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XIII.—*The Life-history of Mycetozoa, with special Reference
to Ceratiomyxa.*

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PLATES X, XI.

THE true Mycetozoa—excluding the Sorophora—form a remarkably compact group of the class Sarcodina of the Protozoa. The course of the life-history is much the same in all members of the family—the spores give birth to swarm-cells; these unite and eventually form plasmodia; the plasmodium at length concentrates to form aerial reproductive bodies producing spores. The spore-bearing bodies consist usually of membranous cases enclosing spores, and are called sporangia; in one species, *Ceratiomyxa*, the stalked spores are borne on the surface of gelatinous processes, the sporophores. The former class constitutes the Endosporeæ, and contains about 260 species; *Ceratiomyxa* is the sole representative of the class Exosporeæ.

In the following notes I propose to rehearse briefly the life-history of one of the Endosporeæ, and then to compare it with that of *Ceratiomyxa*. As an example of the former class, *Badhamia utricularis* may be chosen. It is an abundant species

EXPLANATION OF PLATE X.

Freshly-formed sporophores of *Ceratiomyxa fruticulosa*, magnified about 80 times. From a photograph by J. Howard Mummery.

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in many parts of this country, with conspicuous orange plasmodium that feeds on leathery fungi, and is easily cultivated indoors; the grape-like clusters of small iridescent grey sporangia may be found in favourable seasons, from the summer on into winter, hanging in quantities from the sides of fungus-grown logs in sheltered situations. At the least touch the membranous sporangium-walls break and a shower of dark spores is shed, to be carried away on the breeze, or to be washed down by rain. The spores are not, however, all shed at once, for their dispersion is checked or regulated to some extent by the "capillitium," a structure which in this species consists of a delicate network of tubules, stiffened with deposits of carbonate of lime, and attached to the sporangium-walls. When a ripe spore is moistened, the contents swell, burst the spore-wall, and emerge as a uninucleated swarm-spore or zoospore. This at first creeps about in an amoeboid manner, but soon acquires a flagellum and swims. From the opposite end of the cell to the flagellum pseudopodia are extended, to which bacteria and other food particles adhere, to be conveyed into the interior of the cell and dissolved in digestive vacuoles. After feeding for some time, the swarm-cell divides, its nucleus meanwhile undergoing mitotic division. This process may be repeated several times. Dr. Jahn has proved that these swarm-cells are to be regarded as gametes; they fuse in pairs, their nuclei unite, and zygotes are formed which grow into plasmodia.* The process of fusion was not actually observed, but his cultivations showed numbers of zygotes with large single nuclei, in which when mitosis occurred he could count sixteen chromosomes, whereas the number of chromosomes in the swarm-cell nucleus is eight. The zygotes could often be distinguished at a glance by their habit of absorbing the gametes and devouring them in digestive vacuoles (Pl. XI, figs. 2, 3), while the gametes feed only on minute organisms, such as bacteria. The plasmodia, as the zygotes are termed when they begin to absorb food, increase in size also by uniting with one another. Within their substance a continual rhythmic streaming of granular protoplasm is set up, by means of which all parts are kept in communication. The plasmodium spreads out in a network of veins, searching for food, and grows rapidly; the nuclei meanwhile divide *pari passu*. Several times they have been seen to divide by mitosis simultaneously over a wide extent of plasmodium; considering the many prolonged and unsuccessful attempts that have been made to observe this process, it seems not improbable that they also sometimes divide by direct division. After a time, the length of which varies according to the amount of the food supply, or also, as Dr. Jahn has observed, as the result of cold, the plasmodium concentrates at numerous points to form

* E. Jahn (1911), *Myxomycetenstudien*. 8. Der Sexualakt. Ber. Deutsch. Bot. Ges., xxix. p. 231.

sporangia; sporangium-walls are secreted, and the remainder of the protoplasm, after the capillitium has been formed, divides into spores; before spore-formation the nuclei undergo a reduction division, and each daughter-nucleus forms the centre of a spore.

We may now turn to the course of events in *Ceratiomyxa* (Pl. X and Pl. XI, fig. 7). The sporophores are fragile white branching or anastomosing structures, often appearing in great abundance on the surface of much-decayed wood. The general aspect of a large development closely resembles that of a thin effused *Polyporus*. The colourless ellipsoid spores are borne on slender stalks bristling over the surface of the sporophores; they are readily detached, and are dispersed by currents of air or washed away by rain, which completely dissolves the gelatinous sporophores from which they have fallen. Notwithstanding the naked and unprotected condition of the young spores as compared with those of the Endosporeæ, *Ceratiomyxa* must be regarded as a successful species, for it is abundant in both tropical and temperate regions where decaying wood occurs. The ripe spores differ from those of the Endosporeæ in possessing four nuclei. On being moistened the spore-wall is thrown off with a jerk from the swelling of the contents; the latter at first show slight amœboid movements, and often put out pointed pseudopodia, but very soon the four nuclei divide by mitosis, and the whole cell separates successively into two, four and eight parts; each of the eight uninucleate divisions acquires a flagellum and swims off as a minute swarm-cell (Pl. XI, fig. 7, *a-h*). The further history of these swarm-cells or flagellulæ has not been traced; they have been observed to withdraw their flagella and become amœbulæ, but these have not been observed to conjugate in pairs or to form plasmodia; from analogy with the Endosporeæ however it is probable that such processes occur. Dr. Jahn was able to count eight chromosomes in the nuclei of the swarm-cells and sixteen in those of the plasmodium, showing that when the latter stage is reached the haploid nuclei have become diploid. As the plasmodium lives within rotting wood it is invisible till it comes to the surface to fructify. It then emerges in the form of transparent cushions of jelly. If such a cushion be placed on a glass slide and kept moist, the jelly is seen to be traversed by a dense network of protoplasmic veins in which rhythmic streaming of granules can be watched. The streaming was clearly observed when the shock of placing the specimen on glass had caused part of the plasmodium to gush out from the main cushion; the injured part recovered in half an hour and spread in a thin fan, in which a fine system of interlacing currents was seen; later the fan developed into a flat sporophore adhering to the glass, and formed healthy spores. Five successive stages in the development of the sporophore were distinguished by the Russian botanists, Woronin

and Famintzin, in their classic work on *Ceratiomyxa*.* (1) The *cushion* stage already described. From the cushions finger-like processes grow in (2) the *expansion* stage. In these the plasmodium forms at first a sponge-like network, but as they attain their full length the network concentrates on the surface and forms there an enveloping layer; this is (3) the *network* stage. The network divides up to form (4) a mosaic of cells, which completely covers the upper part of the gelatinous sporophore, and is more loosely distributed in the lower part; this *mosaic* stage soon passes into (5) the *spore-bearing* stage, when each cell pushes outwards and grows into a long-stalked spore. It is at the beginning of the network stage that Dr. Jahn discovered that all the nuclei of the plasmodium undergo a reduction division.† Preparations kindly lent to me by him show nuclei in all stages of mitosis in rather stout strands of protoplasm measuring 11–17 μ across (Pl. XI, fig. 6 *a–d*). When a little later the network has become closer and its strands more slender the daughter-nuclei have already separated. A certain number of the latter stain very darkly and degenerate, and are often to be seen in stainings of young spores lying beside the perfect nucleus (Pl. XI, fig. 6 *f*). It is probable that we see here “a process of elimination” (to use Professor Minchin’s words‡) “of effete or negative chromatin preceding the formation of the gametes

* M. S. Woronin and A. S. Famintzin (1873) “Ueber zwei neue Formen von Schleimpilzen.” Mém. de l’Acad. Imp. Petersburg, sér. 7, xx. p. 4.

† E. Jahn (1908), Myxomycetenstudien. 7. *Ceratiomyxa*. Ber. Deutsch. Bot. Ges., xxvi. d. p. 342.

‡ Minchin (1912), “An Introduction to Protozoology,” p. 142.

EXPLANATION OF PLATE XI.

Figs. 1–3.—*Physarum didermoides* (Ach.) Rost.

„ 4–5.—*Didymium squamulosum* (A. & S.) Fries.

Fig. 7. —*Ceratiomyxa fruticulosa* (Muell.) Macbr.

Fig. 1.—Swarm-cell: *a*, with resting nucleus; *b*, with dividing nucleus.

„ 2.—A zygote or young plasmodium, with a single nucleus undergoing mitotic division, and a digestive vacuole which contains the remains of a swarm-cell.

„ 3.—Young plasmodium, with two nuclei; *a* shows a digestive vacuole containing food.

„ 4.—Ditto, with three nuclei; a swarm-cell lies beside it.

„ 5.—Ditto, with five nuclei.

„ 6.—Strand of protoplasm from the *network* stage of the young sporophore, showing in *a*, resting nuclei; in *b*, *c*, nuclei dividing; in *d*, *e*, daughter-nuclei separated; *e* is from a late *network* stage; *f*, cells from *mosaic* stage. In *c*, *d*, *e*, *f*, darkly-staining degenerate nuclei are seen.

„ 7.—*a*, Ripe spore, with four nuclei; *b* to *e*, spore contents dividing; *f*, group of eight young swarm-cells just acquiring flagella; *g*, *h*, swarm-cells, with lengthening flagella.

All the figures on this plate are drawn from preparations made by Dr. E. Jahn; magnified 930 times.

or their nuclei." In the mosaic stage each cell contains a single nucleus which passes into the young spore, where it undergoes two mitotic divisions *; thus the four nuclei of the mature spore are produced.

We may briefly review the development of *Ceratiomyxa*, and compare it with one of the wood-inhabiting species of the Endosporeæ. In both the plasmodium emerges in the form of cushions of jelly to fructify in the open air. In both the nuclei undergo a reduction division before spore-formation. By a stretch of imagination, the sporophore in the mosaic stage might be regarded as a sporangium with an evanescent or undeveloped wall, and with a large gelatinous columella, over whose surface the spore-cells form only a single layer. But after this stage all attempts to make the two life-histories correspond fail. In the outgrowth of the spore-cells to form stalked spores *Ceratiomyxa* shows a unique arrangement; moreover, in these spores a remarkable process of what may be called precocious development occurs, by which each mature spore contains four nuclei, and these, on germination, at once divide again to take charge of the eight flagellulæ into which the spore-contents separate. In the Endosporeæ the increase of eight flagellulæ from one spore is arrived at leisurely and after repeated intervals of feeding. Thus although *Ceratiomyxa* is undoubtedly one of the true Mycetozoa, it holds a curiously solitary position, apart from all other species of the group.

In conclusion I wish to express my indebtedness to Dr. Jahn for his courtesy in lending me the preparations from which the drawings on Pl. XI were made. I have also to thank Mr. J. H. Mummery for allowing his beautiful photograph of *Ceratiomyxa* to be reproduced on Pl. X.

* These divisions are well illustrated by E. W. Olive (1907), "Cytological Studies in *Ceratiomyxa*," Trans. Wisc. Acad. Sci., xv. pl. xlvii. figs. 11-14.