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TWO NEW SPECIES OF CONIDIOBOLUS OCCURRING IN LEAF MOLD [1]

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AMONG THE ENTOMOPHTHORALES easily culturable forms have come to light so infrequently that they have generally been held to be very meagerly distributed. During the last 68 years there have been fully described only 3 species which, though resembling in their asexual reproduction the insectivorous forms usually assigned to the genus *Empusa,* will develop readily on the artificial substrata commonly employed for growing saprophytic fungi. These 3 species include *Conidiobolus utriculosus* Brefeld (1884) with pyriform conidia described as 50μ long and 35μ wide, *C. brefeldianus* Couch (1939) with globose conidia 10–31μ in diameter, and *Delacroixia coronata* (Cost.) Saccardo & Sydow (1899) with conidia that were represented as measuring 26–45μ in the original diagnosis given by Costantin (1897) under the binomial *Boudierella coronata.* The separateness of *Conidiobolus minor,* a species erected by Brefeld on some relatively small conidia he found intermingled with *C. utriculosus,* is open to serious doubt, for, as Martin (1925) correctly pointed out, the small conidia might well have come from larger ones through prolonged repetitional development. A very robust culturable form which Gilbert (1919) described as producing spherical conidia 48–60μ in diameter could more probably be distinct from the 3 enumerated species, in view of its impressive conidial dimensions and the branching observed in many of its conidiophores. *Basidiobolus ranarum* Eidam (1886) also has been grown readily on various substrata but, since it differs rather conspicuously in sexual and asexual reproduction from the numerous parasitic species of *Empusa* and *Entomophthora* through which the Entomophthorales have become most widely familiar, its ready development on artificial media has not seemed exceptional. Moreover, some adaptation to saprophytic development would appear almost a necessity for a fungus commonly found inside the digestive organs of batrachians and lacertians as well as in the excrement voided by these animals.

By means of a procedure described recently (Drechsler, 1952a) several hundred separate cultures of fungi belonging in the Entomophthorales were isolated during the winter of 1951-1952 from leaf mold and other decaying vegetable detritus. Most of the material was gathered in Maryland and Virginia. A few samples from localities in Florida, Georgia, North Carolina, Arkansas, and New Hampshire served mainly in revealing that this group of fungi was distributed over a broad geographical range. As relatively small portions of detritus—about 0.2 g. of finely crumbled material was commonly used in each Petri dish—often yielded cultures of more than one species, there is reason to believe that the "saprophytic" members of the order, instead of being rare, may collectively persist over wide areas in greater quantity than their relatives of obviously parasitic character. Two species of *Basidiobolus* were obtained abundantly from leaf mold (Drechsler, 1952c) which in many instances came from situations apparently not much frequented by frogs or lizards. In the varied collection of cultures at least 5 species of *Conidiobolus,* besides *C. brefeldianus* and *Delacroixia coronata* (= *C. villosus* Martin), have been found clearly distinguishable (Drechsler, 1952b). Two of these 5 species are herein described as new.

1. CONIDIOBOLUS **firmipilleus** Drechsler, sp. nov. Mycelium incoloratum, saepe copiose ramosum, protoplasmatis dense granulosi maculatim repletum; hyphis sterilibus vulgo 4–12μ latis sed prope conidium germinatum saepius 12–18μ latis, mox septatis; cellulis eorum 30–250μ (plerumque 30–100μ) longis, simplicibus vel aliquid ramosis, inter se vulgo hic illic disjunctis. Hyphis fertilibus incoloratis, simplicibus, erectis vel acclivibus, in aere 20–200μ (plerumque 30–125μ) ad lucem protendentibus, 3–8.5μ latis, parum vel haud inflatis, in apice unum conidium ferentibus; conidiis violenter prosilientibus, vulgo globosis sed quandoque elongato-ellipsoideis, basi papilla praeditis, ex toto 8–40μ longis, 6.5–33μ crassis, papilla eorum rotundo-conica vel hemisphaerica, 1.3–7μ alta, 1.8–9μ lata. Sporis perdurantibus ignotis.

Habitat in foliis quercorum putrescentibus in Arlington, Virginia.

Mycelium colorless, often ramifying abundantly, frequently appearing pronouncedly vacuolated;

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vegetative hyphae commonly 4–12μ wide, but near their origin from a germinated conidium often 12–18μ in width, usually soon becoming septate; hyphal segments 30–250μ (mostly 30–100μ) long, simple or provided with one or more lateral branches, here and there becoming disjointed from one another. Conidiophores colorless, unbranched, erect or sloping, extending 20–200μ (commonly 30–125μ) into the air toward the main source of light, only slightly inflated and often not inflated at all, mostly 3–8.5μ wide, producing a single terminal conidium above a hemispherical protruding wall, which wall often remains visible after the empty tubular membrane has disappeared; conidia springing off forcibly, colorless, most often subspherical but occasionally prolate ellipsoidal, measuring 6.5–33μ in transverse diameter and 8–40μ in total length inclusive of the hemispherical or paraboloidal basal papilla, 1.3–7μ high and 1.8–9μ wide, that results from eversion of the distal layer of the basal wall. Zygospores unknown.

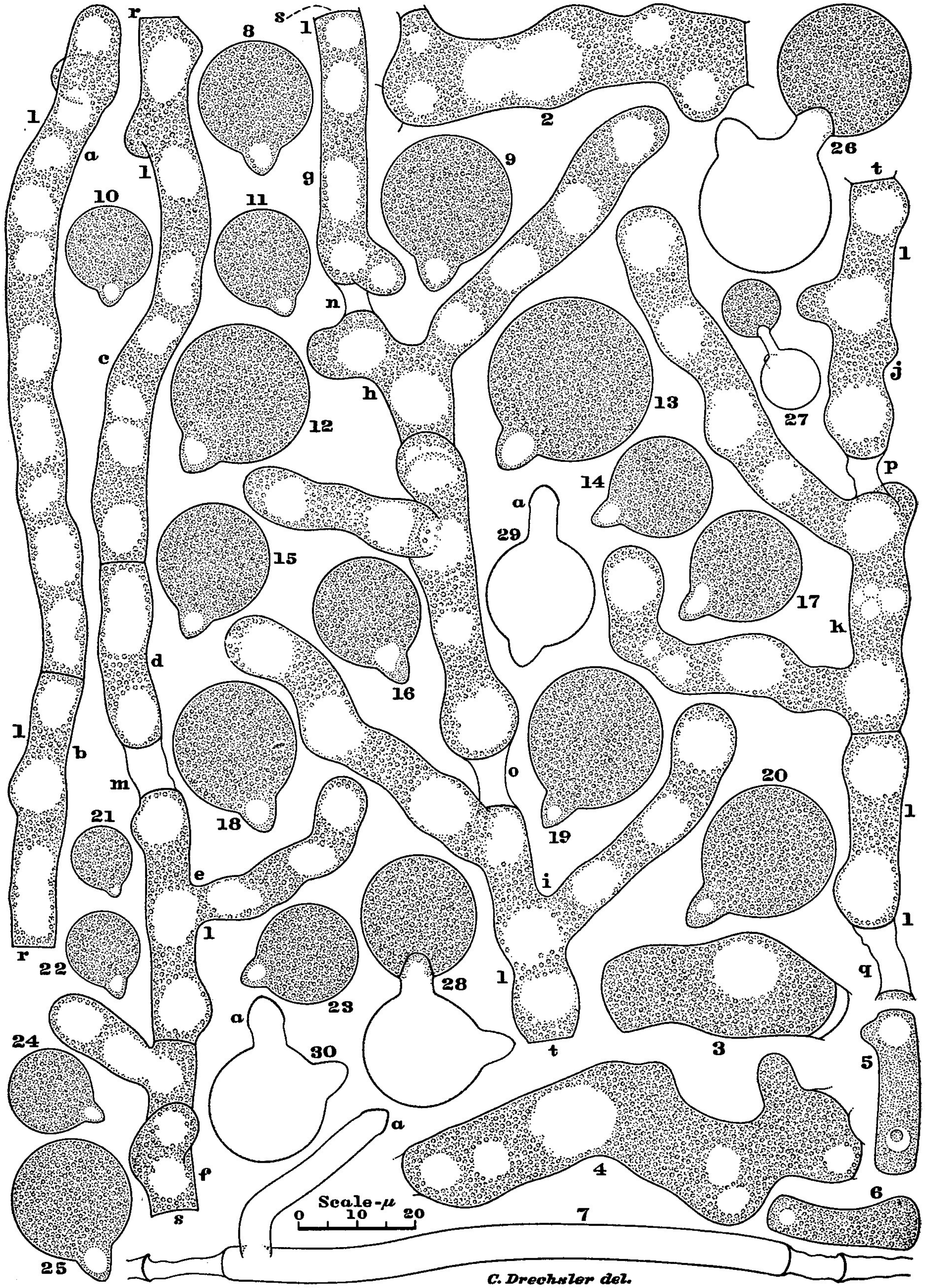
Isolated from decaying oak (*Quercus* spp.) leaves collected on February 28, 1952, in woods along Lubbers Run in Arlington, Virginia. Specimens (microscope mounts and dried agar cultures) have been deposited in Mycological Collections of the Bureau of Plant Industry, Beltsville, Maryland.

When growing unimpeded on an ample expanse of maize-meal agar in a Petri plate culture, mycelia of *Conidiobolus firmipilleus* show at the advancing margin numerous stout, radially-arranged hyphae with markedly vacuolate contents (fig. 1). Along their somewhat crooked courses these hyphae individually may fluctuate in width between 7 and 12μ, though for the most part their range with respect to this dimension is between 7.5 and 10μ. They are little given to distal tapering, the general width of each filamentous part, whether main axis or lateral branch, being usually sustained clear to its bluntly rounded tip. Cross-walls are laid down early, the farthermost septum often being found in axial filaments only 100–150μ from the end. Nevertheless the terminal segment (fig. 1a) usually includes a greater length of axial hypha than is included in most intercalary segments (fig. 1b–1); though some intercalary segments with well-developed branches (fig. 1h,i,k) may exceed the terminal segment in total volume. In many segments all protoplasmic contents are soon withdrawn from one end, and a retaining wall is laid down, thereby in each instance delimiting an empty portion of hyphal envelope (fig. lm–q). Later the emptied membranous parts vanish from sight, so that the individual hyphae become disjointed at variable intervals.

In a mycelium that has grown out extensively from a germinating conidium the segments near the conidium often become exceptionally stout, with widths ranging from 12–18μ (fig. 2–4). They are frequently further distinguished by pronounced irregularities of shape. These peculiarities of cell morphology seem related to the closer and more divergent hyphal branching observable in proximity to the conidium. The massive proximal segments offer strong contrast with segments often only 6 or 7μ wide (fig. 5, 6, 92) that are formed in older cultures as the result of impeded vegetative growth.

Asexual reproduction is initiated early in maize-meal agar cultures of *Conidiobolus firmipilleus*. Each participating hyphal segment, as a rule, produces a single unbranched conidiophore, which swells out at its tip to form a single terminal conidium (fig. 31–34, 65, 66, 93). When the conidium has received all or most of the protoplasmic materials available, it is cut off basally by a hemispherical or paraboloidal wall that protrudes upward into it. Under the tension exerted by turgor pressure generated within the delimited conidium, the peripheral envelope suffers circumscissile rupture and the basal partition splits into two layers as concomitantly the distal layer is suddenly everted. The thicker proximal layer remains behind as a rounded cap on the denuded conidiophore (fig. 7a; 67–71a). The thin distal layer through whose sudden eversion the conidium is thrown forcibly into the air appears on the detached spherical or prolate ellipsoidal spore (fig. 8–25, 35–56, 72–78) as a hemispherical or paraboloidal basal protrusion. Since this basal protrusion or "papilla" is smaller in comparison with the spore than the corresponding modification in *Delacroixia coronata* and *Conidiobolus brefeldianus*, it is noticeably feebler in its propulsive effects. Thus when *C. firmipilleus* is grown on maize-meal agar slants in vertical test tubes 18 mm. in inside diameter its discharged spores evidently fall for the most part on the lowermost area of the slanted surface, where they accumulate in a thick white deposit. In similar cultures of *D. coronata* the discharged conidia more often reach the glass wall opposite the slanted surface of the agar, and after one or two days will commonly form a nearly opaque layer on the inner surface of the tube.

A conidium falling on an ample expanse of sterile maize-meal agar often germinates promptly by putting forth a stout germ hypha (fig. 94) that soon ramifies at wide angles (fig. 79) to grow into a mycelium of the robust type previously discussed. If, however, a conidium falls on substratum already occupied by mycelium of the fungus it produces a more delicate germ hypha, often only 4–5μ in width (fig. 80). Frequently an expanded lobule (fig. 95a) is first formed on the surface of the agar, and from this lobule the narrow hypha (fig. 95b) grows downward into the substratum some little distance before elongating extensively in a direction approximately parallel to the surface. Such elongation often seems to proceed without any considerable intake of nutrients, being accomplished evidently through evacuation of protoplasm first from the conidial envelope and then from progressively more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distal portions of the germ hypha itself. In instances of impeded vegetative development, therefore, a collapsed empty conidial envelope is often found connected by an empty, unbranched, closely septate, tubular membrane (fig. 96) to an unbranched filamentous living hyphal segment perhaps 4–6μ wide and 100–250μ long (fig. 97). As continued elongation entails further progressive reduction in quantity of protoplasm, old cultures usually contain many relatively short narrow segments (fig. 98) whose origin from conidia of impeded germination is obscured through evanescense of their empty tubular connections.

Sometimes a narrow germ hypha, after having been extended procumbently on the substratum to a length of more than 100μ, may grow abruptly upward and on its elevated tip (fig. 81a) give rise to a secondary conidium that like its parent springs off forcibly. Now and then a relatively stout germ hypha, soon after it has been delimited from the parent conidium, puts forth a conidiophore that similarly releases a secondary conidium from its tip (fig. 82a). Much more often repetitional development is not initiated by vegetative germination but takes place in a more direct way: the detached spore extends from its upper side a rather short stout outgrowth that swells out distally to form the young secondary conidium (fig. 57, 83). After it has received all or nearly all the protoplasmic contents of its parent and has been cut off by a protruding basal wall (fig. 26–28, 58, 84) the secondary conidium springs off. The denuded outgrowth on the envelope of the parent spore has a somewhat expanded, convexly protruding cap (fig. 29a–30a, 59a–64a, 99a) much like that of conidiophores arising from mycelial segments.

In cultures of *Conidiobolus firmipilleus* on maize-meal agar repetitional development of conidia often continues briskly for days after production of primary conidia has virtually ceased from exhaustion of the underlying mycelium. It may proceed apparently until minimum conidial dimensions have been reached. The smallest conidia observed in my cultures measured about 6.5μ in width and 8μ in total length (fig. 53). As the largest ones (fig. 52) measured approximately 33μ in width and 40μ in total length, the full range of spore size in the species might permit a succession of 15–20 repetitional generations. Development of 5–10 successive generations is probably not at all infrequent.

Denuded conidiophores of the fungus often retain a substantial remnant of protoplasm. This protoplasm frequently collects in the distal portion of the conidiophore and then secretes a retaining wall proximally. A segment of such terminal origin can be distinguished by the curiously rounded cap at its distal end (fig. 85a–90a, 100a) long after the tubular membranous shaft originally supporting it has vanished. Like other segments of similar size it may grow out vegetatively (fig. 100) or may give rise to a small conidium on a new conidiophorous branch.

When a denuded conidiophore in which no protoplasm is retained falls on moist substratum the empty tubular membrane as a rule soon evanesces in its entirety. Rather curiously, however, the rounded distal cap long remains clearly visible. Accordingly in old cultures numerous empty hemispherical caps (fig. 91) are found strewn about everywhere, suggesting at first sight that perhaps conidia might sometimes be shot off together with a distal part of the conidiophore as in species of *Basidiobolus*. Observations on cultures of varying ages have yielded no evidence that conidial discharge normally entails any rupture of the conidiophore. Since in any case the scattered hemispherical pieces make up a display without parallel among other known species of *Conidiobolus*, their durable character and their outward resemblance to a close-fitting cap have suggested for the fungus a specific epithet compounded of the words *firmus* and *pilleus*. While the fungus most closely resembles *Conidiobolus brefeldianus* it is distinguished from that species by its less prominent conidial papillae and by its failure to produce zygospores.

2. Conidiobolus **heterosporus** Drechsler, sp. nov.

Mycelium incoloratum, mediocriter ramosum, in juventute vulgo protoplasmate mediocriter granuloso omnio farctum; hyphis sterilibus 3.5–15μ (vulgo 5–9μ) latis, mox septatis, hic illic disjunctis; cellulis eorum simplicibus vel aliquid ramosis, 30–250μ (plerumque 50–150μ) longis. Hyphis fertilibus primiformibus incoloratis, simplicibus, in aere vulgo 25–100μ ad lucem protendentibus, saepe aliquid pravis, basi 4–6.5μ crassis, sursum latenscentibus, prope apicem 8–13μ crassis, unum conidium formae globosae ferentibus; conidiis formae globosae violenter prosilientibus, incoloratis, basi papilla 1–5μ alta 3.5–12μ lata praeditis, ex toto 10–35μ longis, 9–30μ crassis, interdum hypham germinationis emittentibus quae saepius in mycelium increscit, interdum alium conidium globosum in apice hyphae fertilis crassae gignentibus, interdum unum conidium vel 2 vel 3 conidia formae ellipsoidae in hypha fertili gracili gerentibus; hyphis fertilibus gracilibus incoloratis, rectis vel curvatis, plerumque 50–100μ longis, basi vulgo 2.5–4μ latis, sursum leniter attenuatis, prope apicem 1.3–1.8μ crassis, vulgo simplicibus sed quandoque prope basim bifurcatis vel trifurcis, unum conidium in quoque apice ferentibus; coni-

Fig. 1–30. *Conidiobolus firmipilleus*, drawn with the aid of a camera lucida from maize-meal-agar cultures, at a uniform magnification; ×1000 throughout.—Fig. 1. Terminal portion of an actively growing mycelial filament, comprising 12 segments, a-l, and 5 empty tubular parts, m-q; the filament is shown in 4 pieces that join at the cross-walls, r–t.—Fig. 2–4. Wide hyphal segments.—Fig. 5–6. Small hyphal segments.—Fig. 7. Empty hyphal segment with denuded conidiophore, a.—Fig. 8–25. Detached conidia.—Fig. 26–28. Empty conidial envelopes, each supporting a secondary conidium. —Fig. 29–30. Empty conidial envelopes, each with a denuded conidiophore, a.

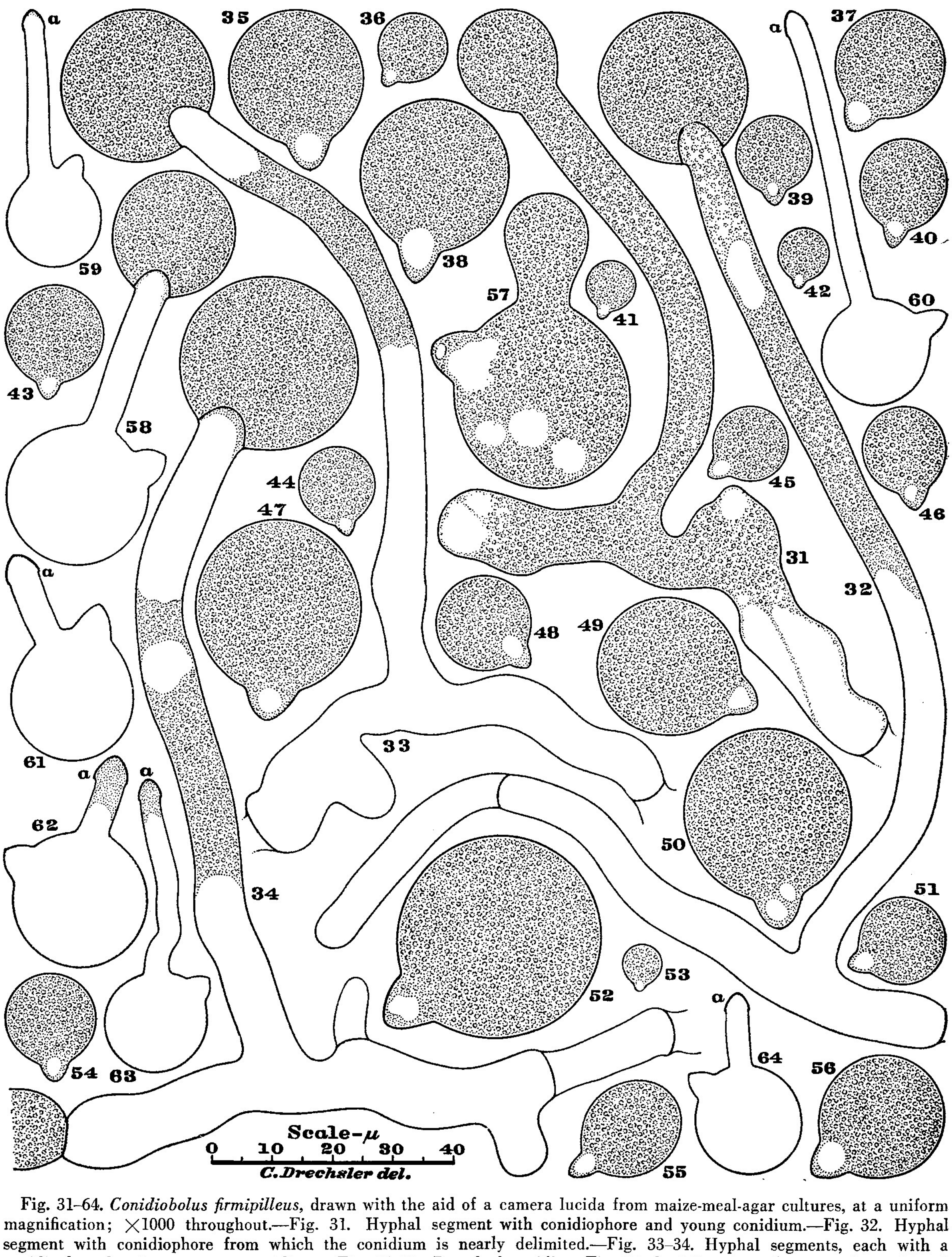

Fig. 31–64. *Conidiobolus firmipilleus*, drawn with the aid of a camera lucida from maize-meal-agar cultures, at a uniform magnification; ×1000 throughout.—Fig. 31. Hyphal segment with conidiophore and young conidium.—Fig. 32. Hyphal segment with conidiophore from which the conidium is nearly delimited.—Fig. 33–34. Hyphal segments, each with a conidiophore bearing a mature conidium.—Fig. 35–56. Detached conidia.—Fig. 57. Conidium in early stage of repetitional development.—Fig. 58. Conidium bearing a conidiophore with a mature condidium.—Fig. 59–64. Empty conidial envelopes, each bearing a denuded conidiophore, a.

Fig. 65–91. *Conidiobolus firmipilleus*, ×1000.—Fig. 65–66. Hyphal segments, each with a conidiophore and conidium.—Fig. 67–71. Empty hyphal segments, each with denuded conidiophore, a.—Fig. 72–78. Detached conidia.—Fig. 79. Conidium with stout branching germ hypha.—Fig. 80. Conidium with slender germ hypha.—Fig. 81. Empty conidium with slender germ hypha terminating in a short denuded conidiophore, a.—Fig. 82. Conidium with stout germ hypha bearing denuded conidiophore, a.—Fig. 83. Conidium in early stage of repetitional development.—Fig. 84. Empty conidium bearing secondary conidium.—Fig. 85–90. Living terminal segments of denuded conidiophores, each with rounded cap, a.—Fig. 91. Detached caps of conidiophores.

diis formae ellipsoideae incoloratis, basi aliquid prominulis, plerumque 15.5–31.5μ longis, 9–16.5μ latis.

Habitat in humo silvestri prope Ellicott City, Maryland.

Mycelium colorless, moderately branched, in young condition commonly filled throughout with protoplasm of moderately granular consistency; assimilative hyphae 3.5–15μ (commonly 5–9μ) wide, soon becoming divided by cross-walls into simple or somewhat branched segments 30–250μ (mostly 50–150μ) long, which here and there become disjointed from one another. Primary conidiophores colorless, unbranched, extending 25–100μ into the air and toward the main source of light, often somewhat crooked, 4–6.5μ thick at the base, widening gradually upward, mostly 8–13μ thick near the tip, forming terminally a single globose conidium; globose conidia springing off forcibly, colorless, measuring 9–30μ in width and 10–35μ in total length inclusive of a basal papilla 1–5μ high and 3.5–12μ wide, sometimes putting forth a germ hypha that may grow into a mycelium, sometimes forming a secondary globose conidium on a broad conidiophore, and sometimes giving rise to an ellipsoidal secondary conidium or to 2 or 3 ellipsoidal secondary conidia on a slender conidiophore; the slender conidiophores colorless, straight or curved, mostly 50–100μ long, commonly 2.5–4μ wide at the base, tapering gradually upward, usually 1.3–1.8μ wide near the tip, mostly simple but occasionally bifurcate or trichotomous some little distance above the base, bearing an ellipsoidal conidium on each tip; ellipsoidal conidia colorless, protruding slightly at the base, mostly 15.5–31.5μ long and 9–16.5μ wide.

Isolated from leaf mold collected on March 18, 1952, in deciduous woods near Ellicott City, Maryland. Specimens (microscope mounts and dried agar cultures) have been deposited in Mycological Collections of the Bureau of Plant Industry, Beltsville, Maryland.

Conidiobolus heterosporus looks markedly different from *C. firmipilleus* at all stages of development. When growing unimpeded in an ample expanse of maize-meal agar its individual mycelia show at the advancing margin numerous radially arranged hyphae which vary commonly from 5–9μ in width (fig. 101). On the whole, separate filaments here fluctuate less pronouncedly and less frequently in thickness than the filaments of *C. firmipilleus.* The young hyphae of *C. heterosporus,* instead of being conspicuously vacuolate like those of *C. firmipilleus,* are filled throughout with protoplasm in which coarse granules are distributed rather evenly. As in *C. firmipilleus,* cross-walls are formed early, the farthermost septum in individual hyphae sometimes being found less than 50μ from the tip, though more often it occurs at distances between 50 and 200μ from the tip. Some hyphal segments long retain their original outward shape (fig. 101a–c) but others soon become noticeably widened and rounded at one (fig. 101d) or both ends (fig. 101e,f), so that the areas of contact with their neighbors are greatly reduced. Complete separation of living segments is accomplished here and there through withdrawal of protoplasmic contents from a portion of hypha (fig. 101h) and deposition of a retaining wall. The segment below an evacuated hyphal part (fig. 101g) often grows out laterally to form a new elongating axial filament.

In *Conidiobolus heterosporus,* much as in *C. firmipilleus,* the central portions of actively growing mycelia often have wider segments than are to be found at the advancing margin. Such segments (fig. 102) may measure as much as 15μ in thickness, and their coarsely granular protoplasm may inclose large vacuoles of irregular outline. Many intercalary segments, whether conspicuously robust or of only moderate width (fig. 103), may put forth a lateral branch at either end or at both ends (fig. 103a,b). Branches extended in a region well back from the periphery of a mycelium commonly measure only 3.5–5μ in width, their slenderness being related apparently to the close presence of the older mycelial filaments.

Asexual reproduction is initiated in *Conidiobolus heterosporus* in much the same way as in *C. firmipilleus.* The conidiophores that are extended from hyphal segments (fig. 108–113) seem to be invariably of the stout type familiar in all members of the genus. They appear more distinctively modified than the conidiophores of *C. firmipilleus* in that they widen out rather markedly toward the tip on which the single globose conidium is produced. In my cultures this widening has been commonly associated with noticeable crookedness. When migration of protoplasmic materials from the hyphal segment and conidiophore has been completed, the conidium is delimited by a convexly protruding basal septum (fig. 113). Soon afterwards it springs off forcibly, following circumscissile rupture of the peripheral membrane, splitting of the basal partition into two layers, and abrupt eversion of the distal layer.

Because of the greater distal width of the supporting conidiophores the basal protrusion or "papilla" on detached globose conidia of *Conidiobolus heterosporus* (fig. 104, 105, 114–126) is broader than the corresponding modification in *C. firmipilleus.* It is, however, generally of less height, so that the propulsive power delivered by its eversion would seem approximately the same as in *C. firmipilleus.* The conidia of the present fungus assuredly are thrown lesser distances than those of *C. brefeldianus* and *Delacroixia coronata* in which, as a rule, the basal protrusion is considerably more prominent. Apart from indicating the distance a conidium may have been thrown, the papilla modifies the basal contour of the discharged conidium in a manner often more or less characteristic of the species. The broadly convex basal contour usual in *C. heterosporus* appears more nearly like that shown in

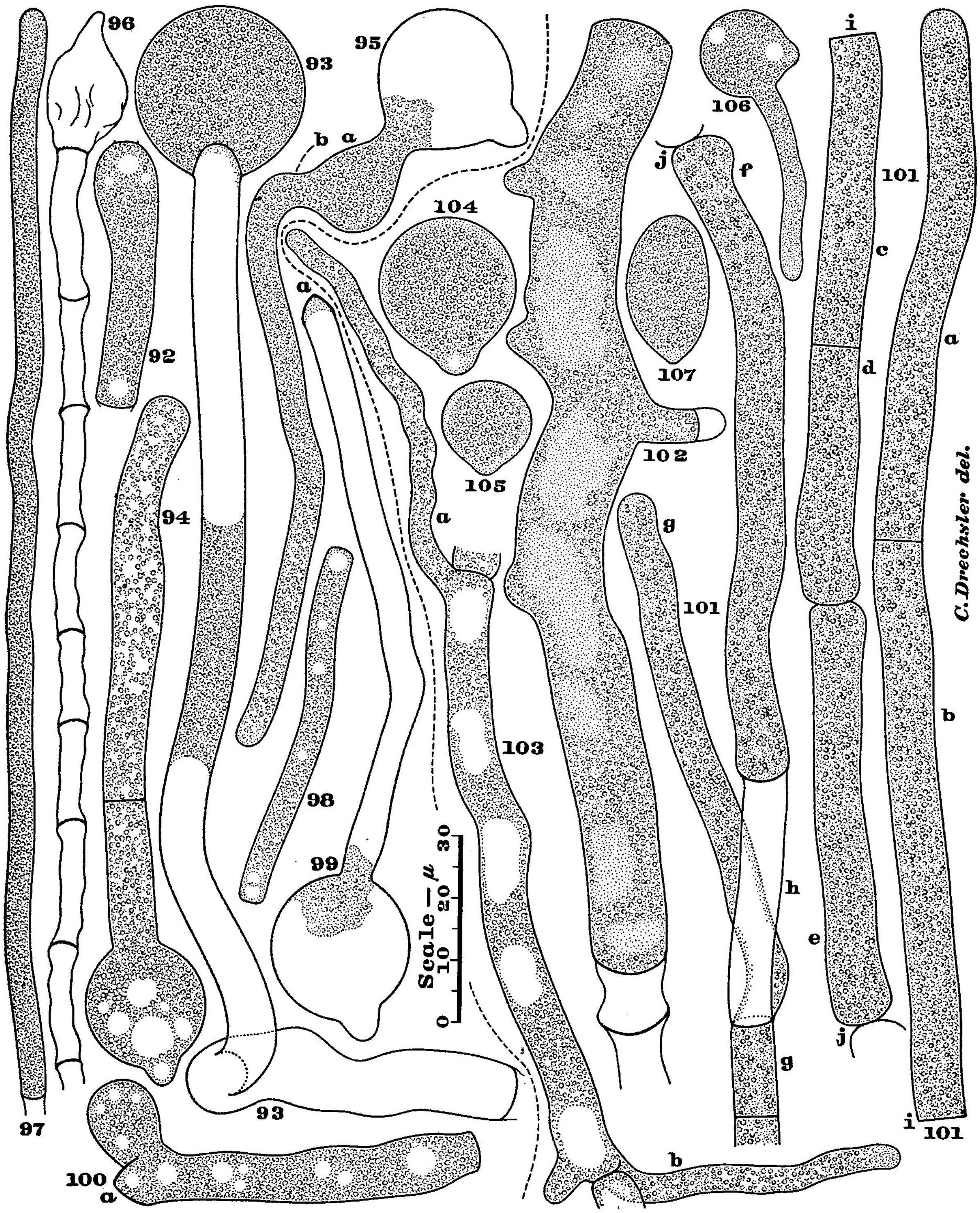

Fig. 92–107.—Fig. 92–100. *Conidiobolus firmipilleus*, ×1000.—Fig. 92. Small hyphal segment.—Fig. 93. Segment with conidiophore.—Fig. 94. Germinating conidium.—Fig. 95. Conidium with thin germ hypha, b, extended from prostrate lobule, a.—Fig. 96. Empty conidium and empty portion of germ hypha.—Fig. 97. Distal part of thin germ hypha.—Fig. 98. Narrow segment.—Fig. 99. Conidium with denuded conidiophore, a.—Fig. 100. Conidiophore segment with outgrowth near cap, a.—Fig. 101–107. *C. heterosporus*, ×1000.—Fig. 101. Distal portion of hypha comprising segments a–g, and empty part h; shown in 3 pieces joining at septa i, j.—Fig. 102. Large segment.—Fig. 103. Segment with branches a, b.—Fig. 104–105. Globose conidia.—Fig. 106. Globose conidium germinating.—Fig. 107. Ellipsoidal conidium.

Brefeld's figures of *C. utriculosus* than like the abruptly protuberant hemispherical basal contour usual in *C. firmipilleus.*

When sporulating material from a maize-meal-agar culture of *Conidiobolus heterosporus* is freshly mounted in water under a cover glass, the detached globose conidia show commonly a rather narrow parietal layer of clear protoplasm surrounding a central mass of densely granular texture. If microscopical examination of the material is continued for 1 or 2 hr. the granular mass undergoes noticeable contraction while the clear parietal layer becomes correspondingly wider. Similar contraction of granular components is observable also in newly formed conidia of *C. firmipilleus* mounted in water under a cover slip, though in the beginning these ordinarily show no clear parietal layer. In cultures of *C. heterosporus* 10–15 days old many subspherical conidia will contain one or more large globules of homogeneous consistency. As these globules are generally absent in newly detached spores, they may represent somewhat abnormal cellular components.

The globose conidia of *Conidiobolus heterosporus* germinate freely in maize-meal agar plate cultures. If the portion of substratum on which an individual spore falls is unoccupied at the time, a robust germ hypha is usually extended, which soon grows out into a mycelium. If, however, the substratum is already permeated with mycelium, a narrow germ hypha will more probably be put forth (fig. 106). Instead of germinating vegetatively the globose conidia of *C. heterosporus,* as in numerous related fungi, often develop repetitiously by putting forth a stout conidiophore whereon is borne a single secondary globose conidium (fig. 127–131) that springs off forcibly like its parent. In cultures several days old they give rise no less frequently to secondary conidia of a different type, with a distinctive elongated ellipsoidal shape (fig. 107, 132–153). The individual globose conidium (fig. 154a–167a) in instances of such development usually puts forth a single, slender, somewhat tapering, unbranched conidiophore that bears at its tip a single ellipsoidal conidium (fig. 154b–167b). Sometimes the slender conidiophore extended from a globose conidium (fig. 168a) bifurcates and bears 2 ellipsoidal conidia (fig. 168b,c), and occasionally it branches trichotomously a short distance from its origin (fig. 169a) to bear 3 ellipsoidal conidia (fig. 169b–d). The ellipsoidal conidia have a minute protrusion at the base where they are delimited by a flat cross-wall. As might be expected from their very ordinary manner of attachment they do not spring off forcibly, but become detached on slight disturbance. After falling on substratum already occupied by mycelium of the fungus, they (fig. 170a–172a) often extend upward a stout conidiophore on which a globose conidium (fig. 170b–172b) is formed that springs off in the manner usual for spores of that type.

In freely sporulating material of *Conidiobolus heterosporus* the slender conidiophores are found arising abundantly and in rather promiscuous confusion, with much variety both in their orientation and in the angular relation to the conidia they support. Many among them are fairly straight and rise vertically into the air. These bear their spores erectly, so that the straight axis of the spore is in alignment with that of the supporting shaft. When viewed from the tip such vertical spores present a circular profile, without noticeable flattening anywhere; and would seem, therefore, to have a close general similarity to the terete melon-shaped secondary conidia Thaxter (1888) found produced in his *Empusa* (*Entomophthora*) *lampyridarum.* It seems possible, however, that the more numerous ellipsoidal conidia that are borne more or less obliquely on distally curved conidiophores may not always present a perfectly circular profile when viewed from the tip, since some inequality of transverse curvature might well accompany the gibbous longitudinal unsymmetry they commonly show in lateral aspect (fig. 155b, 156b, 161b, 167b). Yet it is not evident that the ellipsoidal conidia of *C. heterosporus* are ever flattened in any pronounced degree like the almond-shaped secondary conidia described by Thaxter as occurring in *Empusa fresenii* Nowak. and *Entomophthora sphaerosperma* Fres. as well as in his *Empusa* (*Triplosporium*) *lageniformis,* his *Empusa* (*Entomophthora*) *geometralis,* and his *Empusa* (*Entomophthora*) *occidentalis.*

The ellipsoidal conidia of *Conidiobolus heterosporus* are always broadly rounded at the distal end, never being found terminating in an apical beak like the almond-shaped secondary conidia depicted in Thaxter's figures of *Empusa fresenii.* In one of these figures (Thaxter, 1888, fig. 119) the beak is shown surmounted by a drop-like protuberance. This protuberance Thaxter interpreted as an incipient germ tube, at the same time pointing out that the germinating stage in question bore close resemblance to a perplexing figure given by Eidam (1886, pl. 9, fig. 16) in his original account of *Basidiobolus ranarum* . Eidam's figure purported to show a very young tertiary globose conidium at the tip of a massive, elongated, distally tapering body that was borne aloft on a narrow empty hypha arising perpendicularly from the empty membranous envelope of a secondary globose conidium. It now seems very probable that the massive tapering body was not the expanded propulsive distal part of a conidiophore but a secondary conidium of a distinctive elongated type with a glandular adhesive apical beak. At all events secondary conidia of the elongated adhesive type I described several years ago (Drechsler, 1947) have more recently come to light in two species of *Basidiobolus* widely distrib-

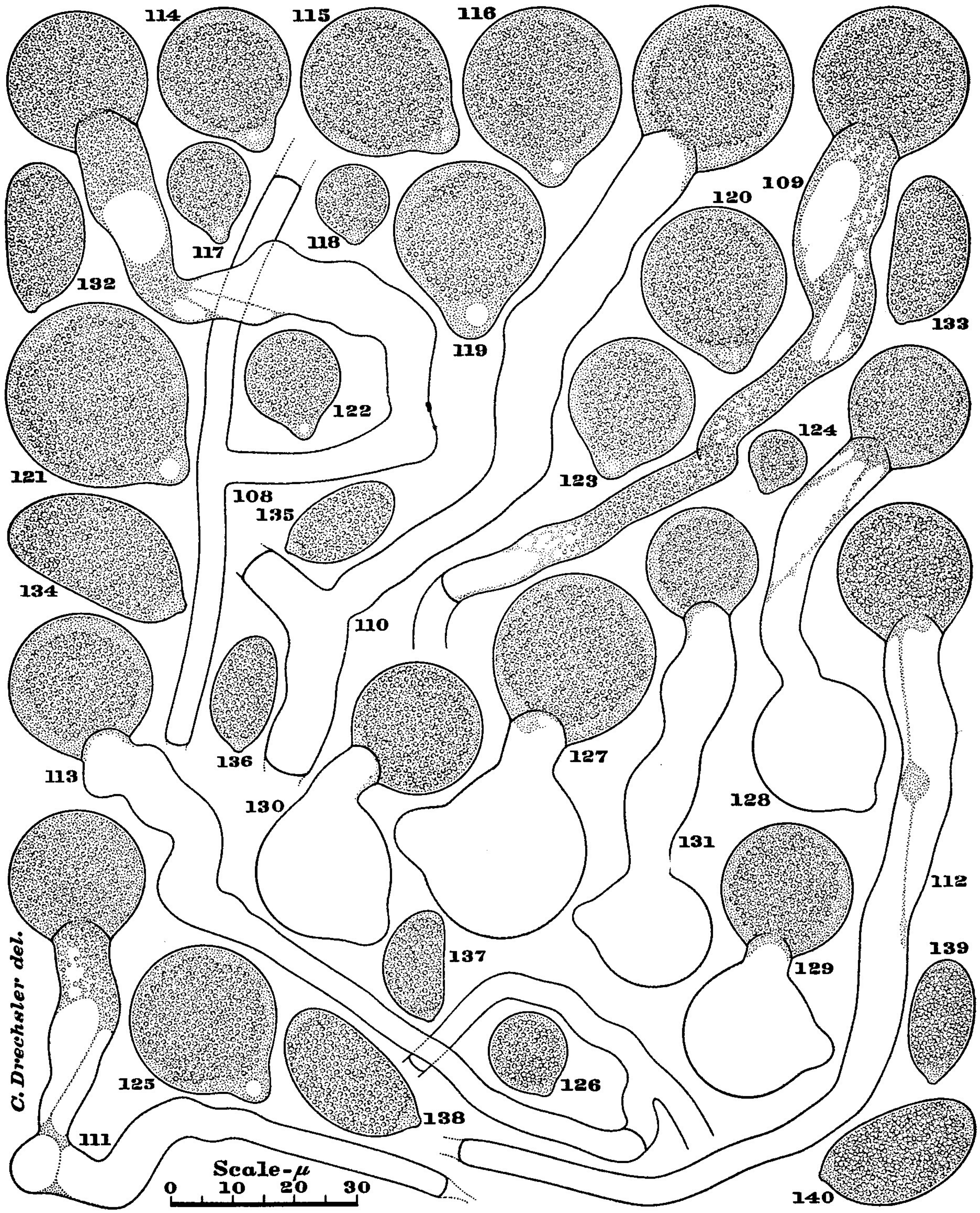

Fig. 108–140. *Conidiobolus heterosporus,* drawn from maize-meal-agar cultures at a uniform magnification; ×1000 throughout.—Fig. 108–112. Five stout conidiophores in successively more advanced stages of development.—Fig. 113. Conidiophore with fully developed globose conidium.—Fig. 114–126. Detached globose conidia, showing usual variations in size and shape.—Fig. 127–131. Globose conidia that have each produced another globose conidium.—Fig. 132–140. Detached ellipsoidal secondary conidia, showing usual variations in size and shape; at the proximal and distal end the protoplasm of the conidium is clearer than in the middle region.

uted in leaf mold (Drechsler, 1952c), being produced only sparingly in the one species with smooth zygospores, but rather abundantly and persistently in the other species with verrucose zygospores. The resemblance in apical conformation between the elongated secondary conidia frequent in *Basidiobolus* and the almond-shaped conidium of *Empusa fresenii* figured by Thaxter is so striking that similarity in localized functional modification is very strongly suggested. No localized glandular modification for secreting adhesive material has been observed either in the distally rounded ellipsoidal conidia of *Conidiobolus heterosporus* or in the globose conidia of this fungus.

The production occasionally of 2 or 3 ellipsoidal secondary conidia on a branching slender conidiophore arising from a globose conidium of *Conidiobolus heterosporus* offers parallelism, at least in a numerical sense, with the development of 3 separate capillary conidiophores on an individual globose conidium of *Empusa fresenii* shown in another of Thaxter's (1888, fig. 124) illustrations. Although the term *Triplosporium* invented by Thaxter for the subgenus to which he assigned *Empusa fresenii* and *Empusa lageniformis* apparently had reference to development of 3 secondary spores, his four other relevant figures of *Empusa fresenii* (Thaxter, 1888, fig. 117–119, 125), as also the 3 similar figures of *Empusa lageniformis* (Thaxter, 1888, fig. 155–157), show only one almond-shaped secondary conidium being produced by each globose conidium. Thus, despite the implication of the name chosen for the subgenus, it may be presumed that the almond-shaped secondary conidia of both *Empusa fresenii* and *Empusa lageniformis*, just like the ellipsoidal conidia of *Conidiobolus heterosporus*, are much more often produced singly than plurally. Because it is usually produced singly the ellipsoidal conidium in *C. heterosporus* most often is nearly of the same size as its globose parent, and like the parent is sometimes large, sometimes small, and sometimes of medium dimensions. Far different dimensional and numerical relations between parent conidia and their progeny are found in the multiplicative reproduction first described by Constantin (1897) in *Delacroixia coronata*. The ellipsoidal spores formed plurally on the globose conidia of that fungus are of relatively uniform size whether the parent is large or small. The larger parents produce many—often 10–15—ellipsoidal spores, while the smaller parents frequently give rise to only 3 or 4 spores. In contrast to the *Cunninghamella*-like sporulation present in *D. coronata* the production of ellipsoidal secondary conidia in *C. heterosporus* would seem interpretable as a modified type of repetitional development. At all events the production of ellipsoidal secondary conidia on slender conidiophores and the absence of zygospore development should serve to distinguish *C. heterosporus* from the much more robust *C. utriculosus* as well as from the more prominently papillate *C. brefeldianus*.

SUMMARY

Readily culturable fungi referable to the Entomophthoraceae are probably far more abundant in nature than the insect parasites through which the family has mainly been known. Though not likely to be found on succulent vegetable materials that are undergoing rapid putrefaction they are widely distributed on firmer plant residues in which decay has proceeded for weeks or months. Two new species of these ubiquitous fungi are described under the binomials *Conidiobolus firmipilleus* and *C. heterosporus*. Both are of generally smaller dimensions than the very robust *C. utriculosus*, and in both the globose conidia spring off the conidiophores less forcibly than in *C. brefeldianus* or *Delacroixia coronata*. In *C. heterosporus* the detached globose conidium may give rise to another globose conidium or may produce an ellipsoidal secondary conidium most closely resembling the melon-shaped secondary conidia of *Empusa* (*Entomophthora*) *lampyridarum*.

Division of Vegetable Crops and Diseases,
Plant Industry Station,
Beltsville, Maryland

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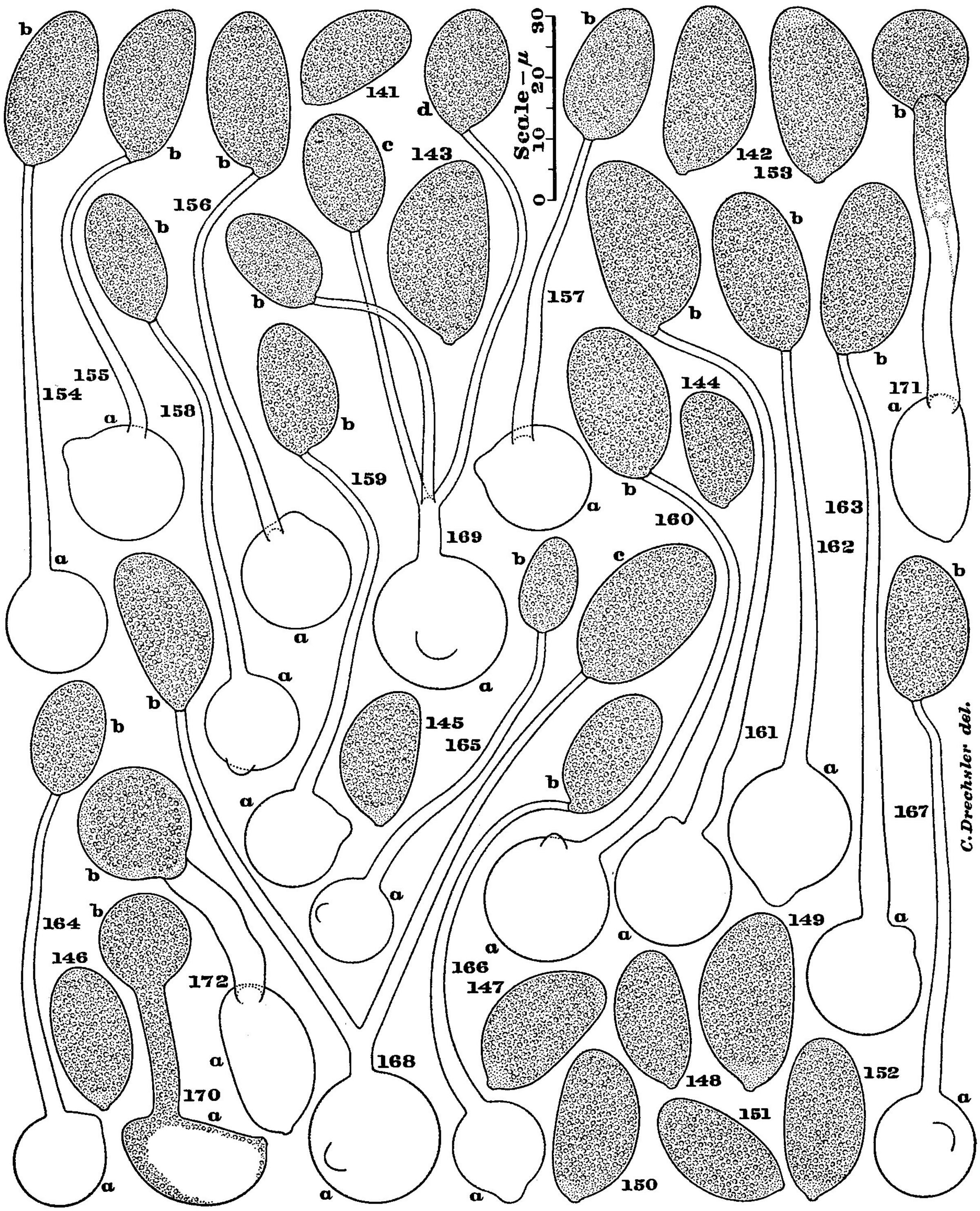

Fig. 141–172. *Conidiobolus heterosporus*, drawn from maize-meal-agar cultures; ×1000 throughout.—Fig. 141–153. Detached ellipsoidal secondary conidia.—Fig. 154–167. Empty globose conidia, a, each supporting a slender empty conidiophore that bears an ellipsoidal secondary conidium, b.—Fig. 168. Empty globose conidium, a, that supports a bifurcated conidiophore bearing 2 ellipsoidal conidia, a and b.—Fig. 169. Empty globose conidium, a, that supports a trichotomous condiophore bearing 3 ellipsoidal secondary conidia, b–d.—Fig. 170–171. Detached ellipsoidal conidia, a, each producing a globose conidium, b.—Fig. 172. Detached ellipsoidal conidium, a, that has produced a globose conidium, b.