

## Review

# Microcycle conidiation—A review

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**Microcycle conidiation is defined as the germination of spores by the direct formation of conidia without the intervention of mycelial growth, as occurs in most normal life cycles. It is a method of asexual spore formation in which the normal life cycle of the fungus is bypassed. Spores formed through sexual reproduction and species with unicellular thalli are not included in microcycle conidiation. The term secondary conidium or secondary spore is usually, but not always, synonymous with microcycle conidiation. In the laboratory various factors, but especially temperature, can induce the microcycle condition in such fungi as *Aspergillus niger*, *Penicillium* and *Neurospora crassa*, providing a useful tool for research. Microcycle conidiation has also been reported in a broad range of species in nature, and comprises a normal part of the life cycle in several groups, including the Entomophthorales, Taphrinales, Clavicipitales, Uredinales, Ustilaginales, Tremellales and Exobasidiales. The presence of a microcycle in such fungi undoubtedly provides a survival mechanism for spores that encounter unfavorable conditions.**

**Key Words**—microcyclic conidiation; secondary conidia; secondary sporulation.

Microcycle conidiation is defined as the germination of spores by the direct formation of conidia, without the intervention of mycelial growth. The term includes both the formation of secondary conidia directly on the spore, as well as on a greatly abbreviated germ tube (Smith et al., 1981). Microcycle conidiation is a method of asexual spore formation in mycelial fungi in which the normal life cycle of the fungus is bypassed. It does not apply to spores formed through sexual reproduction, nor to species with unicellular thalli. Other terms applied to this same general phenomenon include "ascoconidium", "blastoconidia", "capilloconidium formation", "central cell", "conidiation prématurée", "conidiola", "fructificative germination", "indirect germination", "iterative germination", "lag phase sporogenesis", "microconidiation", "microcyclic conidiation", "microcycle sporulation", "microspore formation", "multiplicative sporulation", "paedogenesis", "paedogenetic conidiation", "precocious sporulation", "repetition", "repetitional diplo-netism", "sclerote pedicelée", "secondary ascospores", "secondary ballistospore formation", "secondary chlamydospores", "secondary conidium formation", "secondary sporidia", "secondary sporulation", "secondary zoospore formation", "singular resporulation", "sporulative germination", "sprouting" and "ultimate cells". These terms are generally regarded as synonyms, although Mangenot and Reisinger (1976) distinguish between iterative and secondary sporulation. They use iterative germination for conidia that form conidiophores and conidia directly on the spore, and secondary conidium formation for species in which the conidia are formed directly on hyphal cells, and conidio-

phores are lacking. In this review the formation of conidia directly on hyphal cells is not considered as microcycle conidiation, but rather as a direct form of conidiogenesis. Microcycle conidiation and secondary conidium formation are regarded as synonymous, except in unicellular species in which secondary spore formation is the only form of asexual reproduction.

Microcycle conidiation has been most commonly used to refer to fungi in which the conidia have been induced to produce secondary conidia directly, without mycelium formation, through manipulation of environmental conditions, especially temperature. Anderson and Smith (1971) first used the term to describe the phenomenon they observed in *Aspergillus niger* Tregh. in which conidia subjected to high temperatures swelled and produced conidiophores directly when returned to a lower temperature (Fig. 1). Cortat and Turian (1974) reported a similar phenomenon with macroconidia in *Neurospora crassa* Shear & Dodge, and Rossier et al. (1977) subsequently induced microconidia of *Neurospora crassa* to produce phialides and microconidia directly. Various additional species were demonstrated to behave similarly. The ability to induce microcycle conidiation in various fungi has been a useful tool in biochemical and physiological studies of sporulation, as it has permitted synchronization and simplification of the conidiation process. Species in which the production of secondary conidia has been reported may also germinate by means of germ tubes, but the two types of germination seem not to occur in the same spore.

In the above species the microcycle condition has resulted from manipulation of cultures in the laboratory,

Table 1. Additional species in which secondary spore formation has been reported.

Name	Reference
Entomophthorales	
<i>Basidiobolus ranarum</i> Eidam*	Callaghan, 1969
<i>Entomophthora apiculata</i> (Thaxter) M. Gustafs.	Gustafsson, 1965
<i>E. conica</i> Nowakowski	Gustafsson, 1965
<i>E. curvispora</i> Nowakowski	Gustafsson, 1965
<i>E. elateridiphaga</i> Turian	Remaudière et al., 1976
<i>E. geometralis</i> (Thaxter) M. Gustafs.	Gustafsson, 1965
<i>E. phalloides</i> Batko	Remaudière et al., 1976
<i>E. rhizospora</i> (Thaxter) M. Gustafs.	Gustafson, 1965
<i>E. sphaerosperma</i> Fres.	Sawyer, 1931
<i>Meristacrum asterospermum</i> Drechs.	Drechsler, 1940
Leotiales	
<i>Claussenomyces luteoviridis</i> Ouellette & Korf	Ouellette and Pirozynski, 1974
<i>C. pseudotsugae</i> (Groves) Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>Tympanis alnea</i> Pers.: Fr.	Ouellette and Pirozynski, 1974
<i>T. alpina</i> Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>T. amelanchieris</i> Groves	Ouellette and Pirozynski, 1974
<i>T. confusa</i> Nyl.	Ouellette and Pirozynski, 1974
<i>T. conspersa</i> Fr.	Ouellette and Pirozynski, 1974
<i>T. fasciculata</i> Schwein.	Ouellette and Pirozynski, 1974
<i>T. heteromorpha</i> Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>T. hydrangeae</i> Groves	Ouellette and Pirozynski, 1974
<i>T. hypopodia</i> Nyl.	Ouellette and Pirozynski, 1974
<i>T. hysterioides</i> Rehm	Ouellette and Pirozynski, 1974
<i>T. laracina</i> (Fuckel) Sacc.	Ouellette and Pirozynski, 1974
<i>T. myricariae</i> Höhn. & Rehm	Ouellette and Pirozynski, 1974
<i>T. neopithya</i> Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>T. oxydendri</i> Ell. & Everh.	Ouellette and Pirozynski, 1974
<i>T. prunicola</i> Groves	Ouellette and Pirozynski, 1974
<i>T. pseudoalnea</i> Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>T. pulchella</i> Ouellette & Pirozynski	Ouellette and Pirozynski, 1974
<i>T. rhabdospora</i> Berk. & Curt.	Ouellette and Pirozynski, 1974
<i>T. saligna</i> Tode: Fr.	Ouellette and Pirozynski, 1974
<i>T. truncatula</i> (Pers.: Fr.) Rehm	Ouellette and Pirozynski, 1974
<i>T. tsugae</i> Groves	Ouellette and Pirozynski, 1974
Moniliales	
<i>Alternaria alternata</i> (Fr.) Keissler	Ellis, 1971
<i>A. brassicicola</i> (Schwein.) Wiltshire	Ellis, 1971
<i>A. raphani</i> Groves & Skolko	Ellis, 1971
<i>Aureobasidium caulivorum</i> (Kirch.) W. B. Cooke	Hermanides-Nijhof, 1977
<i>A. lini</i> (Lafferty) Herm.-Hij.	Hermanides-Nijhof, 1977
<i>A. microstictum</i> (Bubák) W. B. Cooke	Hermanides-Nijhof, 1977
<i>Exophiala dermatitidis</i> (Kano) de Hoog	De Hoog, 1977
<i>E. mansonii</i> (Castell.) de Hoog	De Hoog, 1977
<i>E. salmonis</i> Carmichael	De Hoog, 1977
<i>Hormonema dematiooides</i> Legerb. & Melin	Hermanides-Nijhof, 1977
<i>H. prunorum</i> (Dennis & Buhagiar) Herm.-Nij.	Hermanides-Nijhof, 1977
<i>Helicoma tenuifolium</i> Linder	Pirozynski, 1972
<i>Helicomyces fuscopes</i> Linder	Pirozynski, 1972
<i>H. roseus</i> Link	Pirozynski, 1972
<i>Helicosporium pannosum</i> R. T. Moore	Pirozynski, 1972
<i>H. phragmitis</i> Höhn.	Sivanesan, 1984
<i>Leptodontium beauveriooides</i> De Hoog	De Hoog, 1977
<i>Phaeococcus nigricans</i> (Rich & Stern) De Hoog	De Hoog, 1977
<i>Sarcinomyces crustaceus</i> Lindner	Hermanides-Nijhof, 1977
<i>Stemphylium ilicis</i> Tengwall	Neergaard, 1945

<i>Xenosporium mirabile</i> Penz. & Sacc.		Ellis, 1963
	Uredinales	
<i>Chrysomyxa himalense</i> Barclay		Barclay, 1890b
<i>Gymnosporangium cunninghamianum</i> Barclay		Barclay, 1890a
<i>Puccinia coronata</i> var. <i>himalensis</i> Barclay		Barclay, 1891b
<i>P. jasmini-chrysopogonis</i> Barclay		Barclay, 1891c
<i>Uromyces cunninghamianus</i> Barclay		Barclay, 1981a
	Tremellales	
<i>Arrhytidia pustulata</i> Brasfield		Brasfield, 1938a
<i>Basiodendron caesio-cinerea</i> (Höhn. & Litsch.) Luck-Allen		Luck-Allen, 1963
<i>B. cinerea</i> (Bres.) Luck-Allen		Luck-Allen, 1963
<i>B. deminuta</i> (Bourd.) Luck-Allen		Luck-Allen, 1963
<i>B. eyrei</i> (Wakef.) Luck-Allen		Luck-Allen, 1963
<i>B. grandinioides</i> (Bourd. & Galz.) Luck-Allen		Luck-Allen, 1963
<i>B. nodosa</i> Luck-Allen		Luck-Allen, 1963
<i>B. pini</i> (Jackson & Martin) Luck-Allen		Luck-Allen, 1963
<i>B. rimosa</i> (Jackson & Martin) Luck-Allen		Luck-Allen, 1963
<i>B. rimulenta</i> (Bourd. & Galz.) Luck-Allen		Luck-Allen, 1963
<i>B. subreniformis</i> Luck-Allen		Luck-Allen, 1963
<i>Calocera macrospora</i> Brasfield		Brasfield, 1938a
<i>Ceratobasidium mycophagum</i> M. P. Christiansen		Ginns, 1986
<i>Dacrymyces dictyosporus</i> Martin		Martin, 1958
<i>Dacryomitra cystidiata</i> Brasfield		Brasfield, 1938a
<i>D. glossoides</i> Bref.		Brasfield, 1938a
<i>D. stipitata</i> (Peck) Burt		Brasfield, 1938a
<i>Ditiola radiata</i> (Alb. & Schwein.) Fr.		McNabb, 1966b
<i>Ductifera succina</i> (Möller) Wells		McNabb, 1966a
<i>Exidia nucleata</i> (Schwein.) Burt		McNabb, 1966a
<i>Helicogloea lagerheimii</i> Pat.		Ingold, 1992b
<i>Heterotexus flavus</i> Lloyd		Martin, 1936
<i>Jola basidioli</i> Lagerh.		Gäumann, 1922b
<i>J. javensis</i> Gäumann		Gäumann, 1922b
<i>Platygloea sphaerospora</i> Martin		Martin, 1934
<i>Saccoblastia farinacea</i> (Höhn.) Donk		Ingold, 1992b
<i>Sebacina epigaea</i> (Berk. & Br.) Rea		McNabb, 1966a
<i>S. cinerea</i> Bres.		McNabb, 1966a
<i>S. filicola</i> McNabb		McNabb, 1966a
<i>S. megaspora</i> Martin		Martin, 1936
<i>S. mucedinea</i> Pat.		McNabb, 1966a
<i>S. pteridicola</i> McNabb		McNabb, 1966a
<i>S. sublilacina</i> Martin		Martin, 1934
<i>Seismosaria hydrophora</i> Cooke		Martin, 1936
<i>Sirobasidium sanguineum</i> Lag. & Pat.		Martin, 1936
<i>Syzygospora alba</i> Martin		Ginns, 1986
<i>S. effibulata</i> (Ginns & Sunhede) Ginns		Ginns, 1986
<i>S. marasmoidea</i> Ginns		Ginns, 1986
<i>S. norvegica</i> Ginns		Ginns, 1986
<i>S. pallida</i> (Hauerslev) Ginns		Ginns, 1986
<i>S. solida</i> (Berthier) Ginns		Ginns, 1986
<i>S. subsolida</i> Ginns		Ginns, 1986
<i>S. tumefaciens</i> (Ginns & Sunhede) Ginns		Ginns, 1986
<i>Tremella fuciformis</i> Berk.		McNabb, 1966a
<i>T. lutescens</i> Pers.: Fr.		McNabb, 1966a
	Septobasidiales	
<i>Septobasidium acaciae</i> Sawada		Couch, 1938
<i>S. bogoriense</i> Pat.		Gäumann, 1922a
<i>S. jamaicaense</i> Burt		Couch, 1938

\* Binomials are listed as given in the original papers and have not been checked for currency or synonymy.

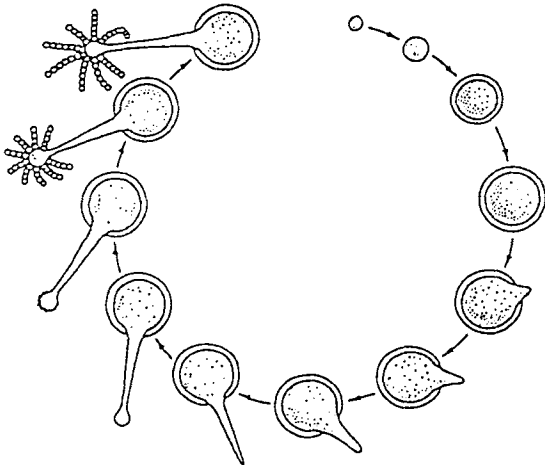
Microcycle for *Aspergillus niger*

Fig. 1. Stages in the microcycle of *Aspergillus niger*. Redrawn from Smith et al. (1981). Drawing by Carol Gubbins Hahn.

but the production of secondary conidia by germinating spores also has been observed in various fungi from field collections or in cultures that have not been subjected to such specialized conditions. Most references to secondary conidium formation are mentioned only incidentally in publications, making them difficult to glean from the literature. Consequently, the examples that follow are meant to be representative rather than exhaustive, although the names of all species encountered that are known to form secondary conidia are included either in the text or in Table 1. In this review emphasis is placed on the taxonomic diversity and variation in behavior of the fungi exhibiting this phenomenon.

### Chytridiomycotina

In certain chytrids the zoospores swim and encyst, after which they may germinate by different methods. In *Anisolpidium saprobium* Karling, *Rhizidiomyces bulbosus* Karling, *R. coronus* Karling, and *R. hirsutus* Karling encysted zoospores can produce secondary zoospores under certain conditions (Karling, 1968).

In the filamentous Chytridiomycete genus *Allomyces* there is normally an alternation of haploid and diploid generations in the life cycle. In subgenus *Cystogenes*, however, the zoospores from the resistant sporangium encyst as in the normal life cycle, but instead of forming a germ tube upon germination, they give rise to secondary zoospores (Emerson, 1941).

In *Blastocladiella emersonii* Cantino & Hyatt the life cycle can be reduced to a unicellular germling that generates and releases a single functional zoospore (Hennessy and Cantino, 1972) when the fungus is cultured in dilute

phosphate buffer.

### Oomycotina

Various members of the Saprolegniales typically undergo a process referred to as "diplanetism", in which a pyriform primary zoospore is released from the sporangium. After swimming it encysts, then gives rise to a reniform secondary zoospore. True secondary spores are formed, however, in *Achlya* and *Dictyuchus*, in which the secondary zoospores can encyst and reemerge repeatedly. This is believed to be influenced by environmental conditions (Sparrow, 1960).

### Zygomycotina

Secondary conidium formation has been observed in a number of species in the Entomophthorales, where it occurs normally in the life cycle. In *Basidiobolus haptosporus* Drechs. the primary conidia germinate by forming a long, slender conidiophore at the tip of which is borne an elongated secondary conidium with an adhesive beak (Drechsler, 1947). In *B. meristosporus* Drechs. the primary conidia are globose. Primary conidia may germinate by forming a globose secondary conidium or an elongate conidium with an adhesive tip. Both globose and elongate conidia may also cleave internally into several spores (Drechsler, 1955b). In *B. microsporus* R.K. Benjamin (1962) primary and secondary spores are formed as in *B. meristogenous*, but in *B. microsporus* the globose conidia, after dividing internally, form large numbers of external spores that Benjamin terms microspores. Several types of conidium germination are found in species of *Conidiobolus*. In *C. brefeldianus* Couch (1939), *C. couchii* Srinivasan & Thirum. (Srinivasan and Thirumalachar, 1968), *C. lobatus* Srinivasan & Thirum. (Srinivasan and Thirumalachar, 1968), *C. firmipilleus* Drechs. (Drechsler, 1953) and *C. rhyssosporus* (Dring, 1958) the conidia may germinate by forming secondary conidia that are also forcibly discharged. In *C. heterosporus* Drechs. (Drechsler, 1953) conidia that fall onto fresh medium germinate by forming germ tubes, but if the conidia fall near existing mycelium they germinate by forming a secondary conidium. In *C. polytocus* Drechs. and *C. chlamydosporus* Drechs. (Drechsler, 1955a) the conidia may also form secondary conidia; in *C. chlamydosporus* this occurs under dry conditions. In both of these species, however, the conidia also may form microconidia on short stalks. From 5-15 microconidia may form on a single conidium. Conidia of *C. obscurans* (Hall & Dunn) Remaudiere & Keller normally produce secondary conidia spontaneously, but if the primary conidia contact moisture before the initiation of secondary conidia, germ tubes form instead (Uziel et al., 1981). In *C. pumilus* Drechs. the primary conidia are globose. When germinated on agar they give rise to two kinds of secondary conidia, one of which is globose, the other ellipsoid (Drechsler, 1955c).

Conidia of *Entomophthora coronata* (Pat.) Kevorkian germinated on agar medium may form either a germ tube

and mycelium or a secondary conidium. Under conditions of abundant moisture, nutrients and warmth, primary conidia may produce a series of short tubes over the surface, each of which bears a microconidium (Kevorian, 1937). In *E. aphidis* Hoffman, *E. fresenii* (Nowakowski) Gustafsson, and *E. planchoniana* Cornu the primary conidia form secondary conidia on the insect cuticle prior to invasion. In *E. thaxteriana* (Petch) Hall & Bell the primary conidium produced a germ tube that invaded the host (Brobyn and Wilding, 1977), but under certain conditions secondary conidia can be produced (Wilding, 1969).

In *Zoophthora phalloides* Batko primary conidia can germinate by forming capilloconidia, in which the primary conidium gives rise to a long, slender tube, at the tip of which is formed the capilloconidium (Glare et al., 1985). Conidia of *Z. radicans* (Bref.) Batko can germinate Y forming a secondary conidium that is forcibly discharged, or by a capilloconidium that is passively released. Capilloconidium formation is greater on water agar than on maltose-yeast-extract medium (Van Roermund et al., 1984).

## Ascomycotina

### Hemiascomycetes

Because of their morphology, the unicellular yeasts of necessity reproduce in this fashion. Ascospores of *Saccharomyces*, e.g., germinate by producing blastospores which continue to reproduce by budding. Because there is no mycelial stage to be bypassed, however, this is not regarded as true microcycle conidiation.

Ascospores of *Taphrina* typically germinate by means of blastospores, which subsequently produce the mycelium. The blastospores themselves may produce secondary blastospores, forming yeast-like colonies in culture. In *T. deformans* (Berk.) Tul., *T. caerulescens* (Desmaz. & Mont.) Tul. and numerous other species, ascospores form blastospores while they are still inside the ascus, resulting in a polysporous ascus (Mix, 1949).

Muthappa (1969) described an unusual method of ascospore budding in a collection of *T. ulmi* (Fuckel) Johanson from winged elm (*Ulmus alata* Michx.). The ascospores put out a short germ tube that grew out through the ascus wall. Conidia were then formed outside the ascus on the tip of the protruding hypha. No conidia formed inside the ascus.

### Discomycetes

Among the operculate discomycetes several species have been shown to produce secondary conidia, including *Cookeina sulcipes* (Berk.) Kuntze (Boedijn, 1929), *C. tricholoma* (Mont.) Kuntze (Boedijn, 1933), *Nanoscypha tetraspora* (Seaver) Denison (Pfister, 1973), *Phillipsia domingensis* (Berk.) Berk. (Paden, 1974) and *P. rugospora* Paden (Paden, 1977), *Sarcoscypha austriaca* (Berk. ex Sacc.) Boud. (Harrington, 1990), *S. coccinea* (Fr.) Lambotte (Alexopoulos and Butler, 1949), *S. coccinea* var. *jurana* Boud. (Rosinski, 1953), and *S. occiden-*

*talis* (Schwein.) Sacc. (Harrington, 1990).

In the inoperculate discomycete *Neobulgaria pura* (Pers.: Fr.) Petrak the ascospores form blastospores while still inside the ascus (Berthet, 1964). In *Encoelia pruinosa* (Ell. & Everh.) Torkelson & Eckblad ascospores discharged onto water agar formed phialides that produced microconidia (Juzwik and Hinds, 1984). In members of the genus *Tympanis* the ascospores typically germinate while still inside the ascus. In some species conidia are formed directly on the ascospore, but in others they are formed on a short "intermediate" cell. Since the pattern of ascospore germination appears to be consistent within different groups in the genus, it has been considered to be of taxonomic importance (Ouellette and Pirozynski, 1974). Ascospores of *Monilinia fructicola* (G. Wint.) form short germ tubes bearing phialides and microconidia when germinated in water.

### Pyrenomycetes

Panuelo Ruiz (1927) reported that the ascospores of *Erysiphe polygoni* DC. and *E. taurica* Lév. germinated by forming numerous small conidia. These conidia subsequently divided into groups of cells.

Bertus (1927) reported that ascospores of *Glomerella piperata* (Stoneman) Spauld. & H. Schrenk sometimes germinated by forming conidia, in addition to the formation of germ tubes.

In *Valsaria insitiva* (Tode: Fr.) Ces. & De Not. the ascospores produce ovoid yeast-like cells upon germination, and these cells in turn reproduce by budding (Glawe, 1985). In *Calosphaeria cryptospora* Munk the ascospores bud while still inside the ascus to produce numerous allantoid conidia (Munk, 1957). In *Romellia tympanoides* M. E. Barr, also in the Calosphaeriales, the ascospores bud while inside the ascus (Barr, 1985). Ascospores of *Bertia moriformis* (Tode: Fr.) De Not. germinated in water can produce phialides and microconidia, as can the ascospores of another lignicolous species tentatively identified as *Ceratospaeria rhenana* (Auersw.) G. Wint. (unpublished observations).

Ascospores of *Nectria aquifolii* (Fr.) Berk., *N. coryli* Fuckel, *Scoleconectria cucurbitula* (Tode: Fr.) Booth, *Thyronectria balsamea* (Cooke & Peck) Seeler, and *T. jamiyi* (Desmaz.) Seeler all form conidia (ascoconidia) while still inside the ascus. Ascospores of *T. berolinensis* (Sacc.) Seaver also form conidia, but only after they are discharged from the ascus (Booth, 1959; Rossman, 1983).

In *Claviceps sorghi* Kulkari, Seshadri & Hegde the macroconidia can reproduce by forming secondary conidia on slender conidiogenous cells (Bandyopadhyay et al., 1990). These secondary conidia then germinate by means of germ tubes. Pazoutová et al. (1978) described a mutant of *Claviceps purpurea* (Fr.: Fr.) Tul. that occasionally formed secondary conidia when grown in submerged culture.

In *Epichloe typhina* (Pers.: Fr.) Tul. ascospores germinate by the formation of conidiogenous cells and conidia (Bacon and Hinton, 1988). The conidia thus

formed also reproduce by microcycle conidiation (Bacon and Hinton, 1991). Since ascospores seem to never form mycelia, microcycle conidiation is considered to be obligatory in this species.

Blackwell et al. (1986) described an unusual phenomenon in a species of *Pyxidiophora* that may be regarded as a variation on microcycle conidiation. The ascospores in this fungus, instead of forming germ tubes, differentiate directly into a hyphomycetous anamorph belonging to the genus *Thaxteriola*. This occurs while the ascospores are still inside the ascus and ascoma. *Thaxteriola* itself is unusual in that it is specialized for insect dispersal. Similar development of an anamorph from ascospores was later discovered in *P. kimbroughii* M. Blackwell & T. J. Perry (Blackwell et al., 1986) and *P. spinuliformis* (Speg.) Lundq. (Blackwell and Malloch, 1989).

### Loculoascomycetes

A somewhat different but related phenomenon was reported in *Fenestella princeps* Tul. & C. Tul. Ascospores of this species germinate by means of germ tubes, but then the ascospore itself becomes transformed into a pycnidium containing conidiogenous cells and conidia (Huhndorf and Glawe, 1990). Thus the intermediate mycelial stage that normally occurs is bypassed.

Gäumann and Dodge (1928) cite Brefeld (1891) in reporting that ascospores of *Sphaerulina intermixta* (Berk. & Br.) Sacc. [= *Sacothecium sepincola* (Fr.) Fr.] may bud under certain environmental conditions. Gäumann and Dodge questioned this report, but later Bond (1946) described a similar phenomenon in *S. mappiae* (Petch) Bond. Clumps of ascospores bearing numerous conidia were found around the ostioles of naturally occurring ascomata. These ascospores were larger than those in the asci and were often 2-3 septate. When freshly discharged ascospores were placed in water they germinated by means of germ tubes. To Bond this suggested that secondary conidia formed under conditions of high humidity, in the absence of free water.

Ascospores of *Metacapnodium spongiosum* S. Hughes & Sivan., *Ophiocapnocomma batistae* S. Hughes, and *O. philophilia* (Fisher) S. Hughes all form phialides and conidia under certain conditions (Sivanesan, 1984), and both the ascospores and conidia of *Tubeufia helicoma* (Phill. & Plowr.) Piroz. are capable of forming secondary conidia (Sivanesan, 1984).

The *Hormonema* states of *Dothiora* and *Pringsheimia* species have been reported to form secondary conidia (Hermanides-Nijhof, 1977).

### Deuteromycotina

Among the conidial fungi, perhaps the most striking examples of secondary conidium formation are found in the "shadow yeasts", in the genera *Bullera* Derx and *Sporobolomyces* Kluyver & van Neil. In both of these genera the unicellular thallus cells form ballistospores that are forcibly discharged onto the surrounding sub-

strate (Phaff, 1971). This is not regarded as true microcycle conidiation, however, since no phase of the life cycle is bypassed.

*Geotrichum candidum* Link reproduces by means of arthrospores, and when grown in the absence of exogenous carbon and nitrogen, these arthrospores can be induced to form secondary arthrospores directly (Park and Robinson, 1969).

*Aureobasidium pullulans* (De Bary) Arn. forms masses of secondary conidia on a variety of agar media (Hermanides-Nijhof, 1977; Hoggan, 1924).

In *Thielaviopsis basicola* (Berk. & Br.) Ferraris endoconidia may germinate and form a short conidiophore that produces secondary endoconidia (Lindeman, 1970; Stover, 1950), instead of the usual hypha. Endoconidia in this fungus also have been observed to form "secondary chlamydospores" that are similar in appearance to the primary chlamydospores (Schippers, 1970; Stover, 1950).

*Aspergillus flavus* Link: Fr., *A. giganteus* A. glaucus Link: Fr., and *A. oryzae* (Ahlburg) Cohn all have been induced to form the microcycle condition in culture (Smith et al., 1981), as have *Paecilomyces varioti* Bainier (Anderson et al., 1978) and *Penicillium urticae* Bainier (Sekiguchi et al., 1975a, b, c). Protoplasts of *A. awamori* van Tieghem released by digestion of the wall sometimes produce conidiophores bearing phialides and conidia six hours after removal from the digestive mixture (Bobbitt and Douglas, 1982). In *A. niger* the initial enlargement of the spore (giant cell formation) is primarily affected by high temperature, with an optimum of 44°C. The temperature range, however, is narrow; at 42°C autolysis occurs and at 46°C there is no activation of the conidia. The addition of L-alanine to the medium provides greater suppression of germ tube formation, and a low concentration of glutamic acid is essential. The addition of CO<sub>2</sub> has little effect on the microcycle and the concentration of glucose is not critical.

In *Penicillium digitatum* (Pers.: Fr.) Sacc. microcycle conidiation could be induced by growing the fungus in medium containing certain amino acids (e.g. glutamic acid) (Zeidler and Margalith, 1973). In *P. notatum* Westling, however, growth of conidia in basal medium containing CaCl<sub>2</sub> induced microcycle conidiation (Hadley and Harrold, 1958), and in *P. italicum* Wehmer the pH of the medium exerts primary influence on conidiation (Van Gestel, 1983).

In the *Colletotrichum* state of *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk secondary conidia are formed when conidia become too crowded. This phenomenon can be duplicated in the laboratory and is considered to be due to growth inhibitors produced by the conidia (Lingappa and Lingappa, 1969).

When grown in a dilute, nutrient-poor medium macroconidia of *Neurospora crassa* produce short germ tubes that become conidiophores. High temperatures are not needed to induce microcycle conidiation (Plesofsky-Vig et al., 1983). Maheshwari (1991) found a naturally occurring isolate of *N. crassa* that spontaneously underwent microcycle conidiation in liquid medium. From this

isolate he derived strains that showed three types of microcycle conidiation: multinucleate blastoconidia, multinucleate arthroconidia, and uninucleate microconidia. Two genes were identified that control the specific patterns of microcycle conidiogenesis in these strains.

Conidia of *Cephalosporium asteris* Dowson germinated in hanging drop culture form a short germ tube that immediately becomes a conidiophore that produces conidia at the apex (Dowson, 1923).

Macroconidia of *Fusarium solani* (Mart.) Wr. form short germ tubes bearing phialides and conidia when germinated in water (Booth, 1960). Park (1956) reported that conidia of *F. roseum* Link: Fr. growing with *Bacillus macerans* Schardinger sometimes germinated by forming secondary conidia directly.

Among the dematiaceous hyphomycetes, secondary spores are induced in *Alternaria porri* (Ellis) Cif. f. sp. *solani* when factors interfere with normal germination patterns. Drying of conidia and lack of nutrients favor microcycle conidiation (Rotem and Bashi, 1969). Drechsler (1923) observed that conidia of *Drechslera catenaria* (Drechs.) Ito (= *Helminthosporium catenarium* Drechs.) and *D. graminea* (Rabenh.) Shoemaker (= *H. gramineum* Rabenh.) naturally formed secondary conidia on short germ tubes produced by the spores. He also reported that when grown on agar under moist conditions, conidia of *D. teres* (Sacc.) Shoemaker (= *H. teres* Sacc.), *D. campanulata* (Lév.) Sutton (= *H. cyclops* Drechs.), and *Bipolaris sorokiniana* (Sacc.) Shoemaker (= *H. sativum* Pammel, C. M. King & Bakke) could germinate while on the conidiophore, and that the conidia in turn formed secondary spores, producing a ramified network. In *B. sorokiniana* conidia formed single germ tubes at each end of the spore bearing a single conidium. This occurred most often in conidia incubated in soil for up to 180 days at 3° and 22°C, then amended with potato dextrose agar (Boosalis, 1962). Conidia of *B. spicifera* (Bainier) Subramanian [= *H. spiciferum* (Bainier) J. Nicot] form conidiophores and conidia directly when germinated in distilled water (Mangenot and Reisinger, 1976). In *Cercospora kikuchii* (Matsumoto & Tomoyasu) M. W. Gardner conidia suspended in distilled water for 24 h commonly formed secondary conidia. Although smaller in size, secondary conidia resembled primary conidia in other respects (Fernandez et al., 1991). Berger and Hanson (1963) observed that when cultures of *C. zebrina* Pass. were grown in an incubator for 12 days with little light, followed by transfer to a laboratory bench, numerous conidia germinated by forming a conidiophore with a secondary conidium. A regime of total darkness reduced but did not eliminate the formation of secondary conidia. Secondary conidia were indistinguishable from primary conidia. When sugarbeet leaves were inoculated with conidia of *C. beticola* Sacc. and kept under continuous high relative humidity (RH), the conidia germinated and formed normal germ tubes. When the RH was lowered for six hours daily, conidia often germinated by forming conidiophores and secondary conidia (Rathaiah, 1977).

Some helicosporous fungi also form secondary

conidia (Linder, 1929, 1931). Pirozynski (1966) has demonstrated the presence of secondary conidia in several species of *Xenosporium*, including *X. africanum* Pirozynski, *X. berkeleyi* (Linder) Pirozynski, *X. pleurococcum* (Höhn.) Pirozynski and *X. thaxteri* (Linder) Pirozynski. Goos (1975) also described secondary conidia in *Helicoma proliferans* Linder [= *Helicosporium viride* (Corda) Sacc.]. These conidia are usually spherical and may be unicellular or dictyosporous. They are formed directly on the surface of the cells of the primary conidia.

In *Itersonilia perplexans* Derx the ballistospores can germinate by forming secondary ballistospores (Webster et al., 1984). The mycelium of *I. perplexans* also forms blastoconidia; these are monokaryotic and they reproduce by budding. The resulting yeast-like cells may also form ballistospores on short sterigmata (Ingold, 1984a).

### Basidiomycotina Heterobasidiomycetes

Interestingly, the formation of basidiospores from teliospores in the Uredinales (rusts) and Ustilaginales (smuts) occurs in the same manner as microcycle conidiation, with the basidiospores forming on short germ tubes (the basidia) produced by the teliospores. Since these are sexual spores resulting from meiosis they are not included in this discussion, but the basic process of spore formation is similar.

Microcycle conidiation does occur in the rusts, however. Barclay (1891a) reported that basidiospores of *Puccinia prainiana* Barclay sometimes form secondary spores when germinated in water, and Colley (1918) and Spaulding and Rathbun-Gravatt (1926) reported the formation of secondary ballistospores by basidiospores of *Cronartium ribicola* Fischer. Such germination was favored by keeping the discharged basidiospores continuously moist. Bega (1960) reported that the basidiospores in *Cronartium ribicola* are capable of repeated spore formation. This apparently occurs in nature, but in the laboratory secondary spore formation is favored by alkaline pH of the medium on which they are germinated. Kais (1963) reported that basidiospores of *C. fusiforme* Hedgc. & Hunt ex Cumm. produce secondary basidiospores in vitro, with up to six generations being formed. Miller and Roncadori (1966) showed that secondary basidiospores in this species are forcibly discharged, and Roncadori (1965, 1968) demonstrated that secondary and tertiary basidiospores are capable of infecting their host and producing typical disease symptoms. Sappin-Trouffy (1896) reported secondary conidium formation in basidiospores of *C. flaccidum* Alb. & Schwein., as well as in *Coleosporium sunchi* Pers., *Endophyllum euphorbiae-silvaticae* DC., *Gymnosporangium sabiniae* Dicks., and *Puccinia malvacearum* Bertero ex Mont. Basidiospores of *G. juniperi-virginianae* Schwein. germinate by forming sterigmata and secondary spores when they are kept constantly moist following discharge (Reed and Crabill, 1915). The ultrastructural details of secondary spore formation in this species have been reported by Mims and

Richardson (1990).

Among the Ustilaginales, members of the Tilletiaceae often form secondary spores. In *Tilletia caries* (DC.) Tul. & C. Tul., *T. tritici* (Berk.) R. Wolf (Ingold, 1987b) and *T. lolii* (DC.) Tul. (Ingold, 1992a) the basidiospores conjugate in pairs, then give rise to ballistospores on sterigmata. In *T. ayresii* Berk. ballistospores may germinate either by repetition or by forming a rod-shaped blastic conidium (Ingold, 1987a). Goates and Hoffman (1986) have studied the ultrastructure of secondary spore formation and discharge in *T. foetida* (Wallr.) Liro (= *T. laevis* Kühn).

The tremellaceous fungi comprise another group in which secondary conidium formation occurs normally. Brasfield (1938b) stated that all species in the genera *Arrhytidia* Berk., *Calocera* Fr., *Dacryomitra* Tul., *Dacrymyces* Nees: Fr., *Femsjohnia* Fr., *Guepinia* and *Guepiniopsis* (Fr.) Pat. form secondary conidia. In *Auricularia auricula-judae* (Bull.: St. Am.) Wetts. and *A. mesenterica* (S.F. Gray) Pers. the basidiospores are capable of germinating by three different methods. When discharged onto agar, basidiospores germinate by forming germ tubes and hyphae. If the basidiospores land near an established mycelium, however, they germinate by forming conidiophores and conidia. If stranded on the hymenium, they germinate by repetition, i.e., the formation of a secondary ballistospore (Ingold, 1982, 1984c). Conidia of *Calocera viscosa* (Pers.: Fr.) Fr., *C. pallidospathulata* Reid, *Dacrymyces stillatus* Nees: Fr., and *Ditiola peziziformis* (Lév.) Reid all germinate by means of germ tubes on agar, but when discharged onto glass slides kept in a saturated atmosphere, they form conidia on tiny conidiophores (Ingold, 1983). In *Exidia glandulosa* (St. Am.) Fr. basidiospores from the surface of the sporophore germinate by forming secondary ballistospores (Ingold, 1982c). This also occurs in *Myxartium nucleatum* Wallr. (Ingold, 1984b). In *Exidia thuretiana* (Lév.) Fr., *Pseudohydnum gelatinosum* (Scop.: Fr.) Fr., and *Tremella encephala* Pers. the basidiospores form blastoconidia (Ingold, 1985). In *Dicellomyces scirpi* Raitv. conidia on agar germinate by forming a short germ tube at the end of each cell, on which is formed a secondary conidium (Ingold, 1985a, b). In *Tremella foliacea* Retz. ex Hooker (Ingold, 1982c) and *T. mesenterica* Hooker (Ingold, 1982b) basidiospores taken from the hymenium of a sporophore germinate by forming secondary ballistospores. When discharged onto agar, however, both species form numerous blastospores over their surface. The blastospores themselves can reproduce by budding (Ingold, 1982c). In *Tilletiopsis washingtonensis* Nyland basidiospores shot onto malt agar germinated by forming elongate blastospores at each end; these can in turn reproduce by budding. Later, hyphae are formed and soon begin forming ballistospores, which occasionally germinated by repetition.

In *Tulasnella cystidiophora* Höhn. & Litsch. basidiospores that remain on the hymenium germinate by forming ballistospores. On malt agar they form conidiophores and stellate conidia (Ingold, 1984c). In *T. helicospora* Raunkiaer, *T. interrogans* P. Roberts, and *T.*

*anguifera* P. Roberts the basidiospores form secondary conidia when mounted for microscopic observation (Roberts, 1992).

In species of *Septobasidium*, such as *S. burtii* Lloyd, the basidiospores may form conidia after discharge (Couch, 1938).

In *Exobasidium vaccinii* (Fuckel) Woron. the basidiospores form elongated blastoconidia when germinated on agar (Ingold, 1985); these in turn can form secondary conidia (Mims and Richardson, 1987). In *E. japonicum* Shir. basidiospores discharged onto agar formed short germ tubes on which were formed elongate conidia. These in turn formed elongate secondary conidia (Ingold, 1985b).

### Summary

Microcycle conidiation is a process whereby the normal life cycle of a fungus may be bypassed, with spores germinating to form secondary spores directly, without formation of mycelium. The term does not apply to spores formed through sexual reproduction nor to species with unicellular thalli that reproduce by budding. Numerous species of fungi in diverse taxa are capable of exhibiting this phenomenon. In some groups of fungi, most notably the Entomophthorales, Taphrinales, Clavicipitales, Uredinales, Ustilaginales, Tremellales, and Exobasidiales this occurs as a natural part of the life cycle. In other groups it may be induced by particular environmental conditions, apparently as a means of survival when suboptimal conditions are encountered. Such factors as drought, reduced nutrition, change in pH, reduced humidity, and temperature all influence conidiation in various fungi. There is no single factor that is effective with all such species. The occurrence of microcycle conidiation under natural conditions provides a significant advantage to species possessing this capability when their spores form and/or are discharged under conditions unfavorable for spore germination. This is especially true of plant pathogens that are able to infect their hosts only under a limited range of environmental conditions. Lastly, the induction of microcycle conidiation in various conidial fungi has proved to be a useful tool in biochemical and genetic studies of the conidiation process in the laboratory.

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