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TWO SPECIES OF CONIDIOBOLUS OFTEN FORMING ZYGOSPORES ADJACENT TO ANTHERIDIUM-LIKE DISTENTIONS

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(WITH 10 FIGURES)

Two readily culturable entomophthoraceous fungi that first appeared on Petri plates of maize-meal agar canopied with moist filter paper to which was affixed some partly decayed plant material are herein described as new species of *Conidiobolus*. The 2 fungi are advantageously discussed together, for although they differ enough to be readily distinguished from each other, both show in an antheridium-like distention often adjoining their zygospores a morphological modification prominently set forth in the figures and description of *C. brefeldianus* Couch (1939), and therefore alike invite comparison with that species. As the original culture of *C. brefeldianus* has unfortunately been long extinct, comparison must be made mainly with Couch's detailed characterization. Supplementary attention is devoted especially to an isolate from central Florida (FIG. 1, A) that I hold properly referable to *C. brefeldianus* and to a rather similar but perhaps not conspecific isolate from northern Wisconsin (FIG. 1, B). Opportunity has been lacking for comparison of my cultures with the "*Conidiobolus*? *brefeldianus*" recently mentioned by Korf (1960) as having been isolated in Highlands, North Carolina, from apothecia of *Peziza proteana* (Boud.) Seav. f. *proteana*. Type cultures of the 2 new species have been transmitted to the American Type Culture Collection, Washington, D. C., and dried material of each has been given to the National Fungus Collections, Plant Industry Station, Beltsville, Maryland. To compensate partly for the very obvious shortcomings of the dried material, figures of reproductive bodies prepared from mounts of living material are supplied in numbers sufficient, it is hoped, to indicate the more usual variations in size and shape.

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Conidiobolus polyspermus Drechsler, sp. nov. (πολύσπερμος, abounding in seed)

In materiis macris oculo nudo saepe aliquid inconspicuus, sed in materiis pinguioribus multo facilius visibilis. Hyphae assumentes incoloratae, mediocriter ramosae, primo filiformes, prope marginem mycelii crescentis plerumque 6–13 μ latae, ibi ex cellulis 40–300 μ longis constantes, hic illic ramos saepius 2–9 μ latos emittentes, postea medio mycelii ex magna parte in cellulas inflatas disjunctas 35–100 μ longas et 12–25 μ latas gradatim transeuntes; hyphae vagae vulgo 40–250 μ longae, 2–4 μ latae. Hyphae fertiles incoloratae, vulgo simplices, in aerem saepius 30–125 μ ad lucem protendentes, plerumque 7–18 μ latae; conidia violenter absilientia, incolorata, globosa, in toto plerumque 15–55 μ longa, 12–48 μ lata, basi papilla saepius 3–15 μ longa et 5–16 μ lata praedita. Zygosporae nunc e copulatione cellularum ejusdem hyphae contiguarum ortae, nunc e copulatione disjunctarum cellularum ejusdem hyphae vel cellularum duarum hypharum oriundae, in maturitate flavidae vel interdum paene incoloratae, leves, globosae vel elongato-ellipsoideae, plerumque 15–48 μ longae, 14–45 μ latae, guttula oleacea 8–30 μ crassa praeditae, muro 1.2–5.5 μ crasso circumdatae.

Habitat in foliis quercorum putrescentibus prope College Park, Maryland. Typus: National Fungus Collections No. 71712; American Type Culture Collection No. 14444.

When growing on substratum of low nutrient content usually rather inconspicuous to the naked eye, but on richer substratum becoming more readily visible, often without production of much aerial mycelium. Assimilative hyphae colorless, at first filamentous, at forefront of a growing mycelium maintaining a rather uniform width mostly between 6 and 13 μ, here divided into cells 40 to 300 μ long, and putting forth branches mostly 2 to 9 μ wide, later in positions behind the forefront usually in large part undergoing conversion into swollen segments 35 to 100 μ long and 12 to 25 μ wide; migratory hyphae often appearing tardily, mostly 40 to 250 μ long and 2 to 4 μ wide. Conidiophores colorless, commonly unbranched, extending 30 to 125 μ into the air toward the main source of light, mostly 7 to 18 μ in greatest width, bearing usually a single conidium; conidia springing off forcibly, colorless, mostly 12 to 48 μ in greatest width, 15 to 55 μ in total length inclusive of an abruptly protruding basal papilla usually 3 to 15 μ long and 5 to 16 μ wide at its attachment. Conjugation sometimes occurring directly between 2 contiguous segments of the same hypha and sometimes either between neighboring segments of the same hypha or between segments of 2 neighboring hyphae after production of a connecting branch; zygospore formed wholly within one gametangium and in immediate proximity usually to a distention of the other gametangium, at maturity often noticeably yellowish but sometimes nearly colorless, always smooth, generally globose or somewhat elongated-ellipsoidal, mostly 15 to 48 μ long and 14 to 45 μ wide, containing a reserve globule 8 to 30 μ in diameter, surrounded by a wall mostly 1.2 to 5.5 μ thick.

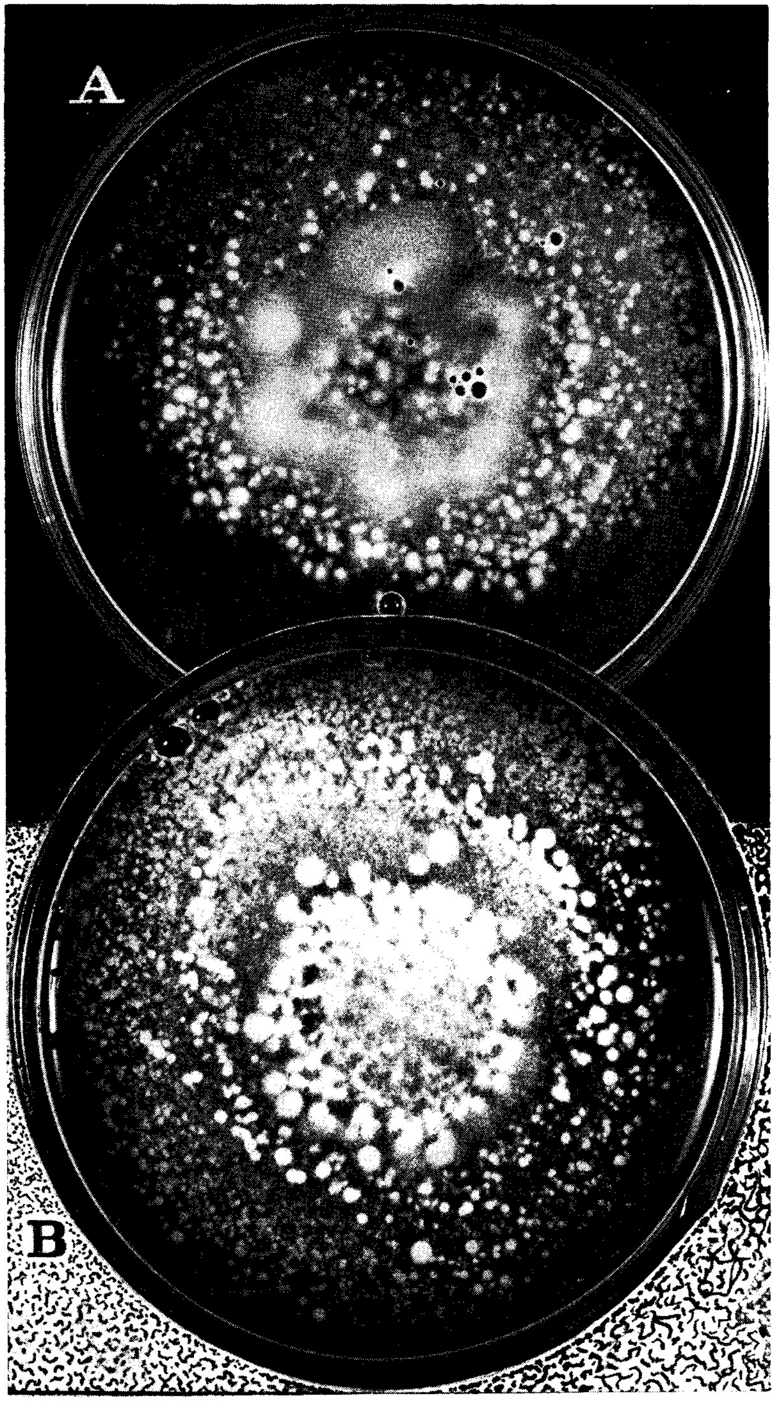

FIG. 1.

Conidiobolus polyspermus was discovered in several Petri plates of maize-meal agar that had been canopied on July 26, 1955, with moist filter paper holding attached some fine detritus sifted from leaf mold newly collected in a wooded area near College Park, Maryland, occupied mainly by white oak (*Quercus alba* L.) and red oak (*Q. rubra* L.). The Petri plates which quite unexpectedly permitted development of many mycelia of *Basidiobolus meristosporus* Drechsler (**1956a**, p. 657) had been incubated at a temperature of 27° C. Not surprisingly they had permitted development also of the ubiquitous *Delacroixia coronata* (Cost.) Syd. & Sacc. emend. Gallaud (**1905**), which on the maize-meal-agar substratum differed little in general appearance from *C. polyspermus,* though after several days the 2 fungi were readily distinguished under the microscope owing to their production of very dissimilar resting spores.

In young maize-meal-agar plate cultures of *Conidiobolus polyspermus* growth of a mycelium is achieved at the advancing margin through apical elongation of hyphae commonly 6 to 9 μ wide (FIG. 3, A). On potato-dextrose agar the elongating hyphae (FIG. 3, B, *a*) at the periphery of a mycelium are noticeably stouter, often measuring 10 to 13 μ in diameter. The long terminal segments in a freshly prepared microscope mount are filled, much as in many congeneric species, with protoplasm of relatively homogeneous texture (FIG. 3, A); and as in congeneric species, too, these segments under microscopical examination soon become divided by cross-walls into shorter cells with vacuolated contents (FIG. 3, B, *a*). Pronounced differences in size of hyphal cells occur in normal development, as is evident when the rather small unicellular migratory hyphae (FIG. 3, B, *b*) in aging tube cultures are compared with the massive resting cells (FIG. 3, C–H) often formed abundantly in Petri plate cultures.

Conidiophores (FIG. 3, I–X) of *Conidiobolus polyspermus* are extended freely from hyphal segments that may be either procumbent on the surface of the substratum (FIG. 3, I, *s*; J, *s*; M, *s*; X, *s*) or submerged under the surface (FIG. 3, K, *s*; L, *s*). Unlike the shaft-like

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FIG. 1. Two *Conidiobolus* isolates grown for 72 hours on Petri plates of potato-dextrose agar confined under an inverted battery jar at 25° C; × 1. A, Isolate considered to be identical with *C. brefeldianus;* it was obtained from detritus of decaying grass leaves taken from a roadside near Saint Petersburg, Florida, on April 15, 1959. B, Isolate that agrees somewhat less closely to *C. brefeldianus* and may belong to a separate species; it was obtained from decayed remnants of a forget-me-not (*Myosotis* sp.) stem taken from marshy ground near Park Falls, Wisconsin, on November 18, 1954.

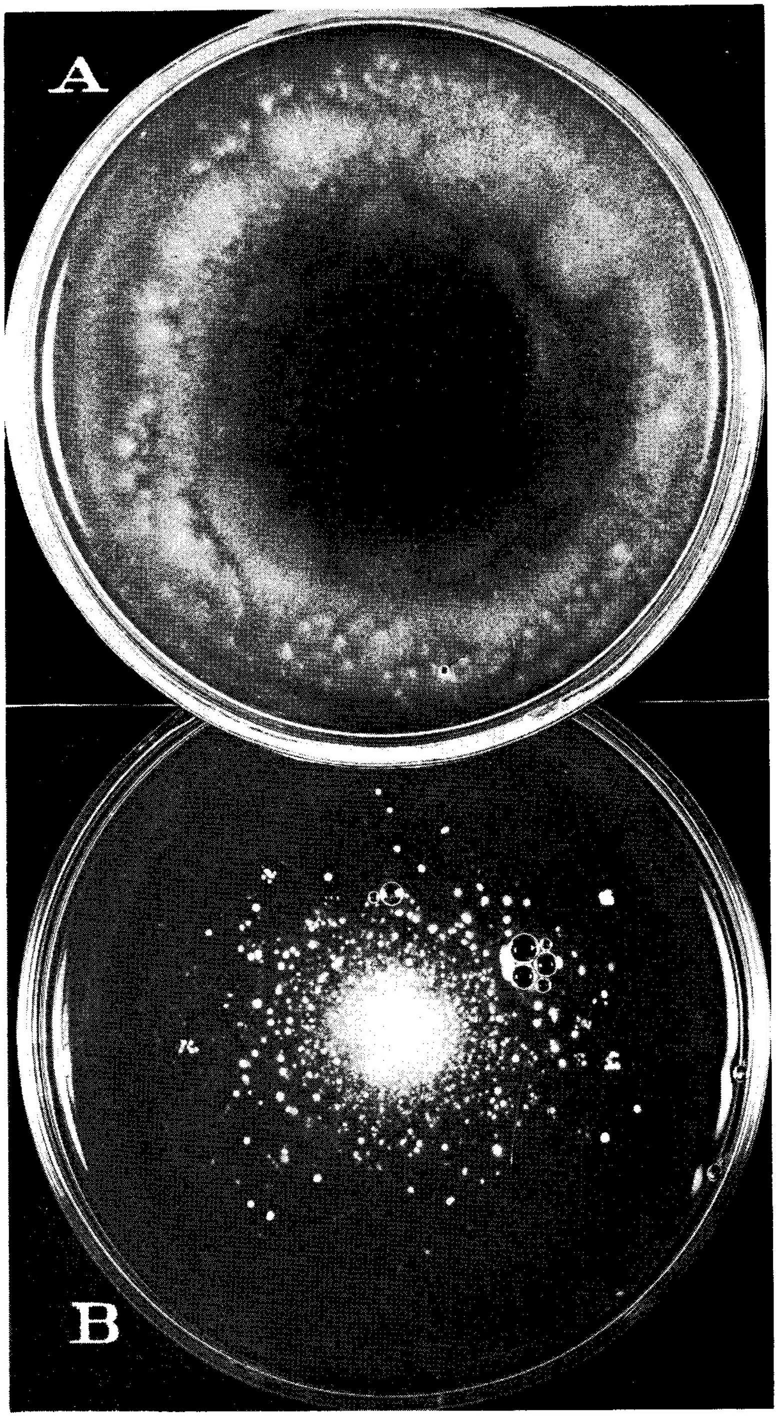

FIG. 2.

cylindrical conidiophores of *Delacroixia coronata*, *C. firmipilleus* Drechsler (1953b), and *C. chlamydosporus* Drechsler (1955) they are often noticeably broadened some little distance—usually about 10 μ—below the attachment of the conidium (FIG. 3, I–L), but in scattered instances they may be widest at the place of attachment (FIG. 3, M) or as much as 20 to 25 μ below the protruding distal septum (FIG. 3, N). Usually when this septum is completed (FIG. 3, M) by deposition of a portion of membrane at its apex, all except a rather small remnant of protoplasm will have migrated into the conidium. Some denuded conidiophores, however, retain considerable protoplasm (FIG. 3, N) and accordingly are capable either of growing out vegetatively or of resuming asexual reproductive development.

Soon after the conidium of *Conidiobolus polyspermus* has been fully delimited, it springs off forcibly through sudden eversion of its basal membrane. The dome-shaped papilla thereby thrust out appears in the detached conidia (FIG. 3, O, *a–o*; FIG. 4, A, *a–v*) rather sharply demarcated from the globose peripheral wall. With respect to outward shape the detached conidia greatly resemble those of *C. brefeldianus*, which, however, would seem from Couch's description to be of generally smaller dimensions. While the conidia of *C. polyspermus* resemble those of *Delacroixia coronata* both in shape and in size, they have never been found transformed into hirsute resting spores. As might be expected from their strong self-propulsion, the conidia of *C. polyspermus* and *D. coronata* are provided with papillae of noticeably greater size than the similarly large conidia of *C. adiaeretus* Drechsler (1953a), *C. chlamydosporus*, and *C. megalotocus* Drechsler (1956b). Many of the very robust conidia produced by *C. polyspermus* in potato-dextrose-agar cultures bear a papilla of broadly rounded hemispherical shape (FIG. 3, O, *i, l, m*; FIG. 4, A, *a, c, d*) rather than of the somewhat tapered paraboloid shape usual in the papillae of smaller spores. In numerous instances the hemispherical papilla contains no vacuole and concomitantly the globose interior is often filled throughout with densely granular protoplasm.

Detached conidia of *Conidiobolus polyspermus* often germinate vegetatively by extending into the substratum one (FIG. 4, B) or two (FIG. 4, C) germ hyphae capable of growing out into new mycelia. Often, too, they extend into the air a single hypha (FIG. 4, D–H) that swells at the tip (FIG. 4, I) and forms there a secondary conidium (FIG. 4, J–L)

FIG. 2. Two new species of *Conidiobolus* grown for 72 hours on Petri plates of potato-dextrose agar confined under an inverted battery jar at 25° C; × 1. A, Type culture of *C. polyspermus*. B, Type culture of *C. gonimodes*.

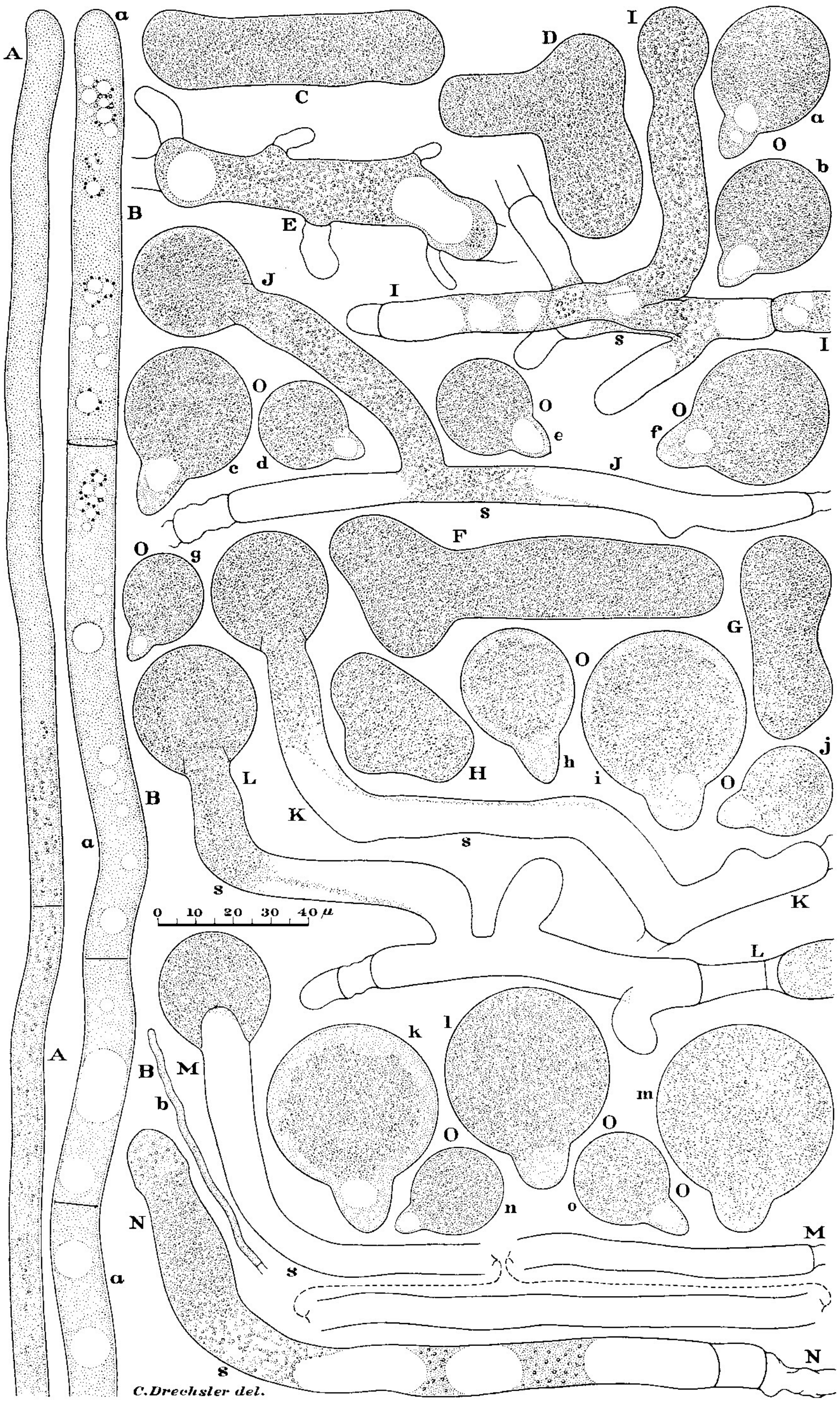
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FIG. 3.

which, like its parent, springs off through sudden eversion of its basal membrane. Continued recurrence of such repetitional development entails progressive reduction in size of the numerous conidia affected. In cultures where evanescence of empty membranes is not too rapid some evacuated conidial envelopes, together with attached tubular remains of germ conidiophores (FIG. 4, M), are found intermixed with thimble-like caps (FIG. 4, N) left by conidiophores of mycelia origin. Multiplicative reproduction by the development of microconidia plurally on short sterigmata has not so far been observed in *C. polyspermus*, though under similar cultural conditions some production of microconidia occurred in the Florida isolate held referable to *C. brefeldianus*.

When *Conidiobolus polyspermus* is grown on maize-meal agar or on lima-bean agar, it forms zygospores in moderate quantity. In potato-dextrose-agar cultures, however, the fungus produces zygospores in extraordinary abundance—a feature which the specific epithet is intended to signalize. In such cultures sexual reproduction is initiated very promptly. Thus, although the Petri plate culture shown in FIG. 2, A, was inoculated only 72 hours earlier, the fungus had become extensively visible in the originally clear potato-dextrose agar, owing in much greater measure to copious development of sexual reproductive apparatus on and under the surface of the substratum than to the moderate formation of conidial apparatus above the surface. In notable contrast, no sexual reproduction whatever had taken place in parallel cultures of the 3 congeneric fungi obtained separately from Florida, Wisconsin, and Illinois (FIG. 1, A, B; FIG. 2, B).

Conjugation often occurs in *Conidiobolus polyspermus* between 2 contiguous hyphal segments (FIG. 5, A; FIG. 6, A) which, through evacuation of adjoining portions of filament, no longer are in direct

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FIG. 3. *Conidiobolus polyspermus* drawn with the aid of a camera lucida; × 500. A, Distal portion of an elongating hypha at advancing margin of a mycelium growing in a maize-meal-agar plate culture, drawn within 5 minutes after material was placed on a microscope slide under a cover glass. B, Two filamentous hyphae of unequal width: *a*, distal portion of an elongating hypha at margin of a mycelium in a potato-dextrose-agar plate culture, drawn 50 minutes after material was placed on a microscope slide under a cover glass and exposed to strong illumination from a microscope lamp; *b*, migratory hypha in a maize-meal-agar tube culture 13 days old. C–H, Large distended segments in central area of a mycelium in a potato-agar-plate culture 6 days old. I, Portion of mycelium with a conidiophore bearing a young conidium. J–L, Portions of hyphae, each with a conidiophore showing early stage in formation of wall delimiting a conidium. M, Hypha with conidiophore bearing a fully delimited conidium. N, Conidiophore denuded of its conidium but retaining some protoplasm in living state. O, Detached conidia, *a–o*, showing variations in size and shape. (*s*, surface of substratum.)

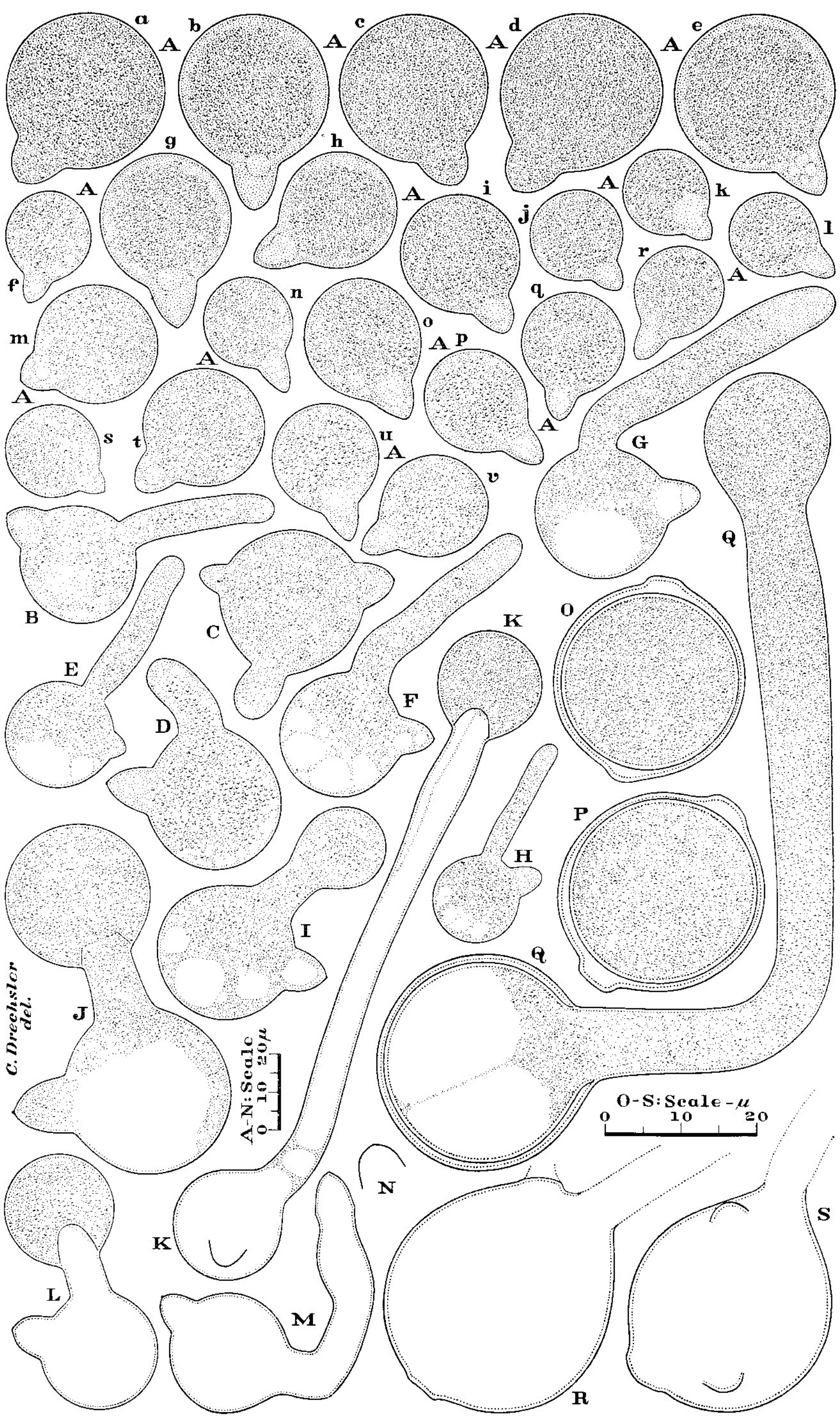

FIG. 4.

contact with any other of their neighbors. As an initial sign of prospective union both segments, especially if they are relatively narrow, may swell rather markedly at their abutting ends. While this preliminary enlargement is taking place, the separating cross-wall seems to remain unchanged (FIG. 6, A). Soon all enlargement ceases in one of the ends, but the other end continues steadily to gain in volume. An opening that permits passage of granular contents now becomes discernible in the flat partition between the increasingly unequal distentions (FIG. 5, A, B), and in one instance 2 such openings could be seen (FIG. 5, C). Beginning, therefore, at a relatively early stage the larger distention receives materials not only from the unmodified portion of the segment to which it belongs but also from the conjoined segment. The migration of protoplasm results in progressive evacuation first of the more distant portions of both segments and later of their closer portions. Successive stages of evacuation are sometimes marked by deposition of retaining walls one after another (FIG. 5, C, D). When the larger distention has received all the contents of both segments, it is walled off proximally and distally as a young zygospore (FIG. 5, E). In somewhat rare instances the contributing segment may retain a substantial remnant of living protoplasm within a cell adjacent to the zygospore (FIG. 5, F). For a while the partition delimiting the zygospore from the contributing segment often appears of unequal thickness (FIG. 5, E, F), its thinner portion corresponding in position to the aperture earlier present between the paired gametangia.

Conjugation often takes place in *Conidiobolus polyspermus* also between 2 hyphal segments that owing to withdrawal of protoplasm from an intermediate portion of filament are no longer contiguous. One of the segments puts forth a branch that makes apical contact with the other segment and unites with it (FIG. 5, G; FIG. 6, B, C). Thereupon the same sequence of developmental events ensues as in pairs of directly

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FIG. 4. *Conidiobolus polyspermus* drawn with the aid of a camera lucida; A–N, × 500; O–S, × 1000. A, Detached conidia, *a–v*, showing usual variations in size and shape. B, C, Conidia germinating by production of 1 and 2 germ tubes, respectively. D-H, Detached conidia, each apparently extending a germ conidiophore. I–L, Conidia at different stages in the production of a daughter conidium. M, Empty membranous envelope of conidium and denuded germ conidiophore. N, Thimble-like distal wall of a conidiophore remaining visible after evanescence of the tubular membrane. O, P, After-ripened zygospores in a maize-meal-agar plate culture 59 days old. Q, After-ripened zygospore germinating by production of a conidiophore and conidium in a maize-meal-agar plate culture 54 days old. R, S, Empty membranous envelopes left behind after germination of 2 zygospores in a 60-day-old maize-meal-agar plate culture was completed.

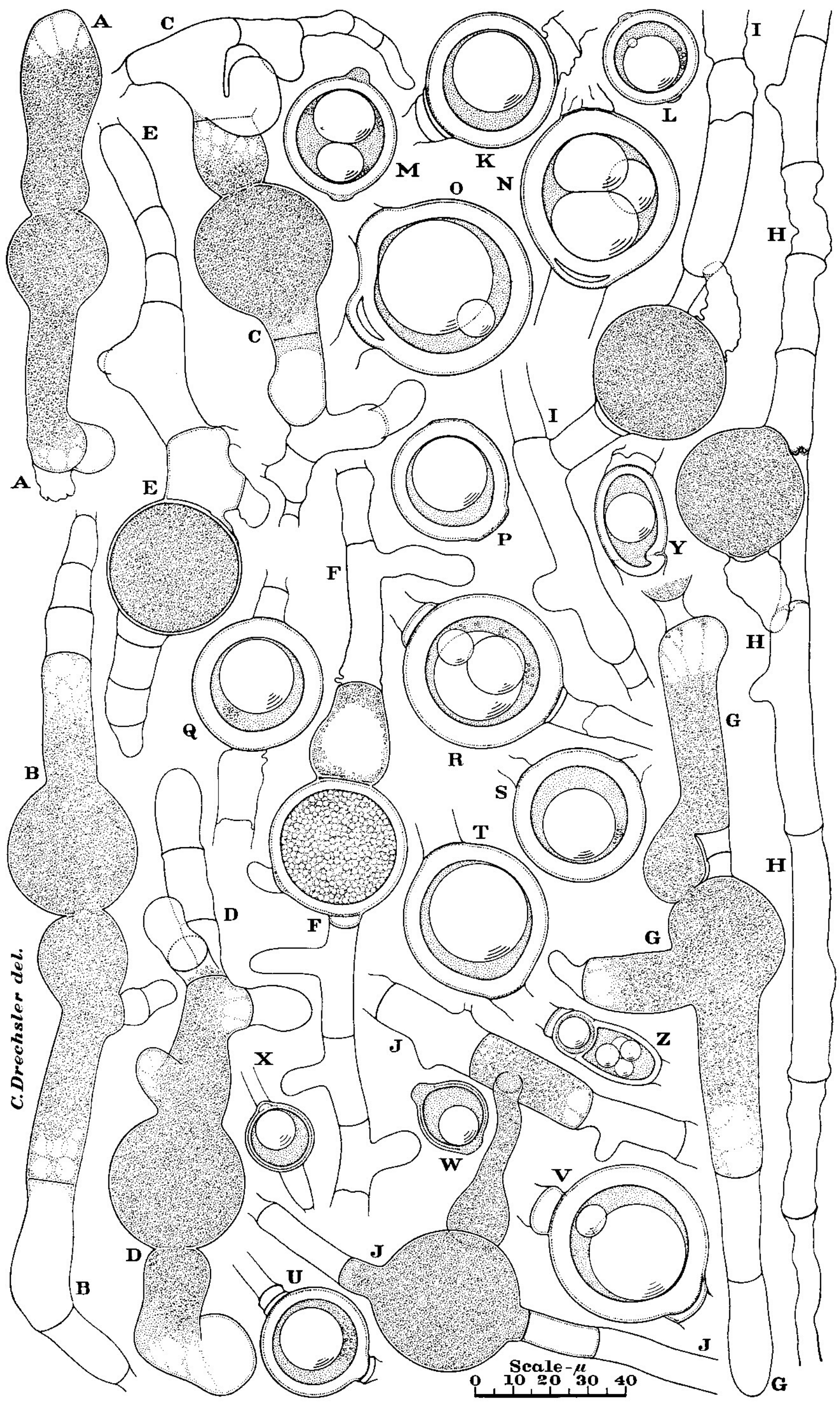
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FIG. 5.

contiguous gametangia, and with the same result that wholly within one gametangium and in immediate proximity to the other a globose distention containing the protoplasm of the entire reproductive unit soon becomes walled off as a young zygospore (FIG. 5, H, I; FIG. 6, D). In scattered instances where the young zygospore is not in axial alignment with the 2 parent hyphal segments but forms a part of the lateral arch (FIG. 5, H) connecting them, it probably was produced distally in the branch. More commonly, however, the zygospore originates in the segment to which the tip of the branch is applied. As a short branch usually applies its tip to the nearest end of the receptive segment, the zygospores produced by paired segments only slightly separated (FIG. 5, G, I); FIG. 6, B) are formed usually in about the same relative position as those produced by paired contiguous segments. A longer branch, on the other hand, may follow a rather circuitous course and apply its tip near the middle of the receptive segment, so that zygospores produced by widely separated consecutive segments often are formed in median positions (FIG. 6, D).

Positional relations are likewise of moment in instances of conjugation between segments belonging to separate hyphae of *Conidiobolus polyspermus*. Segments in 2 neighboring hyphae near the mycelial forefront initiate sexual reproduction by swelling conjointly to form a pair of distentions (FIG. 6, E) side by side, which soon become united laterally. The distention in one segment reaches definitive size about at the time when an aperture becomes discernible in the apposed cohering portions of membrane (FIG. 6, F) and permits migration of protoplasm into the other distention. The latter continues to grow until it has

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FIG. 5. *Conidiobolus polyspermus* drawn with the aid of a camera lucida; × 500. A–D, Sexual reproductive units in which conjugation is taking place between 2 adjoining hyphal segments; in C two openings are visible in the wall separating the paired cells. E, Sexual reproductive unit in which a young zygospore has resulted from conjugation of 2 adjoining segments. F, Reproductive unit similarly derived from 2 adjoining hyphal segments; the zygospore here is half mature, and the adjacent antheridium-like cell representing the delimited distention of the contributing segment retains some living protoplasm. G, Young sexual reproductive unit in which conjugation is taking place by means of a short stout branch connecting 2 segments that are consecutive but not contiguous. H, I, Reproductive units in each of which a young zygospore has resulted from conjugation between noncontiguous consecutive segments; in H the zygospore forms a part of the bridging connection and therefore may have originated distally in the branch extended by one segment to make contact with the other. J, Reproductive unit in which conjugation is effected by means of a branch that connects segments belonging to separate hyphae. K–Z, Mature or nearly mature zygospores, showing variations in size, shape, and arrangement of contents.

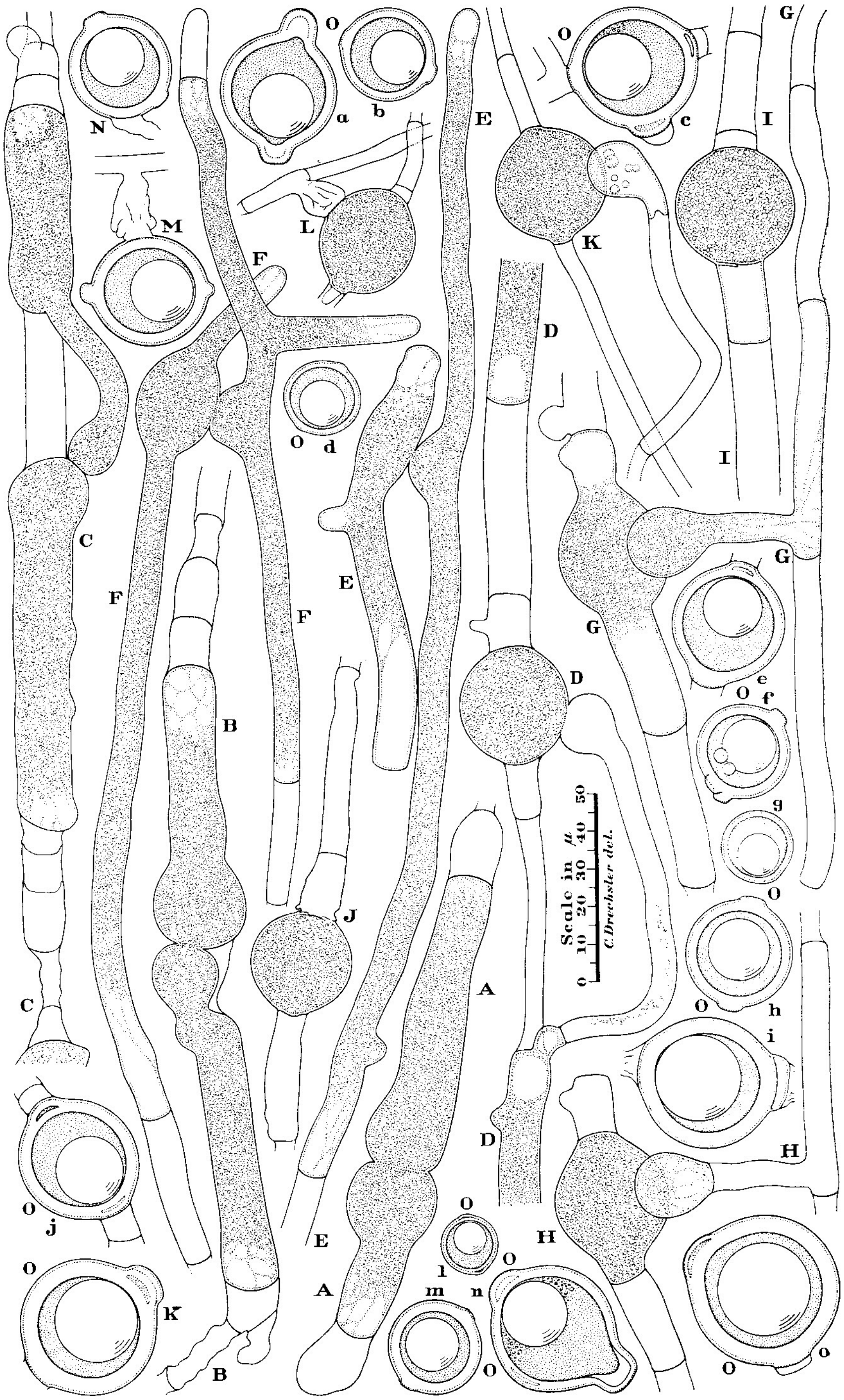

FIG. 6.

received the protoplasmic contents of the whole reproductive unit and is walled off as a globose young zygospore. Conjugation between paired segments in somewhat more widely separated hyphae is accomplished by means of a connecting branch (FIG. 5, J; FIG. 6, G, H), which commonly is extended from the contributing to the receptive segment. Much as in similar conjugation between separated consecutive segments the zygospore here may develop indiscriminately in a middle, a proximal, or a distal position within the receptive cell.

In sexual reproductive units derived from contiguous hyphal segments the globose zygospore together with an adjacent delimited part of the contributing segment (FIG. 5, F; FIG. 6, I, J) gives somewhat the appearance of an oogonium and adjoining antheridium of the familiar *Pythium ultimum* Trow. Owing likewise to parallelism in arrangement of parts, reproductive units of *C. polyspermus* derived from separate consecutive segments (FIG. 5, I; FIG. 6, D) have a suggestive resemblance to monoclinous sexual apparatus of *P. debaryanum* Hesse. Similarly, reproductive units derived from segments of widely separated hyphae may correspond in appearance to diclinous sexual apparatus of *P. debaryanum*, especially in instances where the distal distention of the connecting branch is set off by a cross-wall (FIG. 6, H, K). Since such a cross-wall is usually formed at a late stage in the migration of protoplasm from the contributing segment into the young zygospore, it would seem of no greater significance than other cross-walls that may be laid down at variable intervals as the filamentous portions of the 2 segments are progressively emptied of their contents.

On reaching its definitive size the young zygospore of *Conidiobolus polyspermus* (FIG. 5, E, H, I; FIG. 6, D, I–L) is surrounded by a thin wall and is filled throughout with densely granular protoplasm. Soon

FIG. 6. *Conidiobolus polyspermus* drawn at a uniform magnification with the aid of a camera lucida; × 500. A, Young sexual reproductive unit composed of 2 adjoining hyphal cells. B, C, Sexual reproductive units in each of which a pair of noncontiguous consecutive segments have become connected by a lateral branch. D, Sexual reproductive unit in which a young zygospore has been formed through conjugation between a hyphal segment and a lateral branch. E, F, Young reproductive units in which long segments of separate hyphae have become united laterally. G, Reproductive unit in which 2 segments belonging to separate hyphae are connected by a lateral branch. H, Same unit as G but drawn 25 minutes later when the terminal distention of the lateral branch had been delimited as an antheridium-like cell. I, J, Reproductive units that have each formed a young zygospore through conjugation between adjoining hyphal segments. K, L, Young zygospores to each of which is attached laterally an empty antheridium-like cell. M, N, Mature zygospores with empty membranous parts attached laterally. O, Mature zygospores, *a–o*, showing variations in size and shape.

thereafter its wall increases in thickness and its contents acquire a globuliferous texture (FIG. 5, F). The ripe zygospores (FIG. 5, K–Z; FIG. 6, M; N; O, *a–o*), like those of various congeneric forms, have a relatively thick wall within which usually a single eccentric reserve globule is very largely or wholly surrounded by protoplasm of nearly homogeneous character. Despite their strongly indurated appearance they are capable of rather early germination under conditions that can hardly be considered exacting. Thus, in a set of maize-meal-agar plate cultures, which, after being inoculated were protected against evaporation and for some time with moderate success also against intrusion of alien microorganisms, zygospores began to germinate spontaneously after about 30 days. Without any water added to the aging cultures germination continued for 25 to 30 days, then being halted because of excessive contamination with species of *Streptomyces*. In zygospores ready for germination (FIG. 4, O, P) a thin outer membrane corresponding apparently to the outer layer of the thick wall present during the period of dormancy was found surrounding rather loosely a thin-walled globose cell filled throughout with densely granular contents. A protrusion of the globose cell pushed its way through the outer envelope and elongated externally as a germ conidiophore (FIG. 4, Q) on which was produced a single self-propelling conidium. Some of the empty parts vanished early from sight; so that when the cultures were 55 days old, more than half of the zygospores originally formed in them were represented by only the thin outer membrane together in some instances (FIG. 4, R, S) with a faintly visible proximal portion of the germ tube.

Though capable of early germination the zygospores of *Conidiobolus polyspermus* are capable also of prolonged dormancy. In maize-meal-agar tube cultures that had been stored 4½ years at temperatures near 8° C more than four-fifths of the zygospores appeared to be in a normal living state after sterile water was added to the air-dry substratum. When portions of the softened substratum were transferred to tubes of sterile agar, new cultures of the fungus were obtained promptly.

Conidiobolus gonimodes Drechsler, sp. nov. (γονιμώδης, fruitful.)

In materiis macris oculo nudo parve visibilis, deinde ex parte albidulus et farinulentus, sed in materiis pinguibus vulgo facile visibilis, albidus, aliquid lanatus. Hyphis assumentibus incoloratis, mediocriter ramosis, primo filiformibus, prope marginem crescentis mycelii plerumque 5–8 μ latis sed interdum usque 13 μ latescentibus, ibi ex cellulis vulgo 40–200 μ longis constantibus, hic illic ramos saepius 2–6 μ rarius usque 10 μ latos emittentibus, deinde ex parte in cellulas disjunctas plerumque 15–200 μ longas 6–25 μ latas tarde transeuntibus; hyphis vagis saepe 50–200 μ longis, 2–4 μ latis. Hyphis fertilibus incoloratis, vulgo simplicibus, rarius parce ramosis, in aerem saepius 20–80 μ ad lucem protendentibus, 7–12 μ latis, interdum 5–15 μ subter apicem aliquid inflatis; conidiis violenter absilientibus, incoloratis, globosis, in toto 12–39 μ longis, 11–33 μ latis, basi papilla 2–8 μ longa et 2–9 μ lata praeditis, saepe alium conidium saepe aliquot (2–15) microconidia gignentibus; microconidiis incoloratis, globosis vel elongato-ellipsoideis, rectis vel gibberis, primo 8–16 μ longis, 5.5–11 μ latis, identidem alium microconidium in apice hyphae ascendentis 2–15 μ longae 1–2 μ latae ferentibus, ad postremum quandoque tantum 5 μ longis et 5 μ latis, apice interdum pileo glutinoso praeditis. Zygosporis raro et copulatione cellularum disjunctarum ejusdem hyphae ortis, vulgo e copulatione cellularum contiguarum oriundis, saepius flavidulis, levibus, globosis vel elongato-ellipsoideis, plerumque 15–30 μ longis, 11–25 μ latis, guttula oleacea 6–15 μ crassa praeditis, muro vulgo 1–3 μ crasso circumdatis.

Habitat in foliis herbusculae putrescentibus in Chicago, Illinois. TYPUS: National Fungus Collections No. 71711; American Type Culture Collection No. 14445.

On substrata of low nutrient content at first rather inconspicuous to the naked eye but later often becoming more readily visible by forming on the surface a whitish powdery spore deposit; on richer substrata usually conspicuous, whitish, somewhat cottony, often showing many subsidiary mycelia at the margin. Assimilative hyphae colorless, moderately branched, at first filamentous, near the margin of a growing mycelium usually 5 to 8 μ (rarely up to 13 μ) wide, there consisting of segments mostly 40 to 200 μ long, haphazardly giving off branches mostly 2 to 6 μ (rarely up to 10 μ) wide, later in part slowly undergoing conversion into noncontiguous segments mostly 15 to 200 μ long and 6 to 25 μ wide; migratory hyphae commonly 50 to 200 μ long and 2 to 4 μ wide. Conidiophores colorless, usually unbranched but on a rich substratum sometimes sparingly branched, extending 20 to 80 μ into the air toward the main source of light, mostly 7 to 12 μ in greatest width, sometimes slightly inflated 5 to 15 μ below the tip; conidia springing off forcibly, colorless, globose, mostly 11 to 33 μ wide, 12 to 39 μ in total length inclusive of a basal papilla 2 to 8 μ long and 2 to 9 μ wide at its attachment, very often producing a single daughter conidium on a phototropic germ conidiophore or giving rise sometimes in sessile relationship but more commonly on nonphototropic stalks 2 to 12 μ long and 1.5 to 2.5 μ wide to a progeny of 2 to 15 microconidia: microconidia colorless, globose or elongate-ellipsoidal, straight or gibbous, sometimes provided at the tip with a cap of adhesive substance, in the first generation mostly 8 to 16 μ long and 5.5 to 11 μ wide, often giving rise on a stalk mostly 2 to 15 μ long and 1 to 2 μ wide to another microconidium, through continued recurrence of such development sometimes diminishing in length and in width to 5 μ. Zygospores commonly arising from union of contiguous segments of the same hypha, often slightly yellowish, smooth, commonly globose, less often elongate-ellipsoidal, mostly 15 to 30 μ long and 11 to 25 μ wide, containing a reserve globule 6 to 15 μ in diameter, surrounded by a wall 1 to 3 μ thick.

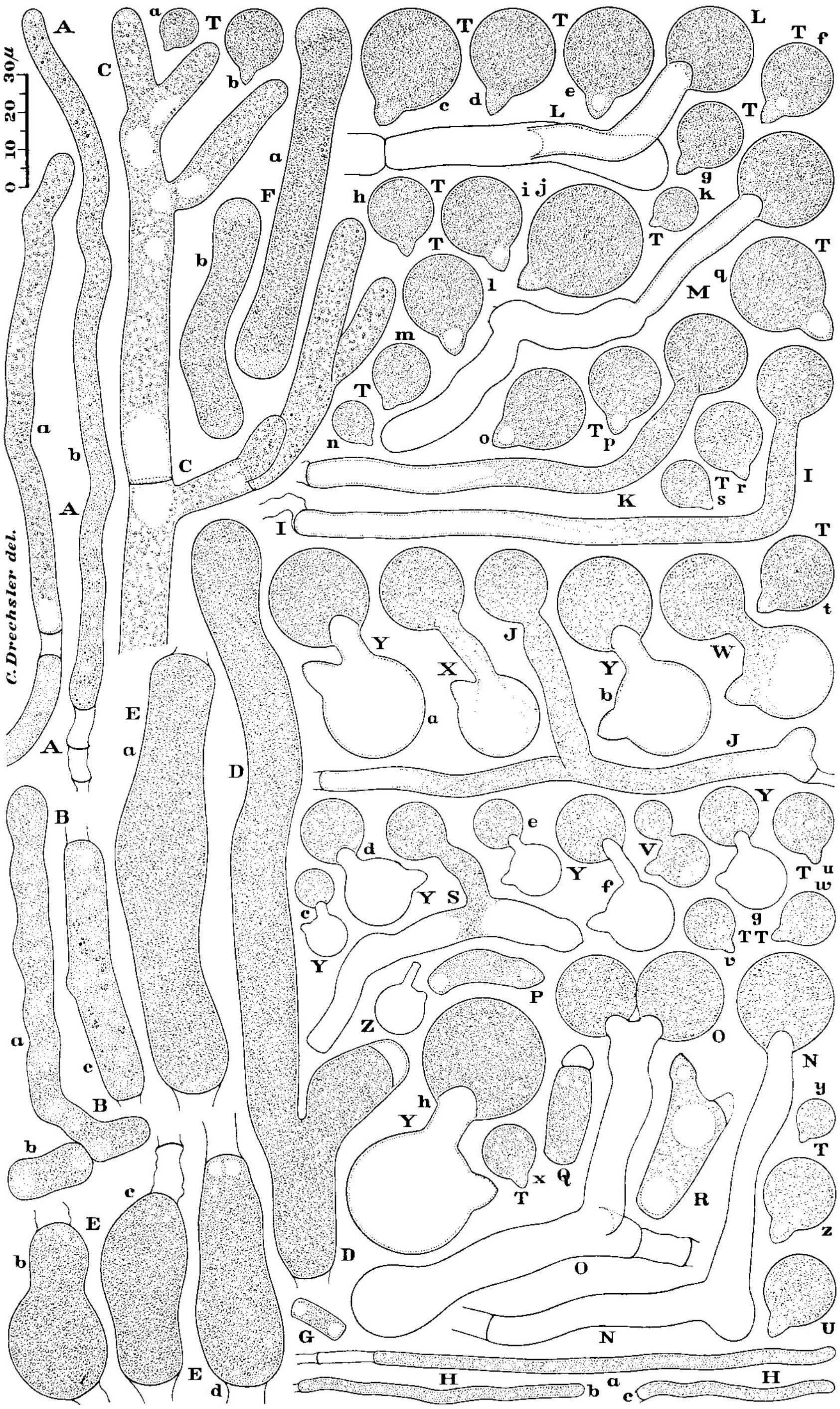

FIG. 7.

Conidiobolus gonimodes was discovered in some Petri plates of maize-meal agar that had been canopied with moist filter paper to which was affixed some fine detritus sifted from decaying herbaceous leaves gathered in an untenanted weedy area in Chicago on November 15, 1954. The submerged mycelium that it pushes through maize-meal agar can be detected with the naked eye when the surface of the culture is viewed at an appropriate angle under a moderately bright light. In Petri plates of potato-dextrose agar, where its growth is readily visible (FIG. 2, B) owing to development of a white downy covering, it shows after 3 days a central area of mycelium surrounded by numerous small mycelia resulting from the germination of individual conidia. The scattered mycelia here seem to merge less freely than in *C. polyspermus,* and in some instances the advance of their peripheral hyphae seems greatly retarded. At an actively advancing mycelial forefront the elongating hyphae (FIG. 7, A, *a, b*) are mostly 5 to 8 μ wide, whereas at a retarded forefront the peripheral hyphae (FIG. 7, C) may measure 8 to 13 μ in width and may show unusually close branching. Backward from the border of an expanding mycelium the hyphae (FIG. 7, B, *a–c*) are found composed of segments mostly 7 to 12 μ wide. Segments 13 to 25 μ wide that can be found here and there in aging cultures (FIG. 7, D; E, *a–d*; F, *a, b*) are perhaps to be considered rather exceptional in view of the moderate dimensions generally characteristic of the fungus. However, in aging cultures are also found some relatively small hyphal segments (FIG. 7, G)

FIG. 7. *Conidiobolus gonimodes* drawn with the aid of a camera lucida; × 500. A, Terminal segments, *a* and *b*, of elongating hyphae at forefront of an actively growing mycelium. B, Hyphal segments, *a–c*, about 3 mm from margin of a growing mycelium. C, Distally branched stout hypha at forefront of a mycelium where advance was halted. D, Large terminal segment at mycelial forefront where advance was halted. E, Wide intercalary segments, *a–d*, from a culture 34 days old. F, Wide intercalary segments, *a* and *b*, from a culture 20 days old. G, Small intercalary segment from a culture 7 days old. H, Migratory hyphae, *a–c*, in a maize-meal-agar tube culture 14 days old. I, Conidiophore arising from one end of a procumbent hyphal segment. J, Conidiophore arising from a position near middle of a prostrate hyphal segment. K, Conidiophore showing early stage in formation of wall delimiting the conidium. L–N, Conidiophores with conidium completely delimited by dome-shaped wall. O, Distally branched conidiophore bearing 2 fully delimited conidia in a lima-bean-agar culture. P–R, Detached cells formed from distal portions of conidiophores in which some living protoplasm was retained. S, Detached cell of similar derivation that is producing a new conidiophore. T (*a–z*), U, Detached conidia showing usual variations in shape and size. V, W, Detached conidia that are each giving rise to a new conidium. X, Late stage in production of a secondary conidium. Y, Empty conidia, *a–h*, each with an empty germ conidiophore bearing a fully delimited new conidium. Z, Small empty conidial envelope left after daughter conidium has sprung off.

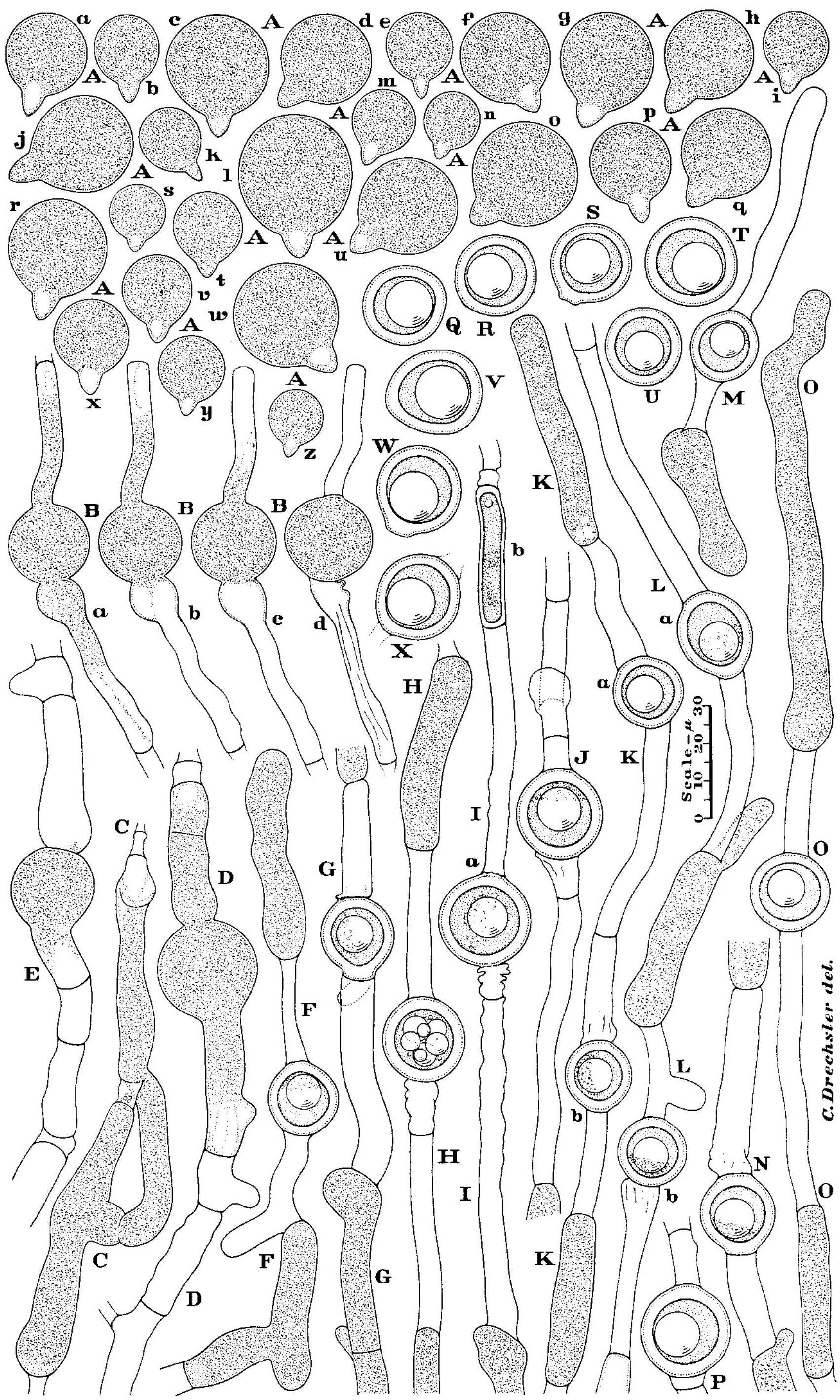

FIG. 8.

as well as scattered unicellular migratory hyphae (FIG. 7, H, *a–c*) that long continue to move through the substratum, steadily expending their limited substance in forming new tubular membrane.

The conidiophores produced abundantly in cultures of *Conidiobolus gonimodes* usually do not project into the air more than 50 μ. Sometimes the aerial shaft ascends from one end of the parent hyphal cell (FIG. 7, I) and at other times it ascends from a middle position (FIG. 7, J). Rather often it is noticeably distended 5 (FIG. 7, J) to 15 μ (FIG. 7, K) below the attachment of the young conidium, but often, again, it shows no pronounced swelling (FIG. 7, I, L, M). During the later stages in the migration of protoplasmic materials from the parent cell a conoidal partition is progressively pushed forward from the base of the conidium (FIG. 7, K). When migration of cellular contents has been concluded, the finished partition protrudes convexly upward (FIG. 7, L–O). In lima-bean-agar cultures somewhat branched conidiophores that bear a conidium on each branch (FIG. 7, O) are found here and there. Soon after being delimited the conidium springs off forcibly through sudden eversion of its basal membrane. A denuded conidiophore, whether simple (FIG. 7, P, Q) or branched (FIG. 7, R), in which considerable protoplasm is retained may put forth a new fertile branch

FIG. 8. *Conidiobolus gonimodes* drawn with the aid of a camera lucida; × 500. A, Detached conidia, *a–z*, showing variations in size and shape. B, Series of 4 stages, *a–d*, in conjugation between 2 adjacent hyphal segments, drawn at intervals of 20 minutes. C, Sexual reproductive unit in which 2 noncontiguous consecutive hyphal branches have been united by means of a lateral branch. D, Reproductive unit in which each of the 2 conjugating contiguous segments has formed at least 2 cross-walls. E, Reproductive unit showing 2 partitions in the empty tubular membrane of the receptive segment and 1 or possibly 2 partitions in the contributing segment. F, G, Portions of hyphae in each of which is intercalated a sexual reproductive unit that contains a mature zygospore and shows no cross-wall in the empty tubular membranes of the paired segments. H, Portion of hypha with an intercalated sexual reproductive unit that contains an approximately mature zygospore with plural reserve globules and shows the wrinkled membrane of the adjacent distention set off by a cross-wall. I. Portion of hypha bearing a sexual reproductive unit in which are included a mature zygospore, *a*, and a thick-walled cylindrical spore, *b*; the wrinkled membrane of the distention adjoining the zygospore is set off by a cross-wall. J, A mature sexual reproductive unit in which the empty tubular membrane of either segment shows a cross-wall about 10 μ from the ripe zygospore. K, L, Portions of hyphae that are each associated with 2 mature sexual reproductive units, *a* and *b*; in K the 2 units are separated by a cross-wall but no cross-wall divides the empty interior of any gametangium. M–O, Portions of hyphae associated with sexual reproductive units that each contain a mature zygospore; no cross-wall divides the empty interior of any gametangium. P, Mature zygospore with adjoining portions of empty hyphal membrane. Q–X, Mature zygospores showing usual variations in size and shape.

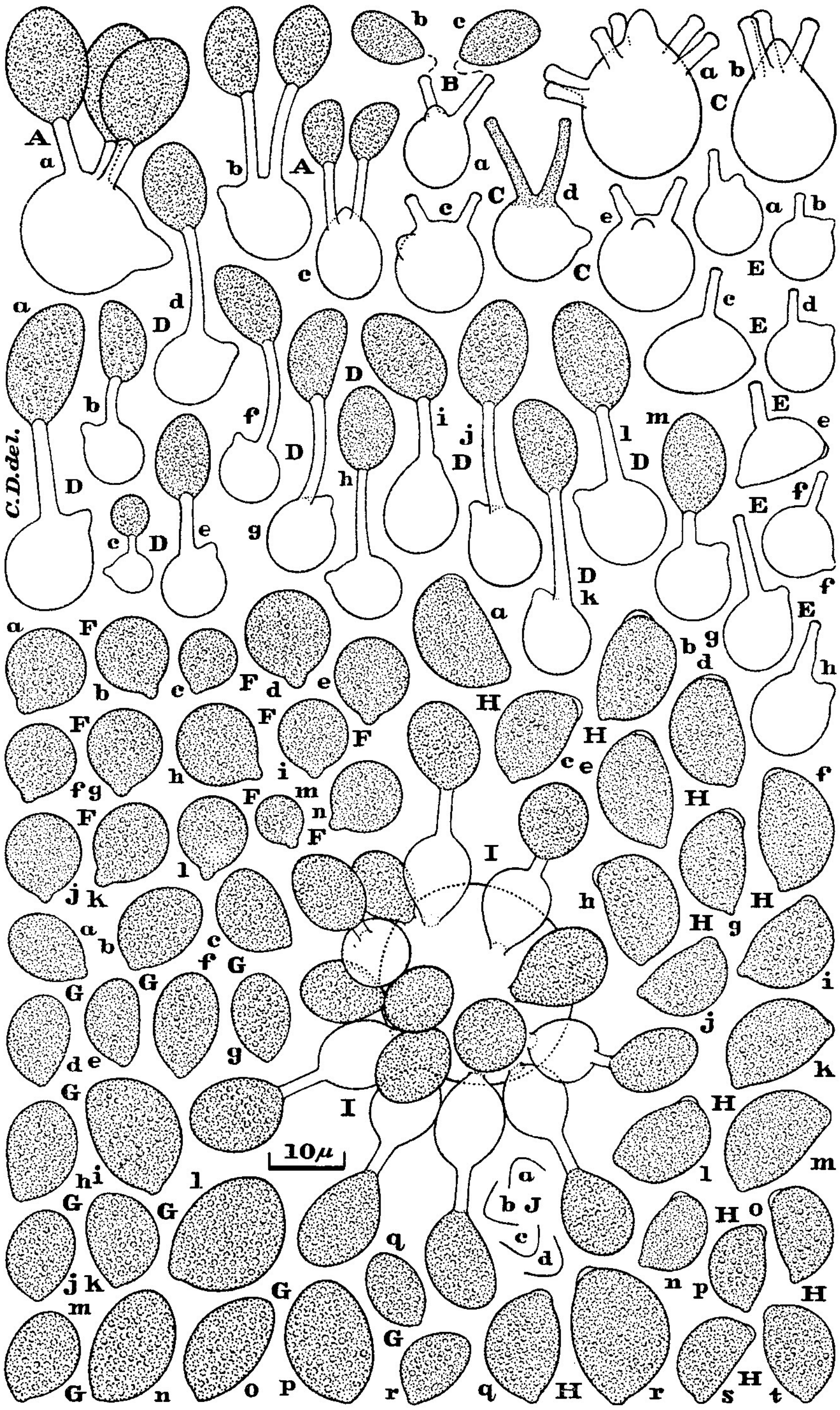

FIG. 9.

(FIG. 7, S) and give rise to an additional conidium. When an empty denuded conidiophore topples on to moist substratum, its tubular membrane may quickly vanish, so that afterwards only the distal wall remains as a visible remnant (FIG. 9, J, *a–d*).

The detached conidia (FIG. 7, T, *a–z*, U; FIG. 8, A, *a–z*) of *Conidiobolus gonimodes*, like those of *C. polyspermus* and *C. brefeldianus*, show an abruptly protruding basal papilla. On a fresh substratum they often put forth 1 or 2 germ hyphae that grow out into a new mycelium. On a substratum already occupied by the fungus they extend in many instances a short phototropic outgrowth (FIG. 7, *V–X*) that soon bears terminally a daughter conidium (FIG. 7, Y, *a–h*), which springs off forcibly, leaving behind the empty membrane of its parent (FIG. 7, Z). The epithet applied to the fungus is intended to be conveniently suggestive of its copious asexual reproduction.

The development of plural microconidia on nonphototropic spurs arising from detached conidia (FIG. 9, A, *a–c*) takes place more freely in *Conidiobolus gonimodes* than in the Florida isolate held referable to *C. brefeldianus*. As the microconidia (FIG. 9, B, *b*, *c*) usually spring off, even if only rather feebly, they are often found lying detached near the parent conidium (FIG. 9, B, *a*). The empty conidial envelopes (FIG. 9, C, *a–c*) usually collapse soon after they become denuded. In aging cultures where all the substratum is already occupied by the fungus, the detached microconidia commonly engage in prolonged repetitional development, each of them giving rise on a rather slender germ hypha to a new microconidium (FIG. 9, D, *a–m*), which springs off, leaving behind the denuded envelope of its parent (FIG. 9, E, *a–h*). In their successive generations the microconidia necessarily incur some reduction in size and usually also some haphazard changes in shape. Many are of a globose shape modified by a basal papilla (FIG. 9, F, *a–n*) usu-

FIG. 9. *Conidiobolus gonimodes* drawn with the aid of a camera lucida; × 1000. A, Globose conidia, *a–c*, that have given rise to plural microconidia. B, Empty conidium, *a*, with its progeny of 2 microconidia, *b* and *c*, lying nearby. C, Empty conidia, *a–c*, with plural stalks, denuded of microconidia, arising from them. D, Empty envelopes of microconidia, *a–m*, each with an empty stalk bearing aloft an elongated daughter microconidium. E, Empty microconidia, *a–h*, each with a stalk denuded of the daughter conidium it earlier supported. F, Microconidia, *a–n*, of globose shape modified at base by an abruptly protruding papilla. G, Microconidia, *a–r*, of elongated ellipsoidal shape with a usually small and rather variable protrusion at the base. H, Microconidia, *a–t*, of gibbous ellipsoidal form, each showing at its tip a cap of adhesive material. I, Globose conidium that produced 14 microconidia, which have remained attached although 8 of them have each given rise to a daughter microconidium. J, Conoidal membranous parts, *a–d*, each representing the distal wall of a conidiophore.

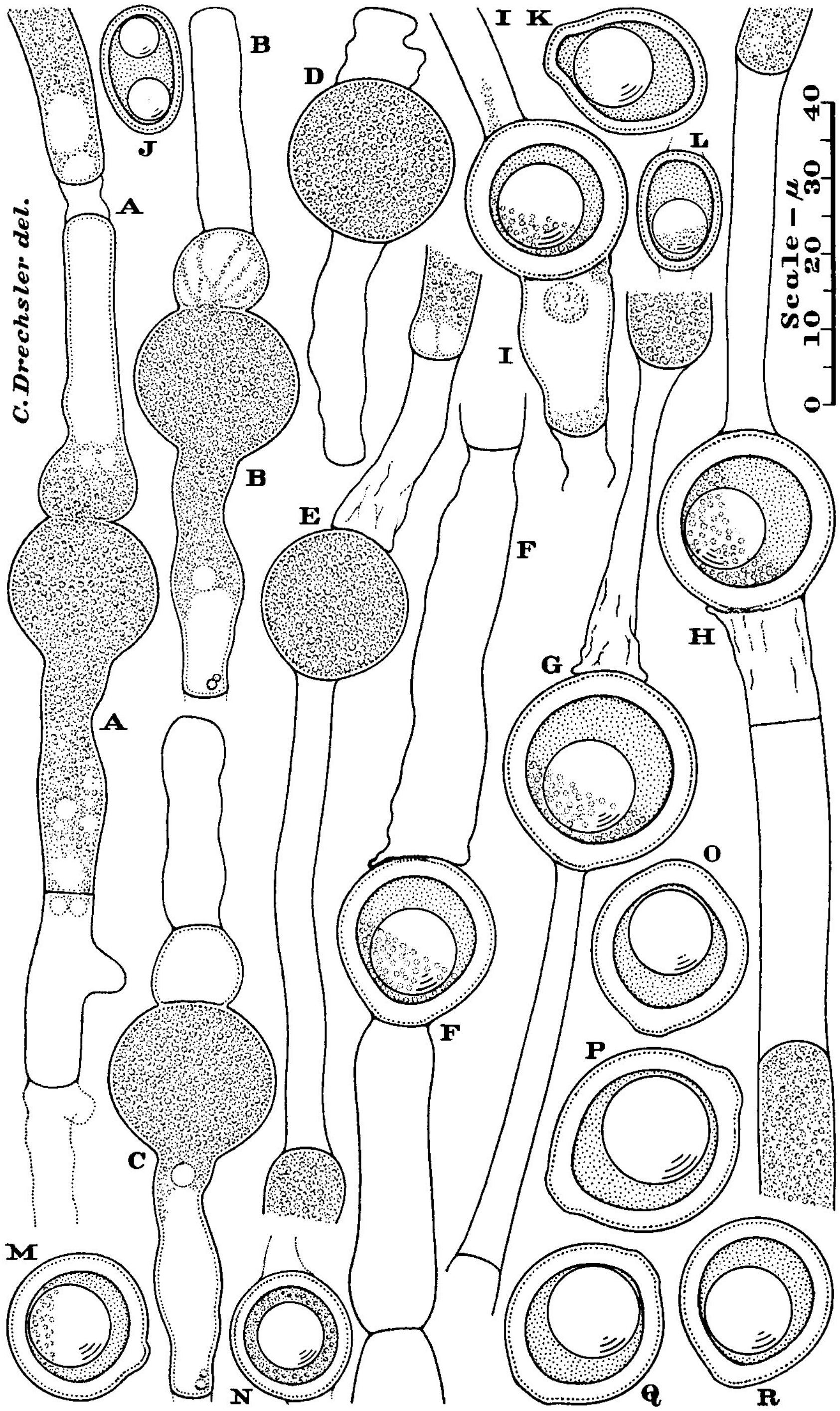
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FIG. 10.

ally somewhat smaller proportionally than the papillae of most large conidia. Others (FIG. 9, G, *a–r*) present an elongated elliptical profile that in many instances is asymmetrical, being nearly semicircular on one side and less prominently curved on the other. The more pronouncedly asymmetrical or gibbous spores often are provided at the tip with a slightly protuberant cap (FIG. 9, H, *a–t*) consisting apparently of adhesive material. Nearly all unsymmetrical microconidia are borne more or less obliquely on their supporting stalks (FIG. 9, I), so that the adhesive cap in gibbous spores is exposed to contact laterally as well as distally.

Similar axially curved or gibbous spores in which an obliquely inclined distal portion bears an adhesive cap in a somewhat lateral position have been observed also in the repetitional development of microconidia in several congeneric fungi. In contaminated Petri plate cultures of *Delacroixia coronata* such spores are often produced with notable consistency by the numerous scattered microconidia that lie partly imbedded in a shallow layer of bacterial slime. Provision for exposing an adhesive apex to contact both laterally and distally would likewise seem present in secondary conidia of the elongate type produced by some members of the Entomophthorales. Thus, while in all species of *Basidiobolus* the proximal portion of the elongate secondary conidium appears usually in axial alignment with the straight slender germ conidiophore supporting it, curvature in the median and distal portions is often sufficient to tilt the adhesive beak well toward one side. Indeed, in a relevant figure given by Eidam (**1886**: Pl. 9, Fig. 16) in the original account of his *B. ranarum* the enlargement that presumably represents the elongated conidium of that taxonomically important fungus is shown obliquely oriented not only in its median and distal portions but throughout its length. In the diagnosis given by Thaxter (**1888**) under the binomial *Empusa (Triplosporium) fresenii* Nowakowski and also in the diagnosis of 3 fungi he newly described in *Empusa* under the epithets *lageniformis, geometralis,* and *occidentalis,* the distinctive almond-shaped secondary

FIG. 10. *Conidiobolus gonimodes* drawn with the aid of a camera lucida; × 1000. A–D, Four stages in conjugation of adjoining hyphal segments, the stages B–D being drawn after successive intervals of 20, 20, and 30 minutes, respectively; after a cross-wall had been formed in the receptive segment another was deposited in the contributing segment at the junction of the distention and the tubular portion of hypha. E, Sexual reproductive unit containing a young zygospore newly walled off. F–H, Sexual reproductive units each of which contains a mature zygospore; only the empty contributing segment in H is divided by a cross-wall. I, Mature zygospore with adjoining portions of hyphal membrane. J–R, Mature zygospores showing variations in size, shape, and internal structure.

conidia were set forth as being "borne obliquely on capillary conidiophores"; and although the term "obliquely" was omitted in his diagnosis of *Entomophthora sphaerosperma* Fresenius, his figures show the almond-shaped conidia of that species likewise in oblique posture.

When *Conidiobolus gonimodes* is grown on maize-meal agar containing some finely divided maize-meal in suspension, it gives rise in moderate number to units of sexual reproductive apparatus (FIG. 8, B, *a–d*; C; D; FIG. 10, C–D, E), which at maturity yield durable zygospores of correct internal structure (FIG. 8, F–H; I, *a*; J; K, *a, b*; M–X; FIG. 10, F–R). In some few instances 2 consecutive segments separated by an empty portion of tubular membrane conjugate by means of an arched lateral branch (FIG. 8, C), but much more often pairing takes place between 2 adjoining hyphal cells. As in *C. polyspermus* the adjoining cells here show their readiness for union by swelling at their abutting ends; and as in that species, again, one of the resulting distentions soon reaches definitive size, whereas the other keeps on increasing in volume (FIG. 8, B, *a–c*; D; E; FIG 10, A–C) until after receiving the protoplasmic contents of both cells it becomes walled off as a young zygospore (FIG. 8, B, *d*; FIG. 10, D, E). The ripe zygospore with its large reserve globule imbedded eccentrically in protoplasm of nearly homogeneous or slightly granuliferous consistency reveals the internal make-up most usual in the several species of *Conidiobolus* for which zygospores are known.

The progressive migration of protoplasm into the growing zygospore is often accompanied by deposition of 1 or 2 cross-walls in either or in both of the conjoined hyphal segments (FIG. 8, D, E; FIG. 10, A–D, H), though in many mature sexual units the empty tubular membrane of each segment shows no cross-wall other than the one originally delimiting it (FIG. 8, F, G; K, *a, b*; L, *a, b*; M–O; FIG. 10, E–G). In instances where a cross-wall in the contributing segment occurs at the junction of distention and unmodified hypha (FIG. 8, H; I, *a*; J; FIG. 10, C, D, H, I) the distention is walled off as a cell that in its position relative to the zygospore presents some outward parallelism with an antheridium in a monoclinous sexual unit of *Pythium ultimum*. This parallelism can hardly be considered important as it appears at a late stage in conjugation. A few mature reproductive units contain, in addition to the globose zygospore, a thick-walled cylindrical spore (FIG. 8, I, *b*) that may possibly be interpreted as a chlamydospore or, perhaps, as a supernumerary zygospore.

The zygospores of *Conidiobolus gonimodes* retain their viability for a long time. New growth of the fungus ensued consistently when transfers were made to newly slanted tubes of sterile maize-meal agar from maize-meal-agar tube cultures that had been stored at 8° C for more than 4½ years and for approximately 3 years of this period had been in a completely air-dry state.

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