BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 84, No. 4, pp. 268–280 JULY, 1957

TWO SMALL SPECIES OF CONIDIOBOLUS FORMING LATERAL ZYGOSPORES

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The two readily culturable entomophthoraceous fungi herein described as new species of *Conidiobolus* came to light in Petri plates of maizemeal agar that had been canopied with small quantities of leaf mold gathered under deciduous trees in northern Wisconsin and in eastern Mississippi. To hold the finely fragmented detritus securely aloft it was affixed to circular pieces of sparingly moistened filter paper, about 55 mm. wide, which were then made to adhere centrally to the ceilings of the Petri dishes. The pieces of filter paper, between 20 and 25 square centimeters in area, were found capable of holding securely a quantity of detritus weighing 30 to 50 milligrams when air-dry. On each ceiling a peripheral zone, 15 to 20 mm. wide, was left unoccupied as a provision against early contamination of the agar plate with molds that commonly grow out from the decaying material, first spreading horizontally to the rim of the glass lid and then pushing downward along the inner surface of the vertical wall.

As the Wisconsin detritus had been stored indoors for 20 months following its collection, and the Mississippi detritus had been gathered after several weeks of dry summer weather, both samples of decaying material had been exposed to prolonged desiccation. Evidently the hyphal segments and asexual reproductive bodies of all species of *Conidiobolus* had perished, for no early development of any fungus referable to this genus was observable in the canopied cultures. Despite their having somewhat greater endurance than conidia or vegetative cells, the hirsute resting spores of *Delacroixia coronata* (Cost.) Sacc. & Syd. emend. Gallaud (1905) must also have succumbed, since this ubiquitous species, which through its rapid mycelial growth and strong conidial propulsion often overwhelms the less obtrusive forms, failed to develop altogether. To encourage the after-ripening and germination of any *Conidiobolus* zygospores that might be present in the adhering detritus the filter-paper canopies were kept suitably moist and at intervals of 7 days were removed to a bed of firm absorbent cotton and there irrigated with distilled water. After such irrigation each freshened canopy was affixed to the lid of a newly sterilized Petri dish and thus superposed over a new maizemeal-agar plate. No entomophthoraceous fungi appeared during the first two weeks but during the third and fourth weeks several species of *Conidiobolus* were obtained. Among them were the 2 new forms presented herein, both of which came from detritus that had remained

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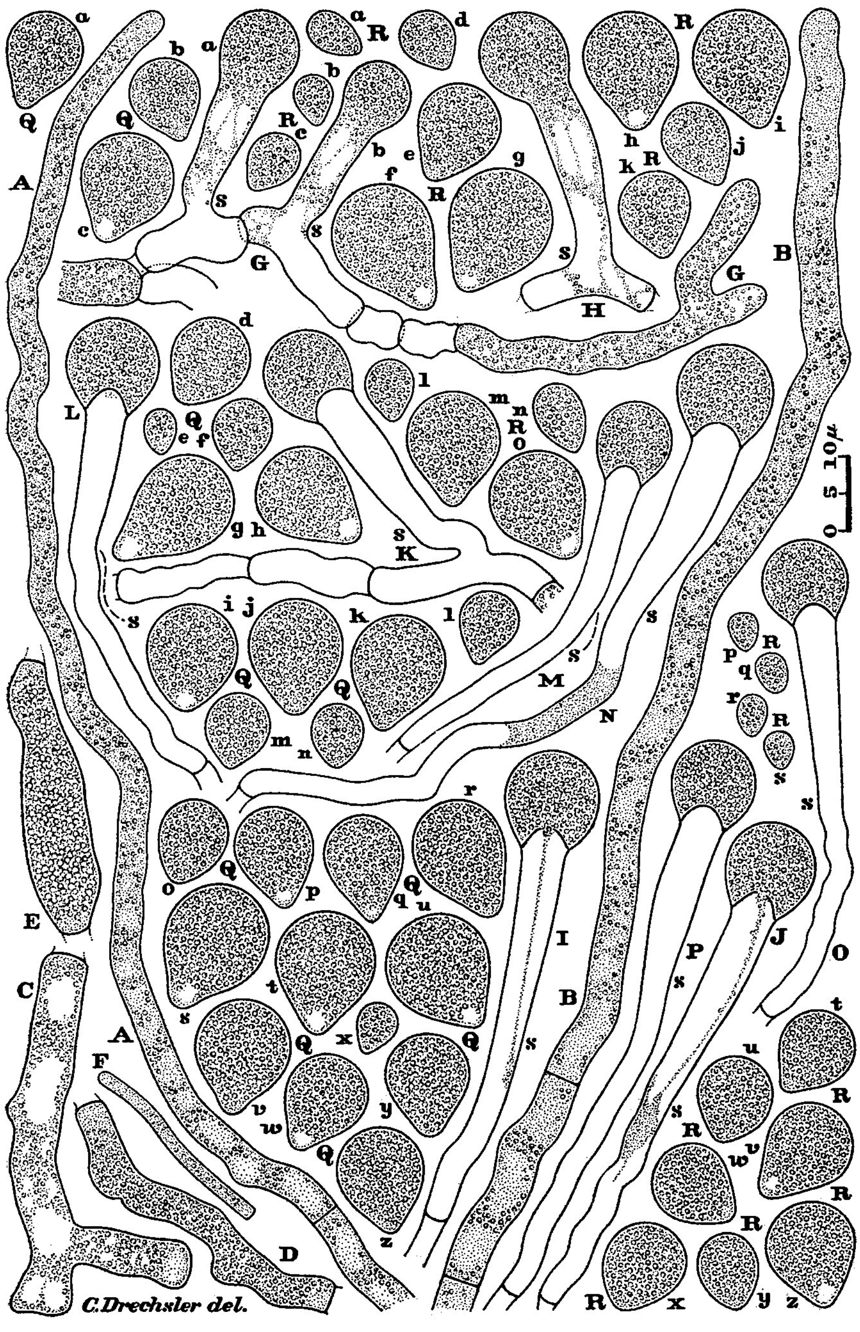
affixed to moist filter paper more than 20 days, and had thus been twice irrigated and twice placed anew over fresh agar substratum.

As various readily culturable Entomophthoraceae can be isolated from small quantities of plant detritus taken at random, whether in Wisconsin or in Mississippi, these fungi would seem distributed very widely and very thoroughly in vegetable materials that have undergone slow and somewhat prolonged decay in moist contact with the ground. In view of their extensive distribution and ubiquitous occurrence there can be little doubt that these fungi exist much more abundantly in nature than has long been supposed. Except perhaps in localities where very numerous insects, such as house flies, grasshoppers, aphides and seventeen-year cicadas, are being, or recently have been, parasitized on a massive scale, the species of *Conidiobolus*, *Delacroixia* and *Basidiobolus* must persist collectively in far greater quantity than the insectivorous species assigned to the genera *Empusa*, *Entomophthora* and *Massospora*.

While among the insectivorous Entomophthoraceae host relationships are very helpful in establishing correct distinctions between species, no characteristic relations to the components of various plant detritus have been observed that might be of similar use in defining species of *Conidiobolus* and *Basidiobolus*. The host relationships set forth in descriptions of species of *Empusa* and *Entomophthora* are often durably attested in dried parasitized insects kept as herbarium specimens; and from many of these parasitized specimens, besides, rather satisfactory microscope mounts of asexual and sexual reproductive apparatus can be prepared. In contrast, owing to extensive collapse and disappearance of membranous parts and to very pronounced disintegrative changes in cellular contents, mounts prepared from dried cultures of species of *Conidiobolus* and *Basidiobolus* usually reveal only poorly the morphology shown in living material. It appears unlikely, for instance, that the difference in sculpture of zygospore wall whereby the 2 new species of *Conidiobolus* are most conspicuously distinguished will in distant years be clearly recognizable in the relevant dried specimens that have been deposited in the National Fungus Collections, Plant Industry Station, Beltsville, Maryland. To make up partly for the shortcomings of the dried specimens the accompanying figures (fig. 1–4) show at a uniform magnification assortments of reproductive bodies that are intended on a small scale to be imitative of the random assortments displayed in microscope mounts prepared from living material. For needs of the less remote future pure cultures of the new species have been supplied to the American Type Culture Collection in Washington, D. C.

1. **Conidiobolus paulus** Drechsler sp. nov. Mycelium incoloratum, vulgo aliquid inconspicuum; hyphae steriles mediocriter ramosae, saepe paulo pravae, plerumque 1.5–7 μ (vulgo 4–5 μ) crassae, mox septatae, postea hic illic disjunctae vel inanitae, in cellulis 20–300 μ longis constantes; fertiles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hyphae simplices, incoloratae, in aerem 15–30 μ ad lucem protendentes, itaque in parte protendenti erectae vel acclives, ibi sursum latescentes, apice 3.5–7 μ crassae; conidia violenter absilientia, incolorata, globosa vel obovoidea, basi papilla 1–5 μ alta et 2–7 μ lata praedita, in totum 5–19 μ longa, 4–14 μ lata; zygosporae evidenter saepe ex conjunctione cellularum duarum hypharum genitae, a latere prope commissuram oriundae, plerumque sufflavae, quandoque ellipsoideae sed saepissime globosae, vulgo 10–15 μ crassae, muro semper levi 0.8–1.8 μ crasso circumdatae.

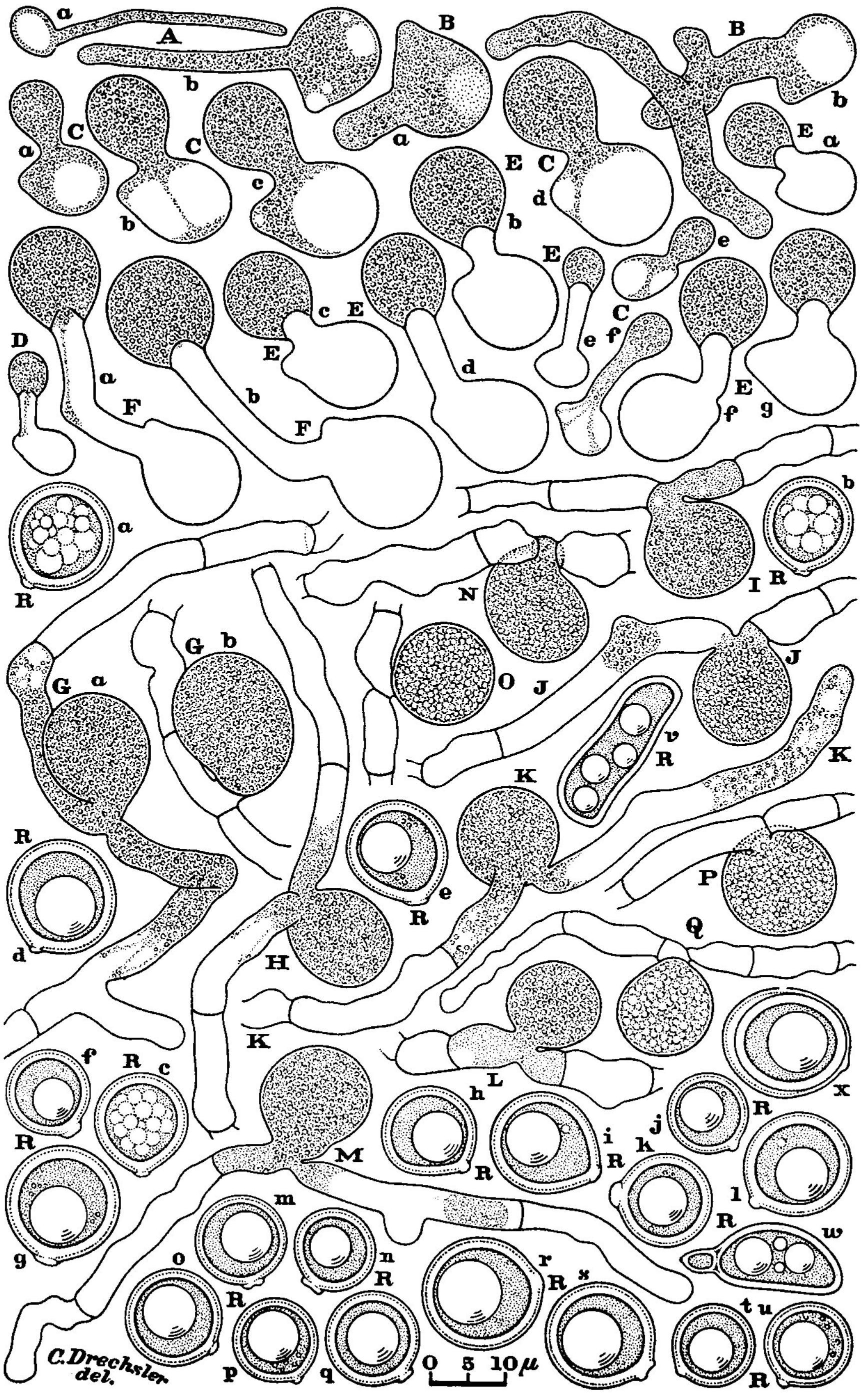
Habitat in foliis arborum (*Aceris, Betulae, Ulmi*) putrescentibus prope Park Falls, Wisconsin.

Mycelium colorless, usually rather inconspicuous; assimilative hyphae moderately branched, sometimes rather markedly crooked, 1.5 to 7 μ (commonly 4 to 5 μ) wide, soon becoming partitioned by cross-walls, when actively growing commonly terminating in a segment 100 to 300 μ long, the other segments being often 20 to 100 μ long and in many places becoming disjointed from one another or separated by empty portions of tubular membrane; conidiophores colorless, unbranched, extending 15 to 30 μ into the air toward the main source of light, the aerial portion (whether erect or inclined) widening upward to an apical diameter of 3.5 to 7 μ; conidia springing off forcibly, colorless, globose or obovoid, 4 to 14 μ wide, 5 to 19 μ in length inclusive of a basal papilla mostly 1 to 5 μ high and 2 to 7 μ wide; zygospores commonly formed laterally near apical union of two segments supplied by separate hyphal branches, usually distinctly yellowish when mature, sometimes ellipsoidal but more often subspherical, mostly 10 to 15 μ in diameter, always smooth except for a slight hilar protuberance, surrounded by a wall 0.8 to 1.8 μ thick.

Isolated from decaying leaves collected in deciduous woods (mainly of maple, birch and elm) near Park Falls, Wisconsin, on November 18, 1954.

Because of the small dimensions of its mycelial hyphae as well as of its reproductive parts *Conidiobolus paulus* belongs in a category with the two dwarfish congeneric species I described earlier (Drechsler 1955a, 1955b) under the binomials *C. pumilus* and *C. nanodes*. When its mycelium grows actively on agar containing some finely ground maizemeal in suspension the relatively long terminal segments (fig. 1, A, B) at the advancing margin commonly vary from 4 to 5 μ in width. The shorter segments, which, one after another, are delimited from the proximal end of the terminal segments, may later become widened to 6 or 7 μ, and, in addition, may undergo modification in shape through extension of branches and protuberances

FIG. 1. *Conidiobolus paulus* as found in maizemeal-agar cultures; ×1000. A, B, Distal portions of two main hyphae at margin of a mycelium. C, D, Hyphal segments about 1 mm. from mycelial margin. E, Somewhat indurated hyphal segment in culture 15 days old. F, Small hyphal segment in culture 15 days old. G, Procumbent hyphal branch with two young conidiophores, a and b; s, surface of substratum. H, Young conidiophore arising from a procumbent hyphal segment; s, surface of substratum. I, J, Distal portions of two nearly mature conidiophores arising from submerged hyphal segments; s, surface of substratum. K, Mature conidiophore arising from procumbent hypha; s, surface of substratum. L-P, Distal portions of five mature conidiophores arising from submerged hyphal segments; s, surface of substratum. Q (a-z), R (a-z), Detached conidia showing usual variations in size and shape.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(fig. 1, C, D). In maizemeal agar cultures 15 days old, segments as much as 8 or 9 μ in width (fig. 1, E) are sometimes found isolated in scattered positions, their strongly granulose contents and noticeably thickened walls being expressive, however, more of a resting than of a vegetative condition. Aging cultures show likewise much less massive segments, including some only 1.5 to 2 μ wide (fig. 1, F), that migrate slowly through the agar in pushing forward at the tip while constantly withdrawing protoplasmic materials from the rear portion. These migrant segments originate as germ hyphae extended by small conidia (fig. 2, A, a) into substratum already thoroughly occupied by mycelium of the fungus.

Asexual reproduction takes place freely in maizemeal-agar cultures of *Conidiobolus paulus*. The phototropic conidiophores extended directly into the air from procumbent hyphal segments (fig. 1, G, a, b; H; K), as also the phototropic aerial prolongations (fig. 1, I, L-P) of narrow hyphae extended from submerged segments, are comparatively short, much as in *C. pumilus* and *C. nanodes*. In gradually widening upward from the surface of the substratum (fig. 1, G-P: s) they resemble more especially the conidiophores of *C. pumilus*.

The young conidium first appears as a globose swelling on the expanded distal end of the conidiophore (fig. 1, G, a, b; H). It increases steadily in size as protoplasmic materials move into it from below. During the later stages in the upward movement of cellular contents it becomes progressively delimited at the base by an intruding partition (fig. 1, I, J). When the supporting shaft has been emptied of granular substance the central aperture of the partition is rapidly walled over. As the dome-shaped septum thus formed, besides being of only moderate convexity, is of large diameter in relation to the globose body it delimits, its everted contour in conidia that have sprung off (fig. 1, Q-R: a-z) is often found virtually in alignment with the adjacent portion of globose membrane. Consequently in *C. paulus* the papilla is not usually seen as an abruptly protruding part, but rather often forms the narrower end of a somewhat obovoid conidium.

Conidia of *Conidiobolus paulus* that spring off on to agar substratum already occupied by the fungus may germinate by extending a rather nar-

FIG. 2. *Conidiobolus paulus* as found in maizemeal-agar cultures; ×1000. A, Detached conidia, a and b, germinating on substratum already occupied by the fungus. B, Detached conidia, a and b, germinating on unoccupied substratum. C, Six conidia, a-f, each with a broad outgrowth on which a secondary conidium is being formed. D, Conidium with aerial outgrowth bearing a partly delimited secondary conidium. E, Seven conidia, a-g, each with a broad outgrowth bearing a completely delimited secondary conidium. F, Two conidia, a and b, which have each put forth a germ hypha that terminates as a conidiophore. G, Two stages of a sexual reproductive unit showing: a, zygospore in active growth; b, zygospore newly delimited 1¼ hours later. H-M, Six sexual reproductive units, each with zygospore in later stages of growth. N-Q, Four sexual reproductive units, each with zygospore newly delimited. R (a-x), Zygospores showing variations in size and shape.

row germ hypha (fig. 2, A, a, b), which in many instances will then elongate without putting forth any branches. On fresh unoccupied substratum a conidium more usually pushes out a wide germ hypha (fig. 2, B, a) that will promptly ramify (fig. 2, B, b) and grow into a mycelium. On either occupied or unoccupied substratum detached conidia display repetitional development abundantly: the individual spore extends upward a broad outgrowth that swells distally into a globose body (fig. 2, C, a-f) which on receiving all the protoplasmic contents (fig. 2, D) is delimited completely by a convex basal partition (fig. 2, E, a-g) and soon springs off as a secondary globose conidium. Sometimes, too, a broad germ hypha, which, in the beginning grew out horizontally, changes its course abruptly and thereupon elongates as a phototropic conidiophore to bear similarly a secondary self-propelling globose conidium (fig. 1, F, a, b). Owing to persistent repetitional development (fig. 2, C, a-f; D; E, a-g) cultures 10 to 20 days old show intermixed with larger conidia of recent primary origin some unusually small conidia (fig. 1, Q, e; R, p-s) among which specimens only 5 μ long or only 4 μ wide can be found. These small conidia are only slightly larger than the minute asexual spores characteristic of the entomophthoraceous tardigrade parasite *Ballocephala sphaerospora* Drechsler (1951). They are not held properly designable as microconidia since multiplicative reproduction has so far never been observed in *C. paulus*.

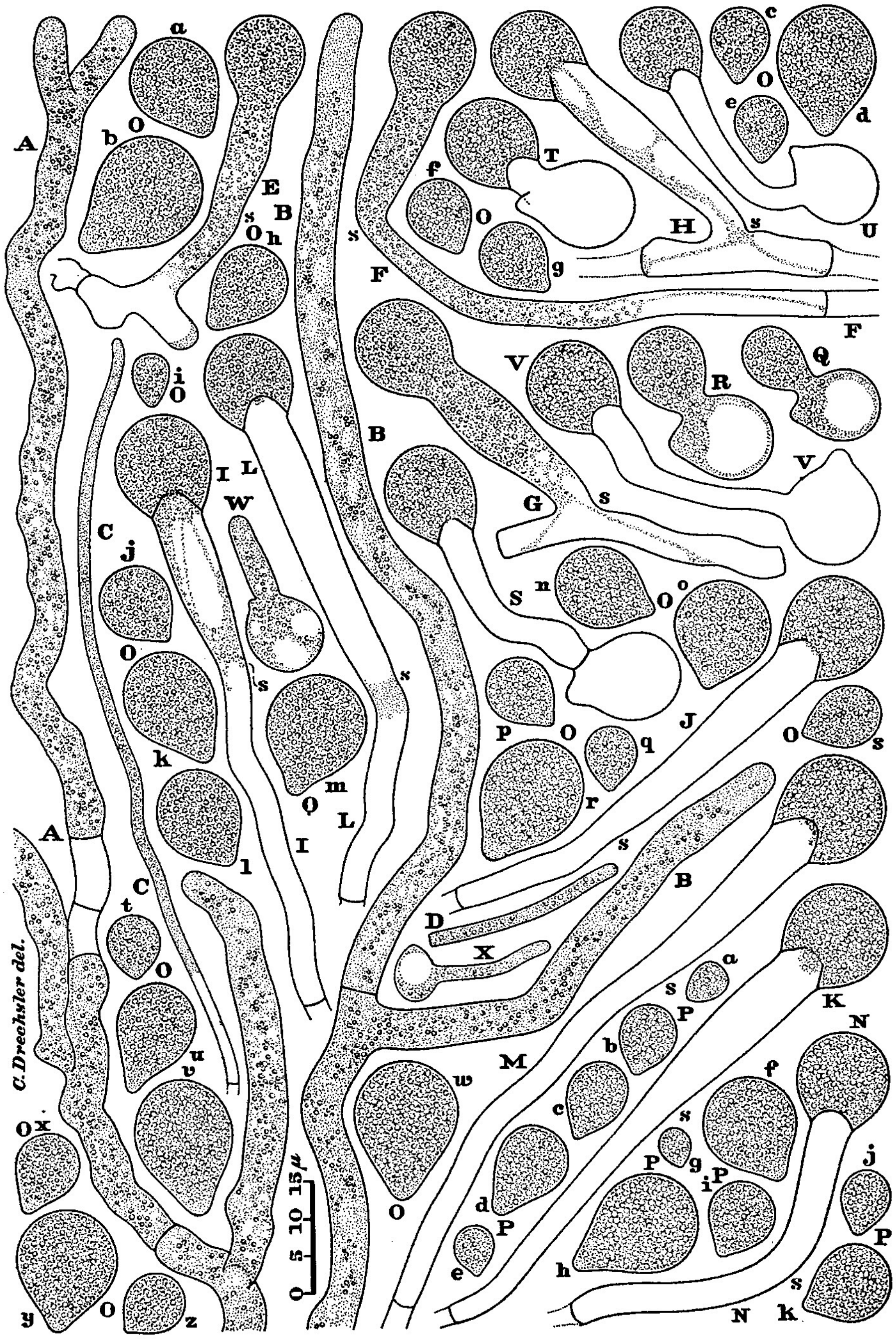
At temperatures near 25° C. zygospores are formed abundantly in maizemeal-agar cultures of *Conidiobolus paulus*. The earliest stages of sexual reproduction are not readily detected, as incipient zygospores look little different from the casual thickenings found here and there on mycelial filaments. Because of the haphazard crookedness of many hyphae it is not easy to infer from the angular relations of the gametangia whether a young zygospore originated through conjugation of 2 adjacent hyphal segments or through apical union of 2 branches given off from separate filaments. Nor can this be easily determined from the mycelial connections of the gametangia, for here, as in many congeneric species, emptied portions of hyphal membrane soon vanish completely. However, since the junction between the 2 gametangia (fig. 2, G, a; H-N) commonly appears as a rather pronounced constriction—an appearance not often presented when adjacent segments are concerned—it may be presumed that conjugation usually takes place between the tips of separate branches.

The young zygospore, in any case, buds forth laterally from one of the gametangia, arising as a globose swelling very close to the junction between the fused segments. As the gametangia become progressively emptied of protoplasm, retaining walls are laid down at intervals to mark successive stages of evacuation. When the gametangium not bearing the zygospore has been emptied of protoplasmic materials a retaining wall is usually laid down that closes the aperture formed earlier in conjugation. A half-hour later this wall is commonly to be seen approximately 1 μ from the septum that in the meantime has been formed to delimit basally the full-grown zygospore (fig. 2, G, b; O-Q), which now is filled with protoplasm containing numerous small globules. Through continued coalescence the globules increase in size and diminish in number (fig. 2, R, a-c) until in the mature zygospore (fig. 2, R, d-u) a single large homogeneous globule is found enveloped in clear protoplasm. The yellow coloration characteristic of the ripe sexual spore would seem to reside mainly in the thickish wall layer deposited within a colorless outer layer corresponding apparently to the membrane that alone surrounded the zygospore when it was delimited. Among large numbers of zygospores a few may usually be found that depart from the normal globose type in having an elongated shape and in containing several globules (fig. 2, R, v, w). Occasionally a specimen is found which along part of its circumference shows the 2 layers of its wall separated by a space (fig. 2, R, x). In such specimens the outer layer is no less smooth than in normal zygospores, never displaying any irregularity in its round contour except in the small, somewhat variable basal protrusion.

2. **Conidiobolus undulatus** Drechsler sp. nov. Mycelium incoloratum, aliquando inconspicuum; hyphae steriles mediocriter ramosae, saepius aliquid pravae, 1.5–7 μ (vulgo 4–6 μ) crassae, mox septatae, postea hic illic disjunctae vel inanitae, in cellulis 25–250 μ consistentes; fertiles hyphae simplices, incoloratae, in aerem 15–40 μ ad lucem protendentes, in parte protendenti erectae vel acclivis, ibi sursum latescentes, subter apicem 4–8 μ crassae; conidia violenter absilientia, incolorata, globosa vel obovoidea, basi papilla 1–5 μ alta et 2.5–8 μ lata praedita, in totum 5.5–19 μ longa, 4.5–14 μ lata; zygosporae interdum ex conjunctione cellularum duarum hypharum genitae, vulgo a latere prope commissuram oriundae, raro intercalares, sufflavae, globosae vel ellipsoideae, plerumque 8–17 μ crassae, muro .7–2 μ crasso in levi interiore corio et undulato exteriore corio vulgo constante circumdatae.

Habitat in foliis arborum (praecipue *Quercus*) putrescentibus prope Starkville, Mississippi.

Mycelium colorless, sometimes inconspicuous to the naked eye; assimilative hyphae moderately branched, often somewhat crooked, 1.5 to 7 μ (commonly 4 to 6 μ) wide, soon becoming partitioned by cross-walls, when growing actively usually terminating in a segment 100 to 250 μ long, the other segments mostly 25 to 100 μ long and in many places becoming disjointed from one another or separated by short portions of empty tubular membrane; conidiophores colorless, unbranched, projecting 15 to 40 μ into the air toward the main source of light, the aerial portion (whether erect or inclined) widening upward, 4 to 8 μ in greatest width near or somewhat below the tip; conidia springing off forcibly, colorless, globose or obovoid, mostly 4.5 to 14 μ wide, 5.5 to 19 μ in length inclusive of a basal papilla 1 to 5 μ high and 2.5 to 8 μ wide; zygospores usually borne in lateral or in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laterally intercalary position, sometimes originating close to junction of gametangia supplied by 2 separate hyphae, yellowish when mature, globose or ellipsoidal, mostly 8 to 17 μ in diameter, surrounded by a wall .7 to 2 μ thick that commonly consists of a smooth inner layer and an undulated outer layer.

Isolated from decaying leaves of deciduous trees (mainly *Quercus* spp.) collected near Starkville, Mississippi, on September 11, 1956.

When *Conidiobolus undulatus* has grown for 20 to 30 days in slanted tubes of maizemeal agar the fungus is plainly visible to the naked eye in the rather opaque upper layer of substratum as well as in the whitish accumulation of conidia overlying the lower half of the slanted surface. The fungus is less conspicuous in maizemeal-agar plate cultures 5 days old, its presence here being most readily noticeable in dappled areas where many small mycelia have developed from globose conidia that after springing forcibly off the conidiophores fell in scattered positions on unoccupied moist substratum. On microscopical examination the growing mycelia are found to consist of hyphae following rather crooked courses and terminating at the margin in elongating segments (fig. 3, A, B) about 5 μ wide; so that the species, like *C. paulus,* may be reckoned among the most delicate members of the genus. In older cultures markedly narrower hyphae (fig. 3, C, D) are produced through vegetative germination of conidia that have fallen on substratum already occupied by mycelium of the fungus.

In both their formative (fig. 3, E-I) and their more advanced stages (fig. 3, J-N) of development the conidiophores of *Conidiobolus undulatus* have much similarity to the conidiophores of *C. paulus,* though apparently in some instances (fig. 3, J, L) they project farther into the air. Apparently, too, their phototropic aerial terminations, in widening upward from the surface of the substratum (fig. 3, E-N:s), more often attain their greatest diameter well below the conidium (fig. 3, E, G, H, K) than the corresponding aerial terminations of *C. paulus.* When the fully delimited conidium of *C. undulatus* springs off its distally widened support, it acquires a broad papilla that merges smoothly with its globose contour. Consequently the

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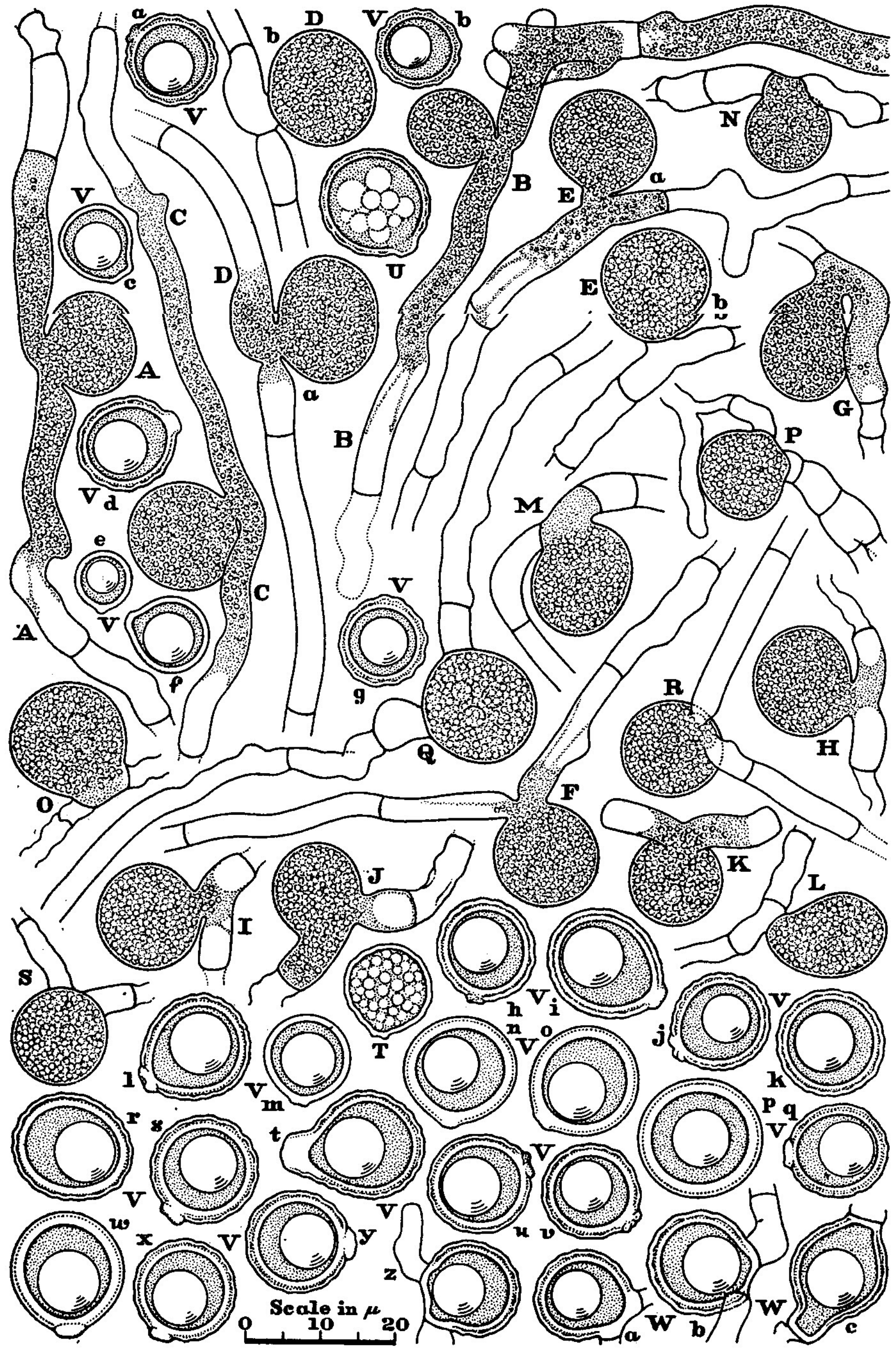
FIG. 3. *Conidiobolus undulatus* as found in maizemeal-agar cultures; ×1000. A, B, Distal portions of two main hyphae at margin of a growing mycelium. C, D, Slender hyphal segments from a culture 24 days old. E-H, Four conidiophores, each arising from a procumbent hyphal segment; s, surface of substratum. I-K, Terminal portions of three conidiophores originating from submerged hyphal segments and bearing partly delimited conidia; s, surface of substratum. L-N, Distal portions of three conidiophores, each of which arises from a submerged hyphal segment and bears a fully delimited conidium; s, surface of substratum. O (a-z), P (a-k), Detached conidia showing variations in size and shape. Q, R, Two conidia, each giving rise to a secondary conidium. S, T, Two conidia, each with an outgrowth bearing a secondary conidium ready to spring off. U, V, Two conidia, each with a germ hypha that terminates as a conidiophore bearing a conidium ready to spring off. W, Conidium germinating in unoccupied substratum. X, Conidium germinating on substratum already occupied by the fungus.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detached conidia (fig. 3, O, a-z; P, a-k) resemble those of *C. paulus* in their rather smoothly obovoid shape as well as in their small dimensions and somewhat densely granular contents. Many detached conidia push up a broad outgrowth on which a secondary globose conidium is formed (fig. 3, Q-T). Others emit a germ hypha, which, after elongating procumbently a short distance, abruptly grows upward as a phototropic conidiophore whereon likewise a secondary globose conidium is borne (fig. 3, U, V). Germ hyphae extended from conidia lying on fresh substratum (fig. 3, W) are commonly wider than those given off by conidia lying on substratum already occupied by the fungus (fig. 3, X).

In maizemeal agar cultures *Conidiobolus undulatus* produces zygospores abundantly. Especially in the earlier stages sexual reproduction proceeds much as in *C. paulus,* the young zygospore nearly always budding forth laterally (fig. 4, A-S) near the junction of the paired gametangia. Since this junction often appears as a constriction (fig. 4, A; B; D, a; F; I; J) it may be inferred that apical conjugation between separate hyphal branches is fairly common. Yet rather often, again, the 2 hyphal arms supplying the growing zygospore show no marked constriction; so that more often than in *C. paulus* the reproductive unit either presents the appearance of having originated from adjacent segments of the same hypha (fig. 4, C, G, H, K, O) or provides no clear indication as to the manner of its origin (fig. 4, E, a; L-N; P-S). In many instances the full-grown zygospore is found delimited by a single basal septum as a globose body sessile on the empty membrane of one of the gametangia (fig. 4, D, b; E, b; L). More often than in *C. paulus* it is delimited by a septum from each empty gametangium, and then appears in laterally intercalary relation to the tubular envelopes of the parent segments (fig. 4, M-S). While the typically lateral or laterally intercalary position of the zygospore is somewhat unusual, being found among known congeneric forms only in *C. paulus,* the earlier stages of sexual reproduction in *C. undulatus,* as in many other members of the genus, are so lacking in distinctiveness that they might readily be mistaken for stages in chlamydospore formation.

Close parallelism with development in congeneric species is likewise shown in the reorganization of contents entailed in maturation of the zygospores. The small globules distributed through the newly delimited subspherical cell (fig. 4, P-S) coalesce to form globules of increasing size (fig.

FIG. 4. *Conidiobolus undulatus* as found in maizemeal-agar cultures; ×1000. A-C, Three sexual reproductive units, each with zygospore in active growth. D, E, Two sexual reproductive units, each showing: a, zygospore in advanced stage of growth; b, zygospore newly delimited 30 minutes later. F-K, Six sexual reproductive units, each showing zygospore in late stage of growth. L, Lateral zygospore newly delimited. M-S, Seven newly delimited laterally intercalary zygospores. T, U, Two slightly immature zygospores having plural globules. V (a-z), W (a-c), Mature zygospores showing variations in size and shape.

4, T, U) until at full maturity only a single large globule is found surrounded by protoplasm of nearly homogeneous appearance (fig. 4, V, a-z; W, a-c). While the internal changes are taking place the enveloping wall gains in thickness. If many thousands of ripe zygospores in a maizemeal-agar culture are examined, a few undersized specimens can usually be found in which the thickened wall is smooth and consists apparently of a single layer (fig. 4, V, c, e, f, m). Diligent search in some cultures may uncover also a few specimens of normal size that closely resemble the zygospores of *Conidiobolus paulus* in being surrounded by a smooth wall in which a thin outer layer, presumably corresponding to the membrane of the newly delimited fusion cell, is everywhere adnate to a thicker inner layer (fig. 4, V, n-p, w). However, owing to the undulate sculpture generally characteristic of the mature zygospores (fig. 4, V, a, b, d, g-l, q-v, x-z; W, a-c), cultures in which sexual reproduction has proceeded for several days show far more conspicuous similarity to *C. rugosus* Drechsler (1955 b) than to any other species. The similarity in sculpture derives mainly from similar differentiation of the zygospore wall into a wrinkled outer layer and a smooth inner layer. In its structure the zygospore wall of *C. undulatus* as well as of *C. rugosus* would seem to agree broadly with that of *Basidiobolus ranarum* Eidam (1886).

Conidiobolus undulatus differs from *C. rugosus* in its narrower mycelial hyphae and in the smaller dimensions of its conidia and zygospores. Its conidia, moreover, show less distinct demarcation of the basal papilla than those of *C. rugosus*. While the zygospores of *C. undulatus* are usually borne in lateral or laterally intercalary position and only rarely can be observed in mesially intercalary position, those of *C. rugosus* commonly develop intercalarily in axial alignment with the parent hyphal segments. The zygospores of *C. undulatus* usually show only faint yellowish coloration, whereas those of *C. rugosus* are distinguished by the most pronounced yellow coloration hitherto seen in any member of the genus.

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