DELINEATIONS OF FOREST FUNGI: MORPHOLOGY AND RELATIONSHIPS OF VARARIA

by

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(with 5 plates)

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INTRODUCTION

Vararia includes corticioid and stereoid species of the basidiomycetous order Aphyllophorales (Polyporales). This discussion of the genus is based on a series of collections from Mississippi by LENTZ (1959), on numerous specimens in the National Fungus Collections, on a few borrowed type collections, and on cultures prepared by LENTZ and various others and maintained in the culture collection of the Forest Disease Research Laboratory. Morphological details of individual species and citation of specimens will be provided in a paper now being prepared.

BASIDIOCARPS

Basidiocarps of *Vararia* develop in a manner entirely unfamiliar to mycologists a few years ago but now becoming well known from investigations of genera such as *Laeticorticium* (DONK, 1956, 1957) and *Aleurodiscus* (LEMKE, 1964). The essential characteristic of this group is formation of basidia at a considerable depth beneath the hymenial surface and the resultant passage of the apical portion of the basidium through a blanketing hyphal mass in order to reach the surface. DONK (1957) used the term hyphidial hymenium for this kind of development, but his "thickening euhymenium" apparently is correlated with the same pattern of basidial development. LEMKE (1964) substituted the term catahymenium for hyphidial hymenium, and DONK (1964) accepted LEMKE's term because, as he said, the blanketing hyphal mass may also include gloeocystidia.

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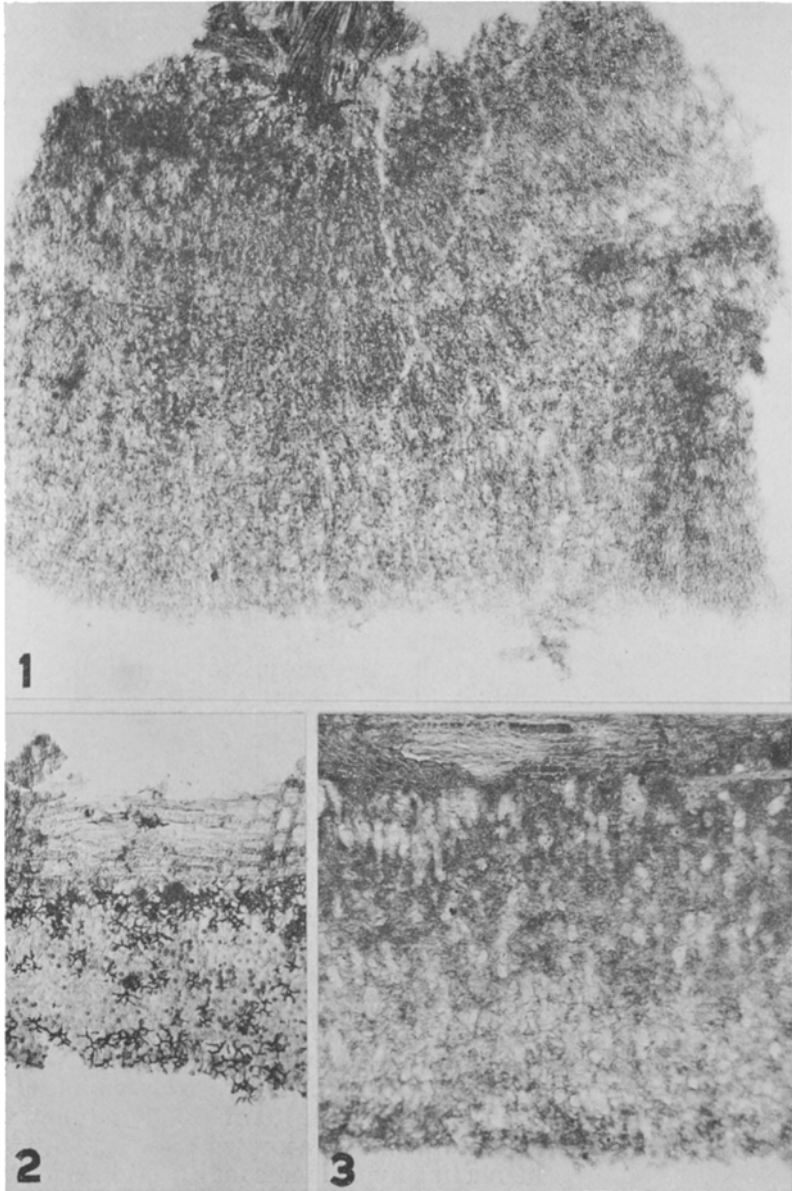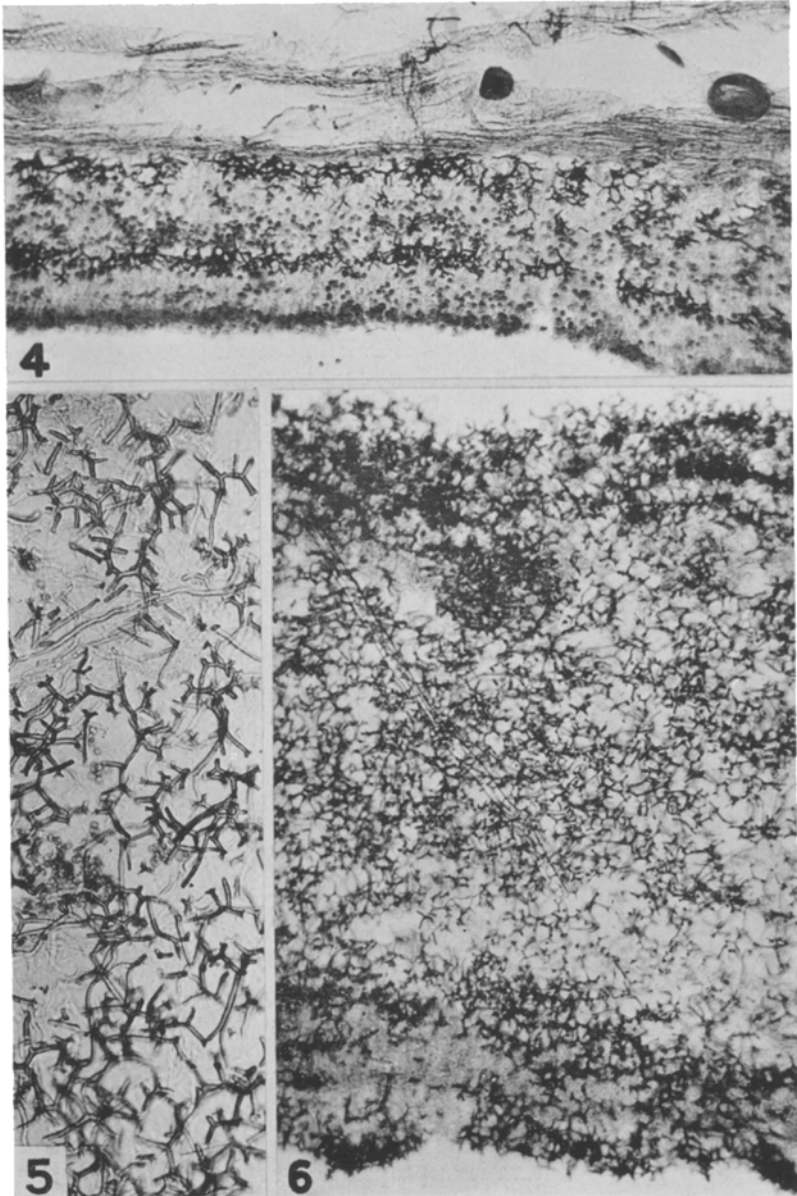
Figs. 1—3. Vertical sections through basidiocarps, × 110. Fig. 1: *Vararia pallescens*, type, BPI* (Michener herb., in NFC), showing tenacious context of dichohyphidia. Fig. 2: *V. effuscata*, F. P. 106774, BPI, showing scattered dichohyphidia and embedded spores. Fig. 3: *Hypochnus (V.) peniophoroides* Burt, type, NY, showing portions of gloeocystidia interspersed among masses of dichohyphidia.
*BPI and NFC refer to the National Fungus Collections at the Beltsville Plant Industry Station; NY refers to the New York Botanical Garden.

Thus, the basidia of *Vararia* are formed as isolated elements in a catahymenium, and their apices push through the surrounding hyphal mass until they extend beyond the surface. However, the hyphal elements of the surface region also continue their growth, and the basidial apices eventually are surpassed and overgrown again. As this occurs, younger basidia develop in their turn. The process, consequently, assumes a cyclical pattern of basidial development at a deep level, growth toward the surface, and eventual re-engulfment by the hyphal mass. This process accounts for the distribution of spores and gloeocystidia throughout all regions of the basidiocarp, as easily observed in vertical sections of basidiocarps of several species and as seen only by assiduous study of basidiocarp sections of other species. Embedded spores in the thickening euhymenium of *Clavulina cartilaginea* (BERK. & CURT.) CORNER were illustrated by CORNER (1950, p. 304). In *Vararia*, the process of spore submersion is essentially the same, except that they are overwhelmed more by hyphal development than by the profuse overgrowth of young basidia.

The term hyphidial hymenium, or catahymenium, has its basis in a system of terminology that DONK (1964) utilizes in writing about the various kinds of specialized hyphal elements that appear in basidiocarps. For example, DONK refers to dentritically branched hyphal structures as dendrohyphidia, rather than dendrophyses. He also substitutes the term dichohyphidia for the specialized dichotomously branched hyphae that PILAT (1926) called dichophyses.

The usefulness of the term dichohyphidium may be illustrated by consideration of the basidiocarp structure of *Vararia*. This structure consists, in many instances, of not much more than a minimal context bearing a thickened catahymenium, as demonstrated by the presence of embedded spores (Figs. 2, 4) throughout the region ordinarily regarded as context. Gloeocystidia of *Vararia* characteristically develop in or near the hymenial region; thus, the submerged gloeocystidia (Fig. 3) are thought to have originated essentially as hymenial elements, rather than in the context. Dichophyses, or dichohyphidia (Figs. 1—15), also appear in the hymenium and constitute the most conspicuous catahymenial elements of *Vararia*. However, in basidiocarps of several species, hymenial development seems to remain relatively limited. In these basidiocarps, the dichohyphidia apparently develop in areas that must be considered as context, not as catahymenium. In such instances, the term dichohyphidium is appropriate, but the term dichophysis is not.

The terms dendrophysis, acanthophysis, and dichophysis all are well known to mycologists who study hymenomycetes, but DONK's terminology is preferable because it emphasizes the hyphal nature of these structures. In some instances, as in *Xylobolus subpileatus* (BERK. & CURT.) BOIDIN, the features that characterize the mo-

Figs. 4—6. Vertical sections through basidiocarps, × 110 (Figs. 4 and 6), × 220 (Fig. 5). Fig. 4: *V. effuscata*, F. P. 107017, BPI, showing scattered dichohyphidia and embedded spores. Figs. 5 and 6: *V. granulosa*, F. P. 105545, BPI, showing dichohyphidia.

dified hyphal elements also may characterize the basidia. If DONK's terminology is applied, the hyphal modifications of *X. subpileatus* include acanthohyphidia, acanthoskeletohyphidia, encrusted skeletocystidia, and encrusted acanthoskeletocystidia. In addition, the basidiocarps may have acanthobasidioles and acanthobasidia formed as fertile or potentially fertile hymenial elements with bottle-brush protuberances. This terminology seems complicated only because, in this instance, it is used to describe a multitudinous assortment of hyphal modifications. The appearance of bottle-brush processes on the basidia and hyphidia of *X. subpileatus* emphasizes the susceptibility of all basidiocarp elements to modification. However, in *Vararia* the ordinary generative hyphae of the basidiocarp produce only dichohyphidia, gloeocystidia, and basidia.

HYPHAE

In nearly all publications about *Vararia*, no distinction is made between the generative hyphae and the specialized hyphal elements known as dichohyphidia. In many instances, the dichohyphidia are referred to as hyphae, thus seeming to imply that the dichohyphidia are the ordinary generative hyphae of the basidiocarp. In all species that have the characteristics of *Vararia*, the generative hyphae are freely branched but not dichotomous. Typically, they are thin-walled and have relatively numerous septa. In most species, they bear clamp-connections (Fig. 16), but the hyphae of a few species are entirely without clamps. Because they usually are thin-walled and pale or colorless, the generative hyphae of *Vararia* are relatively inconspicuous among the dichohyphidia, either in basidiocarp sections or in mounts of mashed hyphal masses. This is especially true of such species as *V. pallescens* (SCHW.) ROGERS & JACKS. and *V. peniophoroides* (BURT) ROGERS & JACKS., in which relatively large dichohyphidia appear throughout the basidiocarp. Generative hyphae usually are much more apparent in basidiocarp sections of species such as *V. pectinata* (BURT) ROGERS & JACKS. and *V. protrusa* CUNN., in which the dichohyphidia are more nearly restricted to a relatively narrow hymenial region.

Generative hyphae of *Vararia* remain pale when immersed in KOH solution and assume a yellowish color in Melzer's iodine reagent. In cotton blue stain, they become less intensively blue than the dichohyphidia.

DICHOHYPHIDIA

No skeletal or binding hyphae are formed in basidiocarps of *Vararia*. Thus, the dichohyphidia are the only elements, other than those of the generative system, that retain a hyphal form. According to TALBOT (1954), dichophyses (dichohyphidia) may appear in the hymenium or context or both, and only in the hymenium
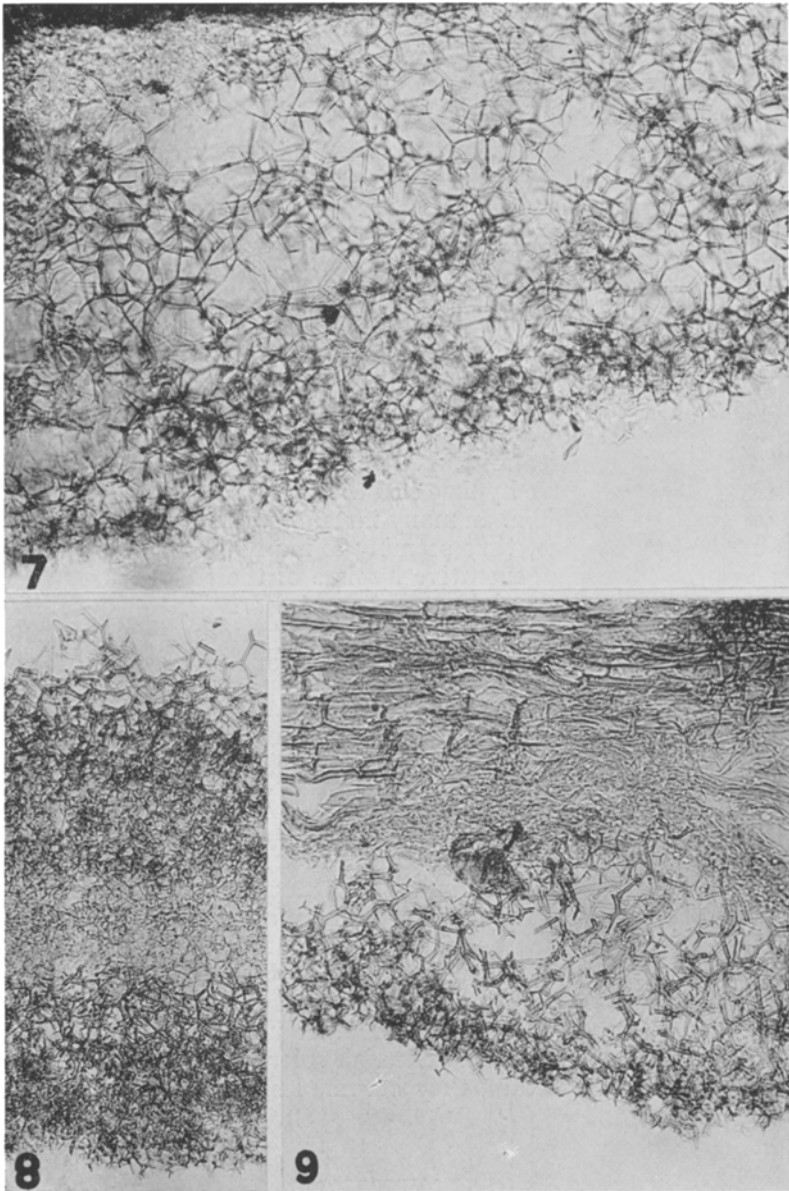
Figs. 7—9. Vertical sections through basidiocarps, × 220. Fig. 7: *V. investiens*, F. P. 100320, BFDL*, showing elastic context of dichohyphidia. Fig. 8: *V. investiens*, F. P. 56445, BFDL. Fig. 9: *Radulum* (*V.*) *investiens* Schw., type, BPI (Michener herb.).
*BFDL refers to the Beltsville Forest Disease Laboratory.

— as a matter of convenience — should they be considered as a type of paraphysis. However, he emphasizes their hyphal nature and believes that this obviates any advantage of considering them as paraphysis-like, even when they occur in the hymenium. For that reason, DONK's terminology seems well applied to *Vararia*.

Dichohyphidia are produced by generative hyphae as specialized forms abruptly set off from their parent hyphae by septa. Beyond the septum that separates a dichohyphidium from the generative hypha, no further septa are formed. Instead, a moderately short or moderately long unbranched stalk, or pedicel, bears a series of branches as a single multi-branched body that constitutes the dichohyphidium. Thus, the dichohyphidia of *Vararia* are hypha-like structures of more-or-less limited growth with branches originating dichotomously and, in turn, giving origin to additional dichotomously- formed branches. Each branch narrows somewhat from base to apex, and the ultimate branches usually are subulate.

The dichohyphidia of *Vararia* have a much greater range of form and size than the literature suggests. Only CUNNINGHAM (1955), in his description of *V. fusispora* CUNN., presents an illustration that adequately shows the considerable range in size and shape that the dichohyphidia of a single basidiocarp may exhibit. Sections from a portion of the type collection of *V. fusispora* reveal that CUNNINGHAM did not exaggerate the prominence of the filiform dichohyphidia that he found in that specimen. Basidiocarps of other species may have similar filiform dichohyphidia in the depths of the context, although usually they are not so conspicuous as those of *V. fusispora*. In fact, usually they are more-or-less difficult to discern, and several species with long, slender dichohyphidia have been described as having only minute or relatively compact dichohyphidia. A good example is *V. investiens* (SCHW.) KARST. Descriptions by a number of mycologists have established its moderately slender and profusely branched acicular dichohyphidia (Fig. 17) as highly characteristic of *Vararia*. No one has revealed that filiform dichohyphidia (Fig. 18) and enormous dichohyphidia with cylindrical branches also may appear in basidiocarps of *V. investiens*, including the type specimen. Obviously, the forms of dichohyphidia described by most authors are simply those most easily observed.

Difference in size, particularly in the length of the branches, greatly affects the appearance of dichohyphidia. The angle at which individual branches narrow from their bases to their apices is more or less directly related to their length, since long branches have a tendency to narrow gradually and short branches to narrow radically. In a few species, including *V. pectinata*, the branches are minute and more nearly peglike than subulate.

The pattern of branching exerts even greater influence than the size of the branches on the form of a dichohyphidium. Branches may develop at very broad angles, as in *V. granulosa* (FR.) LAURILA
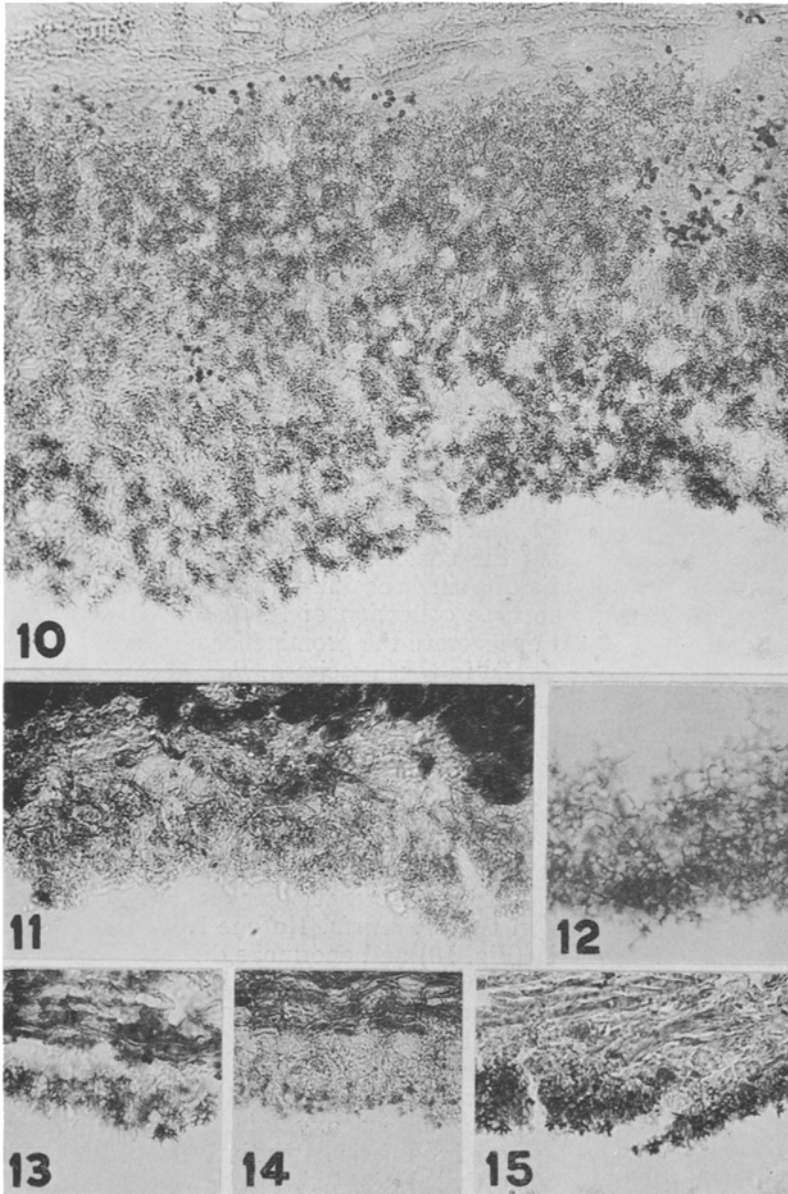
Figs. 10—15. Vertical sections through basidiocarps, × 220. Fig. 10: *V.* sp., F. P. 106809, BPI, showing moderately small dichohyphidia throughout context. Fig. 11: *V.* sp., F. P. 106659, BPI, showing moderately large dichophyses at deeper levels of context and minutely botryose dichohyphidia at hymenial surface. Fig. 12: *V. ochroleuca* (Bourd. & Galz.) Donk, Lundell and Nannfeldt's Fungi Exsic. Suecici 2139, BPI, showing elastic context of dichohyphidia. Fig. 13: *Corticium epiphyllum* sensu Ravenel, type of *V. phyllophila*, Ravenel's Fungi Americani Exsic. 457, BPI, showing delicate hymenial dichohyphidia. Fig. 14: *Corticium (V.) pectinatum* Burt, type, BPI, showing minutely botryose dichohyphidia. Fig. 15: *Corticium (V.) racemosum* Burt, type, BPI, showing small dichohyphidia throughout the thin basidiocarp.

(Fig. 19); or the pedicel may support a few slightly divergent main branches that bear a shrubby mass of small secondary branches (Fig. 20). In *V. fusispora*, the hymenial dichohyphidia may have branching more nearly racemose than dichotomous.

The abundance, size, and form of the dichohyphidia may affect the texture of the basidiocarp. In some basidiocarps of *V. granulosa*, the dichohyphidia are more or less scattered, but in others they are densely massed (Figs. 5, 6). Even those in which they are most densely massed have a less tenacious texture than do the basidiocarps of *V. pallescens*. The dichohyphidia of *V. granulosa* are more robust than those of *V. pallescens* and develop very thick walls. However, they simply intermesh somewhat like the teeth of gears, instead of interlacing and grasping as do those of *V. pallescens* (Fig. 1). The tough texture of *V. pallescens* thus seems directly related to the tenaciousness of the dichohyphidia. The texture of *V. investiens* is notoriously elastic, and this effect is caused by the great masses of well-developed,` moderately slender, profusely branched dichohyphidia that fill the entire basidiocarp (Figs. 7-9). In some species, the basidiocarp remains thin and the dichohyphidia are generally minute; these species are characterized by their tender basidiocarps. *V. phyllophila* (MASS.) ROGERS & JACKS. is an example.

In culture, some dichohyphidia may have such long, slender, loosely branched, threadlike development that they seem almost not to constitute specialized structures. But the developmental tendencies that characterize the dichohyphidia of basidiocarps also appear in the threadlike dichohyphidia that may develop in culture.

The dichohyphidia of *Vararia* bear a resemblance to certain branched or unbranched subulate setae or seta-like structures in basidiocarps of a few genera of hymenomycetes. Some mycologists have been encouraged by this resemblance to regard *Vararia* as a member of a series or family characterized by the formation of setae or branched setae and by darkening of the basidiocarp and its constituent hyphae in KOH solution. This color change is called the xanthochroic reaction. CORNER (1948) wrote about species of *Asterostromella* (*Vararia*) in which the basidiocarps show the xanthochroic reaction, but none has been found in an extensive series of specimens examined during the present work. Dichohyphidia of some species of *Vararia* may be yellowish or somewhat greenish buff, or even pale brownish yellow. In most species, they are nearly or entirely colorless. Application of KOH solution to basidiocarps and dichohyphidia of *Vararia* causes no noteworthy color change, and usually no color change whatsoever. Basidiocarps of the group that includes *V. effuscata* (CKE. & ELL.) ROGERS & JACKS., *V. pallescens*, and *V. peniophoroides* are among those with the darkest color, but they are not appreciably more deeply colored in KOH solution than in tap water.

In Melzer's reagent, dichohyphidia assume a noteworthy reddish-

brown color, the dextrinoid reaction, which is most strongly accentuated when a small particle of the basidiocarp is mashed under the cover slip. In basidiocarp sections, dichohyphidia of the interior may not exhibit the dextrinoid response even though they seem to be immersed in the reagent. The same pattern of response may occur when sections are immersed in cotton blue-lactophenol, for the dichohyphidia of the interior region may become greenish blue instead of the very intense blue assumed by those of the hymenial surface.

GLOEOCYSTIDIA

Gloeocystidia are difficult to find in basidiocarps of some species of *Vararia*. BOURDOT & GALZIN (1928) evidently observed them in only two of the six species that they investigated, and CORNER (1948) said that they occur in some Malayan species but not in others. Although they may be very difficult to find in particular specimens, or even in many or all specimens of a particular species, gloeocystidia probably are characteristic of all species of *Vararia*.

In species such as *V. effuscata* and *V. peniophoroides* (Fig. 3) gloeocystidia may be irregularly inflated structures that appear throughout the basidiocarp. In other species, such as *V. investiens*, the shape or position of the modified element is such that some other term may seem more appropriate. However, study of a great assortment of elements in basidiocarps of many species reveals that the range of form and position is so comprehensive that there is no fundamental difference between the bodies that appear as cystidioles in *V. investiens* (Fig. 22) and those that are characteristically gloeocystidia in *V. effuscata* (Fig. 21).

LEMKE'S (1964) investigations of *Aleurodiscus* led him to refer to the various sterile modified hyphal endings of that genus as pseudocystidia. This seems to follow SINGER'S (1949, p. 42) concept of pseudocystidia as hyphal endings of the laticiferous, oleiferous, and gloeoiferous systems. LEMKE considers pseudocystidia of *Aleurodiscus* as the only cells of a simple conducting system, which includes the structures commonly known as pseudophyses and gloeocystidia. Both LENTZ (1954) and DONK (1964) consider pseudocystidia and gloeocystidia in separate categories, since the term gloeocystidium is reasonably well applied and very firmly entrenched in the literature pertaining to hymenomycetes.

In basidiocarps of many species of *Vararia*, gloeocystidia are evident in the most recently formed subhymenial and hymenial regions. Unless they are very large or very abundant, those in the deeper regions of the basidiocarp usually are found only by very careful examination of basidiocarp sections. Usually they are thin-walled, often empty or with relatively inconspicuous contents, often obscured or almost completely masked by dichohyphidia.
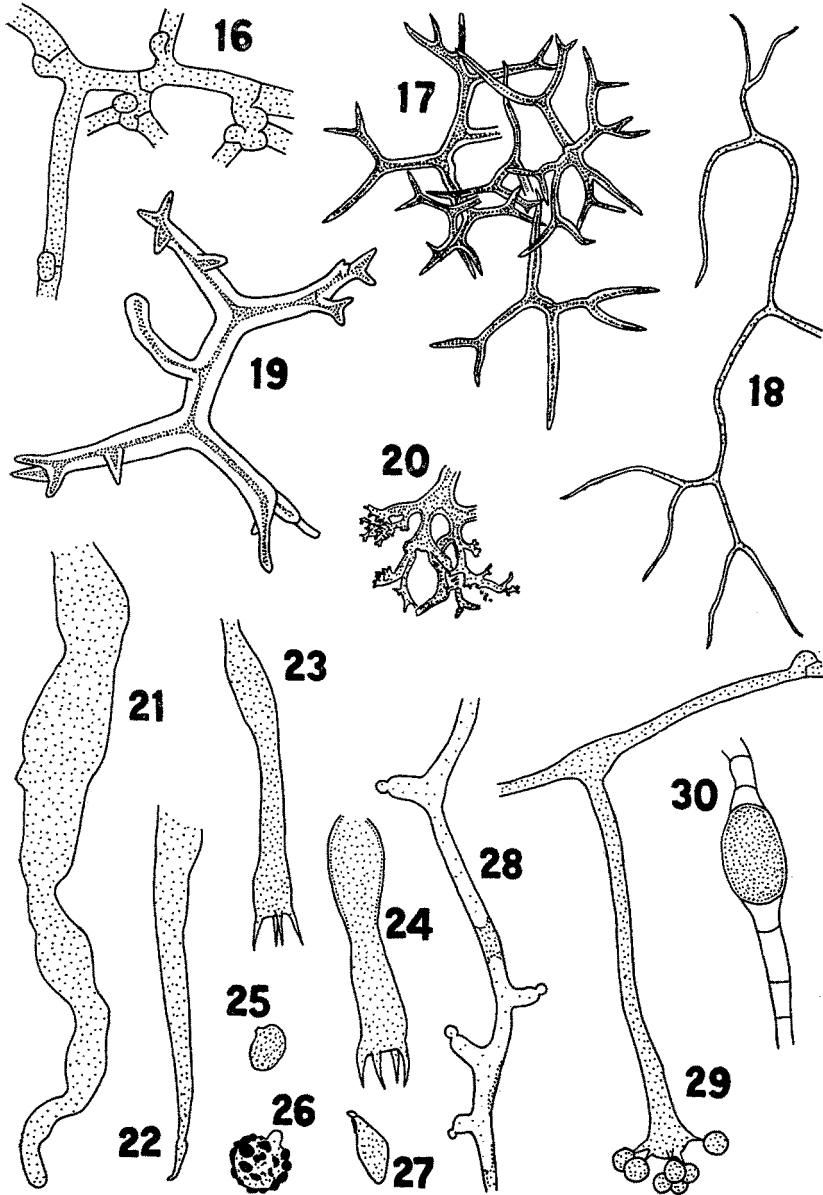
Figs. 16—30. Anatomical elements as shown by drawings made by use of a camera lucida, × 1000. Fig. 16: *V*. sp., generative hypha with clamp-connections. Fig. 17: *V. investiens*, dichohyphidia. Fig. 18: *V. investiens*, filiform dichohyphidium. Fig. 19: *V. granulosa*, dichohyphidium. Fig. 20: *V*. sp., dichohyphidium with botryose tendencies. Fig. 21: *V. effuscata*, gloeocystidium. Fig. 22: *V. investiens*, gloeocysti-dium. Fig. 23: *V. investiens*, basidium. Fig. 24: *V*. sp., basidium. Fig. 25: *V. granulosa*, spore with obscure striate amyloid ornamentation. Fig. 26: *V. peniophoroides*, spore with prominent amyloid warts. Fig. 27: *V. investiens*, spore with small adaxial amyloid plaque. Fig. 28. *V. granulosa*, culture hypha with lateral oil-filled protuberances. Fig. 29: *V. granulosa*, oedocephaloid conidiophore with globose conidia. Fig. 30: *V. granulosa*, chlamydospore.

However, even in *V. investiens*, if searched for arduously, gloeocystidia may be found in all regions of the basidiocarp.

Gloeocystidia in good condition usually stain homogenously and rather weakly in phloxine or cotton blue and become yellowish or smoky yellow in Melzer's reagent. In basidiocarps of some species, such as *V. effuscata* and *V. peniophoroides*, the gloeocystidial contents may appear condensed and waxy-vitreous, and this appearance is retained when they are mounted in a staining reagent. Gloeocystidial form seems relatively constant and characteristic within a particular species, thus gloeocystidia have a certain degree of taxonomic usefulness. However, descriptions of form and size in many instances are inadequate for differentiating gloeocystidia of various species, and direct comparison between microscopic preparations or with illustrations may be required.

BASIDIA

Basidia of *Vararia* (Figs. 23, 24) closely resemble those of several other genera of hymenomycetes, including *Galzinia, Coniophora, Aleurodiscus, Laeticorticium*, and various others. DONK (1964) used the term utriform in referring to the basidia of these genera. Basidia of somewhat similar form have been known for many years in genera such as *Sistotrema* (ROGERS, 1944), where the term urniform has been used. The distinction between utriform and urniform is not pronounced. DONK says that the first nuclear division in the urniform basidium is located near the base of the apical tube and often is longitudinally oriented. In the utriform basidium, the first nuclear division is said to be located near the apex of the tube and usually is transversely oriented. In both kinds of basidia, the structure first formed is a subglobose or ellipsoidal probasidial vesicle. The probasidium subsequently produces a tubular apical prolongation, or metabasidium, which bears the sterigmata. The metabasidial tube of the utriform basidium is said to be less clearly set off from the basal vesicle than is that of the urniform basidium. But its tendency to swell at the apex is said to be more pronounced than that of the urniform basidium, and it may be nearly as broad as the basal vesicle, or even broader. Urniform basidia of a number of species may have more than four sterigmata, often five to eight. Utriform basidia characteristically bear four spores. Regardless of the cytological relationships, utriform is a good descriptive term for the basidial form of *Vararia*, and it can be applied either with or without consideration of the possible phylogenetic significance of this form of basidium.

DONK actually minimizes any implication that the utriform basidium is an indication of primitiveness or of relationship with any of the Heterobasidiomycetidae. Instead, he apparently prefers to regard it as an adaptation to deep-seated origin in the catahymenium or, presumably, in the conspicuously thickened euhy-

menium. The same reasoning often has been applied to explain why heterobasidia often have structural modifications evidently appropriate to their situation as deep-seated bodies in a gelatinous matrix or dense hyphal or hyphidial mass.

A considerable number of basidia of several species of *Vararia* were seen to have one, two, or three septa formed within the apical tube. These were formed as secondary septa, or septa of retrenchment, as the mature basidia began to collapse at the apex. In some instances, the entire basidium became more or less entirely devoid of protoplasm. In many, the protoplasm retreated from the apex of the basidium, was separated from the exhausted portion by formation of a septum, and then remained as densely concentrated in the uncollapsed basal portion of the basidium as it had been in the original probasidium. Thus, except for the presence of the empty, collapsing, apical region of the tube, the retrenched basidium was nearly or completely indistinguishable from probasidia or developing basidioles.

Several authors have described basidia that seem to have some capabilities either of secondary septum formation or of repeated reconstruction of an entire basidium from a single hyphal apex. The basidia of *Galzinia* are somewhat like those of *Vararia* in their development, although the distinction between the basal vesicles and the apical tubes may be somewhat more pronounced in *Galzinia* than in *Vararia*. OLIVE (1954) described the basidia of *G. geminispora* OLIVE as having the tube arising from the vesicle either apically or somewhat laterally and occasionally having one or rarely more than one transverse septum, with rare development of laterally-produced basidiospores in addition to or instead of those ordinarily produced at the basidial apex. Although DONK (1964) does not agree, OLIVE stated that the septation of the basidium of *G. geminispora* may give evidence of a pathway of relationship between the hymenomycetes and the heterobasidiomycetes. Another species of *Galzinia* exhibits a different phenomenon that gives additional evidence concerning the versatility of the basidia of hymenomycetes. According to ERIKSSON (1958), *G. pedicellata* BOURD., as well as *Corticium incrustans* HÖHN. & LITSCH. and a few species referred to the genus *Repetobasidium* ERIKSS., exhibits repeated production of basidia from the same hyphal apex. ERIKSSON described the repetition of basidium production as occurring within the remnants of the old basidium and from the successive growing points subsequently formed at the apex of the hyphal branch.

Secondary septa are formed in some of the cystidiole-like gloeocystidia of *V. investiens* and in the hyphae of many fungi, including *Vararia*, where they may separate living from dead areas of hyphae. Secondary septa also are formed during the process of chlamydospore production in cultures of several species of *Vararia*. Their formation in the basidia of *Vararia* may be without particular significance except as a response to the regression of protoplasm

from the basidial apex. However, the appearance of the basal portions of otherwise exhausted basidia so nearly resembles that of normal probasidia as to suggest the possibility that they may function again in production of metabasidia. No cytological data are available.

SPORES

Two recently published comprehensive taxonomic discussions of hymenomycetes depict the spores of *Vararia* as non-amyloid. CHRISTIANSEN (1960) dealt with two species, of which the only one named was *V. investiens*. Perhaps neither of the two has spores very prominently amyloid. However, at least two of the six species studied by CUNNINGHAM (1955, 1963) have strongly amyloid spores, as was readily ascertained by examintion of specimens that CUNNINGHAM previously had determined as *V. ellipsospora* CUNN. and *V. rhodospora* (WAKEF.) CUNN.

The amyloid material — which becomes grayish blue or blackish blue when immersed in Melzer's reagent — is especially concentrated on the exterior surface of the spore wall in the form of plaques, warts, or ridges. Spores of *V. investiens* may appear yellow in Melzer's reagent, and thus non-amyloid, except for an inconspicuous, small, flat, scarcely thickened amyloid plaque on the adaxial side of the spore just above the apiculus (Fig. 27). Until ERIKSSON (1954) called attention to this minute amyloid area, which may not be visible on a number of the spores of a particular microscopic preparation, the spores of *V. investiens* were thought to be entirely non-amyloid (BOIDIN, 1950). Spores of *V. granulosa* (Fig. 25) and *V. pectinata* have more extensive patterns of amyloid ornamentation but somewhat resemble those of *V. investiens*, in that the blue color may not be very conspicuous. Spores of some species may have even more obscure markings until, finally, the dark areas are so nebulous that their nature is uncertain. Some species of *Vararia* have spores entirely yellow in Melzer's reagent, and thus seem to be completely non-amyloid.

The amyloid patterns on spores of *Vararia* apparently have at least a moderate degree of taxonomic utility. Under some circumstances, though, the ornamentation may be misleading. A considerable amount of pressure on the cover slip of a slide preparation may cause amyloid material to break away from the wall surface and appear as amorphous amyloid debris in the mounting fluid. After loss of amyloid material, prominently ornamented spores of species such as *V. peniophoroides* (Fig. 26) and *V. pallescens* may appear as delicately marked as those of *V. effuscata*. Spores of a few species of *Vararia* may have walls somewhat thickened, but those of most species are thin-walled.

The spore contents of most species of *Vararia* are not particularly noteworthy. However, MARTIN (1937) reported that the pro-

toplasm in spores of *V. investiens* may retract somewhat from the region of the apiculus and leave a vacuous area that becomes delimited by a secondary septum. Occasionally, two septa are formed. This process is reminiscent of secondary formation of septa in the basidia of several species of *Vararia*, in the gloeocystidia of *V. investiens*, and in hyphae of several species in culture, especially in association with production of chlamydospores. MARTIN noted that it also bears a degree of similarity to processes involved in the formation of chlamydospores inside the basidiospores of *Jaapia*.

A particularly remarkable feature of the spores of *Vararia* is the diversity of their shapes. There are at least three or four principal spore groups in *Vararia*, on the basis of shape, and the spores of a few species do not fit into any of these groups very readily. The most extraordinary form is shown by the spores of *V. investiens* and a few other species. A typical spore of this group is fusoid from the apiculus to approximately the middle. Beyond the middle, it is more or less ellipsoid. As the two halves usually are not completely in line with each other, but at an angle, the spore appears somewhat geniculate. An entirely different form is shared by spores of *V. effuscata, V. pallescens, V. peniophoroides,* and several other species. In this group, the spores are essentially globose, with prominent amyloid ornamentation. Several species of *Vararia* have ellipsoid spores, and a few have spores of other shapes, such as cylindric.

CULTURAL CHARACTERISTICS

Very few species of *Vararia* have been studied adequately in culture. This remains the strongest obstacle to a knowledgeable consideration of taxonomy within the group. The present discussion of cultural characteristics is based on a study of isolates representing approximately eight species. When grown in darkness at 25° C, the cultures usually form a soft cottony or woolly growth, occasionally somewhat strigose, more commonly with zones or scattered areas of floccose growth. Cultures usually are white when young but become buffy after several days. The color is considerably accentuated if the cultures are exposed to ample light, when some may become strongly buffy-yellow. In certain isolates of *V. investiens*, the color is especially pronounced. Although the different species of *Vararia* show differences in their growth on gallic and tannic acid agar media, all exhibit a strong oxidase reaction by blackening at least one and usually both of the media. Recognizable hymenial plaques, with gloeocystidia and basidia, are formed in culture by *V. effuscata* and *V. pallescens,* both of which belong among the species with globose, amyloid basidiospores.

In all of the cultures studied, the hyphae characteristically are thin-walled or moderately thin-walled. Those species that have clamp-connections on the generative hyphae of the basidiocarps also have clamps on the hyphae of cultures. Lack of clamp-con-

nections in basidiocarps of *V. phyllophila* (MASS.) ROGERS & JACKS. is substantiated by the absence of clamps from cultures of that species. In cultures of several species, including *V. effuscata, V. pallescens, V. granulosa, V. phyllophila,* and *V. investiens,* oil-filled hyphae are common, and many have distinctive cylindrical, flask-shaped, or mammiform lateral protuberances (Fig. 28). Usually, each protuberance bears a small, globose, apical papilla, and both the protuberance and papilla may also be filled with oily material. WHITE (1951) described the same kind of hyphal modifications and oily contents in cultures of *Corticium galactinum* (FR.) BURT, which more recently has been referred to *Scytinostroma.* Basidiocarps of *Scytinostroma* resemble those of *Vararia* in having dextrinoid hyphidia.

Characteristic dichohyphidia are formed in cultures of several species of *Vararia* and resemble those of the basidiocarps. In addition, or instead, cultures may have dichotomously-branched hyphal structures so greatly elongated and slack that they are hardly recognizable as dichohyphidia. As in the basidiocarps of various species, some dichohyphidia of cultures may be so slender and inconspicuous that they are evident only when they become reddish brown, or even violaceous, in Melzer's reagent. Dichohyphidia could not be found in cultures of *V. granulosa,* nor were any reported by MAXWELL (1954).

Several species of *Vararia* produce oedocephaloid conidiophores (Fig. 29) in culture, and the same species form chlamydospores (Fig. 30). The earliest description of the cultural characteristics of *V. effuscata* by LYMAN (1907), contains descriptions and illustrations of both the conidiophores and chlamydospores. NOBLES (1942) investigated the cytology and reproduction of the same species and concluded that *V. effuscata* exhibits tetrapolar heterothallism. She found that uninucleate conidia are produced on the conidiophores arising from both the 'haploid' (monocaryotic) and 'diploid' (dicaryotic) mycelium. The uninucleate conidia have the ability to dicaryotize monocaryotic mycelium, and a few of the conidia from dicaryotic mycelium may germinate to produce monocaryotic mycelium. In the dicaryotic conidiophores, there is the usual simultaneous nuclear division, but the nuclei enter the conidia singly, according to NOBLES, rather than in conjugate pairs. NOBLES mentioned other species in which uninucleate haploid spores are produced from dicaryotic mycelium, and she said that this ordinarily results from reversion of parts of the dicaryotic mycelium to the monocaryotic condition through separation of the dicaryons in a hypha. BOIDIN (1958b) studied a culture of *V. effuscata* and one of *V. investiens* that seemed to have reverted to the monocaryotic condition. Similarly, an isolate of *Vararia* from Mississippi apparently has developed in the monocaryotic condition, as suggested by its failure to produce the clamp-connections habitually formed by other isolates of the same species. The monocaryotic isolate

belongs in a species rather similar to *V. pectinata*.

Oedocephaloid conidiophores develop in cultures of species with globose basidiospores and in those of the ellipsoid-spored *V. granulosa*. Cultures of several long-spored species of *Vararia* were examined, but none had either conidiophores or chlamydospores. McKEEN (1952) showed that conidiophores are produced by three species of *Peniophora* (*sensu lato*) with considerably elongated basidiospores, thus conidiophores are not limited to hymenomycetes with broad basidiospores. Other hymenomycetes known to form conidiophores of oedocephaloid form in culture include *Stereum sulcatum* BURT, *Corticium furfuraceum* BRES., and *Fomes annosus* (FR.) CKE. In addition, all form clamp-connections in culture, although in many cultures of *F. annosus* clamps are very infrequent. Production of conidiophores in cultures of *Vararia* is associated with formation of chlamydospores, but this association does not seem evident in cultures of the other species. *Stereum taxodii* LENTZ & McKAY produces chlamydospores and apparently is very closely related to *S. sulcatum*. (Both species were placed in *Echinodontium* by GROSS, 1964). Thus, these closely related species, together, have the characteristic structures developed in cultures of individual species of the globose-spored group of *Vararia*.

INTRAGENERIC RELATIONSHIPS

While discussing the taxonomy of the Polyporaceae, TEIXEIRA (1962) said that forms with and forms without clamp-connections should not be considered as congeneric. This is more restrictive than the formula usually applied to taxonomic relationships among hymenomycetes. DONK (1964) says that the value of clamp-connections as a taxonomic feature differs from group to group, and he believes that the occurrence of clamps may even be erratic within a species. *Scytinostroma* and *Gloeocystidiellum* are two genera that include species with, and other species without, clamp-connections. Another is *Lopharia*, but this 'genus' is manifestly artificial. *Botryobasidium* is another group that exhibits heterogeneity for presence of clamp-connections, although segregations from that complex may have reduced the heterogeneity somewhat. ERIKSSON (1950), while writing on *Peniophora* (Coloratae), mentioned that clamp-connections may fail to appear in representatives of some species because the basidiocarp may have developed from monocaryotic hyphae. In another publication, ERIKSSON (1949) reported on a fungus entirely like *Sistotrema commune* ERIKSS., except for complete lack of clamp-connections. ERIKSSON noted that species of the Corticiaceae usually either have or lack clamps constantly, and he said that experimental investigations would be required to determine what the lack of clamp-connections means in fungi such as his *S. commune* f. *efibulatum* ERIKSS.

These examples show that some species or genera of hymeno-

mycetes are not consistent for presence or absence of clamp-connections. However, the pattern of clamp development in a number of genera is remarkable uniform, both as to their presence or absence, and as to the particular ways in which they may develop. A few genera that seem to include only species with clamp-connections on their generative hyphae are *Xenasma* (LIBERTA, 1960; WERESUB, 1961), *Cymatoderma* (BOIDIN, 1960b; WELDEN, 1960), *Podoscypha* (BOIDIN, 1960b,) *Cristella* (DONK, 1957;CHRISTIANSEN, 1960), *Hyphoderma* (DONK, 1957), *Tubulicrinis* (DONK, 1956; WERESUB, 1953, 1961), and *Hyphodontia* (ERIKSSON, 1958; WERESUB, 1961).

Constant presence of clamp-connections also has been cited as a family characteristic, as in the family Auriscalpiaceae, to which MAAS GEESTERANUS (1963) refers *Auriscalpium, Gloiodon*, and *Lentinellus*, the latter having been transferred from the Agaricales. In some genera, the particular distribution of the clamp-connections on the hyphae of the basidiocarp or culture may be a generic characteristic. This seems to be true of *Phanerochaete*, in which the clamp-connections usually are apparent only in the marginal region of the basidiocarp and often are double or multiple, especially as seen in culture. Clamp-connections have not been found in basidiocarps of *Stereum* (LENTZ, 1955, 1960; BOIDIN, 1958a,1958b, 1960a), but single, double, and multiple clamps appear in cultures of all species for which the cultural characteristics are known. ROFF (1964) reported that double clamps appear also on hyphae within host tissue on which *S. sanguinolentum* FR. is growing. Thus *Stereum* is another genus with a very characteristic and unique pattern of clamp formation.

Some genera, families, or series of fungi seem to lack clamp-connections entirely. CORNER (1948), KÜHNER (1950), TEIXEIRA (1962), DONK (1964), and various other authors have cited the xanthochroic fungi as an outstanding example of a group from which clamps are entirely absent. *Cotylidia*, a stipitate segregate from *Stereum*, was defined as lacking clamp-connections (WELDEN, 1958) until BOIDIN (1960b) doubtfully transferred *Podoscypha radicans* (BERK.) PAT. there. All species of *Asterostroma* also lack clamp-connections.

In *Vararia*, clamp-connections apparently always are present in basidiocarps of the globose-spored species in the group that includes *V. effuscata*. They also seem to be constantly present in basidiocarps of the group with geniculately fusoid-ellipsoid spores, including *V. investiens*. However, some species of *Vararia* do not have clamp-connections, either in basidiocarp or culture. The importance of clamps in the classification of the various species is not yet entirely evident, but there may be a relationship between spore form and presence or absence of clamp-connections.

Numerous and notable exceptions can be cited, but in nearly all groups of fungi, the genera that most certainly consist of closely

related species are those in which the spores of the various species have a similar developmental pattern and form. In the hymeno-mycetes, for example, *Stereum, Serpula, Thelephora, Clavulina, Phellodon, Hydnellum, Russula,* and many others are represent-ative of fungi in which the spores of all or nearly all species within a genus have similar form characteristics. *Mycena* (SMITH, 1947) apparently is an example of a genus in which this is not true.

Possibly, *Vararia* eventually will be divided into two or more genera or subgenera, and spore form probably will be an important factor when such a division is made. The globose-spored *V. effus-cata* group seems distinct, as characterized by formation of rela-tively massive dichohyphidia and production of conidia and chlamydospores. Perhaps the group is somewhat less than homoge-neous because of the inclusion of *V. granulosa*, with ellipsoid spores. The only other relatively large group well characterized at present includes the species with geniculately fusoid-ellipsoid spores. *V. investiens* has moderately large dichohyphidia, but those of the other species are inclined to be more or less delicate. According to GILBERTSON (1965), the gloeocystidia of the globose-spored group are benzaldehyde positive, but he could not detect any similar coloration of the gloeocystidia in herbarium specimens of several species outside that group.

SUPRAGENERIC RELATIONSHIPS

CORNER (1948) says that *Asterostromella (Vararia)* is a composite genus "and consists of species related with *Aleurodiscus,* of true xanthochroic fungi, and, probably, of other Thelephoraceous deri-vatives". DONK (1964) places *Vararia* in the family Hymenochae-taceae, subfamily Vararioideae, together with the subfamilies Aster-ostromatoideae and Hymenochaetoideae. This family, with its in-cluded subfamilies, corresponds generally with what CORNER speaks of as the Xanthochroic series. It is based in part on PATOUILLARD'S (1900) Série des Igniaires and his Série des Astérostromes. DONK and CORNER agree that *Asterostroma, Asterodon, Lachnocladium,* and at least part of *Vararia* belong in this group, together with *Hymenochaete, Phellinus,* and various other xanthochroic fungi. CORNER (1950) suggests that the group should be raised to the status of an order, which he would call the Xanthochroales.

Other authors have treated *Vararia* differently. ERIKSSON (1958), for example, included *Asterodon* in the family Hymenochaetaceae but relegated *Vararia* to the Corticiaceae. CHRISTIANSEN'S (1960) arrangement is more or less similar. He includes *Asterostroma* in the Hymenochaetaceae together with *Hymenochaete, Phellinus,* and *Inonotus. Vararia* occupies a position near *Gloeocystidiellum* and between *Scytinostroma* and *Laeticorticium* in the Corticiaceae. According to LEMKE (1964), *Vararia* seems to belong somewhere near the Stereaceae with amyloid spores and macrocystidia (gloeo-

cystidia with sulfaldehyde-positive contents).

CORNER (1948) says that his xanthochroic species of *Asterostromella* (*Vararia*) do not have clamp-connections. And DONK, in his description of the family Hymenochaetaceae, says "clamps lacking," and distinguishes *Scytinostroma* from *Vararia* by saying "the generative hyphae of some species [of *Scytinostroma*] have clamps." During the present study, only a few species of *Vararia* have been found to have hyphae that completely lack clamp-connections. These species without clamps are the very ones least likely otherwise to be regarded as belonging in the xanthochroic series. The basidiocarp context of most such species is nearly or completely colorless, and the majority of dichohyphidia do not resemble setae.

The species of *Vararia* most likely to be regarded as xanthochroic, on the basis of basidiocarp color, are those that have globose spores, coarsely subulate dichohyphidia, and a yellowish coloration of the context elements. Comparison of the KOH reaction of the basidiocarps of these species with those of *Hymenochaete* shows that they are not xanthochroic. Moreover, they consistently have clamp-connections, their spores are amyloid, and they produce oedocephaloid conidiophores in culture. In all of these characteristics, they are different from the xanthochroic fungi.

According to TALBOT (1951), sections of *Stereum albo-cinctum* BERK. & BR. (*Vararia*) darken in KOH solution. TALBOT also includes *Hypochnus pallescens* (SCHW.) BURT among the species that show this reaction. The latter species is *V. pallescens* of the globose-spored group, which shows a decided lack of xanthochroic characteristics. A portion of the type of *S. albo-cinctum* is in the National Fungus Collections. Examination of this specimen reveals that a minimal gross darkening of the section occurs when KOH solution is applied, but direct comparison with sections of *Asterodon ferruginosus* PAT. shows that the darkening of *Asterodon* is vastly greater. This observation is verified by microscopic examination that shows that the color of the brownish hyphae of *S. albo-cinctum*, especially of the dichohyphidia, is hardly changed by the KOH solution. The very slight color change that does occur seems to be well within the limits of the change that would be expected of nearly any brownish hyphal structure upon application of KOH solution. Furthermore, it seems to consist more nearly of a clearing and brightening response than of a darkening and obscuring reaction. This same moderate brightening effect, seen microscopically, seems to be responsible for the very slight macroscopic darkening of sections in basidiocarps of species taxonomically associated with *V. effuscata*. When some of the darker sections of *V. pallescens* are examined, application of cotton blue in lactophenol can be seen to produce the same effect, until the resultant very slight reddish-brown color is masked by the blue stain.

CORNER'S (1948) drawing of a species of *Asterostromella* (*Vararia*) from Malaya illustrates two characteristics strongly reminiscent of

species such as *V. pallescens;* these are globose spores and the profuse development of moderately large dichohyphidia. The basidia are depicted as markedly clavate, a characteristic not observed in any specimen of *Vararia* examined during the present study. CORNER says gloeocystidia may or may not be present in specimens of the various species that he studied, and they apparently are not shown in his illustration. The gloeocystidia of *V. pallescens* often are so rare that they may seem entirely absent from certain specimens, thus CORNER's omission of gloeocystidia does not necessarily remove his species from consideration as being similar to *V. pallescens.*

Inclusion of *Asterostroma* in the xanthochroic series cannot be substantiated much more successfully than the inclusion of *Vararia.* Of the three dozen specimens of *Asterostroma* in the National Fungus Collections, not one is xanthochroic. The color of the asterosetae — unlike that of the asterosetae and setae of *Asterodon* and the setae of *Hymenochaete* — remains entirely unaffected by KOH solution, as does the color of all the hyphae constituting the basidiocarp. This absence of xanthochroic response was verified also by exposure of cultures to KOH solution, both by observation of the mat to which KOH solution was applied and by examination of the individual hyphal elements mounted in KOH solution. Absence of clamp-connections and production of large asterosetae may constitute an inducement for regarding *Asterostroma* as in some sense a member of the *Hymenochaetaceae.* However, these seem to be more than counteracted by absence of xanthochroic response, production of amyloid spores, and development of gloeocystidia. *Asterodon,* so frequently compared with *Asterostroma,* is a typical member of the xanthochroic series. Sections of basidiocarps of *Asterodon* become very dark in KOH solution and the setae, setal hyphae, and asterosetae become dark reddish brown. The other hyphae range from colorless to pale reddish brown, and the generative hyphae are thin walled and do not have clamp-connections. In Melzer's reagent, the setae and other setal elements fail to give a dextrinoid response and the spores are smooth and entirely non-amyloid.

Lachnocladium closely resembles *Vararia* in having dichohyphidia that seem no different in any essential from the subulate dichohyphidia of that genus, except for the fact that they are poorly responsive or unresponsive to Melzer's reagent. When portions of CORNER's types of *L. divaricatum* PAT. var. *cinnamomeum* CORNER, *L. flavidum* CORNER, and *L. molle* CORNER were mounted in KOH solution, no color change could be detected. The specimen of *L. molle* was examined most intensively. Its dichohyphidia are pale yellowish brown or nearly Isabella Color (RIDGWAY, 1912), and most of the other hyphal elements are colorless to very pale yellowish in mass when mounted in KOH solution. Gloeocystidia are present but not very conspicuous. A few dichohyphidia become reddish brown in Melzer's reagent, but most remain yellowish brown. The hyphae lack clamp-connections and the spores are non-amy-

loid. Only in these latter two characteristics does this species share the attributes of the xanthochroic fungi. The basidia were found to be more or less ventricose-elongate, as are those of *Vararia* and *Asterostroma*. However, this fact is of little assistance in the attempt to assess relationships, because at least several strongly xantho-chroic specimens of *Hymenochaete* also seem to have ventricose-elongate (or more or less utriform) basidia. These include speci-mens of *H. mougeotii* (FR.) CKE., *H. sallei* BERK. & CURT., and *H. pinnatifida* BURT. One specimen of *H. tasmanica* MASS. was examined, and the basidia of that specimen apparently are not utriform.

A review of the characteristics of *Vararia, Asterostroma,* and *Lachnocladium* fails to reveal that any is xanthochroic, at least on the basis of the specimens examined. All have gloeocystidia. The basidiocarps of *Vararia*, in addition, often have amyloid spores, and those of *Asterostroma* all do. These genera seem misplaced in subfamilies of the Hymenochaetaceae. If there is a xanthochroic component, no evidence of it can be found among the specimens from North America, South America, Europe, and Asia in the Na-tional Fungus Collections.

The most promising evidences of relationship with *Vararia* seem to occur among those fungi that have gloeocystidia, a well-devel-oped tendency to form clamp-connections, a capability of producing amyloid basidiospores, and perhaps a catahymenial structure asso-ciated with utriform basidia. Therefore, the taxonomic arrange-ments of ERIKSSON (1958), CHRISTIANSEN (1960), and LEMKE (1964) seem appropriate. DONK (1964), also, has written of a 'protean-shaped rhizopod' that may include various extensions from the central mass, such as the Auriscalpiaceae, Bondarzewiaceae, Echi-nodontiaceae, Hericiaceae, an unnamed group of Polyporaceae and 'more doubtfully, *Vararia* and *Asterostroma* (Hymenochaetaceae).' The characteristics that DONK mentions for this group are presence of gloeocystidia and amyloidity of the spore wall. He connects the Hericiaceae to the central mass through *Gloeocystidiellum*, and he suggests that the subfamily Vararioideae of the Hymenochae-taceae may be linked with the central core through *Scytinostroma*. However, he says that the characteristics that seem to unite the genera in the central core all break down completely in various groups; he cites *Aleurodiscus* and objects to LEMKE's restriction of that genus to species with amyloid spores. Through the corti-cioid element of the core, he sees relationships with the stereoid element, including *Stereum.*

Donk has encompassed a very broad spectrum of genera in his discussion, including some that have species in which the basidio-carps are dimitic and others that have species in which the basidio-carps may have non-amyloid spores or lack clamp-connections. As the genus *Vararia* also includes species with non-amyloid spores and without clamp-connections, the entire group seems no more

heterogeneous than *Vararia*. The genus that most nearly shares all of the characteristics of *Vararia* is *Scytinostroma*. These two genera, or groups, both have non-xanthochroic basidiocarps, dextrinoid hyphidia, generative hyphae either with or without clamp-connections, gloeocystidia, and spores of sundry shapes (including globose, ellipsoid, and subfusoid) and either amyloid or non-amyloid.

Summary

Vararia belongs in a group of hymenomycetes characterized by non-xanthochroic basidiocarps in which gloeocystidia are formed rather regularly. Basidia and gloeocystidia originate at a relatively deep level in a catahymenium or hyphidial hymenium; thus they are overgrown by continuing development of the hyphal elements. As a result, they may become deeply submerged in the structure of the basidiocarp, together with embedded basidiospores. Dichohyphidia are formed as dichotomously-branched structures of limited growth. Although commonly subulate, dichohyphidia may show a considerable range of form even within a single basidiocarp. In Melzer's iodine reagent they commonly exhibit a dextrinoid reaction by becoming reddish brown. Hyphae of basidiocarps and cultures of some species have clamp-connections; those of other species lack clamps. Spores of the various species may be fusoid-ellipsoid, ellipsoid, globose, or cylindric, and may have either prominent or obscure amyloid ornamentation or may be apparently non-amyloid. Together with cultural characteristics such as the presence or absence of oedocephaloid conidiophores and various hyphal modifications, the hyphal and spore characteristics of the basidiocarp seem to present a potential basis for division of *Vararia* into several subgenera or generic segregates. The preceding considerations form the basis for a discussion of the position and relationships of *Vararia* within the Aphyllophorales.

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