

Variable proliferation of conidiogenous cells in Diatrypaceae and other fungi

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Conidiogenous cells in Diatrypaceae may proliferate sympodially, percurrently, or both ways in the same species. Reports on conidial ontogeny in Diatrypaceae are reviewed, and mechanisms which might account for variations in proliferative growth in these fungi are discussed. The mechanism considered most likely involves a shift in the location of wall-synthesizing activity within the conidiogenous cell; localization of such activity in the center of the cell apex could result in percurrent proliferation, while localization at subaxial positions could result in sympodial proliferation. Forty-five species outside the Diatrypaceae are listed that exhibit both sympodial and percurrent proliferation of conidiogenous cells.

HUGHES's (1953) paper on conidial ontogeny initiated a new era of research on conidial fungi. While some earlier workers did deal with aspects of conidial development (see MINTER, SUTTON & BRADY, 1983), HUGHES's (1953) paper was the first to focus on conidial development in a substantial number of fungi chosen to exemplify major types of conidial development. His work showed irrefutably that features of conidial development offered valuable additions to the characters used to classify Fungi Imperfecti. His seven major types of conidial ontogeny formed the conceptual basis for all of the subsequent research devoted to clarifying and expanding the understanding of conidial ontogeny and its taxonomic significance. Much of this research has been reviewed earlier in works by KENDRICK (1979), COLE & SAMSON (1979), MINTER et al. (1982), MINTER, KIRK & SUTTON (1983), MINTER, SUTTON & BRADY (1983), and COLE (1986).

A substantial amount of literature now details conidial ontogeny in many fungi. However, the sheer volume of information sometimes obscures patterns of conidial development that occur over a range of fungal groups. Such is the case in the literature dealing with the phenomenon whereby conidiogenous cells proliferate both sympodially and percurrently in single species. This phenomenon appears to be more widespread than generally recognized, possibly because reports generally are scattered among descriptions

of individual fungi. In this paper I cite the reports of this phenomenon known to me, and discuss in some detail its existence in the Diatrypaceae, where it seems widespread.

Conidiogenous cell proliferation in Diatrypaceae

Information on most diatrypaceous anamorphs is based on cultured material since in nature they are inconspicuous, infrequently collected, and are difficult to identify in the absence of the teleomorph (GLAWE & ROGERS, 1984; RAPPAZ, 1987). Conidiogenous cells may be aggregated in palisades within pycnidium-like or sporodochium-like conidiomata; may be formed at the ends of tall, branched conidiophores; or may be formed in hyphomycetous states. Conidiogenous cells tend to be cylindrical, tapering, and hyaline; in species that form melanized conidiogenous cells, the apical regions, where conidia form, are hyaline (GLAWE & ROGERS, 1982b, 1986). Although conidiogenous cells vary in size among different species, the apical, conidiogenous portions generally are approximately 1 μm in diameter. The minute size and transparency of these cells has led to past mistakes in interpreting them; the first attempts to characterize conidiogenous cells in Diatrypaceae (CROXALL, 1950; JOHNSON & KUNTZ, 1978) reported that they are phialides, a conclusion not supported by later studies (Tab. 1).

Each conidiogenous cell gives rise to a number of sequentially-produced conidia. The conidia are single-celled, hyaline, and range in shape from allantoid to filiform and from nearly straight to strongly curved. Mature conidia dehisce schizolytically. Within species, considerable variation in conidial size can occur (e.g., GLAWE & JACOBS, 1987). CROXALL (1950) reported both macroconidia and microconidia in species of *Diatrypella*, but subsequent investigations (GLAWE & ROGERS, 1982a; GLAWE, 1989) on species he investigated failed to confirm this observation.

In all investigated species conidia develop blastically at the apex of the conidiogenous cell. Following production of a conidium, conidiogenous cells frequently proliferate, i. e., the cell grows past the last conidiogenous site. A given proliferation may be too short to be resolved by light microscopy, or may be 1 μm or more long (GLAWE & ROGERS, 1982a, 1986). Percurrent proliferations lengthen the cell along the main axis; this happens when the conidiogenous cell proliferates at the apex, through the remnant of the delimiting septum of the previous conidium. It is the characteristic ring-like frills resulting from successive proliferations that give these cells the appearance of annellides. Frequently, however, the proliferations are subaxial; in these cases the proliferation originates to the side of the secession scar (the remnant of the delimiting septum) of the

previously-formed conidium, and the cell grows past it. As the cell proliferates the secession scar assumes a lateral position. Repeated sympodial proliferation produces the characteristic lateral scarring and somewhat geniculate appearance typical of sympodulae in this family.

A noteworthy feature of diatrypaceous anamorphs is that conidiogenous cells within a species may proliferate either sympodially or percurrently, or both ways (Tab. 1). When both kinds of proliferation occur they may be found in the same culture, conidioma, or even in the same cell. Regardless of how the cell proliferates, conidia produced from it are morphologically indistinguishable. The conidiogenous cells themselves frequently are indistinguishable unless subjected to careful study, and brightfield microscopy alone generally is insufficient to allow accurate characterization of how proliferation proceeds (GLAWE, 1983b).

Tab. 1. Types of conidiogenous cell proliferation in species of Diatrypaceae.

Species	Reference
A. Sympodial proliferation	
<i>Cryptosphaeria populina</i> (PERS. : FR.) SACC.	GLAWE & JACOBS, 1987
<i>Diatrype bullata</i> (HOFFM. : FR.) FR.	ROGERS & GLAWE, 1983
<i>Diatrype stigma</i> (HOFFM. : FR.) FR.	ABE, 1986
<i>Diatrype whitmanensis</i> ROGERS & GLAWE	ROGERS & GLAWE, 1983
<i>Diatrypella favacea</i> (FR.) CES. & DE NOT.	GLAWE & ROGERS, 1982a
<i>Diatrypella frostii</i> PECK	GLAWE, 1983a
<i>Eutypa</i> taxonomic species 2	GLAWE & ROGERS, 1984
<i>Eutypa spinosa</i> (PERS. : FR.) TUL.	GLAWE & ROGERS, 1986
<i>Eutypella</i> sp.	GLAWE & ROGERS, 1982b
<i>Eutypella sorbi</i> (SCHM. : FR.) FR.	ROGERS & GLAWE, 1983
B. Percurrent proliferation	
<i>Cryptosphaeria vicinula</i> (NYL.) KARST.	GLAWE & ROGERS, 1986
<i>Diatrype stigma</i> (HOFFM. : FR.) FR.	ABE, 1986; GLAWE & ROGERS, 1982a; GLAWE & JACOBS, 1987

Tab. 1. (cont.)

Species	Reference
<i>Eutypella angulosa</i> (NITS.) SACC.	GLAWE & ROGERS, 1986
<i>Eutypella cerviculata</i> (FR.) SACC.	GLAWE & ROGERS, 1982b
C. Sympodial and percurrent proliferation	
<i>Cryptosphaeria pullmanensis</i> GLAWE	GLAWE, 1984
<i>Diatrype albopruinosa</i> (SCHW.) COOKE	GLAWE & ROGERS, 1982a
<i>Diatrype stigma</i> (HOFFM. : FR.) FR.	ABE, 1986; GLAWE & JACOBS, 1987
<i>Diatrype virescens</i> (SCHW.) COOKE	GLAWE & ROGERS, 1982a
<i>Diatrypella prominens</i> (HOWE) ELL. & EVERH.	GLAWE & JONES, 1989
<i>Diatrypella pulvinata</i> NITS.	GLAWE & ROGERS, 1982a
<i>Diatrypella quercina</i> (PERS. : FR.) NITS.	GLAWE, 1989
<i>Diatrypella verrucaeformis</i> (EHR. : FR.) NITS.	GLAWE & ROGERS, 1982a
<i>Eutypa armeniaca</i> HANSF. & CARTER	GLAWE & ROGERS, 1982b
<i>Eutypa lata</i> (PERS. : FR.) TUL.	GLAWE & ROGERS, 1982b
<i>Eutypa flavovirens</i> (PERS. : FR.) TUL.	GLAWE & ROGERS, 1982b
<i>Eutypa spinosa</i> (PERS. : FR.) TUL.	RAPPAZ, 1987
<i>Eutypella parasitica</i> DAVIDSON & LORENZ	GLAWE, 1983b
<i>Eutypella sabalina</i> (COOKE) ELL. & EVERH.	GLAWE & JONES, 1989
<i>Eutypella vitis</i> (SCHW.) COOKE GLAWE & JACOBS, 1987	

Variable modes of proliferation in other fungi

While the Diatrypaceae seems to be the only known Ascomycete family where conidiogenous cell proliferation is commonly both sympodial and percurrent within individual species, this phenomenon has been reported in a significant number of fungi representing other Pyrenomycete families, Discomycetes, and Loculoascomy-

cetes. Tab. 2 contains references to species other than Diatrypaceae where this feature has been described or illustrated. The number of taxa listed suggests that this phenomenon may ultimately be found in a larger number of species. The reader should be aware that modes of proliferation likely are not entirely homologous among different groups.

Tab. 2: Species other than Diatrypaceae exhibiting both sympodial and percurrent proliferation of conidiogenous cells

Species	Reference
<i>Ajrekarella polychaetriae</i> KAMAT & KALANI	SUTTON, 1967
<i>Bipolaris tropicalis</i> SIVANESAN	SIVANESAN, 1985
<i>Ceratocystis clavigera</i> (ROBINS.-JEFF. & DAVIDS.) UPADHYAY	TSUNEDA & HIRATSUKA, 1984
<i>Cercoseptoria pini-densiflorae</i> (HORI & NAMBU) DEIGHTON	EVANS, 1984
<i>Colispora elongata</i> MARVANOVÁ	MARVANOVÁ, 1988
<i>Drechslera coicis</i> (NISIKADO) SUBRAM. & JAIN	ELLIS, 1971
<i>Endophragmia biseptata</i> M. B. ELLIS	ELLIS, 1971
<i>Endophragmia uniseptata</i> M. B. ELLIS	ELLIS, 1971
<i>Endophragmiella corticola</i> P. M. KIRK	KIRK, 1982
<i>Endophragmiella hymenochaeticola</i> S. J. HUGHES	HUGHES, 1978
<i>Endophragmiopsis pirozynskii</i> M. B. ELLIS	ELLIS, 1971
<i>Exserticlava globosa</i> RAO & DE HOOG	RAO & DE HOOG, 1986
<i>Gloeosynnema ochroleucum</i> (PENZIG & SACC.) SEIFERT & OKADA	SEIFERT & OKADA, 1988
<i>Graphilbum pleomorphum</i> OKADA & TUBAKI	OKADA & TUBAKI, 1984
<i>Graphium calicioides</i> (FR.) COOKE & MASS.	SUTTON & CAMPBELL, 1978
<i>Hortaea werneckii</i> (HORTA)	NISHIMURA & MIYAJI, 1985

Tab. 2. (cont.)

Species	Reference
NISHIMURA & MIYAJI <i>Hypoxyylon microplacum</i> (BERK. & CURT.) J. H. MILLER	GLAWE & ROGERS, 1986
<i>Lecanosticta cinerea</i> (DEARN.) H. EVANS	EVANS, 1984
<i>Leptographium huntii</i> (ROBINS.- JEFF.) WINGFIELD	WINGFIELD, 1985
<i>Leptographium lundbergii</i> LAGERBERG & MELIN	WINGFIELD, 1985
<i>Leptographium procerum</i> (KEN- DRICK) WINGFIELD	WINGFIELD, 1985
<i>Leptographium terebrantis</i> BARRAS & PERRY	WINGFIELD, 1985
<i>Leptographium truncatum</i> (WINGFIELD & MARASAS) WING- FIELD	WINGFIELD, 1985 (see also WYK & al., 1988)
<i>Microdochium panattonianum</i> (BERL.) SUTTON, GALEA, & PRICE	GALEA & al., 1986
<i>Miurea asiminae</i> (ELLIS & MAR- TIN) v. ARX & O. CONST.	ARX, 1987
<i>Monographella maydis</i> MÜLLER & SAMUELS	MÜLLER & SAMUELS, 1984
<i>Phillipsia crispata</i> (BERK. & CURT. in BERK.) LE GAL	PADEN, 1986
<i>Plectronidium australiense</i> SUT- TON & PASCOE	SUTTON & PASCOE, 1986
<i>Ploiderma lowei</i> CZABATOR	MINTER, 1988
<i>Pseudocercospora helleri</i> (EARLE) DEIGHTON	DEIGHTON, 1976
<i>Pseudocercospora vitis</i> (LÉV.) SPEG.	ELLIS, 1971
<i>Rhinocladiella aquaspersa</i> (BORELLI) SCHELL, MCGINNIS & BORELLI	IWATSU & al., 1987
<i>Rhinocladiella atrovirens</i> NANNF.	TSUNEDA & al., 1986
<i>Rhodesiopsis gelatinosa</i> SUTTON & CAMPBELL	SUTTON & CAMPBELL, 1978
<i>Scopulariopsis koningii</i> (OUD.) VUILL.	HAMMILL, 1971

Tab. 2. (cont.)

Species	Reference
<i>Scedosporium inflatum</i> MALLOCH & SALKIN	MALLOCH & SALKIN, 1984
<i>Seimatosporium kriegerianum</i> (BRESADOLA) MORGAN-JONES & SUTTON	SUTTON, 1964
<i>Sporidesmiella hyalosperma</i> (CORDA) KIRK	ZHANG & al., 1983
<i>Stagonospora delagatensis</i> PARK & KEANE	SWART, 1988
<i>Stagonospora pulcherrima</i> (GAD- GIL & DICK) SWART	SWART, 1988
<i>Stenella anomocanis</i> DE HOOG & BOEKHOUT	DE HOOG & al., 1983
<i>Typhula incarnata</i> LASCH ex FR.	METZLER, 1988
<i>Typhula micans</i> (FR.) BERTHIER	BERTHIER, 1976 (cited in METZLER, 1988)
<i>Vladracula annuliformis</i> (SYDOW & BUTLER) P. CANNON	CANNON & MINTER, 1986
<i>Xylaria longipes</i> NITS.	ROGERS, 1983

Possible mechanisms controlling changes between sympodial and percurrent proliferative growth

At present, little research has been done to determine how and why modes of proliferation vary. Such work seems desirable for two reasons. First, such information may give a clearer indication of the degree to which proliferative modes differ, clarifying their use in taxonomy. Second, understanding the mechanisms of how proliferative modes change may shed light on the control of cell wall synthesis, not only in conidial development, but perhaps also in hyphal growth.

As noted by MINTER (1987) conidial production seems to result from processes basically similar to those involved in hyphal tip elongation. An important aspect of wall synthesis in hyphal growth is that secretory vesicles are concentrated in the cytoplasm at the region where elongation takes place. Similar concentrations of vesicles occur in regions of conidiogenous cells where conidial wall synthesis takes place (MINTER, 1987 and references therein). Unfortunately, relatively few ultrastructural studies are available that characterize the manner in which conidial wall synthesis occurs

(MINTER et al., 1982; MINTER, KIRK & SUTTON, 1983; MINTER, SUTTON & BRADY, 1983). Although no studies have dealt with this aspect of conidial production in Diatrypaceae, it seems likely that cytoplasmic vesicles will be found to play a role in conidial wall synthesis.

One possible explanation for the variable proliferation in Diatrypaceae can be derived from the suggestion (MADELIN, 1979) that a conidiogenous cell proliferates through that site in the wall which is most "physiologically juvenile." This approach suggests that if a delimiting septum is less juvenile (or extensible) than surrounding wall material proliferation would be sympodial. If, however, the delimiting septum is more juvenile than other parts of the wall, the cell would proliferate through the septum. This model may apply to fungi with thickened or melanized conidial secession scars, which might therefore be resistant to plasticization. Conidiogenous regions of diatrypaceous cells, on the other hand, are thin-walled and conidial secession scars appear unthickened (GLAWE & ROGERS, 1982a, 1982b, 1986). Also, wall extension involves a delicate balance between wall lysis and wall synthesis, with both processes being normally involved in regions of cellular extension (GOODAY, 1983). In fungi such as Diatrypaceae, with thin-walled conidiogenous cells, it seems likely that wall plasticization can occur at a variety of locations, both at the site of the delimiting septum (or conidial secession scar), or otherwise.

More recently, WYK et al. (1988) suggested that apparent shifts between sympodial and percurrent proliferation in *Leptographium* LAGERB. & MELIN may be caused by changes in the timing of conidial secession. They suggested that if conidial secession is delayed, proliferation will appear to be shifted to the side of the conidiogenous locus, rather than pushing through the base of the attached conidium. A similar kind of proliferation was described earlier by HUGHES (1978) in *Endophragmiella* B. SUTTON (see also HARVEY, 1974, and SUTTON & CAMPBELL, 1978). WYK et al. (1988) concluded that distinctions between modes of proliferation should be based on wall layers involved in proliferation, even in the case of conidiogenous cells where conidia adhere in a sympodial arrangement.

MADELIN'S (1979) and WYK et al.'s (1988) approaches do seem to explain proliferation in fungi such as species of *Spiropes* CIFERRI, *Pseudospiropes* M. B. ELLIS, *Annellophragmia* SUBRAMANIAN, and other dematiaceous fungi (ELLIS, 1971). In such fungi, thickened conidial secession scars are pushed to the side of a melanized proliferating cell, giving the appearance of sympodial proliferation when in fact the proliferation is at the apex of the cell and parallel to the longitudinal axis of the cell. However, it is not yet clear whether this model can be successfully applied to fungi with hyaline, thin-walled

conidiogenous cells. As MADELIN (1979) noted, the taxonomic significance of different wall layers in conidiogenous regions needs clarification. In fungi with thin-walled, hyaline conidiogenous cells, wall layers frequently are more difficult to distinguish than in dematiaceous fungi. This situation was clearly demonstrated in METZLER'S (1988) ultrastructural study of proliferation in *Typhula incarnata*. Ultrastructural studies on conidiogenous cells in Diatrypaceae (GLAWE & ROGERS, 1982a, 1982b, 1986) provided similar results. Given the facts that such thin-walled conidiogenous cells develop no obvious regions that would structurally interfere with proliferative growth, and that lytic enzymes promoting wall softening are a normal part of wall synthesis, one cannot assume that the site of proliferation is fixed entirely by the cell wall.

In Diatrypaceae and other fungi with similar conidiogenous cells, it seems more likely that proliferation simply occurs where the wall is softened by lytic enzymes. Thus, if the location of wall softening, and concomitant wall synthesis (characterized by localized vesicles within the cell), is precisely restricted to the center of the cell's apex, proliferation would be percurrent and parallel to the longitudinal axis of the cell. If, on the other hand, the location of wall synthesis "wobbles" about the longitudinal axis of the conidiogenous cell, sympodial proliferation would occur. Because conidiogenous cell apices in Diatrypaceae are very small, small shifts in the location of wall-building activity would cause the kind of proliferation to vary.

If this hypothesis is true, one presumably should find that locations of synthetic vesicles differ in sympodially and percurrently proliferating conidiogenous cells, with vesicle locations corresponding to where proliferations arise. In fungi such as Diatrypaceae that exhibit varying modes of proliferation, the location of wall-synthesizing organelles should be less precisely arranged than in fungi such as certain Xylariaceae with exclusively sympodial proliferation, or in certain Diaporthales with exclusively percurrent proliferation. Ultrastructural studies on the cytoplasmic structures and events associated with proliferation in such fungi are needed.

At present, little is known about how environmental or nutritional factors might affect proliferation. Circumstantial evidence suggests that variation in proliferative modes is an inherent characteristic of the organisms, rather than strictly due to environmental influences. While most diatrypaceous anamorphs are known only from culture, *Cryptosphaeria pullmanensis* and *Eutypella sabalina* form both percurrently and sympodially proliferating conidiogenous cells both in nature and in artificial culture, indicating that this phenomenon is not confined to the laboratory (GLAWE, 1984; GLAWE & JONES, 1989). In fact, the environmental fluctuations to

which a fungus is subject in nature (including variations in lighting, temperature, substrate water content, atmospheric relative humidity, etc.) seem far more extreme than those that fungi typically experience in the laboratory. One might go so far as to suggest that single modes of proliferation, if they require stable environmental conditions, should be viewed as artifactual laboratory phenomena.

As shown in Tab. 2, dual modes of proliferation occur in representatives of a wide range of fungal groups. It is possible that different mechanisms account for this phenomenon in different groups. It seems likely that proliferation in Diatrypaceae might not involve the same mechanisms as in Loculoascomycetes with large, heavily melanized conidiogenous cells. The widespread occurrence of variation in proliferative growth in fungi indicates that it is a phenomenon worthy of detailed study, and that additional fungi likely will be found to exhibit it.

Conclusions

In surveying the literature since HUGHES's (1953) paper it is apparent that attitudes regarding the taxonomic significance of conidial ontogeny have undergone periodic shifts. At first, there was a rather slow, measured assessment of conidial ontogeny in a wide variety of fungi, culminating in the account of the first Kananaskis conference (KENDRICK, 1979). By that time many mycologists seemingly came to believe that data on conidial ontogeny would be the single most important class of characters used in classifying Fungi Imperfecti, and it became standard practice to separate otherwise similar fungi into different genera on the basis of differences in conidial ontogeny (or conidiogenous cell proliferation).

More recently, efforts have been directed toward refining basic concepts regarding conidial ontogeny. One important development has been the realization that stages of conidial ontogeny frequently have been confused with the fundamentally separate stages of conidiogenous cell proliferation (MINTER et al., 1982; MINTER, KIRK & SUTTON, 1983; MINTER, SUTTON & BRADY, 1983). MINTER and other authors (MINTER, 1987 and references therein) also focussed attention on the essential similarities between the mechanisms of hyphal growth, conidial development, and conidiogenous cell proliferation. Furthermore, researchers came to realize that certain of the major types of conidial ontogeny recognized by HUGHES (1953) represent points on a continuum of developmental processes. One example of this is the appearance of a number of papers (e.g., MORGAN-JONES et al., 1972; HAMMILL, 1974) noting the similarity of developmental features of annellides and phialides. Similarly, existence of both annellides and sympodulae in a number of fungi suggests that sym-

podial and percurrent proliferation are not fundamentally different (see also GLAWE & ROGERS, 1982a). This increased understanding of proliferation is providing insight into the evolution of conidiogenous cells; for example, GLAWE & ROGERS (1986) recently suggested that diatrypaceous ancestors produced sympodulae, and that evolution is progressing in the direction of increasingly phialide-like cells.

The realization that developmental types can intergrade and can vary within fungi has also served as the basis for reuniting taxa formerly separated because of differences in conidiogenous cell proliferation (e.g., WINGFIELD, 1985). PETRINI & MÜLLER (1986) recently described the anamorph of *Daldinia occidentalis* CHILD as a species of *Nodulisporium* PREUSS on the basis of its overall resemblance to members of that form-genus, even though it differed in producing percurrently rather than sympodially proliferating conidiogenous cells. As the phenomenon of variable conidiogenous cell proliferation has become more widely known, there has developed a clear trend away from giving conidiogenous cell proliferation nearly infinite weight in making taxonomic decisions.

In practice, most evaluations of conidial ontogeny are based on examining secession scars and other features of cell walls. It was logical, therefore, for researchers initially to have emphasized cell walls when investigating and writing about proliferation. Unfortunately, this preoccupation with wall structures has tended to obscure the fact that proliferative growth is the result of processes initiated inside the cell. A much needed change is to shift part of the attention from the conidiogenous cell wall to the cytoplasmic features associated with proliferation. Further application of concepts of wall building proposed by MINTER and colleagues (MINTER et al., 1982; MINTER, KIRK & SUTTON, 1983; MINTER, SUTTON & BRADY, 1983) has the potential to clarify the important issue of how proliferative growth is controlled.

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