

TYPIFICATION OF ALTERNARIA, STEM-
PHYLIUM, AND ULOCLADIUM

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(WITH 12 FIGURES)

Every modern attempt to define the phaeodictyosporic form-genera *Alternaria* Nees ex Fries and *Stemphylium* Wallroth has involved the problem of treating numerous taxa which superficially resemble the type species of one or the other of these genera but which are sufficiently different as to leave a measure of doubt. Chief among these anomalous species are *Stemphylium lanuginosum* Harz and *Macrosporium consortiale* Thümen, both of which have reposed nomenclatorially at one time or another in *Alternaria*, *Stemphylium*, and *Pseudostemphylium* C. V. Subramanian. It is my present purpose to illustrate and to contrast the type specimens of *Alternaria*, *Stemphylium*, and *Ulocladium* Preuss, the latter being an early but generally disregarded generic name appropriate to several pseudoalternarioid and pseudostemphylioid species.

HISTORY OF THE PROBLEM

Wiltshire (29, 30) pioneered in basic studies on this group of Hyphomycetes and in 1933 and 1938 published the results of his examination of the available type specimens and descriptive literature which were fundamental to the then current concepts of *Alternaria*, *Macrosporium* Fries, and *Stemphylium*. His major conclusions were that *Macrosporium* should be suppressed as a *nomen ambiguum* in favor of *Alternaria*, typified by *A. tenuis* Nees, the type specimen of which Wiltshire was unable to locate for examination; and that the limits of *Stemphylium* should be modified to include two sections, *Eustemphylium* for species showing the original characters of the genus (typified by *S. botryosum* Wallr., whose type was available) and *Pseudostemphylium* for species allied to the problematic *S. lanuginosum* Harz, of which no type specimen was or is known.

Groves and Skolko (5) agreed with and retained Wiltshire's sectional treatment of *Stemphylium* in their study on seed-borne species.

Neergaard (14), in his extensive treatment of species of *Alternaria* and *Stemphylium* occurring in Denmark, recognized the same taxonomic problems in handling species similar to *S. lanuginosum*. He also fol-

lowed the lead of Wiltshire by retaining the two sections proposed for *Stemphylium*.

Subramanian (25) proposed that the name *Pseudostemphylium* be raised to generic rank and made a few nomenclatural combinations in the genus, retaining *S. lanuginosum* as the type.

Joly (8), in his survey of *Alternaria*, differentiated *Stemphylium* in its original sense (and in the sense of Wiltshire's section *Eustemphylium*) and disposed in *Alternaria* several of the taxa similar to *S. lanuginosum* which have been considered controversial by earlier students of the group.

The true origin of the problem of differentiating pseudostemphylioid taxa from true *Stemphylium* lies with Harz (6) in his description and excellent illustrations of *S. lanuginosum* and in his failure to recognize that the characters of the conidiophores and conidia of his fungus were foreign to the original concept of *Stemphylium*. Abetting this error has been the general availability of an excellent living culture isolated by Oudemans, originally identified by him as *S. botryosum*, but later reidentified as *S. lanuginosum* and distributed under this latter name. This culture has been examined by most students of the group, and it is this material which actually governs many opinions not only on this species but also on the genus *Stemphylium* itself. It is significant to note that all of the modern taxonomists cited above have recognized the inappropriateness of *Alternaria* and *Stemphylium* as generic placements for species similar to *S. lanuginosum*, either by their nomenclatural proposals or, more importantly, by their invariably excellent illustrations which reveal that conidiophores of members of the *S. lanuginosum* group bear no resemblance whatever to those of *S. botryosum* and that the conidial morphology of the group is fundamentally different from that of the type species of *Alternaria*. It is my contention that the correct relationships of puzzling species of the *S. lanuginosum* group are with *Ulocladium*, typified by *U. botrytis* Pr.

SPORULATION APPARATUS

The conidia of all members of the three genera are porospores. Each conidium originates as an outgrowth of protoplasm through a discrete pore in the apical wall of a sporogenous cell. This cell usually, but not always, is the tip cell of a hyphal branch, the conidiophore, which is morphologically and functionally distinct from vegetative hyphal branches. The only functional connection between a conidium and the cell which produces it is the slender thread of protoplasm passing

through the apical pore of the productive cell; there is complete discontinuity between the cell wall of the conidiophore and that of the conidium which it produces. Conidium release occurs when the protoplasmic thread ruptures; the conidiophore remains intact on release of a conidium without donating any fragment of its apex as a conidium appendage. A basal pore in the conidium wall marks the original position of connection between a conidium and the cell which produced it. Conidia of all three genera mature as dictyospores, although the production of longitudinal septa may be limited or tardy in some species or even absent in individual conidia.

The following characterizations of the sporulation apparatus of *Alternaria*, *Ulocladium*, and *Stemphylium* emphasize the juvenile and mature shapes of conidia and the modes of proliferation of conidiophores and conidia. These developmental characters are illustrated diagrammatically in FIG. 1, which is based on a generalization of observations made on several hundred collections and cultures in addition to the type specimens.

Alternaria (FIG. 1A).—The conidiophore may remain simple, with a single pore at its apex and producing a single conidium through the pore, or it may become geniculate through renewed growth of its apical cell in a region lateral to the existing pore. This new branch may produce a conidium at its apex and may serve as the base for additional geniculate extensions. Individual conidium cells also may give rise directly to functional conidiophores. Conidiophores produced directly by conidium cells and those arising as specialized hyphal branches have the same basic character of a bluntly rounded, slightly swollen, uniperforate apical region.

The fundamental form of conidia is ovoid, i.e., the portion of the conidium which is proximal to the cell which bore it is broader than the distal portion. This ovoid form commonly is apparent at a very early stage in the development of a conidium, often before the first septum is produced. Differences in the degree of distal tapering and in the production of more or less well-defined apical beaks yield obclavate to obpyriform variants of the basic ovate outline. Conidium walls are smooth or variously roughened. Conidium color commonly is a variant of brown (blackish, reddish, greenish, yellowish) but it may approach subhyalinity; albino strains are known. A conidium may remain solitary as produced or it may serve as the basal unit in a chain of spores. Chains are formed when one conidium gives rise to a second one through a simple pore in the tip of its otherwise unchanged apical

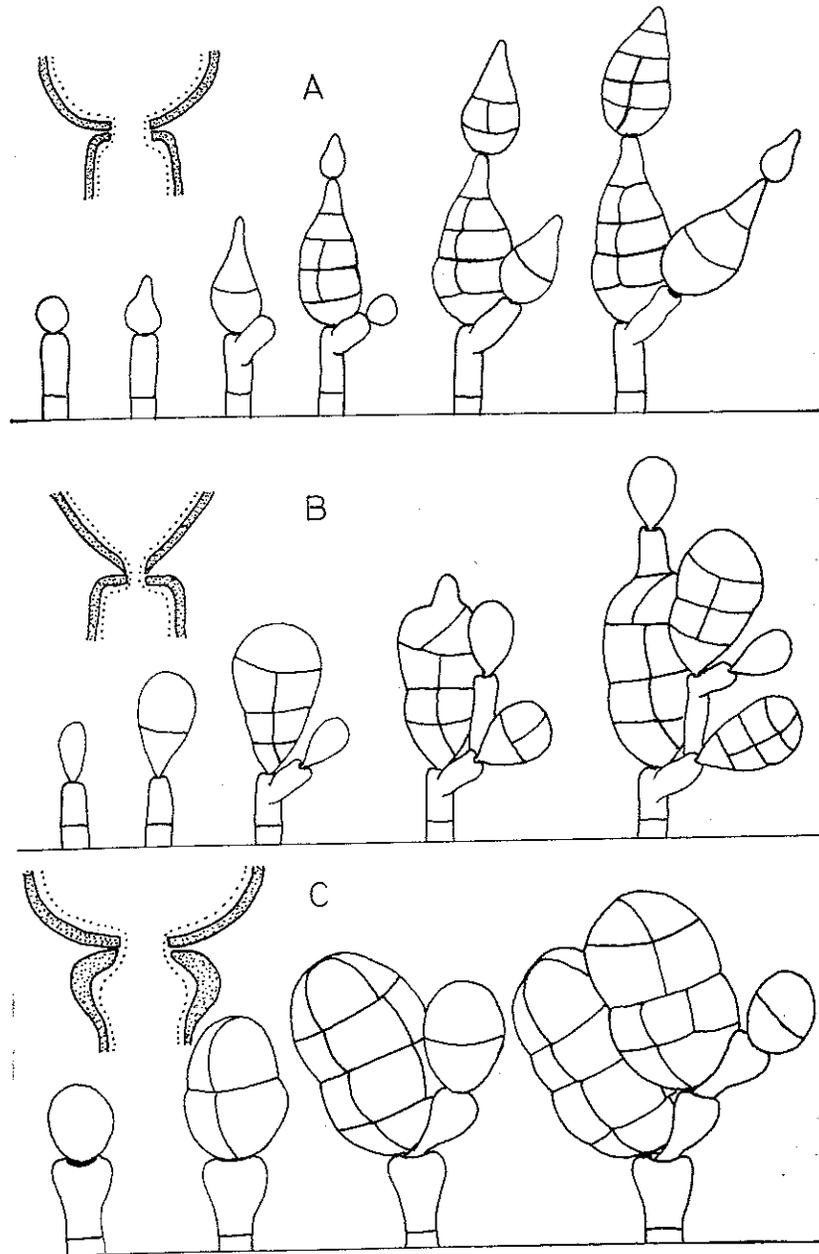


FIG. 1. A. *Alternaria*, B. *Ulocladium*, and C. *Stemphylium*: diagrams of conidiophore proliferation and successive conidium production, with enlargements of the site of contact between conidiophore apex and conidium base.

cell or when the lateral outgrowth of any conidial cell or the renewed terminal growth of the ultimate beak cell becomes converted morphologically and functionally into a conidiophore.

Ulocladium (FIG. 1B).—Some characteristics are shared by *Ulocladium* and *Alternaria*, notably the production of dictyoporospores on well-differentiated conidiophores which commonly become geniculate through successive lateral renewals of growth. Conidia of *Ulocladium*, however, are fundamentally obovoid, i.e., the portion of the conidium which is proximal to the cell which bore it is tapered and narrower than the distal portion. The ultimate shapes of conidia are variants of obovoid, ellipsoidal, and subspherical forms, but the conidia do not taper distally into true beaks. The residual pore in the conidium wall, which is the site of connection between a conidium and the cell which produced it, always is in the narrowed base of the conidium. This narrowed end often terminates in a very small, rounded, subhyaline apiculus, the identity of which may remain visible as the conidium matures and is dislodged or which may become obscured by the thickness and color of the surrounding wall; this apiculus, however, is an integral part of the conidium and does not represent either a broken appendage or a ragged fragment of the conidiophore. Conidium walls may be smooth but more commonly are variously roughened. Conidium color ranges from subhyaline through variant shades of brown to black; albino strains are known.

Conidia occur in clusters when conidiophore development is closely geniculate, or conidia are distant when the geniculations are well-separated. Conidia of some species usually remain solitary as produced without giving rise to secondary conidia. However, individual cells have the potential to germinate while the conidium still is in place on its conidiophore, giving rise apically or laterally to morphological and functional conidiophores. These secondary conidiophores or "false beaks," when apical, have a superficial resemblance to the true conidial beaks of species of *Alternaria*, and it is primarily this character of false beaks which has misled us for many years into attempting to include species of this sort in *Alternaria*. Production of false beaks is rare in some species, e.g., *U. botrytis* and *U. atrum*; moderately common in others, e.g., "*Macrosporium consortiale* Thüm." and "*Stemphylium lanuginosum* Harz"; and very common in "*Alternaria chartarum* Preuss," which in culture produces long chains of conidia with false beaks, thus closely mimicking long-chained species of *Alternaria*. It must be emphasized that production of secondary conidiophores directly

from conidium cells also may occur in *Alternaria* and that this character cannot be used alone to distinguish species of *Ulocladium* from those of *Alternaria*. The distinguishing character is the fundamentally obovoid, nonbeaked form of *Ulocladium* conidia as contrasted with the ovoid, distally tapered or beaked form of *Alternaria* conidia.

Stemphylium (FIG. 1C).—This genus shares with *Alternaria* and *Ulocladium* the general character of producing dictyospores on well-differentiated conidiophores. However, conidiophores of *Stemphylium*, and particularly their mode of proliferation, differ strikingly from those of the other two genera. The apical cell or region of a simple *Stemphylium* conidiophore is slightly to distinctly swollen; a single conidium is produced as a protoplasmic outgrowth through a relatively large terminal pore. Renewed or secondary development of the conidiophore is directly through this terminal swollen region. The previously formed conidium becomes lateral if its protoplasmic connective withstands the thrust of the emerging secondary conidiophore, or it is dislodged if its connective breaks. A conidium may be produced through the apex of this secondary growth; series of three or more apical proliferations and terminal-lateral conidia commonly are produced. Conidiophore walls may be smooth or rough, and the area immediately surrounding the apical pore usually is darker than the remainder of the conidiophore.

Conidia of *Stemphylium* initially may be either ovoid or obovoid. The shapes of mature conidia are variously spherical, ovoid, obovoid, and broadly ellipsoidal to subdoliiform. In some species the distal portion of the conidia narrows gradually into a conical beak; similar broadly conical beaks lateral to the basal pore are known in *S. triglochimicola* Sutton & Pirozynski (26). The relatively large basal pore commonly is surrounded by an area of concentrated pigmentation. Conidium walls are smooth or variously roughened. Conidium color ranges from subhyaline through variant shades of brown; albino strains have not been reported, but their existence is not unlikely. [*Stemphyliopsis* A. L. Smith (24), originally described as a colorless counterpart of *Stemphylium*, has a sporulation apparatus quite unlike that of *Stemphylium*.]

DEFINITION AND DESCRIPTION OF GENERIC TYPES

Wallroth's type specimen of *Stemphylium* has been available in modern times to several students of this group, including Wiltshire (30) who published excellent illustrations based on it. Type or authenticated

specimens of the type species of *Alternaria* Nees were believed no longer to exist until one was found in Persoon's herbarium. The type of *Ulocladium* Preuss was discovered in a small batch of Preuss' specimens acquired by the Botanisches Museum, Berlin; its existence generously was pointed out to me in 1962 by S. J. Hughes.

The following notes and illustrations are intended to define the type status of these specimens and to publicize certain characteristics of the three genera. For my present purposes synonyms listed in this discussion are restricted to those which are obligate.

ALTERNARIA

ALTERNARIA Nees ex Fries [C. G. Nees von Esenbeck, *Das System der Pilze und Schwämme*, p. 72. 1816.]; E. M. Fries, *Systema Mycologicum*, 1: XLVI. 1821.

Type species: *A. alternata* (Fries) Keissler, *Beih. Bot. Centr.* 29: 434. 1912.

[*Alternaria tenuis* Nees, l.c., p. 72, and Tab. V, fig. 68. 1816; invalid pre-starting date epithet.]

Torula alternata Fries, *Syst. Mycol.* 3: 500. 1832.

Fries did not record a name for the type species of *Alternaria* Nees in 1821 when he took up with a pertinent reference, and thus validated, the generic name. When he published the name *Torula alternata* in 1832, citing "*Alternaria tenuis*. Nees!" as a synonym, he established the epithet which is the first one validly published for Nees' species.

Type specimen (neotypus): Rijksherbarium, Leiden (L), No. 910, 262-129, annotated "*misit Nees in herb. Persoon*" and bearing Nees' manuscript label "*Alternaria tenuis mihi*." Although no other pertinent specimen authenticated by Nees is known to exist, it remains impossible to prove that this collection represents Nees' holotype. Fries (l.c.) indicated ("v. s.") that he had seen the species in a dried state; no relevant specimen has been found in his herbarium at Uppsala. For these reasons the specimen cited above is proposed as the neotype of the species.

The neotype specimen, two short fragments of a pithy stem, bears a hyphomycetous mixture of *Alternaria*, *Cladosporium*, and probably a *Scopulariopsis*. The fungus material is closely adherent to the substrate; neither erect conidiophores nor conidia still attached to conidiophores now are observable.

A. alternata (FIG. 2).—Conidiophores and conidia dilute yellow brown to medium golden brown in color. Conidiophores simple, straight or curved, smooth, 1–3-septate, $20\text{--}46 \times 4\text{--}6 \mu$, apically uniperforate, sometimes with the basal cell slightly swollen.

Conidia ovoid, obclavate, obpyriform, or rarely simply ellipsoidal in shape, usually with an easily visible basal pore; beakless when ellipsoidal, or with a short conical, narrowly tapered, or cylindrical beak $2\text{--}3 \mu$ in diam, the apex of which may be narrow and rounded without

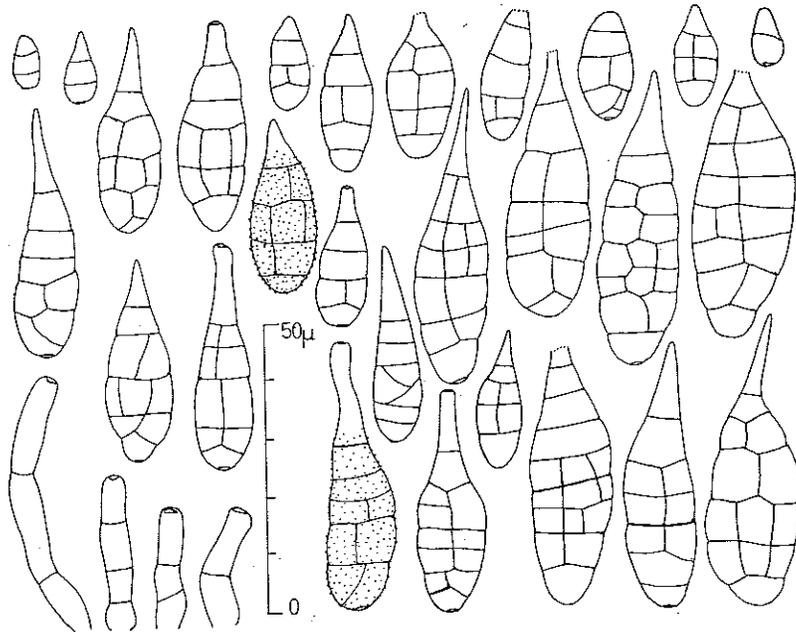


FIG. 2. *Alternaria alternata*: conidia and conidiophores from neotype specimen.

a terminal pore or abruptly blunt with a well-defined pore; beak length up to 25μ , never equaling the length of the conidium body but commonly representing one-fourth to one-third of the total conidium length; beak usually lighter in color than the body. Conidium body $(10\text{--})18\text{--}47 \times (5\text{--})7\text{--}18 \mu$, av. $30.9 \times 12.6 \mu$; $l/w = 1.7\text{--}3.4$, av. 2.4; with (1–)3–8 transverse septa, one or two longitudinal septa in each of 1–6 of the transverse divisions, and commonly a strongly oblique septum in the basal division; distinctly but not deeply constricted at major transverse septa. Conidium wall smooth or very minutely roughened.

STEMPHYLIUM

STEMPHYLIUM Wallroth, Flora cryptogamica germaniae, pars post., p. 300. 1833.

Type species: *S. botryosum* Wallr., l.c., p. 300. 1833.

Type specimen: Institut de Botanique de la Faculté des Sciences, Strasbourg (STR); a single specimen labeled "*Stemphylium botryosum* W. Ad Asparagum." There are other specimens in the *S. botryosum* folder of Wallroth's herbarium, but the specimen cited is the only one which is both mounted on a typical Wallroth specimen card and labeled in his manuscript.

The type specimen, four short sections of asparagus stem, bears predominantly a mixture of the *Stemphylium* and of numerous black, erumpent, pseudoparenchymatous stromata resembling perithecia but within which spores could not be found.

S. botryosum (Fig. 3).—Mycelium extensive within the substrate, septate, about 5 μ diam, forming small pulvinate stromata or clumps of cells from which arise numerous (often 10–15) conidiophores. Conidiophores straight to variously bent or curved, simple or occasionally 1-branched, cylindrical but enlarging apically to the site of spore formation, dilute to medium olive brown, darkest at swollen apex, smooth except for the slightly roughened to distinctly echinulate walls of the apical cell; 1–7-septate; 4–6 \times 20–72 μ with apical cell enlarged to 7–9(–11) μ diam; apical sporiferous cells with a single pore 5–8 μ diam; as many as four successive sporiferous cells produced by successive renewal of conidiophore growth through previously formed apical pores.

Conidia oblong or broadly ovoid to subdoliiform, slightly to conspicuously constricted at the 1–3(–4) transverse and 1–3(–4) complete or nearly complete series of longitudinal septa; dilute to deep olive brown; (12–)15–24(–26) \times (20–)24–33(–35) μ , av. 19.5 \times 28.3 μ ; 1/w = 1.2–1.8, av. 1.5; with a single basal pore up to 8 μ diam; walls conspicuously but minutely warted or echinulate.

ULOCLADIUM

ULOCLADIUM Preuss, in Sturm's Deutschlands Flora, III (Pilze), Heft 30: 83. 1851.

Type species: *U. botrytis* Preuss, op. cit., 30: 83–84; Fig. 42. 1851. The names of the genus and of the type species originally were

published by Preuss, but as nomina nuda, in Bot. Zentralbl. 1: 199. 1846.

Stemphylium botryosum Wallr. var. *ulocladium* Saccardo, Syll. fung. 4: 522. 1866 [as "Var. *Ulocladium* (Preuss)"].

Stemphylium botryosum Wallr. var. *botrytis* (Preuss) Lindau, in Rabenhorst's Kryptogamen-Flora, I, 9(108): 216. 1908.

Type specimen: Botanisches Museum, Berlin (B); a single specimen in the Preuss herbarium, labeled in Preuss' manuscript "265.b. *Ulocla-*

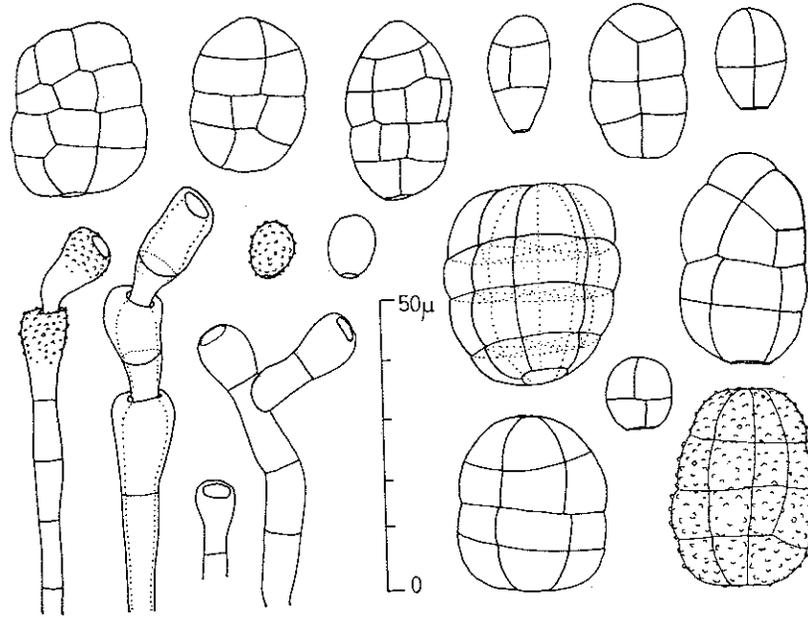


FIG. 3. *Stemphylium botryosum*: conidia and conidiophores from type specimen.

dium botrytis Preuss. Auf dem eichenen Blumenbretchen unter einem Blumentopf in der Rabe." The type specimen is a thin sliver of wood bearing a hyphomycetous mixture dominated by an abundant growth of the *Ulocladium*. This collection is accepted as the holotype specimen, although minor discrepancies exist between the microscopic details of this fungus and the excellent illustration of Preuss; these are noted below in the discussion of *U. botrytis* following the key to nine species of the genus accepted at this time.

SPECIES CURRENTLY ASSIGNED TO ULOCLADIUM

Recognition of the long-ignored *Ulocladium* permits the segregation of a few taxa congeneric with *U. botrytis*. The immediately following taxonomic opinions are based on type material found for species described through 1876, the year of publication of *Macrosporium consortiale* Thüm., which is itself the basionym most frequently used in modern literature for specimens congeneric with *U. botrytis*. Descriptive comments based on suggested representative cultures are specifically noted as such. This treatment of classic materials provides appropriate names for a major portion of pertinent specimens and cultures available in modern times. Included are descriptions of two new species representing unusual pure culture isolates for which there are believed to be no published names. Work in progress will extend this coverage to comparisons in culture as well as to type material of related species described after 1876.

KEY TO SPECIES OF ULOCLADIUM

- A. Conidia usually in chains of 2-10, seldom solitary.....9. *U. chartarum*
- A. Conidia usually solitary, false chains unknown or very rare.....B
- A. Conidia mostly solitary but short chains also common.....D
 - B. Conidia smooth to depressed pustulose.....3. *U. lanuginosum*
 -4. *U. alternariae*
 - B. Conidia becoming densely verrucose.....C
 - C. Conidia mostly obovate with 3 transverse septa.....1. *U. botrytis*
 - C. Conidia mostly subspherical with 1 transverse septum.....2. *U. atrum*
 - D. Conidia grossly tuberculate.....5. *U. tuberculatum*
 - D. Conidia smooth to rough or verrucose.....E
 - E. Conidia smooth to inconspicuously roughened.....6. *U. consortiale*
 - E. Conidia becoming closely and heavily verrucose.....F
 - F. Conidia mostly maturing with 3 dark transverse septa, 7-8 cells, and broadly rounded base.....7. *U. oudemansii*
 - F. Conidia maturing with 3 to commonly 4-7 pale transverse septa, 7-14 cells, and an apiculate to rounded base.....8. *U. septosporum*

1. ULOCLADIUM BOTRYTIS Preuss, in Sturm's Deutschlands Flora, III (Pilze), Heft 30: 83; Fig. 42. 1851. FIG. 4
Stemphylium botryosum Wallr. var. *ulocladium* Sacc., v. s.
Stemphylium botryosum Wallr. var. *botrytis* (Pr.) Lindau, v. s.

Mycelium about 3-4 μ diam, yellow to golden brown, smooth or inconspicuously roughened, septate. Conidiophores erect, ascending, or variously contorted, simple and short, 8-10 \times 3-4 μ , or more commonly simple or branched and elongated to about 100 μ , dilute yellow brown

to medium golden brown, smooth, usually 1-2-septate between the 2-10 uniperforate geniculations. Conidia solitary, obovoid to broadly ovoid or broadly ellipsoidal, rarely subspherical, yellow brown to strongly golden brown to olivaceous, uniformly and closely roughened to verrucose, rarely smooth, $(12.3-13.9-24.6(-27.7) \times (6.2-7.7-15.4 \mu, \text{av. } 18.5 \times 11.5 \mu; l/w = 1.2-2.3, \text{av. } 1.6; \text{ with } (1-2-3 \text{ transverse septa, one or two longitudinal or strongly oblique septa in } 1-4 \text{ of the transverse divisions, and commonly a Y-form septation in the distal division; base tapered or rounded conical, commonly terminating in a minute apiculus; apex rounded.}$

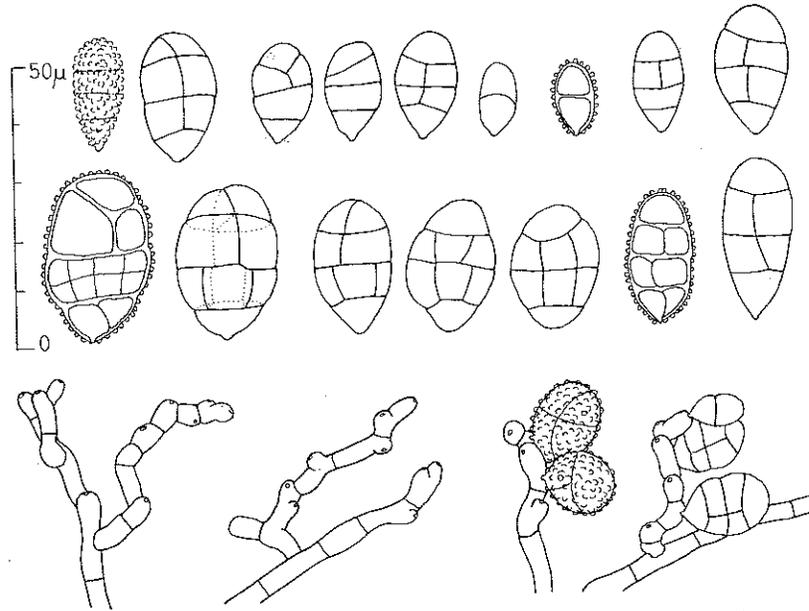


FIG. 4. *Ulocladium botrytis*: conidia and conidiophores from type specimen.

On *Quercus* wood, type in Herb. B (v. s.).

Representative cultures: QM 7878, isol. as a culture tube contaminant, Cambridge, Mass., R. T. Moore, May 1959; QM 8619, isol. ex soil under public garbage litter area, Lassen Volcanic National Park, Calif., W. B. Cooke, LV3-1-4, July 1963.

Preuss illustrated this fungus as having conidia slightly constricted at the septa but without surface ornamentation; transverse septation 3-5. The type specimen yields conidia which agree in shape with those illustrated by Preuss but which usually are uniformly roughened to verrucose and only rarely have more than three transverse septa.

2. *ULOCLADIUM ATRUM* Preuss, *Linnaea* 25: 75. 1852. FIG. 5
Stemphylium atrum (Pr.) Sacc., *Syll. fung.* 4: 520. 1886.

Mycelium about $5\ \mu$ diam, yellow to golden brown, smooth or sometimes minutely roughened, septate. Conidiophores erect, ascending, or variously contorted, simple or branched, golden brown, $5\text{--}8\ \mu$ diam, up to about $110\ \mu$ long, relatively thick-walled, smooth or slightly roughened, with as many as 8 perforate geniculations. Conidia obovoid, broadly ellipsoidal, or most commonly subspherical or sarciniform, golden brown to dark reddish brown to olivaceous, evenly and closely

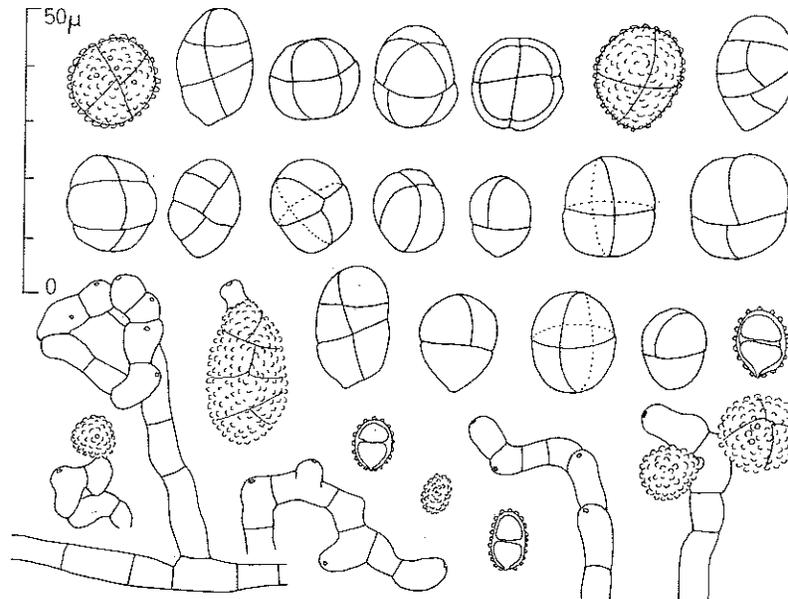


FIG. 5. *Ulocladium atrum*: conidia and conidiophores from type specimen.

verrucose (individual warts about $1.0\ \mu$ diam, larger in culture), $(13.2\text{--})16.5\text{--}19.8\text{--}(22.0) \times (11.0\text{--})13.2\text{--}18.7\ \mu$, av. $18.6 \times 16.0\ \mu$, $1/w = 1.0\text{--}1.3$, av. 1.2; with 1–3 transverse and 1–4 longitudinal or oblique septa, but predominantly with two complete oblique septa intersecting at right angles; base broadly conical or rounded; apex broadly rounded; solitary or very rarely in chains of 2 through production of a short conidiophore (false beak).

On wood of *Betula alba*, type in Herb. B, among Preuss collections as "*Ulocladium atrum* Preuss, auf Birkenästchen"; Preuss, Hoyerswerda, Germany (fide Preuss, loc. cit.).

Representative cultures: QM 7530, isol. ex fruit of *Lycopersicum esculentum*, Davis, Calif., E. E. Butler, S-21, Oct. 1956; QM 8408, isol. ex soil, Calif., P. M. D. Martin, no. 1269, Nov. 1962; QM 7141, isol. ex seed of *Avena sativa*, Kansas, C. T. Rogerson, KSC 0-15-6, 1950; QM 8624, isol. ex river bank gravelly soil, Bellevue, Colo., W. B. Cooke, PR4-4, Oct. 1964.

3. *Ulocladium lanuginosum* (Harz) Simmons, comb. nov. FIG. 6
Stemphylium lanuginosum Harz, Bull. Soc. Imp. Natur. Moscou 44:
 132-133; Pl. III, Fig. 1. 1871.

Alternaria lanuginosa (Harz) Sacc., Syll. fung. 4: 546. 1886;
 lapsus calami, incorrect basionym attributed to description of
Myrosporium hispidum Harz, loc. cit., 44: 131; Pl. IV, Fig. 3,
 1871.

Pseudostemphylium lanuginosum (Harz) C. V. Subr., Current Sci.
 30: 423. 1961.

Alternaria harzii Joly, Encycl. Mycol. 33: 149. 1964.

The original material of this species is believed to be lost. It is believed, in addition, that no isolate currently known to me represents

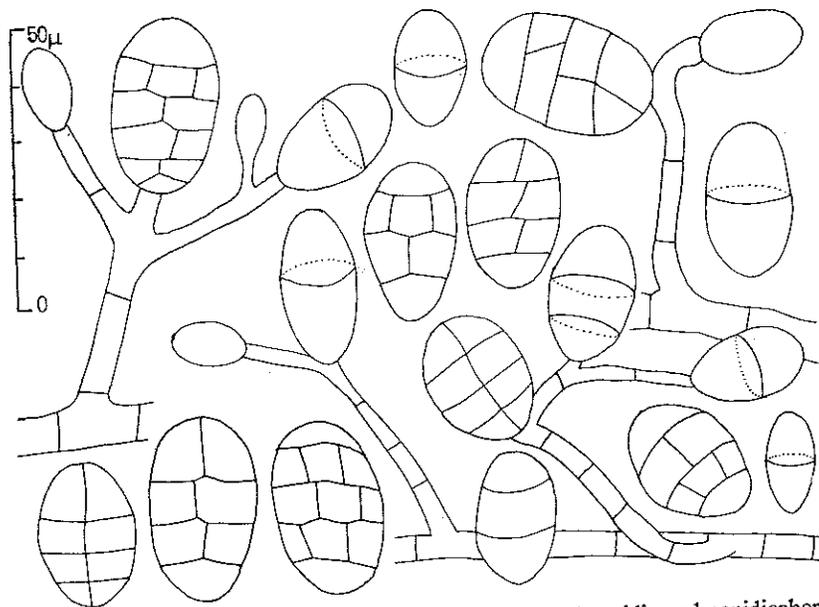


FIG. 6. *Ulocladium lanuginosum*: enlarged redrawing of conidia and conidiophores from type illustration.

this species. This opinion is directed in particular to a culture isolated by Oudemans and deposited by him at the Centraalbureau voor Schimmelcultures, Baarn (= QM 1744), where for many years it has carried the name *S. lanuginosum* Harz in accord with the opinion of Wiltshire. The fungus of Oudemans' isolate differs decidedly from that described and illustrated by Harz; it is used as the basis of a new species described below as *U. oudemansii*.

In the hope that *U. lanuginosum* will be rediscovered Harz's description is presented here in translation, and appropriate portions of his illustration are redrawn (FIG. 6) at an enlargement equivalent to that of the other figures.

Hyphae decumbent, rather thick, closely septate, frequently branched, and colorless, with short lateral branches producing solitary, terminal, colorless, initially 1-celled conidia which develop rapidly and become divided at first into two fairly equal halves through formation of a single transverse septum; as the conidia gradually darken they develop several transverse and longitudinal septa and become squarish, oval, or ovoid with both ends rounded, pale to dark brown, about $30 \times 21.5 \mu$ in size. Elongated side branches commonly arise singly or in opposed pairs below a conidium; side branches in turn produce solitary, apical conidia below which the same manner of branching may be renewed until a cymose or sometimes a unilaterally curved conidial arrangement is formed. On honeycomb from a beehive affected by foulbrood, which had been kept for observation in a damp chamber; appearing as a loose, woolly, abundantly conidial network about 1.5 mm long. Spring 1870, Vienna.

On the basis of Harz's illustration, conidia initially are obovoid becoming broadly ellipsoidal with 3-4 transverse and 1 or 2 longitudinal septa in 3 or more of the transverse divisions; surface ornamentation is lacking, and conidia remain solitary without producing false beaks and chains of conidia. The size range of all conidia with at least one vertical septum is $25-32 \times 18-21 \mu$, av. $28.4 \times 19.0 \mu$; $1/w = 1.4-1.6$, av. 1.5. In contrast, equally mature conidia of *U. oudemansii* rather commonly produce false beaks under moist conditions, retain a broadly obovoid shape, are shallowly roughened to verrucose, and consistently are narrower than mature conidia of *U. lanuginosum*.

No acceptable representative culture of *U. lanuginosum* is known. The name and that of the very similar *U. alternariae* are being retained at least until fresh material of these entities with smooth or shallowly roughened, nonbeaked conidia becomes available for study.

Transfer of *S. lanuginosum* to *Ulocladium* imposes the concurrent

taxonomic synonymy of *Stemphylium* subgen. *Pseudostemphylium* Wilts. (30) and *Pseudostemphylium* (Wilts.) C. V. Subr. (25), both typified by *S. lanuginosum*.

4. *Ulocladium alternariae* (Cke.) Simmons, comb. nov. FIG. 7
Sporidesmium alternariae Cooke, Handb. Brit. Fungi, p. 483. 1871.
Stemphylium alternariae (Cke.) Sacc., Syll. fung. 4: 523. 1886.

Mycelium 4–6 μ diam, pale yellow brown, smooth, septate. Conidiophores golden brown hyphal branches, mostly 4–20 (seldom to 50) \times 4–5 μ , simple with an apical pore or with 1–3 close, uniperforate geniculations. Conidia obovoid to broadly ellipsoidal, golden brown to olivaceous, smooth or depressed pustulose, (18.5–)21.6–30.8(–38.5) \times (10.8–)13.9–20.0 μ , av. 25.4 \times 16.2 μ , 1/w = 1.1–2.0, av. 1.6; with (1–)3–5 transverse septa and 1 or 2 longitudinal or oblique septa in any or all of the transverse divisions; base broadly conical to rounded, sometimes minutely apiculate; apex broadly rounded; solitary, none seen to produce a false beak, no evidence of chains.

On wet wall paper, isotypes in Herb. FH and elsewhere distributed in M. C. Cooke's (1) Fungi Brit. exs. no. 329 as "*Sporidesmium polymorphum* Ca. var. *chartarum* [= nom. nud.], Holloway Mar/70."

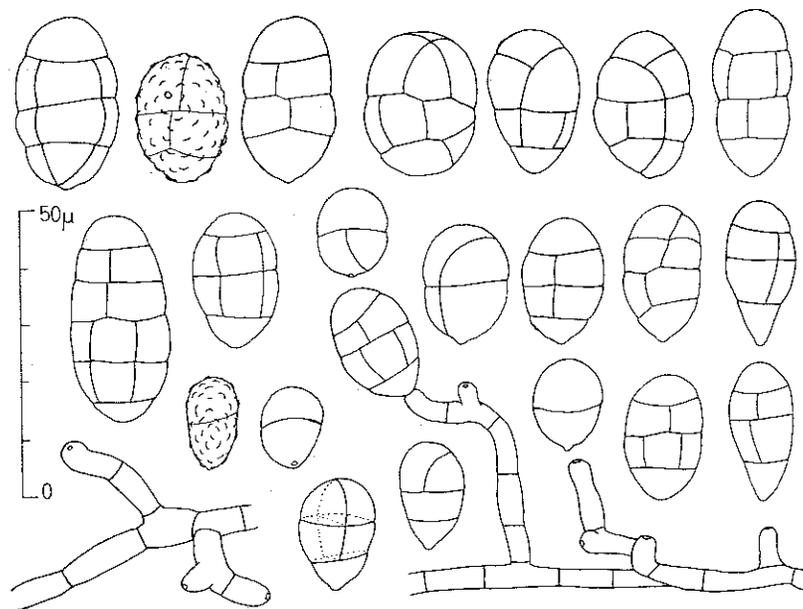


FIG. 7. *Ulocladium alternariae*: conidia and conidiophores from type specimen.

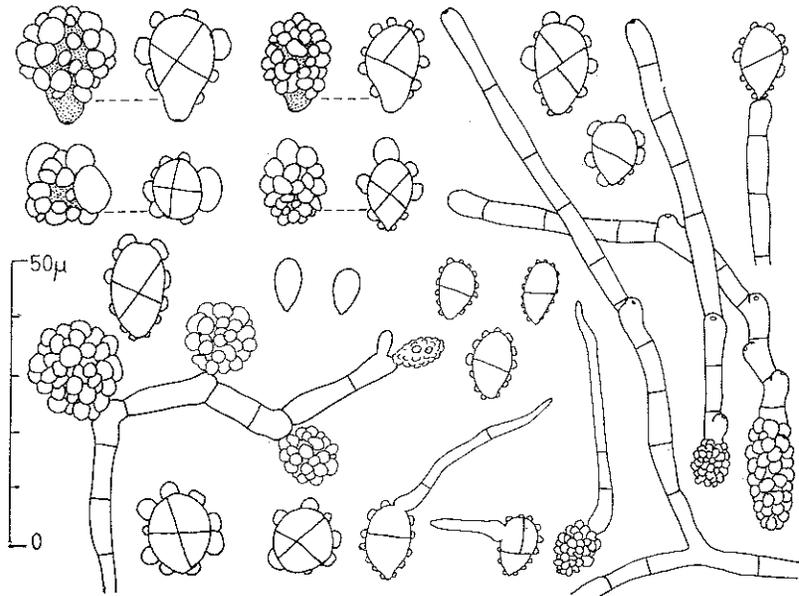


FIG. 8. *Ulocladium tuberculatum*: conidia and conidiophores from type specimen.

No representative culture of this species is known. The unfortunate specific epithet, used originally by Cooke because he saw "indications of a moniliform arrangement of spores" under low magnifications, possibly may be submerged at a later date as a synonym of *U. lanuginosum* if suitable fresh material of these entities with smooth or inconspicuously roughened, nonbeaked conidia ever becomes available for study.

5. *Ulocladium tuberculatum* Simmons, sp. nov.

FIG. 8

Ex culturis in agaro "potato-carrot" descripta. Coloniae cinereo-albae vel atro-brunneae, rapide crescentes. Mycelium ex hyphis septatis, ramosis, subhyalinis vel dilute flavo-brunneis compositum. Conidiophora copiosa, recta vel acclivis, simplicia vel ramosa, ex lateribus hypharum submersarum aeriatarumque oriunda, plus minusve cylindrica, dilute aureo-brunnea, septata, ferme $5\ \mu$ crassa, plerumque ad $200\ \mu$ longa, usque ad 6 genicula sporifera sed vulgo 2-3 remote disjuncta. Conidia initio obovoidea vel ellipsoidea, dilute aureo-brunnea, aspera; deinde aureo-brunnea, dense verrucosa; tum late obovoidea vel subglobosa, atroferruginea, eximie tuberculata; $13.9-18.5(-20.0) \times 10.8-15.4(-16.9)\ \mu$; septo unico principali transverso obliquove per septum secundarium decussato (scilicet in forma X) praedita; solitaria vel aliquando rostrum spurium et sporiferum efficientia.

Habitat: ex solo isolata. Typus: partes ex QM 8614 desiccatae et in Herb. BPI, DAOM, IMI, NY, QM conservandae.

Mycelium 3.0–6.0 μ diam, subhyaline to dilute yellowish brown, smooth or sometimes minutely roughened, regularly septate at distances of 12–18 μ . Conidiophores abundant, erect or ascending from both submerged and aerial hyphae, simple or branched, dilute golden brown, about 5 μ diam, commonly up to 200 μ long, smooth or rarely inconspicuously roughened, septate, bearing solitary conidia at as many as 6 uniperforate geniculations but commonly with only 2–3 widely separated sporiferous pores. Conidia initially obovoid or ellipsoidal, dilute golden brown, roughened; becoming golden brown and heavily verrucose; finally broadly obovoid to subspherical, dark reddish brown, and grossly tuberculate with individual tubercles reaching a diameter of 4–8 μ ; septate conidia 13.9–18.5(–20.0) \times 10.8–15.4(–16.9) μ , av. 16.1 \times 13.4 μ , l/w = 1.0–1.4, av. l/w 1.2; with 1 primary transverse or oblique septum intersected at right angles by 1 secondary septum in one or both of the primary cells, rarely with 2–3 transverse septa in conidia which have elongated in producing a false beak; with base broadly conical to rounded, apex broadly rounded; solitary but sometimes germinating in place and producing a false beak which develops into a typically geniculate conidiophore. Isolated conidia germinate readily on moist substrates, usually producing one rapidly growing hypha per conidium.

Sources: QM 8614 (Type), isol. ex soil, wheat field, northern Utah, W. B. Cooke No. U2-4-1, June 1962; QM 8617, isol. ex bottom slime of water settling basin, San Marcos Dam, Calif., W. B. Cooke no. SM-8, April 1963; QM 8620, isol. ex soil above flood level of Cache la Poudre River, Ft. Collins, Colo., W. B. Cooke No. PR-10-9, Oct. 1964. Described from culture 2 weeks old on potato-carrot agar.

6. *Ulocladium consortiale* (Thüm.) Simmons, comb. nov. FIG. 9
Macrosporium consortiale Thümen, Herb. mycol. oeconom. no. 450. 1876.
Stemphylium consortiale (Thüm.) Groves & Skolko, Can. J. Res., C, 22: 196. 1944.
Alternaria consortiale (Thüm.) Groves & Hughes, in Hughes, Can. J. Bot. 31: 636. 1953.
Pseudostemphylium consortiale (Thüm.) C. V. Subr., Current Sci. 30: 423. 1961.

Mycelium 3–5 μ diam, pale yellow brown, septate, smooth or sometimes minutely echinulate. Conidiophores erect or ascending, simple or branched, translucent yellow to golden brown, about 5 μ diam, up to 60 μ long, with 1–8 perforate geniculations. Conidia obovoid to long ellipsoidal, dilute to medium golden or olive brown, usually smooth to

indistinctly depressed pustulose, rarely definitely verrucose, (18.5–) 20.0–29.3(–33.8) \times (7.7–) 10.8–15.4 μ , av. 23.5 \times 12.4 μ , 1/w = (1.4–) 1.6–2.2(–2.4), av. 1/w = 1.9; with 1–5 transverse and 1–6 longitudinal or oblique septa; base initially conical or rounded, often with a distinct apiculus which may retain its identity as the conidium develops; apex narrowly to broadly rounded; predominantly solitary but occasionally in short chains following apical production of conidiophores (false beaks).

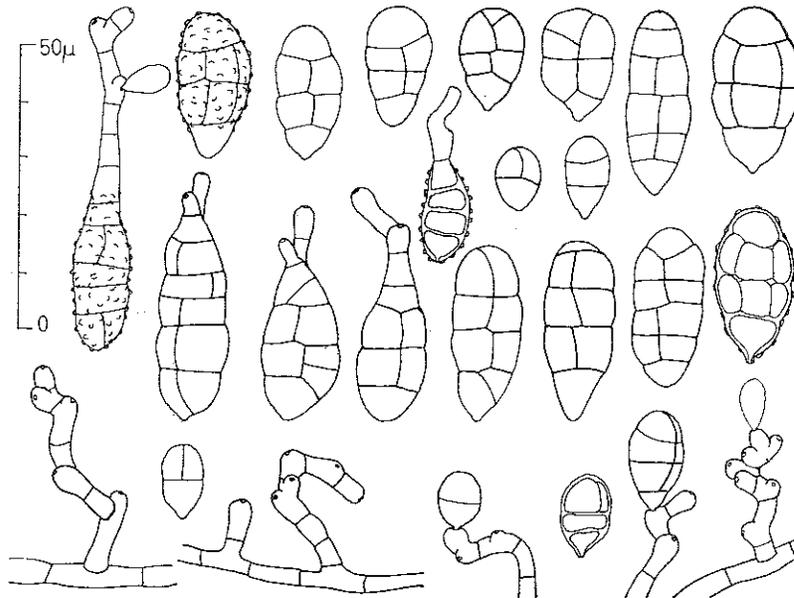


FIG. 9. *Ulocladium consortiale*: conidia and conidiophores from type specimen.

On paper, isotypes in Herb. BPI and elsewhere distributed in Thümen's (27) Herb. mycol. oeconom. no. 450 as "*Macrosporium consortiale* Thm. . . . Bayern: Bayreuth an der Tapete in einem feuchtem Zimmer . . . Winter 1876. leg. von Thümen."

Representative culture: QM 8446, isol. ex dried fruit of *Morus* sp. imported from Afghanistan, Pullman, Wash., S. M. Dietz, 1963.

The name *Macrosporium consortiale* in its several nomenclatural recombinations has come into general use in the past twenty years for numerous isolates of several species of *Ulocladium*. The usage has had a generic consistency, primarily through reference to the excellent illustration of "*Stemphylium consortiale*" by Groves and Skolko (5). This

illustration, however, is either of *U. atrum* or of a closely similar species with dark, conspicuously verrucose conidia. *U. consortiale* is restricted to a species with smooth to inconspicuously roughened conidia of medium color density. *U. atrum* rarely produces false conidial chains, even in culture, whereas *U. consortiale* commonly has false chains, both in the type specimen and in representative isolates.

7. *Ulocladium oudemansii* Simmons, sp. nov.

FIG. 10

Ex culturis in agaro "potato-carrot" descripta. Coloniae cinereo-albae vel atro-brunneae, rapide crescentes. Mycelium ex hyphis septatis, ramosis, subhyalinis vel dilute brunneis compositum. Conidiophora copiosa, recta vel acclivis, simplicia vel ramosa, ex lateribus hypharum praecipue submersarum oriunda, aureo-brunnea, septata, usque ad 6.0–7.5 μ crassa, plerumque 150–250 μ longa, usque ad 5 genicula sporifera praebentia. Conidia initio anguste obovoidea, hyalina, levia; denique crassa obovoidea vel ellipsoidea, atro-ferruginea vel olivacea, tenue salubrosa vel verrucosa; (18.5–)21.6–30.8(–33.9) \times 10.8–16.9 μ ; septis transversalibus 3–5 et longitudinalibus obliquisve 1–2 per partitionem transversam praedita; plerumque solitaria vel interdum rostrum spurium et sporiferum efficientia.

Typus: partes ex QM 1744 desiccatae et in Herb. BPI, DAOM, IMI, NY, QM conservandae.

Mycelium 3–6 μ diam, subhyaline to dilute yellowish brown, smooth, septate at distances of 10–20 μ . Conidiophores abundant, erect or ascending, simple or branched, golden brown, reaching 6.0–7.5 μ diam, commonly in the range of 150–250 μ in length, smooth, septate, bearing solitary conidia at 1–5 uniperforate geniculations. Conidia initially narrowly obovoid, hyaline, smooth; becoming yellowish brown and inconspicuously roughened; finally broadly obovoid or ellipsoidal, dark reddish brown to olivaceous, with basal cell essentially smooth and remainder of spore depressed pustulose to verrucose; (18.5–)21.6–30.8(–33.9) \times 10.8–16.9 μ , av. 25.1 \times 14.8 μ , 1/w = 1.4–2.1, av. 1.7; with (1–)3–5 transverse and one or two longitudinal or oblique septa in any or all of the transverse divisions; base broadly conical to rounded, apex broadly rounded and often more conspicuously verrucose than remainder of conidium; usually remaining solitary, but sometimes germinating in place and producing a false beak which develops as a typically geniculate conidiophore. Isolated conidia germinate readily on moist substrates, producing one or more rapidly growing hyphae per conidium.

Source: QM 1744 (Type), isol. Oudemans, original substrate, locality, and date not known, but originally determined and deposited by Oudemans in CBS as *Stemphylium botryosum*. Described from culture 2 weeks old on potato-carrot agar.

The shape, size, and ornamentation of *U. oudemansii* conidia indicate that this isolate has been misidentified with *U. (Stemphylium) lanu-*

ginosum, q. v. for comments. Oudemans and Koning (16) and Oudemans, in his original determination of his culture, considered that this excellent isolate and similar material represented *Stemphylium botryosum*, an unfortunate misidentification which has misled many of the generic interpretations of *Stemphylium*. Wiltshire (30) proposed a section *Pseudostemphylium* in *Stemphylium* for species similar to *S. lanuginosum* Harz and to this Oudemans isolate. Groves and Skolko

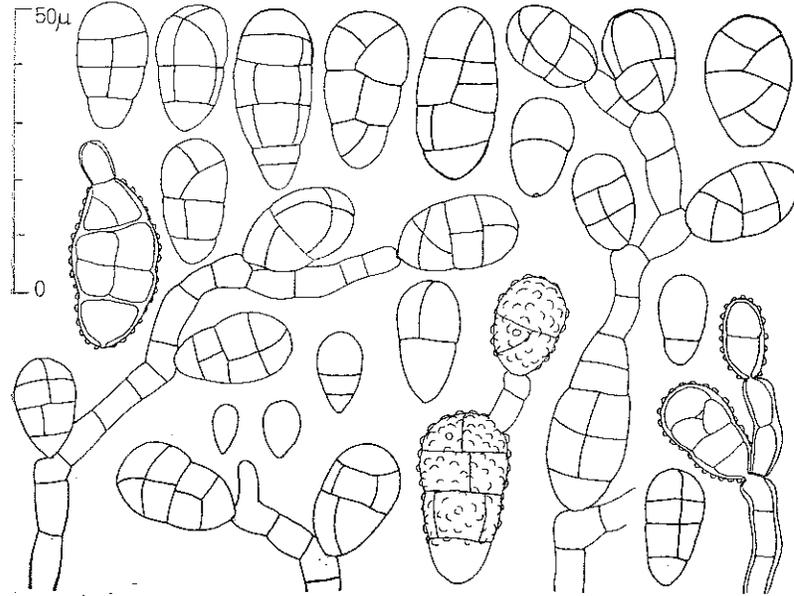


FIG. 10. *Ulocladium oudemansii*: conidia and conidiophores from type specimen.

(5), Neergaard (14), and Subramanian (25) all followed this proposed segregation in one way or another. Wiltshire's perception in this taxonomic problem reaches its logical conclusion in assignment of these species, anomalous in *Stemphylium*, to *Ulocladium*.

8. *Ulocladium septosporum* (Pr.) Simmons, comb. nov. FIG. 11
Helminthosporium septosporum Preuss, *Linnaea* 24: 117. 1851.
Macrosporium septosporum (Pr.) Rabenhorst, *Botan. Zeit.* 9: 454.
 1851.

Mycelium about 5 μ diam, golden brown, smooth, septate. Conidiophores erect or ascending, golden brown to olivaceous, commonly 50–70 \times 4–6 μ , simple with an apical pore or with 2–3 uniperforate genicula-

tions. Conidia obovoid to ellipsoidal, golden brown to olivaceous, inconspicuously roughened to densely and minutely verrucose, $(18.5-20.0-33.9(-35.4) \times 12.3-20.0(-21.6) \mu$, av. $27.0 \times 15.6 \mu$, $l/w = 1.3-2.2$, av. 1.7; with (1-)3-7 transverse septa and 1 or 2 longitudinal septa in each of one or more of the transverse divisions; base broadly conical to rounded, sometimes minutely apiculate; apex rounded; solitary, but with a significant number of conidia producing short, simple or geniculate conidiophores (false beaks).

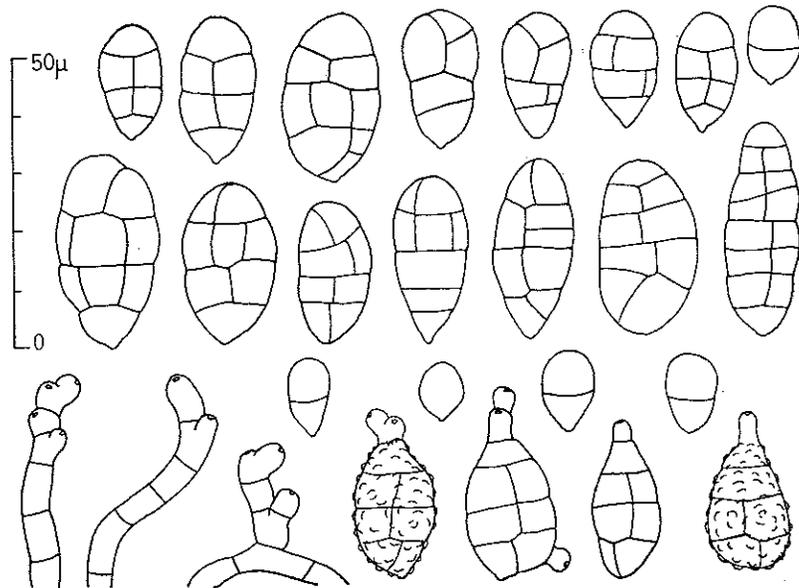


FIG. 11. *Ulocladium septosporum*: conidia and conidiophores from type specimen.

On *Pinus* wood, isotypes in Herb. B, FH, and elsewhere distributed by Rabenhorst (21) in Klotzsch's Herb. vivum mycol. no. 1371 as "*Helminthosporium septosporium* [sic] Pr. Mspt. [= nom. nud.] *Ad ligno decort. in locis suffocatis reposita. Hoyerswerda. Preuss.*"

No available isolate appears to be unquestionably suitable for citing as a representative culture of *U. septosporum*.

9. *Ulocladium chartarum* (Pr.) Simmons, comb. nov.

Alternaria chartarum Preuss, Bot. Zeit. 6: 412. 1848.

FIG. 12

Mycelium about 5μ diam, pale yellow brown, septate. Conidiophores erect or ascending, simple or branched, golden brown, about $5-7 \mu$ diam, up to $40-55 \mu$ long, with 1-8 perforate geniculations. Conidia obovoid.

to short ellipsoidal, medium golden brown to olivaceous, smooth to pustulose roughened (in type) to evenly or irregularly verrucose (in cultures), $(18.5-24.6-32.4(-38.5) \times (10.8-12.3-21.6 \mu, \text{av. } 26.4 \times 14.7 \mu, 1/w = (1.3-1.5-2.0(-2.4), \text{av. } 1/w = 1.8; \text{ with } 1-5 \text{ (commonly } 3) \text{ transverse and } 1-5 \text{ longitudinal or oblique septa; walls and septa often conspicuously thickened to } 2.5 \mu \text{ in type and } 1.5 \mu \text{ in cultures; base initially conical, becoming hemispherical; apex broadly rounded before production of false beaks; solitary or very commonly in chains of } 2-10 \text{ through apical production of short conidiophores (false beaks).$

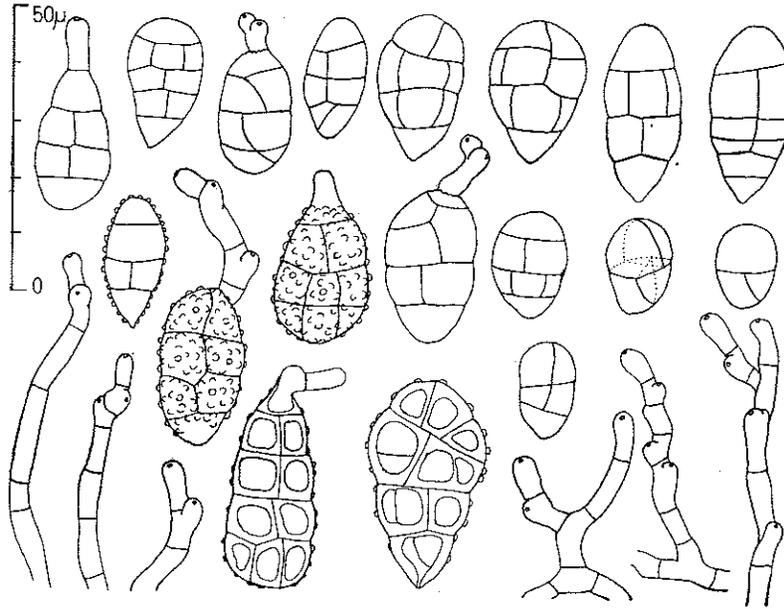


FIG. 12. *Ulocladium chartarum*: conidia and conidiophores from type specimen.

On paper, type in Herb. B, among Preuss collections as "*Alternaria substratiæ chartarum* Preuss, auf Fliegenpapier"; also represented in Klotzsch's Herb. vivum mycol. no. 1284 (ed. Rabenhorst, 21) as "*Alternaria chartarum* Pr. . . . In charta venata muscarum. Hoyerswerda. Preuss."

Representative cultures: QM 8328, isol. ex DAOM 59616(b), on *Populus* plywood, Saskatoon, Canada, S. J. Hughes, July 1957; QM 8610 (= IMI 116369), isol. ex manila fiber, St. Gallen, Switzerland, O. Wälchli, EMPA no. 204, 1965.

U. chartarum is the one species of *Ulocladium* most likely to be misidentified as an *Alternaria*. Conidia typically are produced in rela-

tively long chains which, however, are the result of precocious germination and production of false beaks and conidia by successive elements in the chain. Each conidium is initially obovoid and remains so unless it begins to form a false beak; each beak is in form and function a short conidiophore quite distinct from the gradually tapering true beaks of *Alternaria*.

ALTERNARIA RADICINA

Alternaria radicina Meier, Drechsler & Eddy (11) is a species of considerable importance which has been treated taxonomically with other pseudostemphylioid species (Neergaard, 14; Subramanian, 25). It would be remiss to omit here an opinion on its generic affinities, particularly when a culture derived from its type is readily available and remains in good sporulating condition 45 years after original isolation (QM 1301 = ATCC 6503).

Conidia of *A. radicina* resemble those of some species of *Ulocladium* only in that they usually remain solitary or produce chains sparingly and never develop a narrowly tapered true beak. The conidia, however, are alternarioid in that they are ovoid at a very early age and to a great extent retain an ovoid or broadly ellipsoidal, apically broadly conical shape as they mature. In addition, the basal cell is broadly rounded and has a relatively large pore surrounded by a halo of pigment, a character quite common in *Alternaria* but at variance with the minute and usually inconspicuous basal pore of *Ulocladium*. It is my opinion that the sporulation characteristics of *A. radicina* are fundamentally alternarioid and that the species originally was included correctly in *Alternaria*. Its obligate synonymy is:

- ALTERNARIA RADICINA Meier, Drechsler & Eddy, *Phytopathology* 12: 164, 166; Fig. 1. 1922.
Thyrospora radicina (M., D. & E.) Neergaard, *Bot. Tidsskr.* 44: 361. 1938.
Stemphylium radicinum (M., D. & E.) Neergaard, J. E. Ohlsens Enkes *Plantepatol. Lab., Aarsberetn.* 4: 14. 1939.
Pseudostemphylium radicinum (M., D. & E.) C. V. Subramanian, *Current Sci.* 30: 423. 1961.

ACKNOWLEDGMENTS

A taxonomic review of a genus established more than a century ago can scarcely be considered the sole work of a modern author. Obliga-

tion is acknowledged in particular to directors and staff of the herbaria and culture collections, cited acronymously in the text, in which type specimens and important isolates have been made available to me. The individuals and institutions named as donors of representative cultures may look askance at the generic name resurrected for their isolates, but they are thanked for their materials and for their patience in awaiting identifications.

All cultures cited are deposited with the American Type Culture Collection, the Centraalbureau voor Schimmelcultures, the Commonwealth Mycological Institute, and the U. S. Army Natick Laboratories.

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