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IMPERFECT STATES AND THE TAXONOMY OF THE PEZIZALES*

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(With Plates 20–22)

Certainly only a relatively few species of the Pezizales have been studied in culture. I hope that this paper will stimulate more efforts in this direction. A few patterns are emerging from those species that have been cultured and have produced conidia but more information is needed. Botryoblastospores (*Oedocephalum* and *Ostracoderma*) are frequently found in cultures of *Peziza* and *Iodophanus* (Pezizaceae). Aleurospores are known in *Peziza* but also in other genera. *Botrytis*-like imperfect states are known in *Trichophaea* (Otidiaceae). Sympodulosporous imperfect states are known in several families (Sarcoscyphaceae, Sarcosomataceae, Aleuriaceae, Morchellaceae) embracing both suborders. *Conoplea* is definitely tied in with *Urnula* and *Plectania*, *Nodulosporium* with *Geopyxis*, and *Costantinella* with *Morchella*. Certain types of conidia are not presently known in the Pezizales. Phialospores, porospores, annellospores, blastospores and a few other types have not been reported. The absence of phialospores is of special interest since these are common in the Helotiales. The absence of conidia in certain groups, e. g. Helvellaceae and Theleboleaceae may also be of significance, and would aid in delimiting these taxa. At the species level critical comparison of imperfect states may help clarify taxonomic problems and supplement other data in distinguishing between closely related species. *Peziza*, *Plectania* and perhaps *Sarcoscypha* are examples of genera where such studies might prove valuable.

One large group of the Pezizales in desparate need of study in culture are the tropical species. Very few of these appear to have been cultured. Undoubtedly some surprises are in store for mycologists who culture tropical forms. Species of *Rhizoctonia* may also yield pezizaceous apothecia, as the study of Whitney & Parmeter (*1964*) has shown. Such cultural studies are laborous but must be undertaken if we are to ever approach complete understanding of this group of fungi.

INTRODUCTION

Imperfect states have been known in the Pezizales for over one hundred years, the first report being that of the Tulsane's (*1853*, *1865*) of the *Oedocephalum* state of *Peziza vesiculosa*. Brefeld (*1891*) described and illustrated this imperfect state and the

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Oedocephalum states of *P. repanda*, *P. cerea*, and *P. ampliata*. Molliard (*1904a*, *1904b*) found *Costantinella* conidial states in *Morchella*. Since these early papers, there have been only a few reports of conidial states in the Pezizales until recent years. Commencing with Gremmen's (*1949*) report of the *Verticicladium* imperfect state of *Desmazierella acicola*, more and more reports of conidial states have appeared in the literature, and it is becoming evident that the Pezizales may be rich in undiscovered imperfect forms. Further, as will be discussed in detail below, some excellent correlations between perfect states and imperfect states are becoming evident.

In the remainder of the paper I will discuss the taxonomic implications of pezizaceous conidial states. The system of classification I will follow will be essentially that of Kimbrough (*1970*) except that Korf's (*1970*) division of the Sarcoscyphineae into two families will be adhered to. For the imperfect states I will follow Hughes' (*1953*) system as modified by Barron (*1968*).

METHODS

Spore germination.

Ascospores have been harvested by suspending apothecia or fragments of apothecia over agar and allowing the spores to be discharged. The ascospores of many species of Pezizales germinate readily, however the spores of some species are extremly refringent and germination is difficult or impossible to obtain. Heat shock plus furfural induced a low percentage of germination in *Peziza brunneoatra* ascospores (Paden, *1967*). In *P. saniosa* Fr., germination has been obtained by shooting the ascospores onto 2 % Difco nobel agar, then dropping 50 % aqueous dimethylsulfoxide containing 20 PPM furfural onto the spores and incubating at 13° C. This results in about 1 % germination. The ascospores of *Caloscypha fulgens* (Pers.) Boud. have been induced to germinate only by shooting them onto 2 % Difco nobel agar containing 10^{-4} M n-nonyl alcohol and incubating at 21 to 23° C. About 50 % germination is attained by this technique. The nonyl alcohol method also induces germination in *Aleuria aurantia* (Fr.) Fckl. and *Melastiza chateri* (Sm.) Boud. but less than 1 % of the ascospores germinate.

Potato-carrot agar (PCA) prepared according to the C.M.I. formula (Dade, *1960*) has been routinely employed for pure culture studies. PCA has proven to be by far the best culture medium for most species of Pezizales. A few species of the Sarcosomataceae will grow or sporulate only on a conifer litter decoction (*Paden & Tylutki*, *1968*, *1969*). Cultures have been incubated at 21 to 23° C and given diurnal incandescent illumination. 2.5 PPM aureomycin and 250 PPM streptomycin are incorporated into all media to surpress bacteria.

IMPERFECT STATES PRESENTLY KNOWN IN THE PEZIZALES AND THEIR TAXONOMIC IMPLICATIONS

Suborder Sarcoscyphineae

Family Sarcoscyphaceae (sensu Korf, 1970).

There are few reports of conidial states in this family. Boedijn (*1929, 1932*) described small, globose conidia borne on short conidiophores arising from ascospores in *Cookeina sulcipes* and *C. tricholoma*. Close examination of Boedijn's illustrations indicates that the conidia are probably sympodulospores. Boedijn (*1932*) reports that these conidia germinate readily when placed in water. This latter observation is of considerable interest as I have never been able to germinate the conidia of any species of the Sarcoscyphineae.

Production of conidia in a manner similar to *Cookeina* was reported by Alexopolous & Butler (*1949*) for *Sarcosypha coccinea* (as *Plectania coccinea*). Rosinski (*1953*) also observed this phenomonon in material he considered to be *S. coccinea* var. *jurana*. Rosinski (*1953*) observed only germination by germ tube in *S. coccinea* var. *coccinea*. The drawings of Alexopolous & Butler (*1949*) and the drawings and photomicrographs of Rosinski (*1953*) strongly suggest a sympodulosporous manner of conidium formation in *S. coccinea* var. *jurana*.

I have cultured only what I beleive is *S. coccinea* var. *coccinea* (Paden 571 from British Columbia; Paden 766 from Quebec[1]. Ascospores from both of these collections germinated by germ tube. Colonies on PCA are white, appressed to slightly floccose, and cover a plate in about two weeks. A conidial state develops in two to three weeks (Fig. 1). The conidia are sympodulospores. This conidial state cannot be accomodated in a presently known genus (Hughes, personal communication). Rosinski (*1953*) noted that the apothecial colour and ascospore shape he observed were opposite to that reported by Boudier (*1906–1907*) and that Le Gal (*1941*) had also observed considerable variation and intergradation in ascospores size and shape between the two varieties of *S. coccinea*. The presence of two distict conidial forms and two types of ascospore germination in the species *S. coccinea* is a further basis for distinguishing between the two varieties.

In Korf's (*1970*) scheme *Cookeina* is placed in the Boedijnopezizeae and *Sarcoscypha* in the Sarcoscypheae. If the conidia of *Cookeina* are in fact sympodulospores, then this similar means of conidium formation could be taken as evidence of a close relationship. Hopefully, additional species will be cultured in the future and *Cookeina* reinvestigated. I have cultured *Pithya vulgaris* Fckl. (Sarcoscypheae) but it did not form conidia.

Family Sarcosomataceae (sensu Korf, 1970).

Gremmen (*1949*) first connected *Verticicladium* with *Desmazierella acicola* Lib. in pure culture studies. Hughes (*1951*) determined the imperfect state to be *Verticicla-*

[1] Specimens cited are deposited in the University of Victoria herbarium or in the University of Idaho herbarium (ID).

dium trifidum Preuss. Davidson (*1950*) suggested that *Urnula craterium* (Schw.) Fr. was the perfect state of *Strumella* canker but was unable to obtain conidia in culture. This has been accomplished by Hughes (personal communication). Wolf (*1958a*) obtained conidia of *U. craterium* by innoculating sterile oak branches. The correct name of the imperfect state of *U. craterium* is *Conoplea globosa* (Schw.) Hughes (Hughes, *1960*). It should be noted at this point that both *Conoplea* and *Verticicladium* are sympodulosporous genera.

Recently I have obtained the imperfect states of *Plectania nannfeldtii* Korf and two possibly undescribed species of *Plectania* in culture. The imperfect state of *P. nannfeldtii* is close to or conspecific with *Conoplea juniperi* var. *robusta* (Hughes, personal communication). "Plectanic Taxonomic species II" from California and Oregon is a close relative of *P. nannfeldtii* and also has an imperfect state in the *C. juniperi* group (Hughes, personal communication). "Plectanic Taxonomic species I" from Vancouver Island, British Columbia has an imperfect state in the *C. fusca* group (Hughes, personal communication). The conidia of all *Plectania* species thus far studied possess a germ pore while the conidia of *U. craterium* possess a germ slit. *Plectania* and *Urnula* are without question closely related. Nannfeldt (*1949*) separated them on anatomical grounds. The basic difference in the conidia of the two genera is perhaps evidence for keeping them separate. (The conidia of *Desmazierella acicola* also possess a germ slit.)

Sarcosoma globosa was cultured by Berthet (*1964a*), who did not observe an imperfect state. McCallam (*1919*) germinated the ascospores of *S. globosa* (as *Bulgaria platydiscus*) but was unable to obtain cultures because of contaminants. His figures show germination by one or two germ tubes and no evidence of conidia. Paden & Tylutki (*1969*) cultured *S. mexicana* and did not obtain an imperfect state. The grounds for separating *Sarcosoma* and *Plectania* are tenuous. A case in point is *S. latahensis* Paden & Tylutki (*1969*). This is a borderline species only reluctantly placed in *Sarcosoma*. According to Hughes (personal communication) the conidial state is in the *Conoplea geniculata* group and is not a *Verticicladium*. The presence of a *Conoplea* imperfect state (with a germ pore) is, in my opinion, evidence for including *S. latahensis* in *Plectania*. (The new combination to be made in a separate paper.)

Pseudoplectania is closely related to *Plectania* and should, perhaps, be merged with the latter genus. Imperfect states are not known in *Pseudoplectania* (Korf, personal communication; Paden, unpublished data). Ascospores of *Pseudoplectania* posess a gelatinous sheath, as do the ascospores of some species of *Plectania*. At present, in *Plectania*, there is no relationship between the presence or absence of an ascospore sheath and the presence or absence of an imperfect state.

Imperfect states are unknown in the tribe Galielleae Korf. *Neournula nordmanensis* has never formed conidia (Paden & Tylutki, *1968*) nor has *Galiella rufa* (Schw.) Nannf. & Korf (Paden, unpublished data). There are no records of anyone having cultured *Wolfina*, the third genus included by Korf (*1970*) in this tribe.

Suborder Pezizineae

Family Pezizaceae (sensu Rifai, 1968).

As treated by Rifai, this family includes those genera of Pezizales with J+ asci (excepting some species of the Ascobolaceae). *Oedocephalum* imperfect states are known in *Peziza* (numerous reports) and *Iodophanus* (Korf, *1958*; Gamundi & Ranalli, *1964*). Schneider (*1954*) published the new ellipsoid-spored species *Plicaria fulva* with a description of its conidial state which is an *Ostracoderma*. Korf (*1960*) transferred this species to *Peziza* (as *P. ostracoderma* Korf). An *Ostracoderma* imperfect state (as *Rhinotrichum*) was described by Wolf (*1958b*) for *Peziza trachycarpa* Curr. (as *Lamprospora*). As pointed out by Korf (*1960*) the presence of *Ostracoderma* imperfect states in J+ species with both globose and ellipsoid ascospores is a strong argument for classifying all such species under the older name *Peziza* St.-Amans.

Recently I have obtained *Ostracoderma* conidial states in cultures of *Peziza leiocarpa* Curr. (Fig. 5) and *P. anthracina* Cke., both species with globosa ascospores. This leaves *P. ostracoderma* as the only ellipsoid spored species with a known *Ostracoderma* imperfect state. However relatively few species in the large genus *Peziza* have as yet been cultured and is it very likely that *Ostracoderma* states will be found in additional species with ellipsoid ascospores. The conidial states of *P. leiocarpa*, *P. trachycarpa*, and *P. ostracoderma* are very similar. The conidial state of *P. anthracina* is more compact with shorter conidiophores and broader ampullae. *Peziza anthracina* has been treated as var. *muricata* Grelet of *P. trachycarpa*. However as pointed out by Maas Geesteranus (*1967*), the var. *muricata* was not validly published, and the correct name is *P. anthracina*. The difference in morphology of the conidial states of these species is additional evidence that they should be kept separate.

Paden (*1967*) described an aleurospore-like conidial state in *Peziza brunneoatra* Desm. Recently I have noted both aleurspoores and an *Oedocephalum* conidial state in *P. petersii* Berk. & Curt. (Fig. 2, 4) and aleurospores in *P. saniosa* Fr. (Fig. 6). Possibly aleurospores are common in *Peziza*. I have also seen aleurospore-like structures in cultures of *P. ostracoderma*. Since the *Oedocephalum* and *Ostracoderma* states now known in *Peziza* vary strikingly in morphology, they should be of considerable taxonomic value as more species are cultured and accurate descriptions of conidial states published.

Thecotheus is closely related to *Iodophanus* (Kimbrough & Korf, *1967*), but there are no reports of associated imperfect states. I have been able to culture *T. cinereus* from ascocarp tissue and obtained a few aleurospores on PCA but no other imperfect state.

Imperfect states have not been reported in *Pachyella* or *Sarcosphaera*. I have not been able to germinate ascospores in either of these genera or obtain cultures from tissue explants.

Family Pyronemateceae.

Used in the sense of Rifai (*1968*) and Arpin (*1968*) this family includes the single genus *Pyronema* Carus. Two species, *P. domesticum* and *P. omphalodes* were treated by

Moore & Korf (*1963*). As these authors point out, conidia are unknown in *Pyronema* and earlier reports of conidial states are in error. Berthet (*1964b*) described "oidia" in *P. omphalodes*.

Family Otideaceae Eckblad emend. Arpin.

The limits of this family are in some doubt. As originally defined by Eckblad (*1968*) *Otidea*, *Pustulina* (*Pustularia*), *Sowerbyella*, *Geopyxis*, and *Ascosparassis* were included. Arpin (*1968*) removed *Geopyxis* and *Sowerbyella* to the Aleuriaceae and included *Sepultaria*, *Tricharia*, *Trichophaea*, *Mycolachnea*, and *Pseudombrophila*. Kimbrough (*1970*) suggests that *Jafnea*, *Nothojafnea*, *Jafneadelphus*, *Sphaerosporella*, and possibly *Marcelleina* also belong in the Otidiaceae.

Only a few imperfect states have been reported for species in the Otidiaceae. It has been known for some years the *Trichophaea abundans* (Karst.) Boud. and probably other *Trichophaea* species have *Botrytis*-like imperfect states (Dodge, *1922*; Gwynne-Vaughn & Williamson, *1927*; Kervorkian, *1932*; Webster, & *al.*, *1964*). Whitney & Parmeter (*1964*) note that *Rhizoctonia*-like mycelium may be common among discomycetes and my own studies would definitly confirm this observation. Berthet (*1966*) described aleuro-spore-like conidia in cultures of *T. confusa* (Che.) Berthet. Cain & Hastings (*1956*) published the new species *Sphaerospora minuta* with a *Botrytis*-like imperfect state. The conidia in this species are borne on very broad denticles. However they are botryoblastospores and thus basically like conidia in other "*Botrytis*" species. Since *Sphaerospora* is illegitimate (Eckblad, *1968*) *S. minuta* should perhaps be included in *Trichophaea*.

There are no reports of imperfect states in the related genus *Tricharia*. I have cultured a *Tricharia* sp. (Paden 623) but it did not produce conidia. I have not been able to germinate ascospores of *Otidea* or *Pustulina*. I have cultured *P. catinus* (Fr.) Eckblad (Paden 525) from tissue explants. Cultures are slow-growing and creamy white. There is no conidial state on PCA or malt extraxt.

Family Aleuriaceae Arpin.

Arpin (*1968*) divided the Aleuriaceae into three groups based on carotenoid ratios. Group a includes *Coprobia*, *Cheilymenia*, *Scutellinia*, and *Geopyxis*; group b, *Aleuria*, *Melastiza*, and *Octospora*; group c, *Pulvinula*, *Anthracobia*, *Caloscypha*, and *Sowerbyella*. Kimbrough (*1970*) suggests that *Fimaria*, *Leucoscypha*, *Lamprospora*, *Inermesia*, *Genosperma* and *Rhizoblepharis* belong in the Aleuriaceae.

In group a I have discovered a *Nodulosporium* conidial state in *Geopyxis majalis* Fr. (Fig. 7). This conidial state is formed abundantly on PCA. Cultures of *G. carbonaria* and *G. vulcanalis have remained sterile. Nodulosporium* is sympodulosporous and is related to *Costantinella*, the imperfect genus tied in with *Morchella. Coprobia granulata* was studied in culture by Gwynne-Vaughn and Williamson (*1930*). They do not mention a conidial state. Both Dr. W. C. Denison and myself have cultured *Scutellinia* species and have not seen conidia.

Species in group b lack known conidial states. I have cultured *Melastiza chateri* (Sm.) Boud. and *Aleuria aurantia* (Fr.) Fckl. from germinated ascospores and have

not observed conidia. Berthet (*1964a*) likewise did not observe conidia in cultures of *A. aurantia* or *Octospora euchroa* (Karst.) Boud.

In group c Gwynne-Vaughn (*1937*) and Rosinski (*1956*) studied ascocarp development in *Anthracobia melaloma* (Fr.) Boud. in culture and did not observe conidia. I have cultured *A. macrocystis* (Che.) Boud. (Paden 146, ID) and *Pulvinula archeri* (Berk.) Rifai (Paden 371, ID) and have not seen conidia. *Caloscypha fulgens* (Pers.) Boud. develops an imperfect state on PCA. Colonies are slow-growing, floccose, and a blue-green colouration appears in the agar beneath the colony but does not diffuse further. Conidial formation is sympodulosporous (Fig. 3) and the *C. fulgens* imperfect state is congeneric with the *Sarcoscypha coccinea var. coccinea* imperfect state (Hughes, personal communication). I have discussed the *C. fulgens* problen at some length with Dr. W. C. Denison and we are both of the opinion that the ascus of this species is not suboperculate and that it should not be placed in the Sarcoscyphaceae. The texture and colouration of *C. fulgens* do, however, suggest a sarcoscyphaceous species (Denison, personal communication). Possibly *C. fulgens* is a primitive species of the Aleuriaceae not too far removed from a sarcoscyphaceous ancestry.

Family Morchellaceae.

Molliard (*1904a*, *1904b*) described *Costantinella* imperfect states for species of *Morchella*. I have obtained the *Costantinella* state of *M. elata* Fr. in culture (Fig. 8). *Costantinella* thus seems definitely tied in with *Morchella*. Barron (*1968*) has pointed out the close relationship of *Costantinella* and *Nodulosporium*. Since a *Nodulosporium* state is now known for *Geopyxix majalis* (Aleuriaceae), a possible connection between the two families may be indicated. There are no reports of conidial states in the other genera of the Morchellaceae: *Verpa*, *Ptychoverpa*, and *Disciotis*. Berthet (*1964a*) cultured *D. venosa* (Pers.) Boud. and *P. bohemica* (Krombh.) Boud. but did not observe conidia.

Family Helvellaceae.

At the present state of our knowledge a broad concept of this family such as that of Berthet (*1964a*) should perhaps be adhered to. Conidial states are at this time unknown in species of the Helvellaceae and the ascospores of many have proven impossible to germinate. I have not been able to germinate the ascospores of species of *Helvella*, *Wynella*, or *Discina*. In contrast, the ascospores of *Gyromitra esculenta* Fr. and *G. infula* (Fr.) Quél. germinate readily. Colonies of Gyromitra on PCA are fast-growing, thin, nearly colourless, and do not form conidia. I have obtained a culture of *Rhizina undulata* Fr. from Dr. A. Funk of the Canada Department of Forestry and Rural Development, Victoria, B. C., that had been made by Dr. J. Ginns. Dr. Ginns had told me that he germinated the ascospores by heat shock. *Rhizina undulata* grows rapidly on PCA and forms colourless, somewhat floccose colonies. There is no conidial state.

Family Ascobolaceae.

Oidia are known in a few speciew of *Ascobolus* (Dodge, *1912*; Green, *1931*). These

can act either as vegetative propagules or male cells. A *Papulaspora* state was reported by Dodge (*1920*) for *A. magnificus*, but Lohwag (*1927*) points out that this may represent aborted ascocarps. Some of Hotson's (*1917*) illustrations of *Papulaspora* species are very suggestive of ascogonial initials. Conidia have not been reported in *Saccobolus*. Obrist (*1961*) did not observe conidia in cultures of *Ascodesmis*. The oidia in *Ascobolus* are of little taxonomic significance, except that their presence or absence may help to delimit a given species.

Family Thelebolaceae Rifai.

Kimbrough & Korf (*1967*) have presented a synopsis of this family (as tribe Theleboleae). Kimbrough (*1966*) has summarized all information regarding cultural characters. Imperfect states are not known in the Thelebolaceae at the present time. Since several species have been cultured, it seems likely that the family can be characterized by a lack of imperfect states.

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Note added in proof.

Since this paper was submitted a *Nodulosporium* imperfect state has been found in *Geopyxis carbonaria* (Alb. & Schw. ex Fr.) Sacc. An imperfect state congeneric with the imperfect states of *Sarcoscypha coccinea* var. *coccinea* and *Caloscypha fulgens* has been found in *Pithya cupressina* (Fr.) Fckl.

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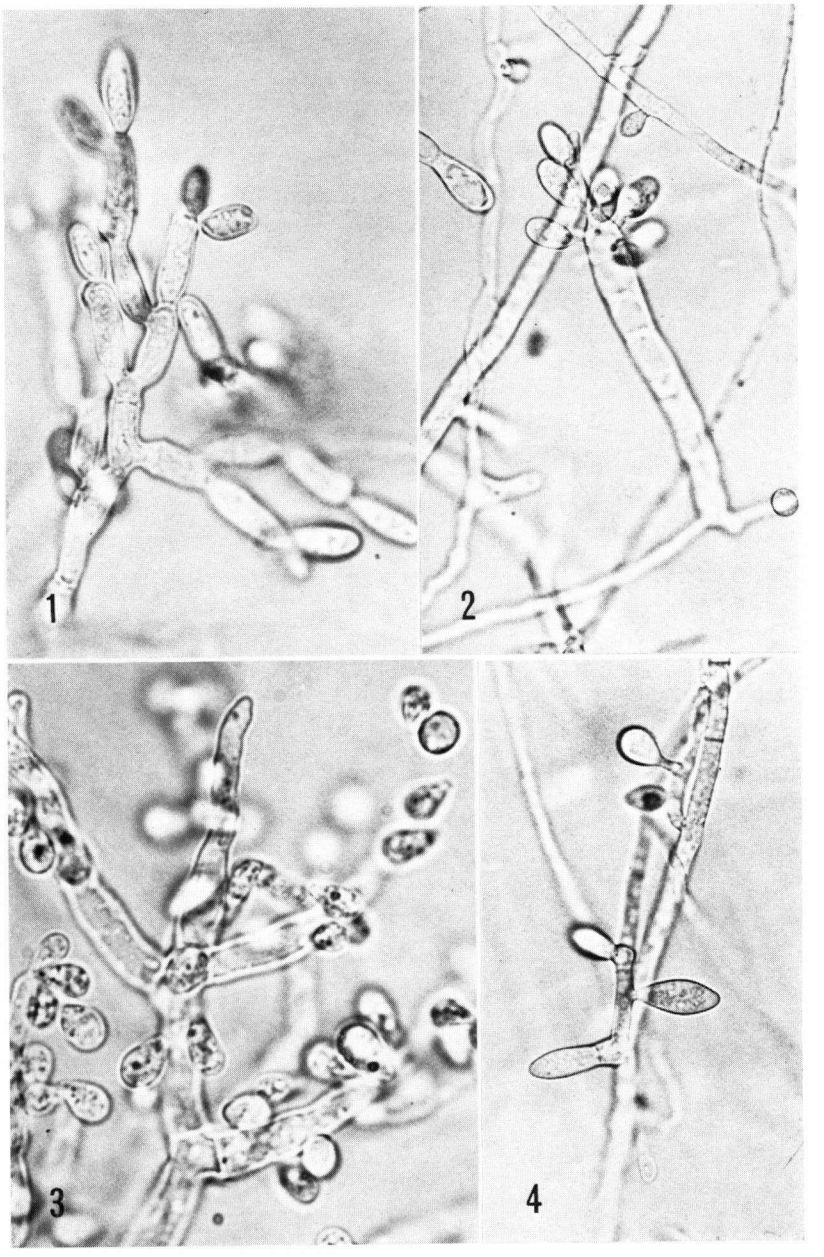
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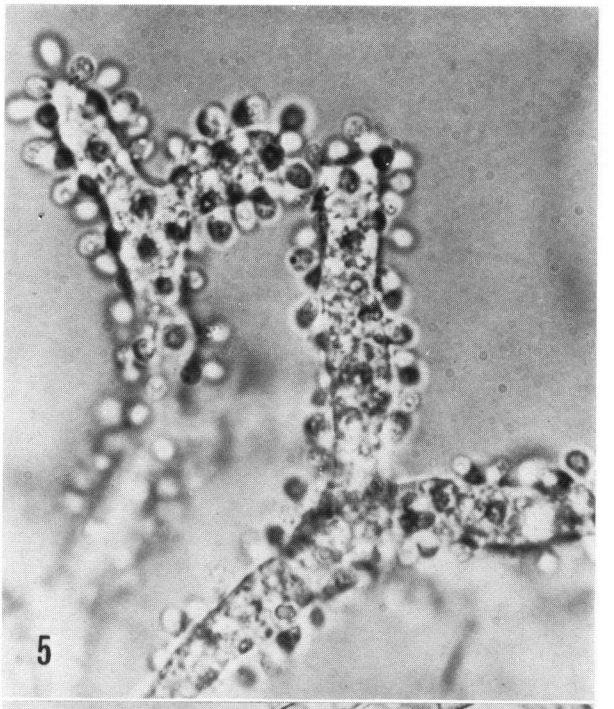
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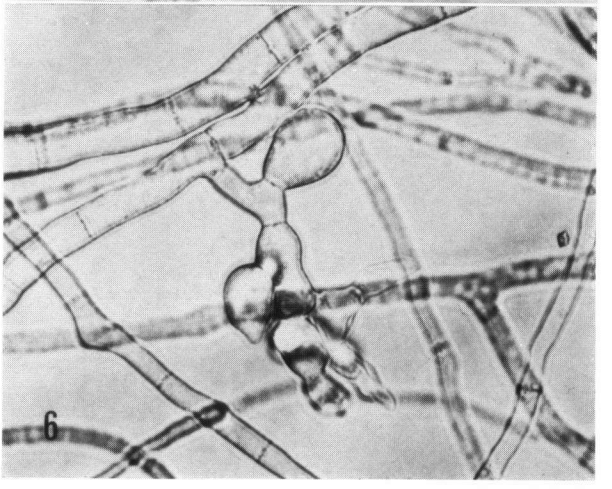
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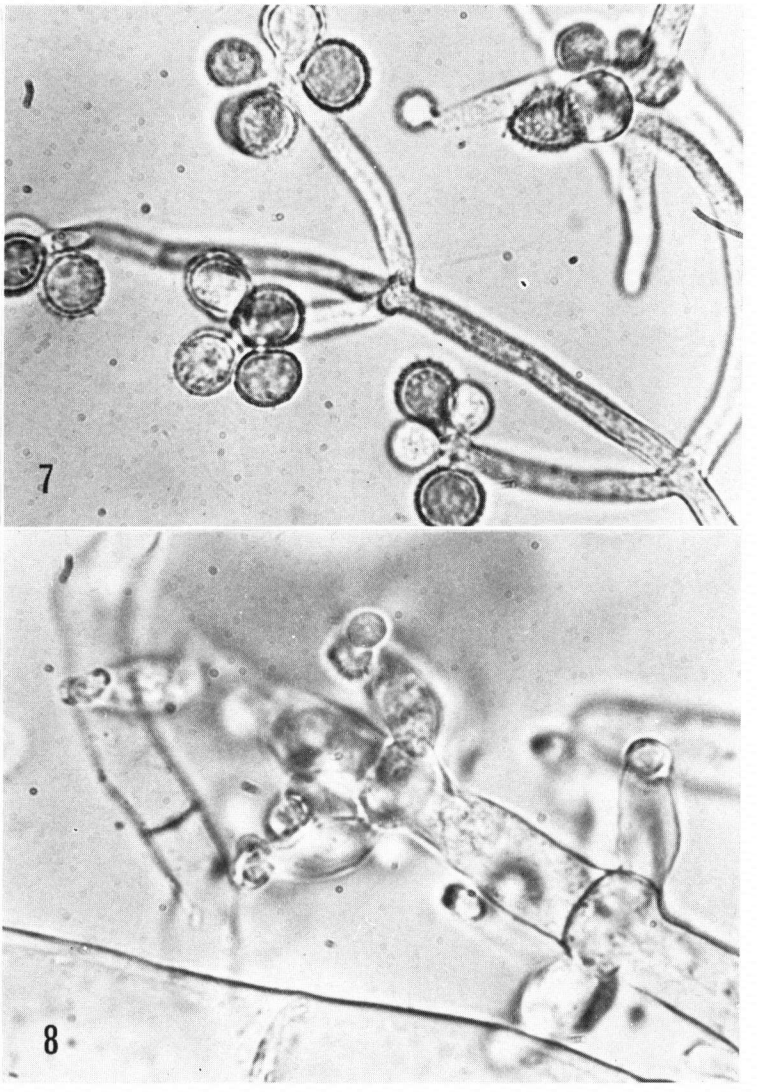
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