and a few hyphal branches bud out from it (fig. 8). By continued development an irregular mass (fig. 9) is formed, which is the primordium of the pycnidium. In a few cases closely lying hyphae may take part in the formation (figs. 10–13), but the typical method of development is the simple meristogenous one from a few cells of a single hypha.

Phoma destructiva Plowr.; isolated at Urbana from fruits of tomato (*Lycopersicon esculentum* Mill.) in September 1915. In all respects the disease and the fungus agreed with the one described by Miss Jamieson (22).

The pycnidial primordium usually arises meristogenously. In most cases a single hypha gives rise to the primordium (figs. 14–17); in other cases 2 or more hyphae share in its formation (figs. 18, 19, 22). In either case adjacent cells swell and divide crosswise and diagonally until a rounded or elongated mass is formed, slightly darker in color than the mycelium. The former (fig. 15) is the simple type of meristogenous development.

Phoma, species indet.; isolated from stems of clover (*Trifolium pratense* L.) at Urbana, Illinois, in July 1916.

Development takes place in a simple meristogenous manner. One hypha only is involved in the formation of the primordium (figs. 23–27). Short hyphal threads sometimes branch from the mass. The cells are usually large and swell into a rounded shape. The mass develops more rapidly at one end than at the other, so that the young pycnidium is slightly conical.

Phoma, species indet.; isolated from a berry of the Concord variety of grape (*Vitis labrusca* L.), from a vineyard near Collinsville, Illinois, September 1917.

A portion of the culture seen under the high power of the microscope showed a very characteristic arrangement of hyphae and of pycnidia in various stages of development (figs. 28–33). The simple meristogenous development of the primordium is similar to that described for *Phoma herbarum* West (figs. 1–5).

Phoma cichorii Passr.; isolated from *Phlox divaricata* L. by Mrs. ESTHER YOUNG TRUE, at Urbana, Illinois, November 1917.

A few adjacent cells of a single hypha or of a number of contiguous hyphal strands divide into short cells (figs. 34, 35). By budding and swelling, short hyphal branches arise, the cells of which swell and divide (fig. 36). The cells of the mother strand or strands also enlarge and divide. The component hyphae anastomose, forming a pseudoparenchymatous, irregularly rounded mass. This mass develops into the pycnidium. The development of this fungus differs from that described for the other species in that, where only a single strand is involved, the mode is simple meristogenous with the original cells and their budding branches anastomosing to form the mass (fig. 36). In instances where 2 or more strands are involved (fig. 37), there has been a similar division, swelling, and branching in each strand, but the whole has been united into a single primordium as described for *Phoma destructiva* (fig. 22). This mode is compound meristogenous.

MACROPHOMA (Sacc.) Berl. and Vogl.

Macrophoma citrulli (B. and C.) Berl. and Vogl.; isolated by Dr. J. A. ELLIOTT from a cantaloupe (*Cucumis melo* L.) leaf procured from Alabama in the autumn of 1915.

Young pycnidia and small sclerotia form in abundance, soon rendering the culture dark brown or black. Usually a single cell in a hypha becomes slightly swollen. It then divides into 2 short cells (fig. 38). These cells in turn divide by cross, longitudinal, and diagonal walls (figs. 39, 40). The swelling continues until the body becomes a rounded or oblong mass much darker than the light brown mycelium (figs. 46, 47). The cells immediately adjacent to the dividing mass may divide into short cells and send out hyphal branches (figs. 42–44). The outer cells of the mass may also send out branching hyphae. The hyphae from all these sources form a network about the enlarging mass. Sometimes the hyphal branches fuse with the mass, and in other cases they appear to have no part in its formation. The body thus developed is the primordium from which the pycnidium arises. It continues to enlarge, becomes pear-shaped, forms an ostiole, and develops spores. This mode of development is meristogenous, with a slight modification in that short hyphal branches either fuse with or form an envelope about the primordium.

Less frequently a second method appears, in which short branches from main mycelial strands direct themselves toward a point. There these branches interweave, swell, and divide to form a network (fig. 48). This network is at other times formed by the looping back or snarling of hyphal branches. The tangle enlarges, becomes more tightly woven, then the cells divide, swell, and anastomose to form a pseudoparenchymatous mass (fig. 49). This method is symphogenous. This species gives rise to both meristogenous and symphogenous developments.

The pycnidia of the species studied in the genera *Phoma* and *Macrophoma* indicate that both meristogenous and symphogenous methods of development may be found. These species present in the main the simple meristogenous mode in which a few cells of a single hypha take part (figs. 1, 6, 15, 23, 29, 38, 44); also a slight variation of the simple development in which hyphal branches both from the dividing cells and from other cells of the mother hypha form a network about the original cells taking part in the development (figs. 36, 39, 47). The compound meristogenous development is that in which 2 or more main hyphae, lying parallel or crossing, begin to divide into short cells at a point of contact, swelling and dividing to form a primordium (figs. 18, 22, 37). A few adjacent cells of each hypha and some surrounding branches take part in this type of development.

SPHAERONAEMA Fries

Sphaeronaema fimbriatum (E. and H.) Sacc.; procured from Dr. BYRON D. HALSTED, October 1916.

HALSTED and FAIRCHILD (18) report and figure the development of the pycnidium of *Ceratocystis fimbriata* as follows:

In its initial stages the pycnidium arises as the swollen and curled or twisted tip of a vegetative hypha, or as a twist or knot in a sporophore between the conidium and its point of union with the main hypha. Although observed to be present in numerous cases, no anastomosing of different hyphae branches seems necessary. Almost simultaneously with the first curving of the hypha tip side branches arise, which, by their growth and formation of septa, form the coarsely cellular membranous wall of the pycnidium.

Single mountings from plate cultures gave all stages of development verifying this description. The usual development was the twisting, budding, branching, and enlarging by cell division of single twisted hyphal branches (figs. 50–52). This is a variation of the meristogenous development.

SPHAEROPSIS Léveillé

Sphaeropsis malorum Pk.; isolated from apple fruits (*Pyrus malus* L.) from Centerville, Indiana, in October 1916.

HESLER (19) gives the development of the pycnidium of *Physalospora cydoniae* Arnaud in agar cultures as follows:

> The dense pseudoparenchyma of the maturer fruit bodies suggests meristematic divisions, but apparently the structure, for the most part, arises symphogenetically. In agar cultures a group of threads may be observed to be directed toward a common point where the pycnidium is to be formed. Here the hyphae are composed of cells 6–7 μ broad, their length varying from 20 to 70 μ, always longer than broad. In the region where the pycnidium is to be developed, the cells become noticeably shorter by the laying down of new walls; the cells also increase in diameter by growth, and the hyphae increase their numbers by branching. The interspaces found in the earlier stages are filled by the growing in of these branches and by a budding-like action of the hyphal cells bordering the space.

Among my own notes upon *Sphaeropsis malorum* Pk., made before the appearance of this description, is an account of the development of the primordium which it seems worth while to give here.

The pycnidial primordium of this species is formed usually according to the method designated by DEBARY as symphogenous. A number of hyphal branches interweave near their ends (fig. 53); these in turn branch and the branches also interweave (figs. 54, 55). The central portion becomes a tightly woven mass. The whole continues to enlarge until a spherical mass is formed, which develops into a pycnidium. Most of these primordia form deeply imbedded in the agar, although a few develop on or near the surface. Those developing imbedded in the agar are smooth, while those on the surface have a fuzzy appearance. A very few pycnidia form by the compound meristogenous method described for *Phoma*. These usually form 2 or more contiguous hyphae in which a few adjacent cells divide, swell, continue to divide, and enlarge until a primordium similar to the one described is formed.

Sphaeropsis citricola McAlpine; isolated at Urbana, Illinois, January 1916, from a kumquat fruit (*Fortunella margarita* Swingle) from Lake City, Florida. The condition produced on the rind of the fruit was that of a very black carbonaceous spotting which finally spread over the whole fruit.

In culture a coarse brown mycelium 5–8 μ in diameter is produced. Numerous pycnidia 80–175 μ in diameter develop from primordia each of which arises either from a single cell or a few adjacent cells in a single hypha. This cell or group of cells (figs. 56, 57) divides by cross and diagonal walls (figs. 58–61), later by the addition of longitudinal walls to form a rounded or elongated mass (figs. 62, 63) which is slightly darker in color than the mycelium. This mass becomes globose, light brown, carbonaceous and reticulated, and is the primordium. Development is usually simple meristogenous. The compound meristogenous mode is seldom found (figs. 64–66). From pycnidia developing from these masses small hyaline spores $5–7 \times 4–5\ \mu$ exude.

The genus *Sphaeropsis* presents a variation of the symphogenous development in that the branches interweave near their ends at a point some distance from the main mycelial strands (fig. 53). It also shows the more usual symphogenous type (figs. 54, 55) described for *Macrophoma* (figs. 48, 49). Simple meristogenous development occurs in one species. The compound mode seldom occurs in the species studied.

Coniothyrium Corda

Coniothyrium pyriana (Sacc.) Shel.; pure culture isolated from twigs of apple (*Pyrus malus* L.) from Savoy, Illinois, October 1916.

A few adjoining cells of a main hypha become slightly swollen and divide into short cells (figs. 67, 68). These cells swell, divide by cross, diagonal, and longitudinal divisions, and continue to swell and send out short hyphal branches by budding (figs. 69, 70). This body increases in size, becoming darker in color. Branches from adjoining cells or closely lying hyphae may interweave with the branches from the mass, at length forming a primordium (fig. 71). from which a pycnidium develops. Usually this primordium arises from a single main hypha, but occasionally 2 or more contiguous hyphae are included in its formation. The mode of development is meristogenous, with small hyphal branches at times included in the formation. Both simple and compound modes are found, but the compound mode seldom occurs.

Coniothyrium, species indet.; culture procured from the air of the laboratory in the summer of 1917 by W. S. BEACH.

A few adjacent cells in a single hypha divide into shorter cells. These cells branch profusely (fig. 72). A few of the cells continue to divide and swell, and the branching hyphae divide and branch (fig. 73). The whole becomes a more closely formed mass (fig. 74) which forms a globose, dark brown, finely reticulated primordium. From this the pycnidium develops. The mode of development is simple meristogenous.

The genus *Coniothyrium*, so far as studied, presents only the meristogenous development.

SEPTORIA Fries

Septoria polygonorum Desm.; isolated from its host *Polygonum persicaria* L. at Urbana, Illinois, July 1916.

The development of the primordium in most cases is by the usual meristogenous method, but in some instances it is atypical. Some of the primordia arise from a single hypha, 1 or 2 cells of which divide transversely and diagonally, and, swelling slightly, continue to divide (fig. 75). Later this mass develops into a globose, finely reticulated, pale brown body. In some instances the compound mode appears in which 2 or more hyphae are involved in the formation (fig. 76). In other cases primordia are to be found arising from a main hyphal strand with numerous branches of nearby hyphae intermingling in the mass (fig. 77). This involves both the meristogenous and the symphogenous methods, and so may be considered a combination of the two. The principal method of development is meristogenous.

Septoria scrophulariae Pk.; isolated from its host *Scrophularia leperella* Bicknell by Mr. Walter S. Beach during the summer of 1917.

In pure culture it produces a closed sporing body, the primordium of which arises either from a few cells of a single hypha or from 2 or 3 closely lying hyphae (figs. 78, 79). These primordial cells divide, swell, and continue to divide to form a small ball-like structure which later develops into 1 or more pycnidia. They thus arise either by the simple or compound meristogenous mode.

Septoria helianthi E. and K.; isolated from its host *Helianthus grosseserratus* Mortens by Mr. Walter S. Beach in the summer of 1917 at Urbana, Illinois.

Pycnidia form readily in culture. A single cell or a few adjoining cells in a hypha become slightly swollen. These then divide into shorter cells which swell and send out very short branches (fig. 80). The swelling continues until a rounded mass is formed, slightly darker in color than the pale brown mycelium (fig. 81). The body thus formed becomes almost globose in shape. The outer portion or covering becomes membranous with a cellular appearance. This primordium continues to enlarge, and becomes ovate or elliptical in shape. The development is simple meristogenous, within a single strand of mycelium.

The genus *Septoria* can hardly be judged by these few species, but these, with those reported in the literature, indicate that the 2 main methods of development, namely, meristogenous and symphogenous, and even a combination of these two, may occur.

Sphaeronaemella Karst.

Sphaeronaemella fragariae Stevens and Peterson; procured from Dr. Alvah Peterson, Urbana, Illinois.

A few cells of a single hypha divide, producing very short cells. These bud and branch profusely, usually in one direction, into short hyphae (fig. 82). These branches anastomose (fig. 83), twining about in a circular manner. They then divide and swell, forming a small mass which usually protrudes from one side of the main mycelial strand from which it arises (fig. 22). The body thus formed is the primordium from which the pycnidium arises.

In the genus *Sphaeronaemella* a striking variation of the meristogenous development is found. A few cells of a main mycelial thread begin to divide as in the simple meristogenous mode, but short hyphal branches arise from these, usually on one side, curling and twisting about each other to form a ball-like mass. In some cases this mass envelops and includes the main hypha (fig. 84).

Gloeosporium Desmazières and Montaigne

Gloeosporium rufomaculans (Berk.) Thüm.; isolated from fruit of apple (*Pyrus malus* L.) from Neoga, Illinois, September 1917.

The primordium of the acervulus arises from a number of neighboring hyphae. These branch into short hyphae which branch in turn, forming a loosely woven network. A spreading tuft arises from this loosely woven base (fig. 87). This cushion with its tuft of short hyphae is the primordium. It usually originates symphogenously, sometimes meristogenously.

Gloeosporium musarum C. and M.; isolated from a banana (*Musa sapientum* L.) from the Champaign market, July 28, 1916.

Short hyphal branches from main mycelial strands interweave near their ends. Other hyphae intertwine about this initial portion. Some branches fold or loop back upon themselves, while still others branch again. The cells of the interwoven mass divide, swell, and branch (fig. 88). At length a cushion-like base is formed. This is the primordium of the acervulus, from which short conidiophores arise which bear conidia. In terms of pycnidial development it arises symphogenously. In culture this fungus bears many spores, either sessile or upon short conidiophores outside of acervuli, scattered freely upon the mycelium. These spores appear before the formation of acervuli, making the study of the beginning of acervuli difficult.

Colletotrichum Corda

Colletotrichum lagenarium (Pers.) E. and H.; isolated from a watermelon (*Citrullus vulgaris* Schrad.) procured on the Champaign market, September 1917.

The primordia of the acervuli begin their formation deeply imbedded in the media, even near the bottom, by the time the culture is 4 cm. in diameter and no more than 4 or 5 days old. At this age no conidia have developed upon the short conidiophores or as buds from cells of hyphae, as often occurs when the culture becomes older. The primordia arise by 2 methods: (1) from a few cells of a main hypha arise a few or many short budlike hyphae (figs. 89–92); these elongate, intertwine, and branch to form a cushion-like base from which very short conidiophores arise; (2) hyphal branches from a few neighboring or contiguous mycelial strands intertwine, some of the threads forming short loops which mass, intertwine, and branch (figs. 93–96), forming an irregularly shaped, loosely made, cushion-like base from which conidiophores arise as in the other type. Irregular large acervuli, or acervuli-like groups, bearing numerous conidia, arise in this latter type. The first mentioned type may be considered as meristogenous, both simple and compound modes appearing; the second is symphogenous.

The genera *Gloeosporium* and *Colletotrichum* have been extensively studied by SHEAR (36), STONEMAN (42), SOUTHWORTH (38, 39), EDGERTON (11), and others. Late stages of development and cross-sections of different stages have been figured from fixed material in host tissues, but little has been said in regard to the early development of the acervulus. The 3 species studied give insight only into the origin of the cushion-like base from which the acervulus arises. They present 2 distinct types, the simple loosely woven base that arises from a single hypha or from a few contiguous hyphae, and the more complexly interwoven base which arises symphogenously.

PESTALOZZIA De Notaris

Pestalozzia palmarum Cke.; pure culture procured from the Centralstelle für Pilzkulturen, Amsterdam, Holland.

A few hyphae, usually 2–6, lying side by side form a bed in which a few cells begin to divide into shorter cells. These cells may be in only one of the hyphae (fig. 97*a*), or they may be contiguous cells of 2 or more hyphae (fig. 100). These cells swell and continue to divide by cross and longitudinal walls, at length forming a protruding oval or obovate body (fig. 97*b*) which is the primordium of the pycnidium-like body which later forms. This primordium arises by either simple (fig. 97*a*) or compound meristogenous (fig. 100) development. It soon becomes globose and membranous, with a cellular outer wall, but remains light of color, so that a few dark spores may be seen within (figs. 98, 99). At this stage the structure is to all appearances a young pycnidium (fig. 101). Within a few days the top breaks, the few spores already formed are extruded, sometimes rather forcibly (fig. 102), and the cavity then becomes saucer-shaped. Conidiophores arise in profusion, and many spores are produced. When the first spores are noted the body is a pycnidium, if observed in a later stage it appears like an acervulus. In *Pestalozzia capiomanti* similar facts were noted by BAINIER and SARTORY (4), while LEININGER (24) in his studies of *P. palmarum* speaks of these bodies as pseudopycnidia.

Pestalozzia guepini Desm.; isolated from the fruit of a kumquat (*Fortunella margarita* Swingle) from Lake City, Florida, January 1916.

A few pycnidia were produced in plate culture. In the beginning stages a number of branches of closely lying or nearby hyphae branch, snarl, and intertwine (figs. 103, 104). Cells within the more closely twined part of the mass swell and divide by continued cross and longitudinal divisions until a rounded mass is formed, which is the primordium of the pycnidium (fig. 105). This primordium arises symphogenously. The development of the final sporing body from this stage is very similar to that described for *Pestalozzia palmarum*.

Pestalozzia, species indet.; isolated, by the author November 1916, from leaves of peony (*Paeonia officinalis* Retz) procured by Dr. H. A. ANDERSON near Crawfordsville, Indiana.

A good growth of mycelium and numerous sporing bodies were produced in plate cultures. The mycelial threads are slightly larger than those of other species of *Pestalozzia* studied. Pycnidial primordia arise usually by the compound meristogenous method (figs. 107, 108). As these bodies develop from the pycnidial stage to the open type, the formation of spores within (fig. 109), a breaking open of the pycnidium, and its further development into what appears to be an acervulus may be seen.

Pestalozzia, species indet.; pure culture procured from Dr. G. P. Clinton, New Haven, Connecticut, in November 1916. It had been isolated from dead maple (*Acer*) bark in October 1910.

This *Pestalozzia* was the most vigorous of all those cultured. Sporing bodies were produced in abundance. Two or 3 contiguous hyphae, or in some cases as many as 10 or 12, take part in the formation of the primordium. A few cells continue to swell and divide until a small mass is formed (fig. 110). They branch slightly (fig. 111) until a primordium of tissue-like type is formed. It is of compound meristogenous development, especially pronounced in cases where 10 or more hyphae take part. The young pycnidia-like bodies continue to develop, produce spores, then break open (fig. 112) and change into the acervulus form as in the previous species mentioned.

In *Pestalozzia* a condition is found that is quite distinct from any other acervulus-forming fungus studied, in that it first produces a sporing body which morphologically is a pycnidium. These pycnidia arise by any of the various modes previously described. The different species vary in the manner of development, but whatever the method there first appears a pycnidium which later breaks open and becomes acervulus-like.

Patellina Speg.

Patellina fragariae Stevens and Peterson; pure cultures procured of Dr. A. Peterson, September 1916. It was also isolated from strawberries (*Fragaria chiloensis* Duschesne) from Centerville, Indiana, June 1916.

This fungus forms numerous sporodochia in concentric rings in plate cultures. These sporodochia arise in 2 rather typical ways. A few cells of a hypha divide into very short cells. These cells swell and bud, producing numerous branches in some cases (fig. 115), in other cases a tuft of 2 or 3 branches. These branches elongate slightly to form a pedicel (fig. 116), then branch at the tips and radiate to form a distinct urnlike body (fig. 117), within which a cushion or bed forms and gives rise to the conidiophores. The sporodochia are usually produced singly by a simple meristogenous mode. In other instances sporogenous areas develop, and in these 1 or 2 cells, in each of the closely lying hyphae, branch profusely (fig. 113). Many of these branches unite into a mass and, without the formation of a definite pedicel and peridium (fig. 114), give rise to hundreds of conidiophores.

Patellina, species indet.; from a quince (*Cydonia vulgaris* L.) procured on the Champaign market, November 1917.

Strands of 6–20 hyphae are formed, and at some definite point within the strand a few adjacent cells branch; thus a tuft of a number of branches is formed (fig. 118). This tuft becomes slightly larger at the upper end by continued branching, while the lower portion constitutes a pedicel consisting of a few large branches, where a few hyphae enter into its formation. A more substantial closely formed pedicel or base is present if a larger number of hyphal branches are concerned in its origin (figs. 118, 119). The upper half or less becomes cuplike, and the outer hyphae curve inward as a superficial covering, while within conidiophores and conidia are formed. The type is compound meristogenous.

In *Patellina* the sporodochium develops in a very characteristic manner, arising by the meristogenous method. A single isolated mycelial thread gives rise to a very simple sporodochium. If a number of mycelial strands are crowded together, each branches characteristically, and the branches form a sporodochium of the compound type. The type of sporodochium varies with the type of base formed.

VOLUTELLA Tode

Volutella fructi S. and H.; procured from Mr. WILMER G. STOVER, Ohio State University. It was isolated by G. C. MECKSTROTH in the winter of 1916 from a fruit of apple (*Pyrus malus* L.) grown in western Ohio.

The sporodochia form in abundance in plate cultures, the primordium arising from a main hypha. A definite portion, 1, 2, or 3 cells in length, takes on a brownish color. These cells divide and some of them branch, usually from one side only (figs. 120, 124), forming a small tuft (figs. 120, 125), the branches of which elongate and then divide again, forming a larger tuft (figs. 121, 122). The first interwoven branches form a short pedicel. This cuplike structure may be regarded as the primordium of the sporodochium (fig. 123), from which a bed of short conidiophores is formed. The development is clearly simple meristogenous. Other larger bases are quite often formed symphogenously. Then hyphal branches from all adjacent mycelial threads interweave and anastomose, forming a black mass of sclerotial character from which hyphae arise and interweave into a cuplike bed from which conidiophores develop.

Volutella circinans (Berk.) Stevens and True; from a white globe onion (*Allium cepa* L.) at Urbana, Illinois, September 1917.

Primordia arise by either of 2 methods, simple meristogenous (fig. 126) or symphogenous (figs. 128–130). In most instances a black stroma-like mass of interwoven hyphae is formed symphogenously (figs. 130, 131), from which the sporodochium later develops. Setae may be found arising as hyphal branches (fig. 127).

Volutella is very similar to *Colletotrichum* and *Gloeosporium* in the origin of the sporing bodies; the meristogenous and symphogenous methods are both found. The principal distinction is in the formation of a more compact and usually larger base or subicle upon which the sporodochium is produced. The origin of this subicle if it is simple is usually meristogenous, but if a complex subicle is formed it arises symphogenously by the interweaving of numerous hyphal branches.

Epicoccum Link

Epicoccum, species indet.; isolated from a plate culture in which it appeared as a contamination in October 1917.

The sporing body of this fungus arises from 2 or more closely lying hyphae which produce erect branches from a rather localized area. Two or more such hyphae arise which branch in turn near their tips. These form a spreading tuft of conidiophores each bearing a conidium at its end. This is a simple form of sporodochium (fig. 132). The development is compound meristogenous.

PYCNIDIAL STAGE OF MELIOLA(?) CAMELLIAE (Catt.) Sacc.

This pycnidium was studied from herbarium material collected by Dr. F. L. STEVENS in Porto Rico. The fungus, which usually is reported as *M. camelliae* and is perhaps better known as "sooty mold" (48), is plainly not a true *Meliola*, as the genus is limited by recent writers (16, 40), and the position of its ascigerous stage has not been definitely determined.

A small pycnidium arises from a single cell of the main hypha or a single cell of a hyphal branch. The initial cell is usually an intermediate cell, but it may be a terminal one. In either case it divides by transverse and diagonal walls into 2, then 4 cells (fig. 133), and by swelling and dividing becomes an elliptical, finely reticulated, dark brown body (figs. 134–137). The mode is simple meristogenous.

These observations do not essentially disagree with the descriptions as given by ZOPF (53) and TULASNE (43), who studied early stages of the development of the pycnidium of the sooty molds.

Discussion

Two main methods of origin and early development are found in pycnidial formation, namely meristogenous and symphogenous. The meristogenous method resolves itself into 2 modes, simple (figs. 1, 2, 4, 5) and compound (figs. 18, 22, 37). In the simple mode the pycnidium develops from a single cell or a few adjacent cells of a single hypha. In the compound mode adjacent cells of 2 or more contiguous hyphae divide, swell, and sometimes branch, all of these then anastomosing freely to form a pseudoparenchymatous mass. Variations of these 2 modes are found in *Macrophoma citrulli* (figs. 39, 43, 47), *Coniothyrium pyriana* (figs. 69–71), *Septoria polygonorum* (figs. 76, 77), *Sphaeronaema fimbriatum* (figs. 50–52), and *Sphaeronaemella fragariae* (figs. 82–85).

The symphogenous method (figs. 48, 49, 54, 55) is less often found in the species studied. In this method of development, branching hyphae from main mycelial threads are directed toward a common point, loop back, and interweave to form a loose network which later becomes more close. The hyphae of this ball anastomose into a pseudoparenchymatous mass from which the pycnidium develops.

Table I gives the species and the methods of development found in each of the pycnidium-forming species. *Phoma herbarum, Phoma pirina, Phoma* from clover, *Phoma* from grape, *Sphaeronaema fimbriatum, Coniothyrium* species indet., *Septoria helianthi, Sphaeronaemella fragariae*, and a pycnidium of *Meliola*(?) *camelliae* show a simple meristogenous origin and development, and other methods of development seldom or never appear.

TABLE I

Species	Simple meristogenous	Compound meristogenous	Symphogenous
Phoma herbarum West	+	−	−
Phoma destructiva Plowr	+	+	−
Phoma pirina (Fries) Cooke	+	−	−
Phoma from clover	+	−	−
Phoma from grape	+	−	−
Phoma cichorii Passr	+	+	−
Macrophoma citrulli (B. and C.) Berl. and Vogl	+	+	+
Sphaeronaema fimbriatum (E. and H.) Sacc	+	−	−
Sphaeropsis malorum Pk	−	+	+
Sphaeropsis citricola McAlpine	+	+	−
Coniothyrium pyriana (Sacc.) Shel	+	+	−
Coniothyrium, species indet	+	−	−
Septoria polygonorum Desm	+	+	+
Septoria scrophulariae Pk	+	+	−
Septoria helianthi E. and K	+	−	−
Sphaeronaemella fragariae S. and P	+	−	−
Pycnidium of Meliola (?) camelliae (Catt.) Sacc	+	−	−

In *Phoma destructiva, Phoma cichorii, Sphaeropsis citricola, Coniothyrium pyriana*, and *Septoria scrophulariae* the pycnidial primordia arise by either the simple or compound meristogenous modes, the simple mode being the more common.

Macrophoma citrulli, Sphaeropsis malorum, and *Septoria polygonorum* give rise to their pycnidial primordia by either the symphogenous or meristogenous methods. In *Sphaeropsis malorum* the symphogenous method is the main one. The compound meristogenous method appears occasionally. In *Macrophoma citrulli* the simple meristogenous mode prevails, but the others are often found. In *Septoria polygonorum* the compound meristogenous mode is more often found, although a few primordia arise by the symphogenous method, and occasionally the simple meristogenous mode appears.

Variations of these 3 modes of development are found. No 2 species give exactly the same development. In symphogenous development a few branches from nearly hyphal strands may interweave near their ends, or intermingling hyphae may loop back, branch, and interweave or snarl into a knotlike mass. In the simple meristogenous mode the origin may be a single cell which swells and divides, or a number of cells that swell and divide simultaneously. In some cases branches arising from the dividing cells anastomose with the enlarging mass. In other cases branches arise from more distant cells of the same strand and take part in the development. In a few instances short budlike branches arise from a few cells of a hyphal strand, enlarge, divide into short cells, intertwine, and anastomose to form a pycnidium.

Neither have the acervuli-forming fungi in the Melanconiales been studied as to the early development of their sporing bodies, nor has the origin of the sporodochium been given special attention. SHERBAKOFF (37), in studies of *Fusarium*, describes a simple type of sporodochium found in cultures. TULASNE (43), STONEMAN (42), SOUTHWORTH (38, 39), WOLF (50, 51), and others figure and describe later stages of the development of acervuli, and the later development of sporodochia are referred to in the literature, but the subject is considered merely incidentally.

The fungi that form acervuli and sporodochia may be classed according to the manner of origin and development of the primordia on the same basis as the pycnidia-forming species.

In table II fungi of the Melanconiales and Tuberculariaceae that were studied are listed, indicating the method or methods of development of the primordia. In *Gloeosporium rufomaculans*, *Gloeosporium musarum*, and *Pestalozzia guepini* the primordia originate by the symphogenous method. In *Colletotrichum lagenarium* and *Volutella circinans* the symphogenous method prevails, although the simple meristogenous mode occurs occasionally. The compound meristogenous mode is well exemplified by *Pestalozzia palmarum*, *Pestalozzia* from peony and from maple. *Epicoccum* and *Pestalozzia* from maple have only the compound meristogenous mode. The simple meristogenous method of development appears in *Colletotrichum lagenarium*, *Pestalozzia palmarum*, *Pestalozzia* from peony, *Volutella fructi*, and *Volutella circinans;* it also is at times observed in the development of isolated sporodochia of *Patellina fragariae*. This mode is more seldom found than either the compound meristogenous or symphogenous method in the development of acervuli and sporodochia.

TABLE II

Species	Simple meristogenous	Compound meristogenous	Symphogenous
Gloeosporium rufomaculans (Berk.) Thüm.	–	–	+
Gloeosporium musarum C. and M.	–	–	+
Colletotrichum lagenarium (Pers.) E. and H.	+	+	+
Pestalozzia palmarum Cke.	+	+	–
Pestalozzia guepini Desm.	–	–	+
Pestalozzia from peony	+	+	–
Pestalozzia from maple	–	+	–
Patellina fragariae S. and P.	+	+	–
Patellina from quince	–	+	–
Volutella fructi S. and H.	+	–	+
Volutella circinans (Berk.) S. and T.	+	–	+
Epicoccum, species indet.	–	+	–

The species of *Pestalozzia* studied present a type of sporing structure which is in need of further investigation in other genera and species. From the mature structure it has been classed as an acervulus, but from its origin and development it is not a true acervulus, for it arises as a pycnidium and opens to form an acervulus when mature. This may be called a pseudo-acervulus.

According to POTEBNIA (30) and DIEDICKE (10), some species of *Septoria* and *Ascochyta* have open-topped sporing bodies arising by the interweaving of hyphae to form a bed from which arises a peridium partially surrounding the inner sporing surface. Such a structure is designated by POTEBNIA as a pseudo-pycnidium.

Study of the origin and development of the sporing bodies of the many genera and species of the Sphaeropsidales and Melanconiales which have not yet been investigated will no doubt add to these 2 types.

In the pycnidia-bearing fungi studied the meristogenous method of development is the more prevalent, the symphogenous type seldom appearing. In species forming acervuli and sporodochia, the tendency is toward the more complex methods, especially if *Pestalozzia* be regarded as belonging to the Sphaeropsidales. As was to be expected, in the pycnidial development no sexual organs, ascogenous hyphae, or nuclear fusions were observed.

Summary

1. Pycnidia originate and develop by 2 main methods, namely, meristogenous and symphogenous.

2. The meristogenous method resolves itself into 2 modes, simple and compound.

3. Variations of the meristogenous method are found, for example, in *Coniothyrium pyriana* and *Sphaeronaemella fragariae*.

4. The symphogenous method is less often found and is variable.

5. Acervuli arise in the same manner as do pycnidia, simple acervuli by the simple meristogenous mode, and complex ones usually by the compound meristogenous or symphogenous method.

6. Complex subicles usually arise symphogenously, although they may arise by the compound meristogenous mode.

7. Simple sporodochia, especially those appearing on single isolated strands, originate by the simple meristogenous method.

8. Complex sporodochia, with a large base or subicle, usually arise either by the compound meristogenous mode or symphogenously.

9. The pseudo-acervulus of the species of *Pestalozzia* studied arises and develops as a pycnidium which breaks open and appears like an acervulus.

10. The simple meristogenous development is the more often found in the Sphaeropsidales, while the compound meristogenous and symphogenous modes are the more usual in the Melanconiales and Tuberculariaceae.

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EXPLANATION OF PLATES XVII–XXII

The drawings were made with a Leitz camera lucida and a Leitz one-twelfth oil immersion lens or a no. 6 objective. The scale appears on the plates.

PLATE XVII

Phoma

FIG. 1.—*P. herbarum* West: 4-celled stage of pycnidial primordium of simple meristogenous origin.

FIG. 2.—Slightly later stage.

FIG. 3.—Stage similar to fig. 2.

FIG. 4.—Young pycnidium with light colored rostrum where ostiole will form.

FIG. 5.—Mature pycnidium and spores formed by simple meristogenous development.

FIG. 6.—*P. pirina* (Fries) Cooke: few-celled stage; simple meristogenous origin.

FIG. 7.—Slightly later stage.

FIG. 8.—Many-celled pseudoparenchymatous stage with branches protruding from mass.

FIG. 9.—Irregular mass from which pycnidium develops.

FIGS. 10, 11.—Few-celled stages in origin of which 2 or more hyphae are involved; compound meristogenous origin.

FIG. 12.—Similar to fig. 11, but slightly older.

FIG. 13.—Primordium in which a 3-parted hyphal strand is involved.

FIGS. 14–16.—*P. destructiva* Plowr.: beginning stages in pycnidial development; simple meristogenous origin.

FIG. 17.—Slightly later stage.

FIGS. 18, 19.—Compound meristogenous development in which 2 or more hyphae are involved.

FIG. 20.—Development near end of hypha with branches budding from mass.

FIG. 21.—Irregular meristogenous development.

FIG. 22.—Typical compound meristogenous development with 3 parallel hyphae involved.

PLATE XVIII

FIGS. 23, 24.—*Phoma* from clover: beginnings of pycnidia.

FIG. 25.—Slightly older stage with a few short budding branches.

FIGS. 26, 27.—Later stages with one end enlarging slightly.

FIG. 28.—*Phoma* from grape: mycelial threads with different stages of pycnidial development.

FIG. 29.—Beginning stage: simple meristogenous.

FIGS. 30–32.—Later stages.

FIG. 33.—Mature pycnidium.

FIG. 34.—*P. cichorii* Passr.: early stage in development; short cells formed which divide and branch.

FIG. 35.—Early stage in which is much branching.

FIG. 36.—Medium stage in simple meristogenous development.

FIG. 37.—Typical compound meristogenous development.

Macrophoma

FIG. 38.—*M. citrulli* (B. and C.) Berl. and Vogl.: 2-celled stage in origin of pycnidium, from drop culture; simple meristogenous development.

FIG. 39.—Same 12 hours later.

FIGS. 40, 41.—Early stages of other pycnidia, from drop culture; slight variation from simple meristogenous type in that many branches are involved.

FIGS. 42, 43.—Early stages in which much branching takes place; drop culture.

FIGS. 44, 45.—Early stages from Petri dish culture.

FIGS. 46, 47.—Later stages.

PLATE XIX

FIG. 48.—*M. citrulli* (B. and C.) Berl. and Vogl.: symphogenous development in which branches from a number of main strands interweave.

FIG. 49.—Later stage in which a winding of the hyphae and cell division have taken place forming a pseudoparenchymatous mass.

Sphaeronaema

FIGS. 50–52.—*S. fimbriatum* (E. and H.) Sacc.: early stages of pycnidium in which a hypha coils, branches, and divides to form knotlike mass.

Sphaeropsis

FIG. 53.—*S. malorum* Pk.: Early stage in symphogenous development in which branches *a*, *b*, *c* interweave near their ends to form a ball.

FIG. 54.—Interwoven hyphae in early stage of symphogenous development.

FIG. 55.—Slightly later stage.

FIGS. 56, 57.—*S. citricola* McAlp.: very early stages in origin of simple meristogenous development of pycnidia.

FIGS. 58, 59.—Slightly later stages.

FIGS. 60–63.—Later stages with short hyphae branching from masses.

FIGS. 64–66.—Unusual examples of developments in which more than one hypha is involved; compound meristogenous.

Coniothyrium

FIGS. 67, 68.—*C. pyriana* (Sacc.) Shel.: early stages in development.

FIGS. 69, 70.—Later stages in which numerous branches from dividing mass are involved.

FIG. 71.—Pseudoparenchymatous mass from which a pycnidium arises.

PLATE XX

FIG. 72.—*Coniothyrium* species from laboratory air: early stage showing short cells and short branches as origin.

FIG. 73.—Slightly later stage in which cells and branches from main hypha divide into short cells and anastomose.

FIG. 74.—Stage slightly more developed than fig. 73; slight variation from simple meristogenous type.

Septoria

FIG. 75.—*S. polygonorum* Desm.: beginning stage of simple meristogenous development.

FIG. 76.—Development in which original hypha and numerous branches are involved.

FIG. 77.—Pseudoparenchymatous primordial mass formed by symphogenous method.

FIGS. 78, 79.—*S. scrophulariae* Pk.: early stages in compound meristogenous development.

FIG. 80.—*S. helianthi* E. and K.: early stage in beginning of simple meristogenous development.

FIG. 81. Later stage.

Sphaeronaemella

FIG. 82.—*S. fragariae* S. and P.: early stage of simple meristogenous development.

FIG. 83.—Later stage in which branches and original hypha have anastomosed to form a mass on one side of main strand.

FIG. 84.—Later stage in which mass surrounds main strand.

FIG. 85.—Late stage which has developed by a winding and dividing of hyphal branches from a few cells upon one side of main strand.

Gloeosporium

FIG. 86.—*G. rufomaculans* (Berk.) Thüm.: early stage of meristogenous development; this method rarely occurs.

FIG. 87.—Side view of an acervulus formed by symphogenous method: compressed so that cushion-like bed of conidiophores is pulled away from basal hypha.

FIG. 88.—*G. musarum* C. and M.: top view of partially developed acervulus; development symphogenous.

Colletotrichum

FIG. 89.—*C. lagenarium* (Pers.) E. and H.: very early stage in which acervulus originates in a few short branches from a single hypha.

FIG. 90.—Numerous budding branches from a few cells of one hypha forming beginning of an acervulus; simple meristogenous.

FIG. 91.—Early stage in development of acervulus.

FIG. 92.—Primordium in which a few branches are involved.

FIG. 93.—Early stage in symphogenous development: hyphal branches loop and interweave in this mode.

FIG. 94.—Same as fig. 93, 24 hours later.

FIG. 95.—Beginning stage of symphogenous development.

FIG. 96.—Later stage.

PLATE XXI

Pestalozzia

FIG. 97.—*P. palmarum* Cke.: *a*, very early stage in meristogenous development, a few cells divided and swelling; *b*, later stage.

FIGS. 98, 99.—Pycnidia with young spores developed within.

FIG. 100.—Primordium of compound meristogenous origin.

FIG. 101.—Young pycnidium at stage just before opening.

FIG. 102.—Pycnidium opening and extruding spores: following this stage cuplike interior formed, longer conidiophores develop, and body becomes a pseudo-acervulus.

FIGS. 103, 104.—*P. guepini* Desm.: early stages in symphogenous development.

FIG. 105.—Later stage; pycnidia of this species form spores within and later break open as pseudo-acervuli.

FIG. 106.—*Pestalozzia* from peony: meristogenously developed pycnidial mass.

FIG. 107.—Early stage in symphogenous development.

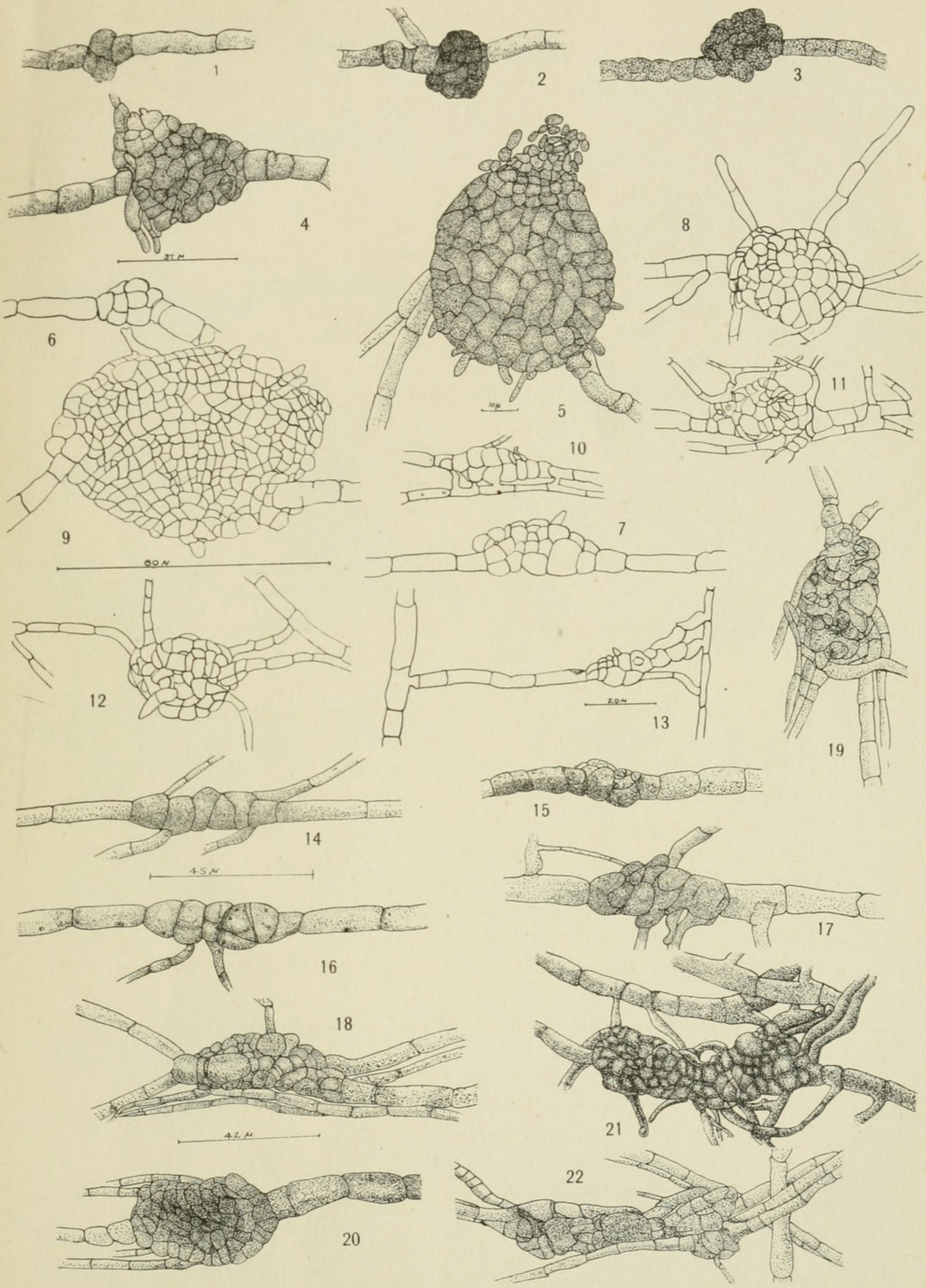
FIG. 108.—Later stage.

FIG. 109.—Pycnidium which has opened, surface view.

FIG. 110.—*Pestalozzia* from maple: compound meristogenous development from a number of parallel hyphae.

FIG. 111.—Later stage.

FIG. 112.—Young pycnidium breaking open on one side: spores show within.



KEMPTON on PYCNIDIUM