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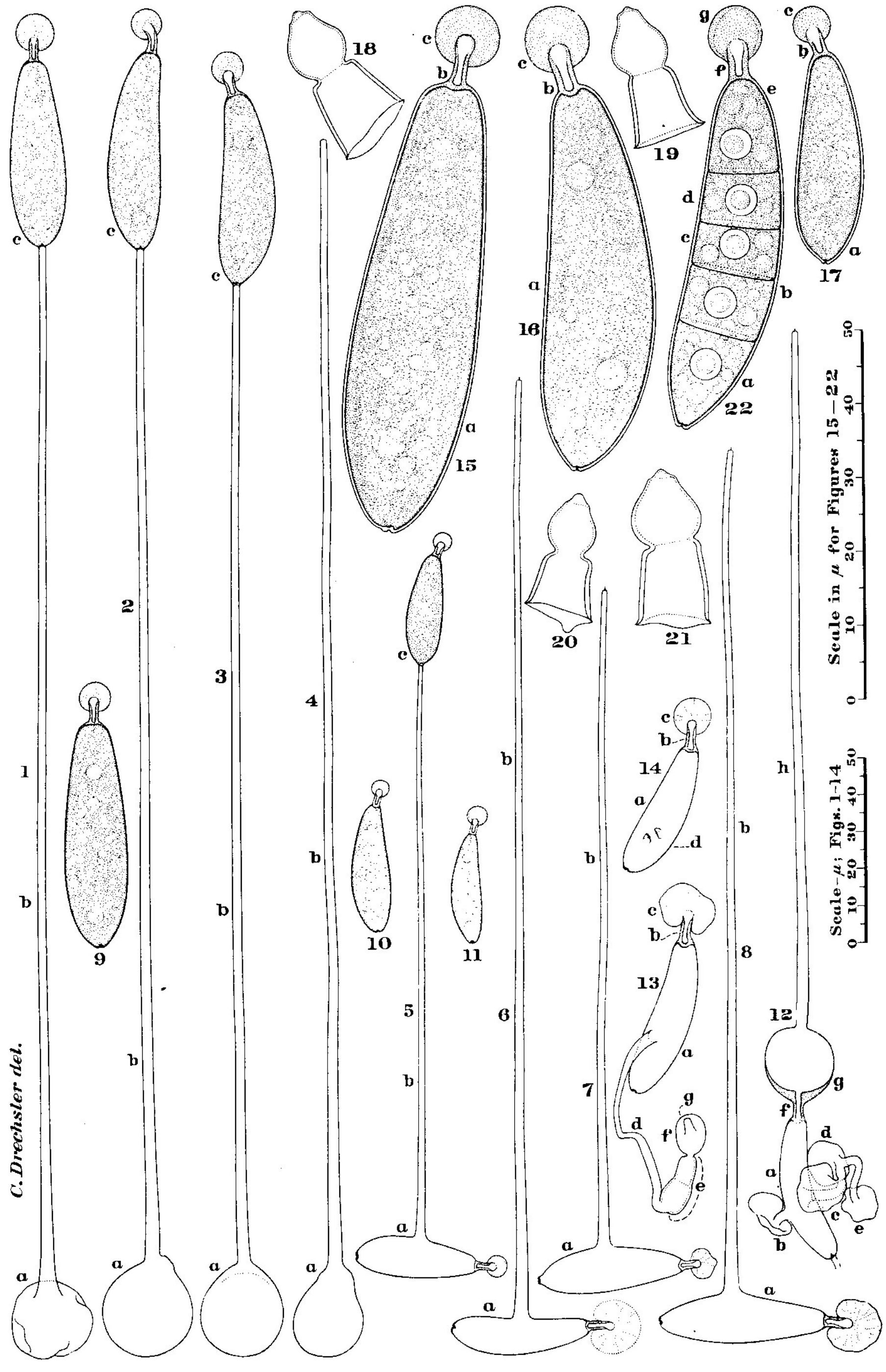
A BASIDIOBOLUS PRODUCING ELONGATED SECONDARY CONIDIA WITH ADHESIVE BEAKS

CHARLES DRECHSLER[1]

A maizemeal-agar plate culture which after being permeated with *Pythium ultimum* Trow had been further planted with small quantities of friable leaf mold collected on November 14, 1945, in a deciduous wood near Mercer, Wisconsin, showed after 50 days about a hundred globose conidia scattered sparsely over an area of approximately 75 square millimeters bordering one of the deposits of forest detritus. Nearly all of the globose bodies were empty of protoplasmic contents, and thus were represented only by membranous envelopes many of which had become misshapen from partial collapse (fig. 1, a). The globose envelopes that had suffered no collapse (figs. 2, a; 3, a; 4, a) revealed, like the few globose conidia that retained their protoplasmic contents, a rather broadly protuberant irregularity in their rounded contour, which gave them an unmistakable similarity to the subspherical conidia characteristic of many insectivorous Entomophthoraceae as well as of the few related forms in the genera *Conidiobolus* and *Delacroixia*. Many of the empty globose envelopes were found bearing individually an erect slender conidiophore (figs. 1, b; 2, b; 3, b; 4, b) usually about 300 μ high, on whose tip was supported an elongated ellipsoidal or strobiliform secondary conidium (figs. 1, c; 2, c; 3, c) prolonged at its distal end into a narrow beak which terminated in a relatively large spherical mass of yellow material. While in many instances the empty conidiophore was found denuded (fig. 4, b), and often, besides, had fallen over prostrate on the substratum, it was clear that all of the empty globose conidia had used their contents in producing aloft a secondary conidium of the beaked strobiliform type. In no instance had germination taken place by the production of a mycelial hypha.

Nor was vegetative germination observable in any of the beaked conidia. When these fell on the moist substratum (figs. 5, a; 6, a; 7, a; 8, a) they usually would send up a slender conidiophore (figs. 5, b; 6, b; 7, b; 8, b), most frequently from a position about midway between base and apex, to produce a tertiary conidium (fig. 5, c), which, like its immediate parent, was strobiliform and drawn out distally into a beak surmounted by a subspherical yellowish mass. The same reproductive development would commonly be

[1] Pathologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture; Plant Industry Station, Beltsville, Maryland.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repeated a second and a third time, each repetition entailing some reduction in size of the spore; so that whereas the first generation of strobiliform conidia often measured 64 to 73 μ in total length and 14.5 to 17.5 μ in greatest width (figs. 1, c; 2, c; 3, c; 9), many of their descendants (figs. 5, c; 10; 11) showed corresponding dimensions only half as large.

Departures from the usual course of repetitional development were manifest in a number of instances. In one such instance the empty spore envelope of elongate elliptical outline (fig. 12, a) bore in its median region four empty collapsed membranous pouches, one of them being attached by a short hyphal outgrowth (fig. 12, b), the others (fig. 12, c–e) being borne at intervals on a hyphal outgrowth that must have been produced by successive elongation. That these collapsed pouches may originally have had a subspherical shape was strongly indicated in the distal modification of the beak (fig. 12, f) into a globose inflated part (fig. 12, g) that bore a slender sporophore (fig. 12, h) whereon had evidently been produced a conidium of the strobiliform type. The inflated part at the tip of the beak would seem perhaps best interpretable as a somewhat abortive conidium of the globose type interpolated between two generations of strobiliform conidia. The four collapsed membranous

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Explanation of figures 1–22

Basidiobolus haptocladus, drawn with the aid of a camera lucida; magnification ×500 in figures 1–14, and ×1000 in figures 15–22. FIGS. 1–3. Globose primary conidia, a, each of which has put forth an erect conidiophore, b, whereon is borne an elongate secondary conidium, c, with its apical beak supporting a mass of yellow adhesive material. FIG. 4. Empty envelope of a globose conidium, a, with the empty membrane of the erect germ conidiophore, b, from which an elongate conidium has become detached. FIG. 5. Elongate conidium, a, which has put forth an erect conidiophore, b, and on its tip has produced an elongate beaked daughter-conidium, c. FIGS. 6–8. Empty envelopes of elongate conidia, a, each bearing an empty erect conidiophore, b, from whose tip a daughter-conidium of elongate type has become detached. FIGS. 9–11. Detached conidia of elongated beaked type, showing differences in size and shape. FIG. 12. Empty envelope of elongate conidium, a, bearing laterally on two short empty hyphal outgrowths the collapsed membranous envelopes of four globose bodies, b–e, and bearing distally on its apical beak, f, a fifth empty globose body, g, whereon is supported an empty erect conidiophore, h, now denuded of the elongate daughter-conidium produced on its tip. FIG. 13. Empty envelope of elongated conidium, a, with terminal beak, b, and flattened body of adhesive material, c; it bears laterally a germ conidiophore, d, which tapers narrowly before widening out to bear an abortive "basidium," e, surmounted by the empty envelope of an abortive globose conidium, f, supporting a sterigma, g, from which an elongate conidium was disjointed. FIG. 14. Empty envelope of elongate conidium, a, with apical beak, b, and mass of adhesive material, c; it bears laterally a short, distally reflexed, empty, tubular membrane, d, left behind after the violent discharge of an expanded "basidium" and globose conidium. FIGS. 15–17. Elongate conidia, a, each with an apical beak, b, whereon is borne a globose mass of yellow adhesive material, c. FIGS. 18–21. Empty membranous remains of expanded distal parts of propulsive conidiophores ("basidia") found lying scattered on substratum after each functioned in the violent discharge of a globose conidium. FIG. 22. Elongate conidium which has become divided internally into five cells or sporangiospores, a–e, each showing a large nucleus near its center; f, apical beak; g, globose mass of yellow adhesive material.

pouches seem likewise interpretable as abortive globose conidia that with respect to function had suffered complete frustration.

Another and somewhat different departure from the usual course of repetitional development was brought to light in a strobiliform conidium whose empty envelope (fig. 13, a), correctly provided at its apex with beak (fig. 13, b) and mass of yellowish material (fig. 13, c), was found bearing in the usual median position an empty conidiophorous filament (fig. 13, d), which at a distance of 35 μ from its origin, on tapering to a width of 1.3 μ, widened out to 2.5 μ and maintained this width for a distance of 20 μ to bear a thick-walled expanded part (fig. 13, e) surmounted by a thin-walled, somewhat globose, empty bladder (fig. 13, f). This bladder bore an empty, blunt, sterigma-like projection (fig. 13, g) from which assuredly a daughter-conidium must have become abjointed. Judging from the narrow apex of the projection, the daughter-conidium most probably was of the beaked strobiliform type. Here, again, the globose bladder may best be construed as a poorly developed abortive conidium of the subspherical type that was interpolated between two generations of beaked conidia.

That, nevertheless, a conidium of the strobiliform type may sometimes give rise successfully to a daughter-conidium of the globose type was inferred from an empty spore envelope (fig. 14, a) which showed a fully characteristic elongated-elliptical outline and at the apex was prolonged into a beak (fig. 14, b) bearing a subspherical mass of yellow material (fig. 14, c). The only membranous part present on this envelope that could have been operative in conveying away the protoplasmic contents was a short lateral tube (fig. 14, d), open at the end, and with its distal portion markedly widened and reflexed; the cylindrical portion of the tube measuring about 2.5 μ in length and width, while its reflexed mouth showed a width of approximately 5.5 μ. As the slightly lipped basal hilum in elongated beaked conidia (figs. 15, a; 16, a; 17, a), with its darkened minute central scar, is usually not more than 2 μ wide, the likelihood that a conidium of this type could have been disjointed from so broad an attachment can be dismissed from consideration. The manner in which the reflexed tube must have come into being was made evident through the presence near the leaf mold of more than twenty thick-walled empty structures (figs. 18–21) consisting individually of a bell-shaped part, slightly flaring at the open mouth, together with a slightly shorter dome-shaped part that at the closed end showed a minute thin-walled protrusion; the two parts being demarcated from one another by a fairly pronounced transverse constriction. The close resemblance of these curious structures to the "basidia" figured by Eidam (10, *pl. 10, fig. 22, a–c*) in the original account of his *Basidiobolus ranarum,* as well as to Thaxter's (20, *pl. 21, figs. 411, a; 412, a*) illustrations of the same objects, identified them unmistakably as thick-walled envelopes of the expanded terminal parts thrown off in the violent discharge of conidiophores pertaining to a species of *Basidiobolus*. Manifestly the reflexed tube on the empty strobiliform conidial envelope represented the proximal portion of such a propulsive conidiophore that was left attached when the expanded distal portion, together with the daughter-conidium borne on it, was projected into the air. The conidiophore here must have been very short since the expanded part had evidently been borne on a narrow stalk only 2.5 μ long. Further, the meager length of the reflexed rim of the empty tube would seem to indicate that rupture of the conidiophore here took place considerably farther toward the base of the expanded part than would seem illustrated by Ingold (13) for *B. ranarum*.

There is reason to believe that in the present fungus the narrower stalk-like part of the propulsive conidiophore may often attain greater length than in the specimen shown in figure 14, d. As the thick-walled expanded part shown in figure 13, e, almost certainly represents an abortive "basidium," the somewhat widened portion of supporting filament immediately below it may very probably have developed as the stalk of the "basidium," whereas the narrowly tapering proximal portion of supporting filament offered more the appearance of having been produced as the prospective stalk of an elongated beaked conidium. Direct observations on the forcible discharge of the "basidium" and globose conidium are lacking, because unfortunately the projection of these bodies on to the transparent agar, evidently from a source some distance within the deposit of leaf mold, had come to an end when the fungus was first seen; and because, further, the repetitional development of conidia on the agar took place, with very few exceptions, by the production of elongated beaked conidia on inert slender sporophores.

Spores corresponding to the beaked conidia of the Wisconsin fungus do not seem to have been ascribed to *Basidiobolus ranarum* in the rather extensive literature on that species. Nor apparently do any references to such spores occur in the less abundant writings on *B. lacertae* Eidam (10, 15), which species Levisohn (14), after ample comparative study carried out with excrement of frogs, toads, salamanders, blindworms, and lizards, concluded should be reduced to synonymy with *B. ranarum*. Mention of elongated beaked conidia likewise seems absent in Fries' original account of *B. myxophilus* (11), a species which its author (12) later seemed inclined to regard as also being identical with *B. ranarum*, on learning that the gelatinous masses in which it developed might have consisted of material voided from the oviducts of frogs. Of problematical import in this connection is a figure of *B. ranarum* given by Eidam (10, *pl. 9, fig. 16*) wherein is shown a globose conidium with a long slender erect germ-conidiophore that supports an expanded structure tapering markedly toward a narrow apex on which is attached a small globose body. The expanded structure was construed by

Eidam as a "basidium" that had begun to bud forth a tertiary conidium. Thaxter (20, p. 145, 146) noted its similarity to the nearly almond-shaped secondary conidia often produced by *Empusa sphaerosperma* Fres., *E. Fresenii* Nowak., and allied insectivorous species. These secondary conidia Thaxter found borne on long slender capillary conidiophores from which they were not forcibly discharged; and he observed them to germinate by means of an irregular hypha that begins "as a drop-like protuberance from the apex of the spore." One of his figures of *E. Fresenii* (20, *pl. 16, fig. 119*) shows a globose primary conidial envelope that has become emptied of its contents in sending up a capillary conidiophore on whose empty tubular membrane is supported aloft an almond-shaped secondary conidium, which, while still attached, has begun to germinate by putting forth a small spherical protuberance at its tip. This figure, as also Eidam's figure referred to, reveals with respect to the outward shape and general arrangement of component parts a suggestive approximation to the asexual reproductive units of the Wisconsin fungus in which a secondary elongate beaked conidium has been produced from a globose primary conidium.

Although the elongate beaked conidia here under discussion appear truly homologous with the almond-shaped conidia of *Empusa Fresenii,* they show some distinctive differences. As far as I have been able to determine they are always terete, never being flattened laterally in any noticeable degree. The beak (figs. 15, b; 16, b; 17, b; 22, f) with which they are regularly provided cannot well be regarded as a product of incipient vegetative germination, seeming rather to represent a product of spore differentiation. In mature conidia it consists of a sturdy narrowed cylindrical prolongation of the spore envelope. It commonly ranges in length from 4 to 8 μ, and in width from 1.5 to 2.5 μ. Its wall is distinctly yellow and except at the distal end has usually a thickness of 0.5–1 μ. The empty and frequently narrow lumen of the beak is separated from the protoplasmic interior of the living cell below by a septum which likewise is thick and distinctly yellow. Distally the tubular wall diminishes pronouncedly in thickness, so that at the very tip it may be discernible only as a thin convex line of demarcation setting off the colorless lumen from the homogeneous globose mass of yellow material, 5–10 μ in diameter, that surrounds the terminal portion of the beak (figs. 15, c; 16, c; 17, c). In some instances the subspherical mass may show at its periphery a perceptibly different shade of coloration, either lighter (fig. 22, g) or deeper than through its interior. After the spore has fallen on the substratum, the mass often flattens out somewhat irregularly and may then show a variable number of radial striations (figs. 6, a; 7, a; 8, a; 13, c; 14, c). These striations strongly recall the radial markings frequently observable in the globose masses of adhesive material utilized by my *Nematoctonus haptocladus* (9) in the capture of nematodes, and very probably likewise merely represent minute folds formed in a thin film-like outer layer when the mass becomes flattened under external pressure. Parallelism with *N. haptocladus* is further evident in that the yellow material of the Wisconsin fungus is of an adhesive character, and obviously is secreted from the thin-walled distal portion of the beak. Among phycomycetes the glandular conidial beak, together with the globose adhesive mass secreted by it, has an approximate counterpart in my *Stylopage rhynchospora* (4, p. 394–397), where, however, transformation of the conidial beak into a glandular part is more often omitted than accomplished.

Presumably the special function of the adhesive beak is to attach the spore securely to a passing animal. Although a possibility exists that such attachment be serviceable merely in achieving dispersal after the manner of cocklebürs (*Xanthium* spp.), analogy with other fungi whose spores are equipped with similar organs while still attached to their sporophores—e.g. *Dactylaria haptospora* Drechsl. (6, p. 456–461) and *Nematoctonus leptosporus Drechsl.* (7)—or whose spores develop comparable adhesive organs after they fall on the substratum—e.g. *Dactylella asthenopaga* Drechsl. (3, p. 496–499) and *Nematoctonus pachysporus* Drechsl. (7)—seems strongly indicative of a parasitic or, perhaps, predaceous relationship. To some degree the fungus would seem to betray a dependence on some other organism also by its failure to grow vegetatively on the agar culture wherein it appeared. In restricting its development to the production of successive generations of spores it showed a behavior much like the behavior that on a few occasions was found displayed by some insectivorous entomophthoraceous forms in similar cultures which had been prepared by adding detritus from herbaceous crop plants evidently containing intermixed remains of parasitized aphids. By way of contrast, when in several instances *Delacroixia coronata* (Cost.) Sacc. & Sydow (1; 19, p. 457) developed from plantings of decaying material, it gave rise to an extensive vegetative mycelium that yielded an abundance of conidia and resting spores.

Among the many elongated beaked conidia that came under observation, two individuals—one of them shown in figure 22—arrested special attention, for instead of giving rise to another spore externally they became divided internally by transverse cross-walls. The five resulting cells (fig. 22, a–e), though not accurately equal in size, showed no great differences in volume. The two subconical or dome-shaped cells at the base and tip (fig. 22, a, e) measured about 13 μ in length, and about 10 or 11 μ in diameter at the circular end directed toward the middle of the spore; while the three intermediate segments (fig. 22, b–d), of cylindrical shape, measured 6.5–8 μ in length and 10–11.5 μ in diameter. Each of the segments contained near the center of its vacuolate protoplast a spherical nucleus, 4–4.5 μ in diameter, which showed a clear hyaline outer layer surrounding a noticeably darker subspherical nucleolus commonly 2.2–2.5 μ in diameter. Owing to its relatively large size and its ready visibility in an unstained condition within the living cell, the nucleus here had much resemblance to the nucleus of various rhizopods, such as *Amoeba verrucosa* Ehrenb., for example, where similarly a hyaline outer layer surrounds a slightly darker subspherical central body. Eidam remarked on the unusually large size of the nucleus in *Basidiobolus ranarum*, and mentioned being able to see it in unstained living material. He further characterized the nucleolus of his species as being very large, though judging from his figures it would seem to be somewhat smaller in comparison with the entire nucleus than the nucleolus of the Wisconsin fungus. While for the most part, again, Eidam figured the nucleus of *B. ranarum* with an elliptical outline, the nucleus in the conidial segments of the Wisconsin fungus appeared to be very nearly spherical. It seems unlikely, however, that specific differences are concerned here, since in the figures given by Raciborski (18), Olive (17), and Levisohn (14), the nucleus of *B. ranarum* shows considerable variation in shape and in relative size of the nucleolus.

The two segmented conidia were left on the surface of the agar where they had fallen. They were examined at intervals until after 12 days the culture was ruined through burrowing of small annelids. During these 12 days they showed no sign of further change. In becoming divided internally into several cells they evidently developed in accordance with their primitive character as sporangia. The several cells formed within them must be regarded as sporangiospores homologous with the endogenous immotile spores of my *Gonimochaete horridula* (8) as well as with the cells which according to Levisohn's account are liberated from the globose conidial envelopes of *B. ranarum* inside the digestive tubes of frogs and lizards. Moreover, the several cells of the elongated conidium may readily be homologized with the multiple segments of the helicoid hyphal terminations of my *Meristacrum asterospermum* (5), each of which gives rise exogenously, by budding, to a single conidium of rather small size. To the small conidia of *M. asterospermum*, therefore, as also to the similarly small conidia produced plurally on multiple stalks put forth by the large globose conidia of *Delacroixia coronata* and *Conidiobolus Brefeldianus* Couch (2), the multiple spore segments of the Wisconsin fungus would seem to bear the same relationship as the sporangiospores of *Rhizopus* bear to the conidia of *Cunninghamella*.

It is not known whether the leaf mold used in planting my culture contained excrement of any of the animals habitually harboring *Basidiobolus ranarum* in their digestive tracts, for though the material was collected on rolling upland in a site well removed from any pond or permanent stream, some species of frogs and toads roam about so widely that their excrement might be distributed, even if only in meager quantity, almost anywhere. Consequently the source of the detritus provides no certain indication as to the separateness of my fungus from *B. ranarum;* and, indeed, caution would seem here all the more necessary in view of Möller's report (16, p. 5–8) that several times *B. ranarum* developed spontaneously in decaying plant residues he collected on the side of a forest brook in Brazil. My fungus, however, would appear distinguished decisively from *B. ranarum* by its abundant production of elongated secondary conidia with adhesive glandular beaks. If similar conidia were formed in *B. ranarum,* they could hardly have been overlooked by the several very competent investigators who have given that species prolonged study. Even if the structure which Eidam interpreted as a "basidium" bearing a small tertiary conidium on its tip, should have been, as Thaxter hinted, a conidium of the secondary type occurring in *Empusa Fresenii,* the pronouncedly tapering shape evident in Eidam's figure, and the absence of any indication of a thick-walled cylindrical part below the globose protuberance, would yet offer features quite alien to my fungus. Further, if the particular "basidium" in question were to be construed as a secondary conidium, its nodding posture would relate it more accurately to the secondary conidia of *E. Fresenii* and *E. lageniformis,* which Thaxter described as "borne obliquely on capillary conidiophores," than to the secondary conidia of the Wisconsin fungus, which like those of *E. Lampyridarum* Thaxt. (20, p. 169–170), among insectivorous forms, are "borne vertically on capillary conidiophores," their axes always being in alignment with the supporting hyphae.

Because its adhesive organs are very unusual among phycomycetes, and, besides, almost certainly imply a destructive biological relationship to some species of animal, the fungus is described as new despite the lack of knowledge concerning its vegetative and overwintering stages.

Basidiobolus haptosporus Drechsler, sp. nov. Conidiis primariis incoloratis, globosis vel late ovoideis, plerumque papilla subtruncata praeditis, vulgo circa 25 μ crassis, in maturitate cum "basidio" inflato violenter emissis, mox hypham fertilem erectam 250–325 μ altam basi 3.5–4.5 μ crassam sursum 2 μ latam saepe porrigentibus et in apice ejusdem conidium secundarium gerentibus. Conidiis secundariis saepe in totum 64–73 μ longis, in cellula viventi et rostro vacuo glutinoso consistentibus; cellula viventi incolorata, elongato-ellipsoidea, recta vel leviter curvata, saepe 50–61 μ longa, 14.5–17.5 μ lata, apice ab rostro septo flavo divisa; rostro tubuliformi, 6–8 μ longo, 2–2.5 μ crasso, muro ejus flavo, magnam partem 0.8–1 μ crasso sed sursum rotundato et valde attenuato et guttula globosa materiae glutinosae flavidae 8–10 μ in diametro vestito. Conidiis ordinum tertii et quarti et quinti modo rarius ad instar primariorum globosis denique cum "basidio" violenter emissis, plerumque ad instar secundariorum elongatis rostratisque sed minoribus, interdum tantam modo 35 μ longis et 8 μ latis, denique rostro eorum interdum tantum 4 μ longo et 1.5 μ lato, et hypha fertili germinationis interdum tantum 150 μ alta, basi tantum 2.2 μ crassa, apice tantum 1.2 μ crassa. Cellula viventi conidiorum elongatorum cujusque ordinis quandoque aliquot septis in plura (interdum 5) loculamenta (sporas) divisa.

Habitat in humo silvestri prope Mercer, Wisconsin.

Primary conidia colorless, globose or broadly egg-shaped, usually provided with a blunt protuberance, commonly about 25 μ in diameter, when fully developed regularly discharged forcibly together with the inflated distal portion of the conidiophore, thereupon often producing a secondary conidium erectly at the tip of an erect conidiophore usually 250–325 μ high, 3.5–4.5 μ wide at the base, and 2 μ wide near the apex. Secondary conidia often 64–73 μ in total length, consisting individually of a living cell and an adhesive apical beak; the living cell colorless, elongated, ellipsoidal, straight or slightly curved, often 50–61 μ long, 14.5–17.5 μ wide, delimited distally from the beak by a thick yellow septum; the apical beak tubular, at maturity devoid of protoplasmic contents, commonly 6–8 μ long and 2–2.5 μ wide, its wall yellow, in large part 0.8–1 μ thick but always very thin at the rounded apex, which is surrounded by a globose mass of yellow adhesive material 8–10 μ in diameter. Conidia of the third, fourth, and fifth orders only seldom resembling the primary conidia with respect to globose shape and violent manner of discharge, being usually similar to secondary conidia in shape and beaked apical modification, though of smaller size, sometimes measuring only 35 μ in total length and 8 μ in width, the beak then often only 4 μ long and 1.5 μ wide, and the erect germ-conidiophore frequently extended by them then sometimes measuring only 150 μ in height, 2.2 μ in basal width, and 1.2 μ in apical width; the living cell in elongated conidia of whatever order occasionally becoming divided by several cross-walls into plural (sometimes 5) cells or sporangiospores.

Occurring in deciduous leaf mold near Mercer, Wisconsin.

UNITED STATES DEPARTMENT OF AGRICULTURE
BELTSVILLE, MARYLAND

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