

## Contributions of Electron Microscopy to Fungal Classification

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**SYNOPSIS.** Such characters as surface ultrastructure of asexual and sexual propagules, wall and septal ultrastructure, the fine structure of ascus tips, and ultrastructural aspects of nuclear division have taxonomic significance for major groups of fungi. Information derived from fine-structural analyses can be correlated with that obtained from light-microscopic, chemical, and developmental investigations. The versatility of electron-microscopic facilities makes them powerful research tools in the hands of the innovative taxonomist.

### INTRODUCTION

An eminent botanist and taxonomist, who shall remain anonymous, once told me that classifications represent man's frustrated attempts to recognize order amongst living things, and in return for his efforts, nature reveals inconsistencies and anomalies that mock his categories. This rather pessimistic statement was made about the processes of systematization, which G. C. D. Griffiths (1974) has defined as "the ordering of organisms according to relations within a system." Attempts to discover natural relationships between organisms are often based on subjective decisions concerning phylogeny. They usually lead, at least in fungal systematics, to futile efforts to order taxa according to their evolutionary relatedness. Classification, on the other hand, is simply the ordering of organisms into classes and "class membership is dependent on possession of certain essential or contingent attributes" (Kavanaugh, 1978). With the scanty fossil record of ancestral fungi, we can do little more than speculate on the phylogeny of these cryptogams and their interrelation-

ships with members of other kingdoms—Monera, Protista, Plantae, and Animalia (Whittaker, 1969; Cain, 1972; Ainsworth, 1973; Pirozynski and Malloch, 1975; Malloch, 1977; Margulis, 1977). From a practical standpoint, however, we can do a great deal toward providing a functional classification of various groups of fungi by incorporating data from many different sources into our concepts of taxa (von Arx, 1977). Kendrick (1978) suggested "that in order to define many of our taxa properly, we must consider not simply the morphology of a sexual or an asexual state, nor morphology supplemented by development, nor even those augmented by knowledge of the entire life history, but all of the above, placed in an environmental context that specifies the ecological demands made by each species." This holistic approach to fungal taxonomy is not a simple task. It does, however, emphasize the need to re-evaluate and revise existing classifications of the fungi, classifications which are based largely, and often exclusively, on morphological characters derived from light microscopy alone.

The principal aim of this paper is to demonstrate that information obtained from electron-microscopic studies of organisms may be useful in providing supplementary data for improving classifications as they now exist. At the outset, however, it is necessary to delimit this group of microorganisms. Whittaker (1969) as-

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signed the fungi the status of a kingdom in his popular five-kingdom system. In the current taxonomic approach, fungi are separated into the slime molds (Division: Myxomycota) and the mycelial fungi (Division: Eumycota) (Ainsworth *et al.*, 1973a, b). Only the Eumycota will be considered in this discussion. The assimilative phase of this group is typically filamentous (*i.e.*, consisting of hyphae) but may also exist in a yeast (*i.e.*, globular) form. The Subdivision Mastigomycotina is distinguished from other members of the Eumycota by the presence of motile cells (zoospores). Members of the Deuteromycotina are distinguished by the absence of a perfect (*i.e.*, sexual) state. They reproduce asexually by yeast budding or conidium formation. The remaining Subdivisions, Zygomycotina, Ascomycotina, and Basidiomycotina, are largely differentiated on the basis of the ontogeny and morphology of their perfect-state spores—zygospores, ascospores, and basidiospores, respectively.

Fine-structural data obtained from the scanning and transmission electron microscopes and the freeze-etch techniques have augmented our capabilities for morphological comparisons by resolving cellular details which are beyond the resolution of conventional light microscopy. (*e.g.*, Beckett *et al.*, 1974). In choosing ultrastructural characters to incorporate into taxonomic schemes, several factors must be considered. Morphological features which appear to be biologically important and genetically stable are usually regarded as taxonomically valid. Considerations of the biological importance and genetic stability of characters, however, require comparative examination of large numbers of specimens. Because material to be studied by electron microscopy requires complex and time-consuming preparation, only a few specimens may be examined before a decision concerning the taxonomic value of a particular ultrastructural character is made. Limited sampling is an undeniable restriction in the application of electron microscopy to taxonomy. In the case of scanning electron microscopy there is less of a problem (Reimer and Pfefferkorn, 1977;

Hyatt, 1978). New facilities have been developed for the SEM which allow many specimens to be examined (*e.g.*, multiple specimen holders and a dual magnification system which enhance the operator's ability in sample searching and data reporting). The quality and ease of preparation of fungal samples for the SEM has improved with development of many new procedures (Zeyen and Shearer, 1974; Cole, 1975; Kinden and Brown, 1975; Sweney and Shapiro, 1977; Edelman, 1978; Samson and Stalpers, 1978; Steffens, 1978). The application of cryotechniques to scanning electron microscopy (Nei and Asada, 1974, 1975; Nei *et al.*, 1974; Tokunaga *et al.*, 1977; Echlin, 1978) permits rapid ultrastructural examination of unfixed, non-dehydrated, and uncoated fungal samples (Watanabe, 1975; Hasegawa *et al.*, 1976). A chamber has been developed that attaches to the SEM and that is used for fracturing and coating biological samples (Pawley and Norton, 1978). Such a device may be particularly useful for examining internal cellular structures of fungi (Laane, 1972, 1974; Bole and Parsons, 1973; Kirschner and Rusli, 1976). Application of X-ray microanalysis to fungal taxonomy is in the pioneering stage and may be another useful technique for future investigations (Ernst and Winkelma, 1977; Meisch *et al.*, 1977; Thibaut *et al.*, 1977; Doerge *et al.*, 1978; Urbanus *et al.*, 1978).

The esoteric nature of electron microscopy and inaccessibility of ultrastructural data to many taxonomists may create skepticism concerning the real value of fine structure in classification. The taxonomic applications of these data are more appreciated in correlative morphological studies involving both light and electron microscopy (Michaels *et al.*, 1972; Cole and Ramirez-Mitchell, 1974; Cole and Behnke, 1975; Konishi *et al.*, 1976). The introduction of Nomarski interference contrast optics for the light microscope has significantly increased the ease of such correlative studies. For instance, ultrastructural investigations of conidiogenesis in the Deuteromycotina have clarified developmental concepts (Cole and Samson, 1978), and ontogenetic characters have

been incorporated into a classification of this fungal subdivision (Kendrick, 1971; Kendrick and Carmichael, 1973). Early light-microscopic examinations of conidial ontogeny did not provide clear definitions of the various modes of development. However, the light microscopist can now reexamine large numbers of imperfect fungi, and on the basis of a morphological comparison with existing ultrastructural data can make an accurate decision about the kinds of conidium and conidiogenous cell ontogeny demonstrated by a particular species and place it into the proper developmental category. Practically every major laboratory involved in taxonomic studies of fungi in the United States and Europe makes use of electron-microscopic facilities. Perhaps as fungal taxonomists become more familiar with the kinds of information which can be obtained from electron microscopy, their appreciation and utilization of ultrastructural data will grow.

#### SURFACE TOPOGRAPHY OF ASEQUAL AND SEXUAL PROPAGULES

Because of the limited space in this paper, it is not possible to present a comprehensive discussion of the surface topography of fungal cells and its relevancy to the classification of these microorganisms. Many examples of taxonomic applications of surface ultrastructure of fossil spores, zoospores, sporangia, ascospores, conidia, and basidiospores have been documented in the literature. Only the surface features of asexual and sexual propagules produced by members of the Zygomycotina are considered below.

#### *Sporangiospores and zygospores*

Carbon-replica preparations of sporangiospores in members of the Kickxellaceae show spines in patterns that are considered diagnostic in the classification of this family (Young, 1968, 1973a, b, 1974). All known species of *Piptocephalis* (Family: Piptocephalidaceae) examined by light microscopy were considered smooth, delicately reticulate or minutely roughened (Benjamin, 1959, 1963, 1966). Examined with the elec-

tron microscope, however, they can be seen to have distinctive patterns of warts and ridges (Young, 1969a). Fine-structural examinations now include representatives of most families of sporangiospore-producing fungi (Jeffries and Young, 1975, 1978).

In the Entomophthorales, the SEM has illustrated morphological differences between *Entomophthora virulenta* and *Conidiobolus coronatus* (Matanmi and Libby, 1975; Krejzova, 1977) and provided support for maintenance of these fungi in separate genera. Turian and Wuest (1977) proposed the transfer of *Entomophthora myrmecophaga* to *Zoophthora* (*Z. myrmecophaga*) based on data from light- and electron-microscopic examinations of the surface of asexual propagules and morphology of rhizoids. Using the SEM to investigate the morphology of reproductive structures, Krejzova (1978) verified the taxonomic position of a fungal parasite isolated from mosquitoes as *Basidiobolus ranarum*. The asexual, often violently discharged propagules of the Entomophthorales are commonly referred to as conida (Waterhouse, 1973). However, thin sections have revealed the double-walled nature of these structures (Turian and Wuest, 1977), suggesting their homology to monosporous sporangia. Additional developmental and ultrastructural investigations of this order of Zygomycetes are required.

In the Mucorales, largest order of the Zygomycetes, morphological and developmental features of asexual reproductive structures have been used as the most important taxonomic characters in separating families and genera (Cole and Samson, 1978). In a few of these fungi (e.g., species of *Mucor*, *Zygorhynchus*, *Mortierella*), the zygosporic sexual states have facilitated delimitation of species and genera (Gams, 1969; Gams *et al.*, 1972; Kuhlman, 1972, 1975; Schipper *et al.*, 1975). However, in most zygomycetes the sexual spores are either completely lacking, not reported, or difficult to induce in culture. The elaborate wall ornamentations of zygospores have been examined in both the SEM and TEM and utilized as taxonomic criteria (Hawker and Beckett, 1971; Chien *et al.*, 1974;

Schipper *et al.*, 1975; Kirk, 1977; Egans and Samson, 1977). O'Donnell *et al.* (1978) pointed out that the mature zygospore of mucoraceous fungi is encompassed by an outer (exospore) layer derived from the zygosporangium and an inner (endospore) layer formed by the zygospore proper. These authors examined the potential value of the exospore and endospore surface topography "as a set of taxonomic characters which might indicate intrageneric relationships and aid in species recognition." On the basis of light microscopic examinations and examinations of thin-sectioned sexual spores of members of the Harpellales (Trichomycetes), Moss and Lichtwardt (1977) concluded that these structures are typical zygospores. However, lack of ultrastructural data on zygospores produced by members of the Kickxellales and Entomophthorales prevent structural and developmental comparisons between the trichomycetous and zygomycetous fungi. This is another promising area for future contributions of electron microscopy to fungal taxonomy.

#### WALL CHEMISTRY AND ULTRASTRUCTURE

Most morphological characters described above have been used for generic, specific, and infraspecific delimitations. Many biochemical and physiological aspects of fungi, on the other hand, have been involved in phylogenetic consideration (Klein and Cronquist, 1967; Bartnicki-Garcia, 1969). For example, Bartnicki-Garcia (1968) divided the fungi into eight groups based on chemical composition of the cell walls. These groups demonstrate a high degree of consistency in composition of related forms. Although cell wall formation has "a certain latitude for quantitative and even qualitative changes . . . in response to environmental alterations or associated with . . . ontogenetic development," the mechanism of fungal wall construction is a conservative process which cannot tolerate "erratic departures" in its chemical makeup (Bartnicki-Garcia, 1969).

Examinations of ultrastructural features of cell walls have been correlated with studies of chemical composition (Hunsley

and Burnett, 1970). Together these investigations provide the taxonomist with significant information. For example, the walls of conidial fungi (Subdivision Deuteromycotina) have received considerable attention from both biochemists and ultrastructuralists (Jones *et al.*, 1972; Kitajima *et al.*, 1972; Reisinger and Bonaly, 1972; Nozawa *et al.*, 1973; White *et al.*, 1973; Laborda *et al.*, 1974; Barran *et al.*, 1975). The formation of chlamydospores in these fungi represents an important taxonomic character. Although biochemical and ultrastructural aspects of chlamydospore wall differentiation have been examined (Stevenson and Becker, 1972; Griffiths 1973a,b, 1974; Schneider and Seaman, 1974; Van Eck, 1976; Schneider *et al.*, 1977), the application of these data to taxonomic studies has not been explored. Deuteromycetes that produce "dematiaceous" or pigmented vegetative and reproductive cells that are not enclosed in sporocarps have been classified together for convenience (M. B. Ellis, 1971, 1976). However, the presence of melanin in the walls of most, or perhaps all these fungi may be phylogenetically significant. Ultrastructural and chemical analyses of melanin formation have been made by a few workers (Rowley and Pirt, 1972; Ellis and Griffiths, 1974, 1975; Griffiths and Swart, 1974; Wheeler *et al.*, 1976; Ola'h *et al.*, 1977). The surfaces of conidia, revealed by freeze-etch technique, demonstrate a microfibrillar wall layer composed of "rodlets" (Hess *et al.*, 1968). These structures have been found on the surface of dry, deciduous conidia (Fig. 1) produced by several species of the Deuteromycetes (Hess and Stocks, 1969; Cole and Aldrich, 1971; Cole, 1973, 1975; Cole *et al.*, 1979b), as well as sporangiospores (Cole and Samson, 1978;), basidiospores (Bronchart and Demoulin, 1971; Hess *et al.*, 1972; Wessels *et al.*, 1972; Hess and Weber, 1976) and actinomycete (filamentous bacteria) spores (Takeo, 1976; Smucker and Pfister, 1978). The chemical composition of the rodlet layer in conidial fungi has been examined only in *Trichophyton mentagrophytes* (Hashimoto *et al.*, 1976; Wu-Yuan and Hashimoto, 1977) and *Aspergillus niger* (Cole *et al.*, 1979b). Rodlets of these fungi are considered to be pro-

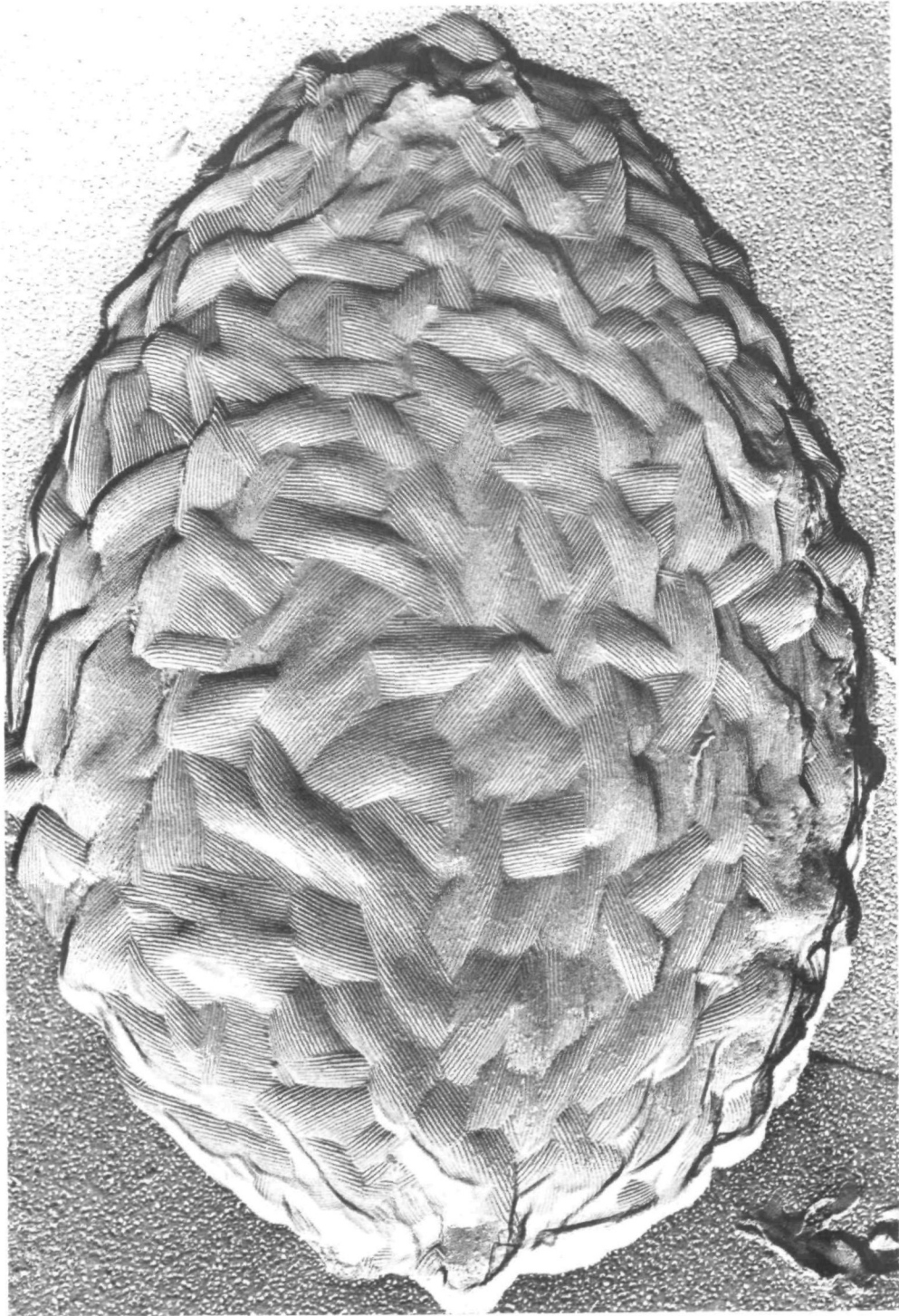


FIG. 1. Freeze fracture of a conidium of *Penicillium* sp. showing "rodlet" fascicles.  $\times 16,000$ .

teinaceous and the matrix in which they are embedded is apparently a glucomannan complex. Wessels *et al.* (1972) suggested that the rodlets of the basidiomycetous fungus *Schizophyllum commune* are composed of S-glucan. Comparative studies of rodlet fine structure and chemical composition in major groups of fungi may reveal features which support phylogenetic concepts. Although the function of rodlet fascicles is unknown, it has been suggested that they represent a hydrophobic layer which provides buoyancy to the conidia during dispersal in a humid environment or aquatic habitat (Beever and Dempsey, 1978). It has also been proposed that rodlets, along with other components of the cell wall surface of pathogenic deuteromycetes, elicit significant immunological activity of the host during the infection process (Kitajima and Nozawa, 1975; Smith, 1977; Cole *et al.*, 1979b).

The imperfect, or asporogenous yeast are morphologically uniform (Doby *et al.*, 1978) necessitating "a special taxonomic treatment for the differentiation of species" (Kreger-Van Rij, 1973) in which physiological, biochemical and molecular characteristics are used (Lodder, 1970; Phaff *et al.*, 1978). Ultrastructural and chemical aspects of the yeast cell walls, especially the mannan component, have been considered valid taxonomic criteria (Phaff *et al.*, 1978).

Many yeast and conidial forms are capable of dimorphism, involving a reversible yeast-to-mold conversion, and these are fungi often pathogenic to man (Cochrane, 1958; Ramano, 1966). Ultrastructural and chemical aspects of wall morphogenesis in dimorphic fungi are fundamental to our understanding of this developmental process (Oujezdsky *et al.*, 1973; San-Blas and Carbonell, 1974; Yamaguchi, 1974; Yamaguchi *et al.*, 1974; Garrison and Boyd, 1975; Dorn and Roehnert, 1977). In a study of dimorphism in *Mycotypha poitrasii* (Zygomycetes), Cole *et al.* (1979a) described an "intermediate" form whose wall chemistry and ultrastructure were different from that of the yeast and hyphae (Figs. 2,3). Examinations of these three developmental stages in *M. poitrasii* suggested that interrelationships exist between the alterations in

cell wall chemistry and morphogenetic aspects of dimorphism. It may be possible to isolate and examine similar intermediate forms among other dimorphic fungi. Dimorphism has been observed with keen interest by medical mycologists, and such studies may yield valuable information for clinicians, morphogeneticists, and taxonomists.

#### SEPTAL ULTRASTRUCTURE

The phylogenetic implications of septal ultrastructure are uncertain. Heath (1975) suggested that variations in septal structure may simply reflect a "physiological peculiarity of the species concerned" and warned that phylogenetic conclusions should not be drawn from limited ultrastructural data. However, electron-microscopic examinations of the kinds of septa present in fungi have provided at least some valuable taxonomic data that have sometimes supported and sometimes contradicted concepts of taxa (Blanchard, 1972; Johnson-Reid, 1972; Schneider and Dargent, 1972; Kreger-Van Rij and Veenhuis, 1973; Strullu and Gourret, 1974). These and similar studies have been particularly useful in decisions on whether certain imperfect fungi have an ascomycetous or basidiomycetous affinity (Cooper *et al.*, 1973; Terracina, 1974; Bronchart and Demoulin, 1975; Evans *et al.*, 1978; Hanlin, 1978).

#### FINE STRUCTURE OF THE ASCUS

The ascus is recognized as a fundamental, diagnostic structure in ascomycete classification (Schoknecht, 1975; Stiers, 1977). The Pyrenomycetes, a major class of the Ascomycotina, is divided into two series, Bitunicatae and Unitunicatae, on the basis of the structure of the ascus wall (Luttrell, 1951). Thin-section examinations of asci at different stages of development have revealed taxonomically significant features of wall differentiation in other groups of the Ascomycetes. For example, Schneider and Dargent (1977) demonstrated that the ascus wall of *Taphrina* (Protoascomycetes) consists of several tunicae that "could be assimilated to the endoascus and exoascus

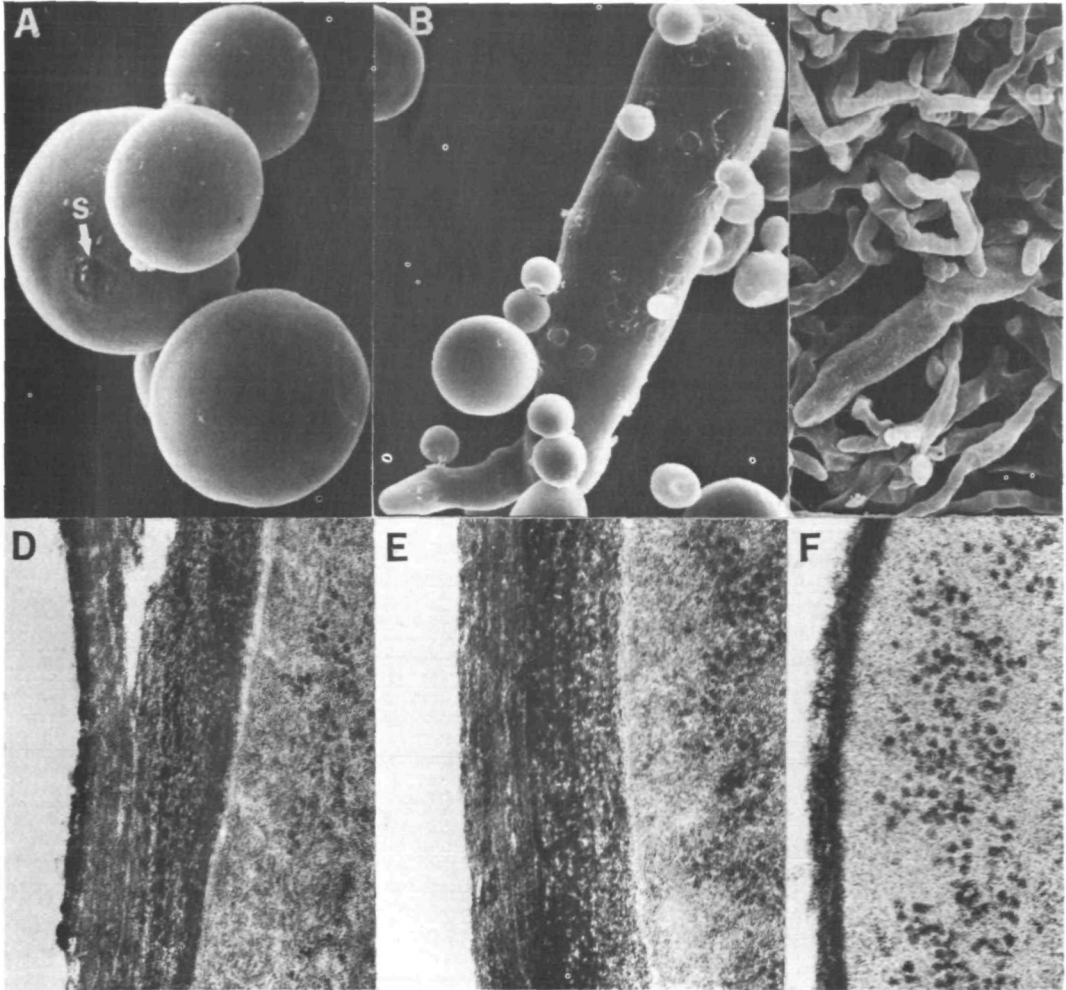


FIG. 2. Yeast (A, D), intermediate (B, E) and hyphal forms (C, F) of *Mycotypha poitrasii*. Structural and dimensional differences in the wall of each form are

shown (D-F,  $\times 204,000$ ). S, bud scar. A,  $\times 1,700$ ; B,  $\times 1,300$ ; C,  $\times 2,400$ . (From Cole *et al.*, 1979a).

of higher Ascomycetes." Light- and electron-microscopic features of the ascus apex have also been utilized in the taxonomy of Pyrenomycetes and Discosmycetes. Paraguy-Leduc (1977) demonstrated that the apical apparatus of pyrenomycetes is differentiated into an apical and subapical ring. The lower ring, or thickening of the ascus wall, forms a projection into the epiplasm, and a central pore or papilla penetrates this projection. At the time of dehiscence, the subapical ring undergoes eversion, and the ascospores are pushed out through a narrow pore formed

by dissolution of wall material. Stiers (1977) has indicated differences in the nature of the apical apparatuses among pyrenomycetes but "all the observed variations can probably be regarded as elaborations of a basic structure." Electron microscopy, in this author's opinion, has demonstrated that the differentiated ascus apex is much less complex than previously published data based on light microscopy suggest. Bellemere (1977) showed that the apical apparatus of inoperculate discosmycetes, although also composed of two adjacent rings, is different from that of the pyreno-



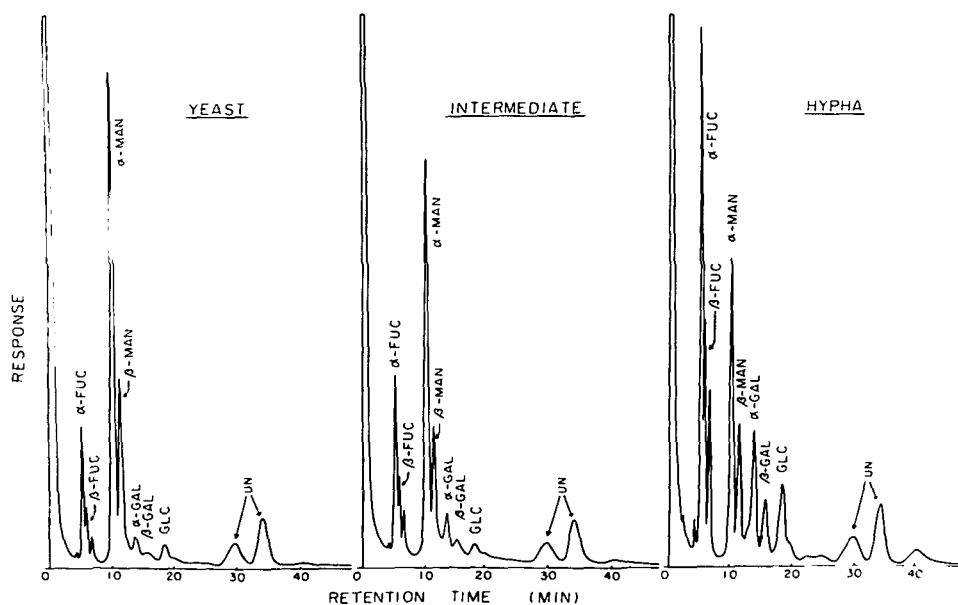


FIG. 3. Gas-liquid chromatographic patterns for yeast, intermediate, and hyphal walls of *Mycotypha potrasii*. Operational conditions for the GLC and preparatory procedure for each sample were identical.

Major peaks are labeled; FUC, fucose; MAN, mannose; GAL, galactose; GLC, glucose; UN, unknown. (From Cole *et al.*, 1979a)

mycetes. Samuelson (1975) examined the ultrastructure of a group of discomycetes with suboperculate, or obliquely operculate asci (Le Gal, 1946). His electron-microscopic examinations of the apical apparatus of several representatives of this group demonstrate unique characters that support the classic taxonomic distinction of suboperculate fungi from other discomycetes.

#### DEVELOPMENTAL ULTRASTRUCTURAL CHARACTERS

Early workers recognized that conidia and conidiogenous cells of deuteromycetous fungi (Subdivision Deuteromycotina) arise by several different methods (Constantin, 1888; Vuillemin, 1910a, b, 1911; Mason, 1933, 1937) and that these developmental features may be of taxonomic value. However, it was Hughes (1953) who provided the first experimental scheme based on differences in the modes of conidium ontogeny. His synthesis provided a valuable supplement to Saccardo's (1886) classification, which was not entirely satisfactory

because of its many inconsistencies and ambiguities. However, due to the limited resolving power of the light microscope, the differences between kinds of conidiogenesis were not clearly understood. Ultrastructural features of the development of conidial fungi have been documented recently (Cole and Samson, 1978), and these have clarified developmental concepts and permitted formulation of categories of conidium and conidiogenous cell ontogeny.

Nicot (1977) presented a review of the problems and perspectives in the classification of Fungi Imperfecti. In it he suggested that the application of ultrastructural, developmental, and biochemical characters to the taxonomy of this group has initiated a new and promising period of study. Although most examinations of conidiogenesis have involved members of the Form-Class Hyphomycetes, Sutton (1973, 1976) has been optimistic that developmental studies of the coelomycetous fungi (Form-Class Coelomycetes) will provide equally valuable taxonomic information. Few ultrastructural investigations of conidiogenesis in this group have been pre-



sented (e.g., Ekundayo and Haskins, 1969; Boerema and Griffin, 1974; Marasas *et al.*, 1974; Swart and Griffiths, 1974; Boerema and Bollen, 1975; Brisson *et al.*, 1975; Jones, 1976). Efforts are now underway in my laboratory to explore the mechanisms of conidial and conidiogenous cell development in the Coelomycetes. The reproductive propagules of these fungi are usually very small and are enclosed within fructifications. The material is being examined both by scanning and transmission electron microscopy.

As mentioned previously, the taxonomy of the Zygomycetes depends to a large extent on morphological aspects of the imperfect forms. For example, in recent classifications of the Mucorales (Zycha *et al.*, 1969; von Arx, 1970, 1974; Pidoplichko and Milko, 1971; Hesseltine and J. J. Ellis, 1973), morphological and developmental features of the asexual reproductive structures have been used as the most important taxonomic characters to separate families and genera. The asexual aplanospores produced by zygomycetous fungi like *Cunninghamella* and *Entomophthora* are termed sporangiospores, but are often incorrectly referred to as conidia. The latter are actually asexual, nonmotile, usually deciduous propagules produced by the Fungi Imperfecti (Subdivision Deuteromycotina). Conidia are usually formed by the blowing out of a hyphal tip to form a terminal cell which is separated from the fertile hypha by a basal septum (Cole and Samson, 1978). The septum later undergoes schizolysis resulting in conidial secession. On the other hand, in developmental and ultrastructural examinations of *Cunninghamella echinulata*, Khan and Talbot (1975) demonstrated that sporangiospores are formed within monosporous sporangiola, and that this process is ontogenetically related to cleavage in multispore sporangia (e.g., *Gilbertella persicaria*: Bracker, 1966, 1968). The monosporous sporangiolium, therefore, is simply a reduced sporangium (Khan, 1975). Similar ultrastructural observations of *Cunninghamella echinulata* and *Mycotypha microspora* were reported by Benny (in Cole and Samson, 1978). Young (1973a) demonstrated that the monosporous merosporan-

gia of *Coemansia aciculifera* each secede from a pseudophialide and the endogenous sporangiospore emerges through the outer, merosporangial wall. In an ultrastructural examination of *Piptocephalis*, Jeffries and Young (1975) concluded that the "presence of a membrane . . . around the asexual spore of *P. unisporea*, which often persists even on germinating spores, suggests its spore-like nature." Turian and Wuest (1977) illustrated the double-walled nature of "conidia" produced by *Zoophthora myrmecophaga* (Entomophthorales), suggesting that these cells are actually sporangiospores and homologous to the asexual propagules of other zygomycetes. Although electron microscopy has revealed differences between the mechanisms of sporangiosporogenesis and conidiogenesis, functional similarities do exist between these two kinds of aplanospores which are the result of convergent evolution (Cole and Samson, 1978).

The different modes of sporangiosporogenesis in mucoraceous fungi have been reexamined by electron microscopy. New features have been revealed which, in some cases, have clarified developmental concepts (Fletcher, 1972, 1973; Khan and Talbot, 1975; Baker *et al.*, 1977; Jeffries and Young, 1978). In an examination of the patterns of sporangiospore development in Zygomycetes, Cole and Samson (1978) used the SEM and light microscope to illustrate developmental differences between representative species of mucoraceous fungi. For example, in an ultrastructural comparison of *Mycotypha poitrasii* and *Cokeromyces recurvatus*, differences in the mechanisms of sporangiolar dehiscence were demonstrated (Fig. 4). These observations support the proposal by Benny and Benjamin (1976) to synonymize *Cokeromyces poitrasii* with *Mycotypha poitrasii* partly because the sporangiola of *Mycotypha* (e.g., *M. microspora* and *M. africana*) are typically "freed from the subtending vesicle by circumscissile, subbasal rupture of the pedicel." The pedicels of *Cokeromyces* do not differentiate a dehiscence zone.

In taxonomic revisions of the families Cunninghamellaceae and Thamnidaceae (Benny and Benjamin, 1975, 1976; Jeffries

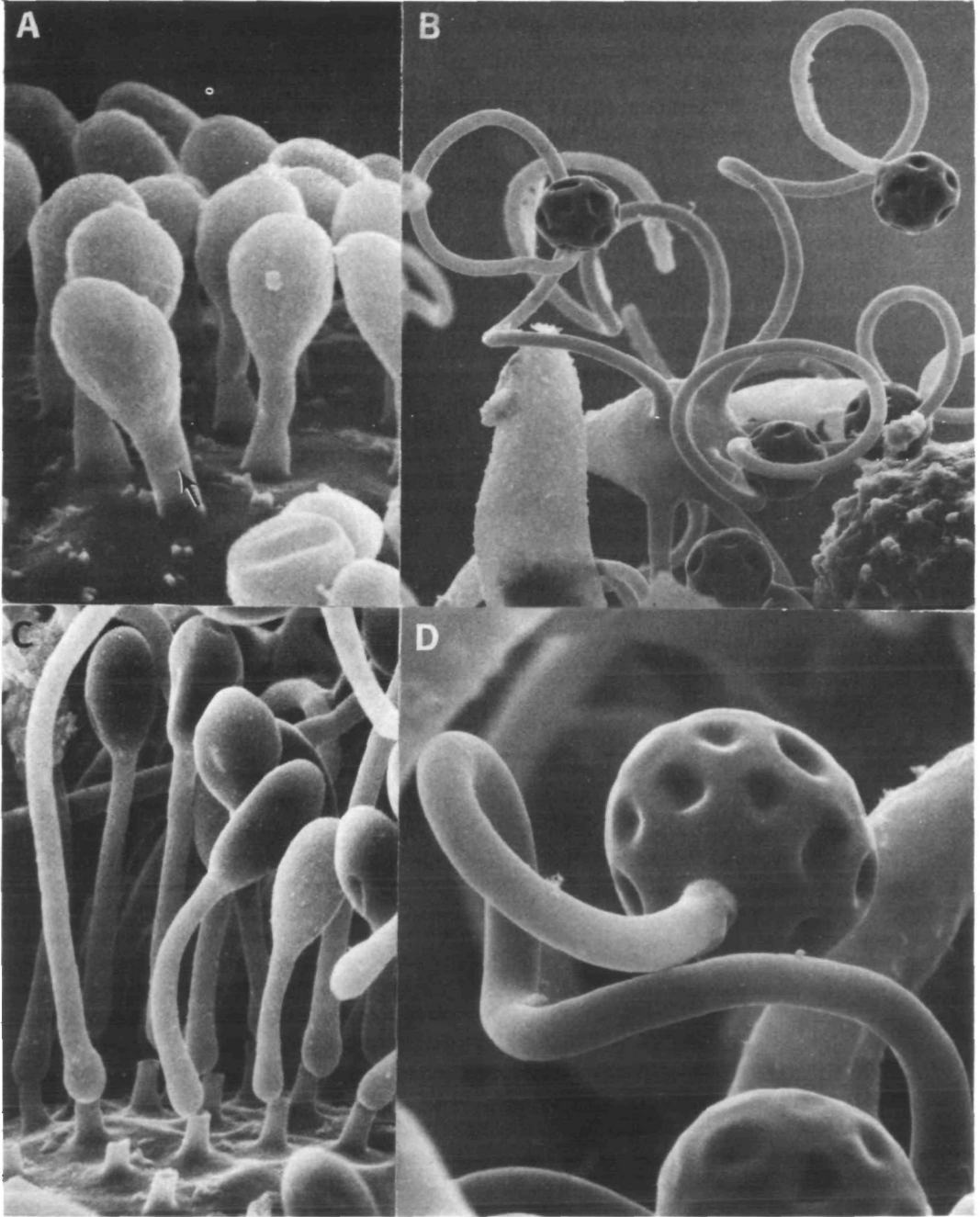


FIG. 4. Stages of monosporous sporangial development in *Mycotypha poitrasii* (A, C) and few-spored sporangial development in *Cokeromyces recurvatus* (B, D). Note the presence of a cross wall at the base of the sporangium of *M. poitrasii* (arrow in A) which ap-

pears before pedicel elongation. This same cross wall later functions in the process of dehiscence (C). In *Cokeromyces recurvatus*, no such dehiscence mechanism occurs. (From Cole and Samson, 1978) A,  $\times 7,260$ ; B,  $\times 1,320$ ; C,  $\times 5,250$ ; D,  $\times 3,740$ .

and Young, 1978), fine structural studies of sporangiosporogenesis have played a significant role. Ultrastructural examinations of zygospore (sexual propagule) development have so far included only a few species (O'Donnell *et al.*, 1977*a,b,c*, 1978).

Applications of ultrastructural, developmental data to the taxonomy of other groups of fungi have been poorly explored. Although numerous studies have been reported on the fine-structural aspects of zoosporogenesis (*e.g.*, Bland and Amerson, 1973; Barron and Hill, 1974; Harrison and Gareth Jones, 1974; McNitt, 1974; Barstow and Lovett, 1975; Schnept *et al.*, 1978) and ascosporeogenesis (*e.g.*, Rooney and Moens, 1973; Hill, 1975; Kreger-Van Rij and Veenhuis, 1975), comparable investigations of many additional members of the Mastigomycotina and Ascomycotina are necessary before this information can be accurately incorporated into the existing classifications.

#### ULTRASTRUCTURAL ASPECTS OF NUCLEAR DIVISION

Robinow and Bakerspigel (1965) pointed out that "fungal mitoses are of several different kinds and have peculiarities that set off from the better known ordinary forms of nuclear division." Fuller (1976) suggested that a natural separation exists between classes of fungi that have centric and those that have noncentric nuclear division, *i.e.*, with and without centrioles, respectively. With few exceptions, the centric forms are found among the lower, flagellated fungi while the noncentric forms are among the higher fungi (Zygomycetes, Ascomycetes and Basidiomycetes). The centric forms have classical features of inter-polar and chromosomal microtubules and a metaphase plate. On the basis of serial section analyses, Heath (1974) classified spindle microtubular arrangement into four groups: (1) continuous or inter-polar tubules, (2) interdigitating tubules, (3) polar tubules, and (4) chromosomal tubules, which sometimes terminate in kinetochores. Centrioles are present in most centric fungi, and their structure is similar in basic aspects to other eukaryotes.

Also, the nuclear envelope of most centric forms is persistent during division. Pickett-Heaps (1971), however, challenged the theory that centrioles have functional significance in nuclear division. He has proposed that these organelles are involved rather in flagellation, and that their association with the process of nuclear division is simply to ensure equal distribution of centrioles to each daughter cell. If this hypothesis is correct, the absence of centrioles in noncentric fungi presents no difficulty and is of little consequence in the evolution of the mitotic apparatus in fungi (Fuller, 1976).

Pickett-Heaps (1972) also presented a theory of the sequence of events in the evolution of fungal spindles. He suggested that closed spindles in the lower fungi gave rise to open spindles in the Basidiomycetes. However, the evolution of the open spindle may not be as important a phylogenetic event as previously suspected (Fuller, 1976). Both closed and open spindles are found in the Chytridiomycetes (posterior uniflagellate forms) while the Oomycetes, considered by most workers to be an advanced group of flagellate fungi, have closed spindles.

The fate of the nucleolus during fungal mitoses is still unclear (Wright *et al.*, 1978). Pickett-Heaps (1970) recognized four classes of nucleolar behavior during mitosis: (1) autonomous, (2) persistent, (3) semipersistent and (4) dispersive. In all fungi, an organelle on or near the nuclear envelope in a ribosome-free region is associated with the spindle. This structure has been given many names, including microtubule-organizing center, or MTOC (Pickett-Heaps, 1969), and spindle pole body, or SPB (Aist and Williams, 1972). There is some argument against the use of "MTOC" because of its functional connotations. However, all SPBs so far examined are associated with microtubules some time during karyokinesis, and Fuller (1976) suggested that SPBs "may ultimately turn out to be a special class of MTOCs." In the flagellate fungi, the MTOC is intranuclear and opposite the centrioles. In those forms demonstrating noncentric mitosis (*e.g.*, ascomycetous yeast), the SPB may be intimately

associated with the nuclear envelope, as in *Saccharomyces cerevisiae*, or lie outside the nuclear envelope during mitosis, as in *Schizosaccharomyces pombe*. The SPB of members of the Ascomycotina is a plaque-like structure. The SPB of most basidiomycetes is a dumbbell-shaped structure, composed of two fibrillar, globular elements joined by an electron dense middle piece (Wells, 1977). Some authors have suggested that there is a chemical distinction between the ascomycete and basidiomycete SPBs (McDonald and Weijer, 1966; Girbardt, 1968, 1971; Zickler, 1973). On the other hand, the SPB of the Uredinales is disk-like (Heath and Heath, 1975; Wright *et al.*, 1978), and nuclear divisions in the rusts may differ from those in other basidiomycetes. Wells (1977) proposed that "the characteristics of nuclear divisions in the Uredinales are intermediate between those of the Ascomycotina and those of the remaining orders of the Basidiomycotina." Fuller (1976) suggested that comparative cytological studies of fungi support the existence of a coherent group, the Zygoascobasidiomycotina. He concluded that the SPB of Zygomycetes (closed spindles) is probably derived from the intranuclear MTOC of the flagellate fungi. Following another evolutionary pathway from ancestral flagellates, the SPB of Ascomycetes and Basidiomycetes may have developed from the extranuclear MTOC. Observing mitoses in fungi, Fuller (1976) concluded that the SPB of most Ascomycetes became closely associated with the membranes of the nuclear envelope. In most basidiomycetes the nuclear membranes became disorganized. In some ascomycetes and basidiomycetes polar fenestrae developed during mitosis.

#### OTHER CYTOLOGICAL CHARACTERS

The significance of other cytological aspects in the phylogeny and taxonomy of fungi has not been extensively examined. Thin-section studies of protoplasmic differentiation associated with hyphal tip growth (Fig. 5) have revealed three types of organization of apical vesicles (Grove and Bracker, 1970; Bartnicki-Garcia, 1973).

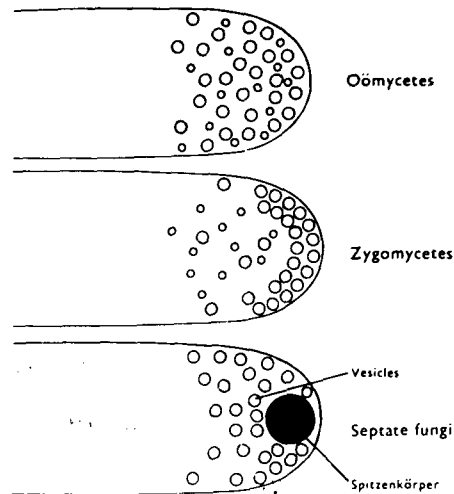


FIG. 5. The three kinds of organization of apical vesicles in hyphal tips of fungi. (After Grove and Bracker, 1970)

The consistency of this cytological character in Oomycetes, Zygomycetes and septate fungi requires further exploration (Wang *et al.*, 1975; Roos and Turian, 1977). Typical dictyosomes, demonstrating a stacked arrangement of cisternae and an elaborate membrane system in which the "nuclear envelope, endoplasmic reticulum, Golgi apparatus, and secretory vesicles form a structural and functional unit" are apparently restricted to the Oomycetes (Bracker *et al.*, 1971). Other groups of fungi, like the Zygomycotina and Deuteromycotina, have simple dictyosome-like organelles often composed of cisternal rings (Fig. 6) from which secretory vesicles are presumably liberated (Bracker, 1968; O'lah, 1974; Cole and Aldrich, 1971; Cole and Samson, 1978). Perhaps associated with the absence of a well differentiated dictyosome, the endoplasmic reticulum in fungi demonstrates a high degree of morphogenetic plasticity and the various ER complexes may function as Golgi equivalents (Thielke, 1972; Steele and Fraser, 1973; Robb, 1974; Bojović-Cvetić and Vujičić, 1976; Vannini, 1976; Khan, 1978). Although Moore's (1971) statement that "aquatic fungi are characterized by the presence of the Golgi system while terrestrial fungi are not" may have been premature, these observations have generated questions and speculations

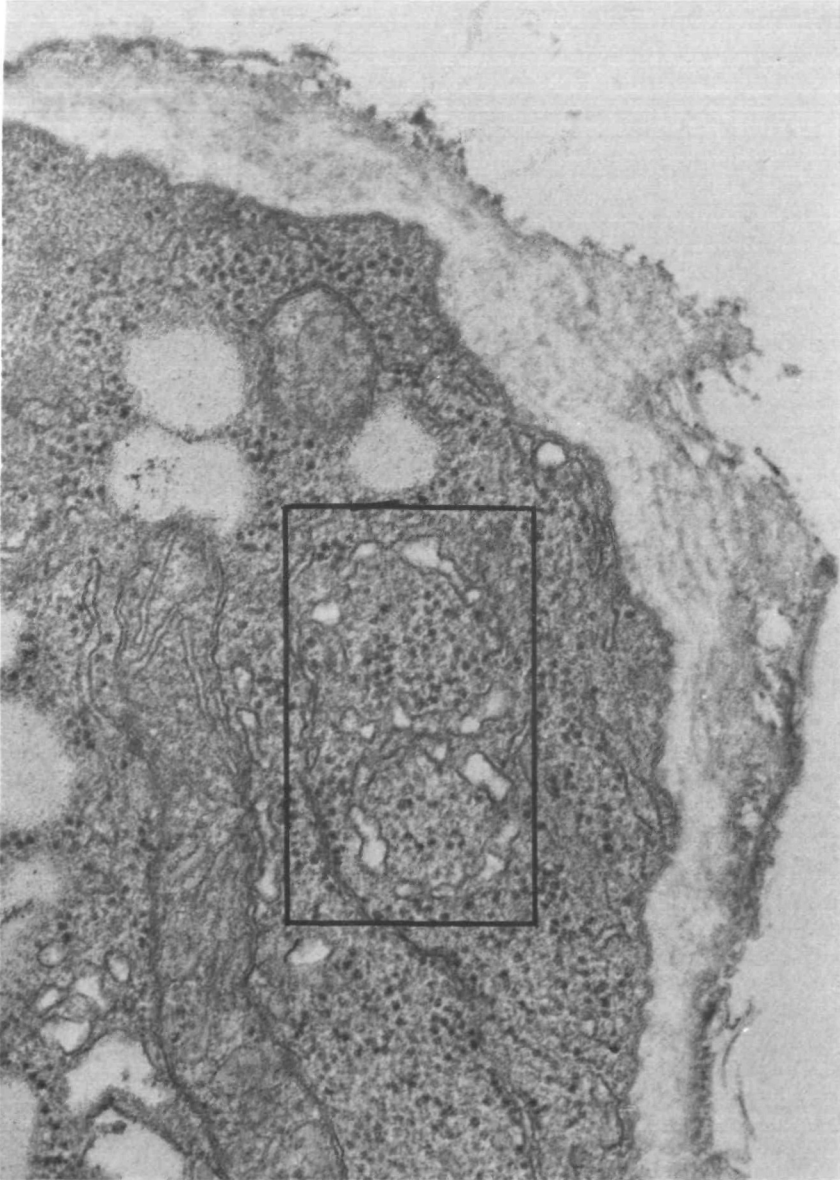


FIG. 6. Cisternal rings (enclosed by rectangle), considered Golgi equivalents, in the cytoplasm of a young

conidium of *Scopulariopsis brevicaulis*  $\times 51,000$ .

on the phylogeny of fungi. Moore (1971) recognized that members of the Blastocladales (Mastigomycotina) are notable exceptions to his statement; they have well-developed dictyosomes. These same fungi are characterized by the presence of distinctive nuclear caps and formation of gamma particles (Olson, 1973; Barstow and Lovett, 1974, 1975; Pommerville and Fuller, 1976;

Cantino, 1977; Manier, 1977). The nuclear cap is found in zoospores and gametes and contains suspended RNA. The cap may be bounded by the nuclear envelope or have its own limiting membrane (e.g., *Blastocladia*). These fungi lack a defined nucleolus and the nuclear cap may represent its functional equivalent. The role of gamma particles at least in *Blastocladia emersonii*,

appears to be involved with cell-wall synthesis (Cantino, 1977). The phylogenetic significance of these findings in the Blastocladales is unclear. The lomasome, found adjacent to the hyphal wall of many fungi, is an important organelle which may function in secondary wall intussusception and apposition (Moore and McAlear, 1961; Boissiere, 1972; Marchant and Moore, 1973; Weisberg and Turian, 1974; Cole and Samson, 1978). Although lomasomes are not unique to the fungi (Bouck, 1962; Manocha and Shaw, 1964), their high frequency in many kinds of fungal cells suggests that these organelles are phylogenetically important.

#### CONCLUSION

The fungi represent a challenging group of microorganisms to which taxonomists must apply all their skills in the formulation of functional classifications. Electron-microscopic investigations have been particularly fruitful in providing much new information which has been effectively incorporated into taxonomic schemes. Electron microscopy is more than a simple extension of light-microscopic investigations differing only in its finer resolution of morphological details. Using such auxiliary electron-microscopic facilities as energy dispersive X-ray equipment, it is possible to combine ultrastructural with elemental analyses of wall and cytoplasmic components. In addition, electron microscopy combined with cryotechniques, allows examination of both the surface and internal ultrastructure of fixed or unfixed frozen cells without breaking vacuum. Current scanning-transmission electron microscopes (STEMs) permit studies of macromolecular structure as well as the morphology of intact cells or entire microorganisms. In the hands of the innovative taxonomist, these facilities can be powerful research tools used in the formulation of experimental classifications.

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