SPECIAL ARTICLES

HETEROTHALLISM IN PUCCINIA TRITICINA[1]

CRAIGE[1, 2] discovered in 1927 that the spermatia (pycniospores) of the rust fungi are active functional spores which serve in some way to initiate the sporophyte generation of the rust. Since then other workers have proved by greenhouse investigations that these spores can be used in producing hybrids between physiologic forms of a rust, and a beginning has been made by cytological methods in learning how these spores function. C. F. Andrus, in a paper presented before the Botanical Society of America in December, 1930, reports the occurrence in the gametophyte generation of *Uromyces appendiculatus* (Pers.) Fries of trichogynous hyphae which "are much branched and highly septate organs having their terminus at the epidermis of the host leaf where they project through stomata or between epidermal cells and make contact with spermatia." Nuclei of spermatia enter these trichogynous hyphae and initiate the sporophyte generation.

Puccinia triticina Eriks., the leaf rust of wheat, has its aecial generation upon species of Thalictrum. The sporidium, formed by the germinating teliospore, in the spring, is a haploid spore, and when it falls upon a Thalictrum leaf it germinates, enters directly through the outer epidermal wall, and forms a 4- to 6-cell hypha in the epidermal cell, which in turn gives rise to haploid, intercellular mycelium.

After 6 or 7 days of vegetative growth reproductive activities set in. Spermogonia (pycnia) form at both surfaces of the leaf. A count of a hundred spermogonia in 11-day infections shows that 46 open upon the upper surface and 54 upon the lower.

At the same time that spermogonia are forming, hyphae near the lower surface of the leaf grow into stomatal apertures. A hypha in a stoma is short-lived, but successive hyphae present themselves at the same stoma. It is not uncommon to find 5 or 6 hyphae in the same stomatal aperture, only the last of which is living. In addition to this an occasional hypha at the upper epidermis forces a passageway between epidermal cells to the upper leaf surface. In older leaves this development at the upper epidermis is limited. In infections on young tender leaves it is more abundant. There may even be an extensive subepidermal growth of mycelium giving rise to groups of upright hyphae that push up to the surface. Hyphae reaching the lower or upper leaf surface through stomata or between epidermal cells are regarded as receptive hyphae.

In the substomatal air space, beneath a stoma occupied by one or more receptive hyphae, the hyphae grow and branch rapidly, forming a dense little nest of cells—the beginning of an aecium. If, as not infrequently happens, practically all the stomata in an infected area are occupied, there is not room for so many aecial primordia, and only a part of them develop. Over a large vein, where stomata do not occur, aecial primordia are absent.

Puccinia triticina is heterothallic. A monosporidial infection may bear both spermogonia and receptive hyphae, but, if kept isolated, it will remain sterile. Unless spermatia are brought to it from another and different infection, the aecia remain haploid and after the first differentiation into an upper area of small dense cells and a lower area of large empty cells, the whole aecium gradually degenerates and dies. With rare exceptions the sterile aecium consists of uninucleate cells from beginning to end.

A comparative study of a number of young infections of the same age shows that some have many spermogonia and few receptive hyphae; others have comparatively few spermogonia and more receptive hyphae; and a few have no spermogonia whatever and abundant receptive hyphae. The intermediates in this series are more numerous than the extremes, although some, at first classed as intermediates, have since been proved to be of multisporidial origin.

This is not just a temporary condition of young infections. In one sterile infection 42 days old there were 103 spermogonia and only 23 small sterile aecia. In another large sterile infection from the same lot of material there were over 200 sterile aecia and no spermogonia whatever. Moreover, in this latter, the average size of the aecium was much greater than in the spermogonial infection. The infections of *Puccinia triticina* can be arranged into a series with an almost exclusively spermogonial type at one end and a completely aecial type at the other.

Before fertilization, the receptive hyphae, like the haploid mycelium producing them, consist of uninucleate cells. When fertilization takes place, the receptive hyphae at the stomata are found crowded with nuclei. Two to 6 nuclei are common and as many as 11 nuclei in a cell have been seen. Growth from these cells permeates the aecium. The young fertile aecium grows vigorously and is composed of

[1] J. H. Craigie, "Experiments on Sex in Rust Fungi," *Nature*, 120: 116–117, 1927.

[2] J. H. Craigie, "Discovery of the Function of the Pycnia of the Rust Fungi," *Nature*, 120: 765–767, 1927.

a matrix of haploid cells interspersed throughout with cells containing 2 or more nuclei. The aecium becomes differentiated into a lower half of large vacuolated cells, which later die, and an upper half of smaller denser cells. In this upper area multinucleate cells are abundant. The number of nuclei varies, ranging in extreme cases to 15 or 20 per cell. With further growth and cell division the number of nuclei per cell decreases. From this mass cells grow down to form the sporogenous layer of "basal" cells. Young basal cells contain from 2 to 8 nuclei. The extra nuclei are used in forming the first spores and by the time the spore chains are well started the basal cells are regularly binucleate.

The question of the effectiveness of the receptive hyphae that grow to the upper surface of the leaf is still an open one. Aecia occur that open on the upper surface, but they are uncommon. Either fertilization of the upper receptive hyphae is rare, or those that are fertilized grow to the lower surface before developing further. So far this has not been observed.

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THE REDIA OF THE GASTEROSTOMES[1]

AN intermediate generation has been found in the life history cycle of the trematode order *Gasterostomata,* thereby bringing this form into line with normal life histories of other digenetic trematodes. The adult of this generation, the redia, is found in abundance in the lumen of the young mother-sporocysts. Young redia dissected from the mother-sporocysts are very active swimmers due to the covering of long cilia over the entire surface of the body. Older specimens indicate a loss of cilia followed by a coating of spines which are similar in character to the final adult. Two eyes are present. The redia is hermaphroditic. The testis is large, median in position with an extensible penis. In a live redia, mature active spermatozoa have been observed. The ovary is small, below the testis on the left side. Laurer's canal is long and apparently functions in cross-fertilization as a sperm-duct leading to the ovary. The vitelline complex in two lateral rows is very well developed. Eggs are shed through a short oviduct into the cavity of the mother-sporocyst and give rise to cercariae.

The origin of the redia was found to be in the gonads of the mother-sporocyst, and localized in the distal ends of the branches. The testis is large and situated below the tip of the branch previous to the expanded portion of the lumen. The ovary in the mother-sporocyst of *Bucephalus pusillum* appears in the form of "stroma." In *B. elegans* the ovary is located in a "plug" extending downwards into the lumen. This "plug" is composed of the ovary and nutritive glands, both in the form of "stroma" which, as development proceeds, extend for a considerable distance through the lumen even in older branches heavily packed with cercariae.

[1] Contribution from the Zoölogical Laboratory of the University of Michigan.

Spermatogenesis has been worked out in detail for all three generations; in the mother-sporocyst, redia and final adult.

It is therefore concluded that each of the three generations starts with a fertilized egg and gives rise to hermaphroditic "adults." Maturation with polar bodies and reduction is evident. There is no parthenogenesis or metagenesis. The life history of the trematodes as witnessed in this order is simple, with comparable embryological and larval stages in each of the three generations. The differences in the adults undoubtedly has evolutionary significance and is probably due to parasitism: first, within a mollusk; second, within the mother-sporocyst, and third, within the vertebrate.

Other species, not related to the gasterostomes are being studied by the author to find out how universal this method of reproduction is, among the class *Trematoda.* Material to be examined must be young before the reproductive stage is over and before the nutritive phase increases to confuse observation. Completely known life cycle material is preferable. Differential staining is advisable.

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VARIATIONS IN THE EVENING PRIMROSE INDUCED BY RADIUM

GENETICISTS are now aware that x-rays and radium are agents by which genetic changes, both genic and chromosomal, may be produced. However, in the several years since 1927, in which many investigators have published on the genetic effects of irradiation on both plants and animals, nothing, in so far as I am aware, has appeared dealing with the irradiation of the evening primrose. For the past three years the writer has been making such an investigation, using radon (radium emanation) in the treatment of *Oenothera Lamarckiana* and *Oe. franciscana,* a preliminary account of which appears here.

The method of treatment was to insert an unfiltered tube of radon parallel with the buds in a flowering cluster, thus treating buds in all stages of development at distances varying from direct contact to 4 cm. As the flowers opened after treatment they were