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Contributions from the Cryptogamic Laboratory of Harvard University. XXIX.

New or peculiar American Zygomycetes. I. Dispira.

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WITH PLATE XXXIV.

Among the many interesting forms studied by Van Tieghem in his classic "Études sur les Mucorinées"¹ are several genera of doubtful affinities which this writer is inclined to consider hyphomycetous conditions of certain Ascomycetes. Of these, several named genera (Martensella, Coemansia, Kickxella) have been included in a family of Coemansiae, clearly distinguished by their peculiarly differentiated sporophores and spores, and must still be considered incertae sedis, although one of them has been not too definitely connected with an ascomycetous form. In addition to these, two nearly related genera are included in the same category, both parasitic on species of Mucor and distinguished by producing fertile heads which recall in some respects those occurring in Aspergillus or Sterigmatocystis: the one, Dimargaris, characterized by an erect solitary fertile hypha, terminated by a large spheri
cal head from which arise compound sterigmata bearing spores in chains: the other, Dispira, producing also solitary erect fertile hyphae which become distally several times dichoto
mous, the branches spirally twisted in a characteristic fashion and bearing numerous fertile heads associated with sterile horn-like branches.

Since the publication of Van Tieghem's paper the writer is not aware that this or any other species of Dispira has been observed. During the past spring, however, a package of rat dung was received by Mr. W. H. Rush, a student in the

laboratory, who was the first to observe in cultures of this material a clear white fungus which on examination was found to be very similar to Van Tieghem's *Dispira cornuta* and was provisionally so named. The form was subsequently cultivated and studied more carefully by the writer and proved interesting not only from the fact that it appears to be quite distinct from Van Tieghem's species but was found in some instances to produce its sexual spores in abundance, thus determining beyond question its position in the system.

As described by Van Tieghem, *Dispira cornuta* is characterized by producing erect septate fertile hyphae which become terminally symmetrically dichotomous, the same type of branching being several times repeated in planes successively at right angles to one another. Each successive branch is distinguished by a septum at its base and all become spirally twisted. The last formed are somewhat irregular, the ultimate divisions being either sporiferous or forming curved sterile horn-like branchlets. The fertile branchlet becomes terminally swollen into a spherical head from the surface of which bud out in all directions papillae that subsequently develop into sterigmata. The sterigma consists of a single cell with a median constriction, or more commonly this constriction is replaced by a septum which divides it into two superposed cells, the upper of which bears terminally a single chain of six spores. The two main branches which are, in the younger condition, at first erect, and give to the fructification the appearance of a closed umbrella, gradually separate as they grow older, so that at maturity it becomes shaped like the letter T.

The American species, however, shows important differences in several essential points of structure, and although its general habit is similar, it is very evidently falsely dichotomous, one of the main divisions of the fertile hypha being a lateral outgrowth (fig. 2) below the base of the other, which is thus in reality a terminal modification of the primary axis. The same false dichotomy characterizes the secondary branching, although the resultant fructification, except for a certain asymmetry in its general habit, closely resembles its ally, showing the same characteristic spiral modifications and sterile horn-like ultimate branchlets. In addition to its usual asymmetry, the fructification differs in that it does not undergo the characteristic change of position above described. The
sporiferous heads, moreover, though similarly formed at the tips of ultimate curved branchlets, are clearly distinguished from the fact that the sterigmata are invariably two celled, the upper budding from the lower and not a result of septation, each cell bearing terminally several spore chains, or sporangia, if we adopt the terminology of Van Tieghem, each spore chain consisting of but two spores instead of six.

The characters of the non-sexual form of reproduction are of secondary importance, however, as compared with those of the sexual, which was not observed in connection with *D. cornuta*, but appears to be common in the American species and are quite without parallel among the Mucorineæ. The vegetative mycelium is composed of rather irregular branching hyphae, for the most part aseptate and much smaller in diameter than the fertile ones. From these vegetative hyphae are produced lateral branches which, becoming slightly swollen terminally, attach themselves usually to the fertile hyphae of mucors. This lateral branch fixes itself firmly to the host filament by a sucker-like tip which eventually penetrates the host by means of an irregular protrusion, usually not conspicuously developed though sometimes extending a short distance beyond its point of entrance along the inner surface of the wall of its host. These suckers are the only parasitic organs which were observed in the material examined, and it is uncertain whether they are characteristic of the ordinary hyphae or invariably represent the first stages in the production of zygospores, since they were always found associated with the latter.

The successive stages in the formation of the zygospores are illustrated by figs. 10–13. The lateral branch already mentioned after it has fastened upon the host, becomes divided into two parts by a septum, usually nearer the filament from which it arises, and these two parts proceed to conjugate with one another, the outer becoming eventually separated from the parent filament and receiving from the inner the material derived from its parasitic union with the mucor. The outer gamete soon becomes nearly spherical, enlarging greatly to form the zygospore itself, while the inner, which gradually assumes the appearance of a mere outgrowth from the mucor, sends out simple or once-branched finger-like processes which grow about half way round the mature spore and are at first more or less yellowish from the
presence of the yellow oily material in the cell contents so often associated with zygosphoric reproduction in mucors generally. As far as can be judged with a one-twelfth oil immersion there seems to be eventually a direct connection between the contents of the mucor hypha, and the supplying gamete. The finger-like outgrowths from this gamete become roughened by scattered and not very conspicuous prominences, and although they suggest the protective branches which surround the zygospores of Absidia or Phycomyces, do not seem to have any very definite function in the present instance, since they arise on one side only of the spore which they but half enclose. In general appearance they recall to some extent the characteristic parasitic attachments found in Chaetocladium, and might readily be mistaken for these organs, when, as sometimes occurs, a number of parasitic branches have attacked a mucor hypha in close proximity to one another, and the finger-like processes are developed in dense groups arising from what would at first sight be taken for a general distortion of the host, instead of a mass of partly coalescent supplying gametes.

The only case of conjugation among Zygomycetes, which seems in any way comparable to that which has just been described is found in the genus Basidiobolus Eidam, where the vegetative hyphæ become divided by septa into a series of cells which conjugate with one another as a result of the absorption of the septa separating adjacent cells, the contents of one such cell passing into the other and there forming the zygospore. In the present genus, as has been seen, the process is similar in that a parasitic branch divides into two cells which conjugate with one another, one being receptive, the other supplying; but apart from this circumstance the two types are not to be compared.

The close relationship which exists between the present genus and Dimargaris is evident from Van Tieghem's figures; in fact Dispira Americana corresponds far more closely in the details of its non-sexual fructification to the type of the first than it does to that of the last mentioned genus, and the discovery of additional species may necessitate the union of the two, their separation being at present based on a mere difference of habit. Among the Mucorineæ they may be provisionally included in the Cephalidæ, although perhaps sufficiently aberrant in their mode of sexual reproduction to form a group by themselves.
Van Tieghem has called attention to the septa of the fertile hyphae in the present genus (which by an oversight were not inked in the accompanying illustrations before reproduction) and described the disc-like thickening for which they are remarkable. The same thickenings occur in Dimargaris, and, as was first noted by Van Tieghem, also in the second group of uncertain genera already referred to as constituting the family of Coemansiae. It may be mentioned in this connection that the writer has cultivated certain of the latter forms (Coemansia reversa, Kickxella alabastrina and several others) on nutrient agar-agar in an absolutely pure condition some of them for a period of years, under various conditions, without ever having observed the production of any perithecia, and although Kickxella has been connected with an ascigerous condition, the evidence on which this connection is based is of the most unsatisfactory nature, and the reference of the group to the Hyphomycetes seems based on practically no reliable information. In the writer's opinion the peculiarities of the sporophores, the coherence of the gelatinous spore mass when ripe, together with the peculiarities of the septa just mentioned, as well as the general habit of these plants would indicate a connection with the Mucorinae rather than with any other known fungi.

**Dispira Americana**, nov. sp.—Vegetative hyphae slender branched, creeping on the substratum or running on species of *Mucor* to which they become parasitically attached, giving rise to single erect septate colorless fertile hyphae which become terminally several times more or less regularly falsely dichotomously branched, the divisions spirally twisted, the curved ultimate branchlets either sterile or bearing terminally a white fertile head. Fertile heads spherical, producing numerous sterigmata which bud in all directions and consist of two superposed cells, the upper formed as a bud from the apex of the lower, each giving rise distally to several short spore chains of two spores each. Zygospores always formed in connection with a mucor filament, from one of two gametes without suspensors, nearly spherical, pale brownish, slightly roughened, partly surrounded by a rosette of slightly roughened finger-like processes from the supplying gamete. Fertile hyphae about 1 mm high, 10–12 μ in diameter. Fertile heads 35–45 μ in diameter. Spores 3 × 1 μ. Zygospores 35–65 μ in diameter.
On rat dung from Greenville, Ohio (W. H. Rush), parasitic on Mucor.  

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**Explanation of Plate XXXIV.**  

*Dispira Americana* Thaxter.

Fig. 1. Terminal portion of a small fertile hypha.

Fig. 2. A young fertile hypha showing false dichotomy.

Fig. 3-4. Fertile heads from which sterigmata are budding.

Fig. 5. Fertile head from which the terminal cells of the sterigmata have been formed by budding from the basal cells.

Fig. 6. Optical section of a fertile head showing mature sterigmata from which the spore chains are in process of budding.

Fig. 7. The same with nearly mature spore chains.

Fig. 8. Sterigma with two mature spore chains *in situ.*

Fig. 9. Two spores stilladherent to one another.

Fig. 10. Fertile hypha of *Mucor mucedo* attacked by parasitic branches of Dispira which are producing zygospores in various stages of development.

Fig. 11. The same showing younger parasitic branches and zygospores more highly magnified.

Fig. 12-13. Two mature zygospores.

**Note.**—The original figures have been reduced by photo-lithography 1/2 and were drawn with the following approximate magnifications in diameters: Figs. 1, 2, 10, x 240. Figs. 3-9, x 925. Figs. 11-13, x 420.