

investigate the plants before flowering, but it is not believed that the differences found are due entirely to the fact that the females are changed in nutritive condition by the production of fruit. The production of embryos can have no relation, however, to the parallel results obtained with the *Mucors* in which sexual reproduction was prevented in the plants investigated.

The data presented we believe show more or less striking average differences in green plants between the sexes in respect to the Manoilov reaction, the color of leaf extracts, the presence of oxigenase, peroxigenase and total acidity.

Further parallel tests may give us a more complete biochemical picture of cell products and cell processes and enable us to distinguish those primarily associated with male and female protoplasm from individual non-sexual peculiarities.

¹ Part of paper presented before the Physiol. Sect. of the Bot. Soc. of America, Dec. 31, 1925. The investigation was carried on under a grant from the Committee of the National Research Council for Research on Sex Problems to whom the authors gratefully acknowledge their indebtedness.

² Minenkov A., *Naouc. Agr. Journ. (Moscow)*, **1**, 29-47 (1924).

³ Schreiner O., and Sullivan M., *Science*, **31**, 310-311 (1916).

⁴ Manoilov, E., *Münch. Med. Wochenschr.*, **51**, 1784-1789 (1924).

⁵ The apparent equality of this species in respect to the Manoilov reaction is probably due to the fact that, in this as in other species listed in table 3, those individuals were included which were earlier listed as reversals in table 2.

THE *MUCOR* PARASITE *PARASITELLA* IN RELATION TO SEX¹

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STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR, N. Y.

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Parasitella simplex is a member of the group of fungi known as *Mucors*. It is commonly parasitic on other *Mucors* although it may be grown as a saprophyte. As a parasite it produces galls, which, when mature, resemble zygospores with curious outgrowths. The early stages are like those in conjugation or in the reaction known as imperfect hybridization.

It was from the resemblance of gall formation to conjugation and from the apparent sex-limited relation between *Parasitella* and host, discovered in the course of his brilliant investigations of sex and parasitism among *Mucors*, that Burgeff² was led to believe that parasitism had developed by way of an imperfect sexual reaction. Lacking a true imperfect hybridization between the sexual races of *Parasitella* and known (+) and (-) races of other *Mucors*, there was no method of knowing which sex of the

parasite was (+) and which (-). The terms (+) and (-), it may be mentioned, have been used to designate the opposite sexes in *Mucors* in which morphological differences between the two sexes did not allow the use of the terms male and female. With certain species, like *Rhizopus*, Burgeff found that both sexes of *Parasitella* formed galls with both sexes of the host. With *Absidia glauca* and *A. caerulea*, however, what he was led to call the (+) race of *Parasitella* formed galls only with the (-) sex of the host and what he called the (-) race of *Parasitella* formed them only with the (+) sex.

Our problem was to test this hypothesis of Burgeff and to discover reliable methods, if possible, of determining which sex of *Parasitella* is (+) and which (-). For convenience of discussion we may use the terms (+) and (-) for the same sexes of *Parasitella* that apparently were so designated by Burgeff. We can confirm in the main the curious cytological behavior in gall formation which he found. Without going into details, we may say that the cell content of host and parasite become mixed in the formation of a gall cell with basal outgrowths which is subtended by a thick-walled storage cell. Burgeff found no open connection in his material between the gall and the storage cell, but in our material we find stages which indicate that the intervening wall becomes dissolved and that nuclei enter the storage cell from the gall. When grown on certain *Mucors* as hosts, *Parasitella* forms only imperfect galls in which there is no mixture of cell contents of host and parasite nor development of storage cells nor of outgrowths.

Our investigations have to do with 4 races of *Parasitella*, 3 which for convenience of discussion we will call (-) and one (+). Morphologically they are similar, though differing somewhat in heights of growth. Contrary to the experience of other investigators, we find that when grown together saprophytically, the opposite sexes of *Parasitella* form numerous zygospores and also a certain number of perfect galls. We have found formation of perfect galls to take place in certain combinations between races of *Parasitella* belonging to the same sex, when no other *Mucors* were present. This, we believe, is a matter of some significance, although the galls were small and not numerous.

Each race of *Parasitella* was contrasted with 54 *Mucor* races (in 9 genera and 17 species). These selected host *Mucors* belong to both homothallic and heterothallic forms. The latter contained neutral races and weakest as well as strongest (+) and (-) races.

Table 1 shows the results of contrasts with 8 *Mucor* species of high sexual strength. In this and the other tables, perfect reactions are shown by capital letters—formation of imperfect galls by small letters. The strengths of reaction are indicated by the grades A to D. As may be seen, there is no difference in the kind of reaction in regard to the sexes of the parasite and

hose. Parasitella I, II and III, belonging to one sex, and Parasitella IV to the opposite sex, all give an A reaction with 3 pairs of races, imperfect galls with 3 other races—with a single exception which was a "0" and no reaction with 2 pairs, irrespective of the sex. A slight difference can be noted only in strengths of the imperfect reaction.

TABLE 1
GALL FORMATION BETWEEN OPPOSITE SEXES OF PARASITELLA AND (+) AND (-) SEXES OF OTHER MUCORS (HELICOSTYLUM, CIRCINELLA SPINOSA, ABSIDIA REPENS, SYNCEPHALASTRUM, MUCOR MUCEDO, MUCOR V, RHIZOPUS NIGRICANS, CHAETOCLADIUM BREFELDII⁶)

(+) RACES								PARASITELLA								(-) RACES								
HELIC.	C. SPN.	A. REP.	SYNC.	M. MUC.	M. V.	RHIZ.	CHAET.	(-) ? RACES								CHAET.	RHIZ.	M. V.	M. MUC.	A. REP.	HELIC.	C. SPN.	SYNC.	
0	0	0	0	0	A	A	A	P. I								A	A	A	0	0	0	0	0	0
0	0	c	b	a	.	.	.	P. II								.	.	.	a	c	d	0	0	0
0	0	0	0	0	A	A	A	P. III								A	A	A	0	0	0	0	0	0
0	0	c	b	a	.	.	.	(+) ? RACE								.	.	.	a	d	0	0	0	0
0	0	0	0	0	A	A	A	P. IV								A	A	A	0	0	0	0	0	0
0	0	d	b	a	a	b	b	0	0	0

There also was no difference in the kind of reaction in regard to the sexual races of Parasitella, when contrasts were made with 2 homothallic species and 5 neutral races³ not shown in the table.

Particular attention was given to the contrasts with Absidia glauca and A. caerulea, the 2 species which, according to Burgeff's observations, have a sex-limited relation in regard to parasites. In all, 30 races were used, 21 races of A. caerulea and 9 races of A. glauca. Table 2 shows that

TABLE 2
GALL FORMATION BETWEEN OPPOSITE SEXES OF PARASITELLA AND (+) AND (-) SEXES OF ABSIDIA CAERULEA. (PERFECT REACTIONS SHOWN BY CAPITAL LETTERS, IMPERFECT REACTIONS BY SMALL LETTERS)

ABSIDIA CAERULEA								PARASITELLA								ABSIDIA CAERULEA												
NEUTRAL RACES				(+) RACES				(-) ? RACES								(-) RACES												
437	443	440	441	436	911	913	536	537									442	914	535	434	532	533	534	445	435	444	531	439
0	0	0	0	0	0	0	0	A	P. I								0	0	0	0	0	0	0	0	0	0	0	0
0	d	0	c	b	b	b	a	.	P. II								b	c	d	c	d	b	0	d	0	0	d	c
0	0	0	0	0	0	0	0	A	P. III								D	0	0	0	0	0	0	0	0	0	0	0
0	d	c	c	b	b	a	a	.	P. IV								b	b	c	b	c	b	c	d	c	c	c	c
0	0	0	0	0	0	0	0	A									0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	c	d	a	.									0	d	0	0	0	0	0	d	0	0	0	c
0	0	0	0	0	0	0	0	0									B	B	D	0	0	0	0	0	0	0	0	0
d	d	c	b	c	d	c	0	d									.	.	a	a	a	a	a	b	b	b	b	c

Parasitella IV (a (+) race by Burgeff's test) has a certain tendency to react more with the (-) races of *A. caerulea*; and the (-) race of Parasitella I, II and III—more with the (+) races of *A. caerulea*. This tendency is not an absolute one, since, out of the 4 Absidia (+) races, it is only one which develops perfect galls with the 3 (-) Parasitellas, and out of the 12 (-) races of the Absidia, only 3 which form galls with the (+) Parasitella. Moreover, one of these 3 (-) races (442) develops galls with Parasitella II, also a (-) by assumption.

If we consider the imperfect gall formation, the table shows that it is only the (-) Parasitella III which shows in fact any definite tendency not to react with the (-) races of Absidia and which fails entirely to react with the neutral races of this species. Furthermore, the other (+) and (-) races of Parasitella develop imperfect galls with nearly all the 21 Absidias, whether the latter are (+), (-) or neutral.

Table 3 shows the result of contrasts with Absidia glauca. It may be seen that the tendency of the (+) Parasitella IV to react preferentially with the (-) races of Absidia appears even weaker than in the previous case. The (+) Parasitella IV forms galls with 3 races only out of the 5 (-) Absidias while the same race of the parasite develops perfect galls with 2 (+) races of Absidia. A similar condition will be noted concerning the (-) Parasitellas I and II. They show a certain tendency toward preferential reaction with the (+) Absidia races, although they do not develop galls with one of them (915), and do form galls with a race of the same (-) sex (669).

TABLE 3
GALL FORMATION BETWEEN OPPOSITE SEXES OF PARASITELLA AND (+) AND (-) RACES OF ABSIDIA GLAUCA. (PERFECT REACTIONS SHOWN BY CAPITAL LETTERS, IMPERFECT REACTIONS BY SMALL LETTERS)

	ABSIDIA GLAUCA (+) RACES			PARASITELLA (-) ? RACES	ABSIDIA GLAUCA (-) RACES				
	915	917	667		668	669	666	919	918
0	B	B	B	P. I	C	0	0	0	0
b	d	0	0	0
0	B	B	B	P. II	B	0	0	0	0
b	d	0	0	0
0	B	C	B	P. III	0	0	0	0	0
c	.	.	.		0	d	0	0	0
				(+) ? RACE					
0	0	C	C	P. IV	B	B	B	0	0
c	0	b	c

If we consider the total reactions with the 2 species of Absidia, there are 2 facts which appear of significance: (1) the lack of gall reactions between races of Parasitella and the majority of the races of the sex toward which the parasite shows a certain tendency—in other words, between (+)

Parasitella and (−) Absidia and vice versa; (2) the definite gall reaction between races of Parasitella and races of the same sex of the Absidias.

Burgeff based his conclusions upon a single pair of races each of Parasitella and of the 2 Absidia species. The results we have obtained, however, with a larger number of races of Parasitella and of Absidia, emphasize the necessity of basing conclusions in regard to the relation between host and parasite upon a large number of individual races. The fact that gall formation can take place between both sexes of Parasitella and selected races of both sexes of the Absidias and the fact that gall formation fails to take place between both sexes of Parasitella and certain (+) and (−) races of Absidias, added to the fact that gall formation does occur between races of the same and opposite sexes of Parasitella, indicate that one is not dealing with a truly sex-limited relation between parasite and host.

It cannot be denied, however, that a tendency does actually seem to exist for one sex of the parasite to react preferentially with a single sex of the host in the two species of Absidia. The significance of this evident tendency cannot as yet be explained, although it may conceivably be related to predominant biochemical differences between the sexes, which we have demonstrated in other Mucors.⁴ We applied to the Mucors some of the tests which we had used with male and female higher plants (cf. preceding papers, these PROCEEDINGS). It is interesting to note that the (+) Mucor races correspond in biochemical behavior to the females of higher plants and the (−) Mucor races correspond to males. It is perhaps significant that Parasitella IV, which showed a preferential tendency to form galls with (−) Absidias and should be ranked according to Burgeff with the (+) races, gave the characteristic female reactions with the tests used with this race, while the Parasitellas I, II and III, which according to Burgeff should be called (−), correspond in biochemical behavior to male plants.

From their biochemical behavior, therefore, with the possible additional evidence from gall reactions, which are doubtless biochemical in nature, we may provisionally assign the terms (+) and (−) to the sexual races of Parasitella.

¹ Paper presented before the Mycological Section of the Botanical Society of America, December 31, 1925. The experimental part of the work on gall reactions was completed in 1923. The biochemical tests with Parasitella cited from a previous paper in these PROCEEDINGS were made while working under a grant from the Committee of the National Research Council for Research on Sex Problems.

² Burgeff, H., *Botan. Abhandl.*, 4, 1-135 (1924).

³ Homothallic species: *Zygorhynchus heterogamus*, *Mucor genevensis* (2 races). Heterothallic species: *Mucor spinosus*, *M. Rouxianus*, *Mucor* sp., *Pilaira*, *Mortierella* sp.

⁴ Satina, S., and Blakeslee, A. F., these PROCEEDINGS, 11, 528-534 (1925).

⁵ We have not yet determined the sex of the races of *Chaetocladium* by imperfect reactions but the gall formation with Parasitella is the same for each sex. When either

sex of *Chaetocladium* was grown with either sex of *Parasitella*, both species acted as host to the other parasite and galls were produced characteristic of both *Parasitella* and *Chaetocladium*. The parasitic behavior of *Chaetocladium* has been described in detail by Burgeff.²

THE PHYSIOLOGICAL PRINCIPLE OF MINIMUM WORK. I.
THE VASCULAR SYSTEM AND THE COST OF BLOOD VOLUME

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Introduction.—Physiological organization, like gravitation, is a “stubborn fact,” and it is one task of theoretical physiology to find quantitative laws which describe organization in its various aspects. Just as the laws of thermodynamics were known before the kinetic theory of gases was developed, so it is not impossible that some quantitative generalizations may be arrived at in physiology which are independent of the discrete mechanisms in living things, but which apply to organic systems considered statistically. One such generalization is the principle of the maintenance of steady states—a principle which furnishes definite equations (of the type indicating equality of intake and output of elementary substances) applicable to the hypothetical normal individual. The purpose of these studies is to discuss the possible application of a second principle, the principle of minimum work, to problems concerning the operation of physiological systems.

The concept of adaptation has been treated in a quantitative manner by experimental morphologists, students of growth and form, who have shown again and again the tendency toward perfect fitness between structure and function in all sorts of plants and animals. Only rarely, however, has the concept of fitness been used as a *premise* for physiological deductions. The beginnings of theoretical or deductive physiology are to be found in the works of Galileo¹ and of Borelli,² who argued from the principle of similitude, as others have done since. Thompson’s fascinating book³ contains a wealth of material on this subject. Henderson’s classic essay⁴ covers the history of the teleological problem, and presents his own proof that the teleological aspect of nature (until Darwin’s time associated with the minutiae of biological adaptations, and in the latter part of the last century associated with primitive theological doctrine) has its real roots in the properties of matter and in the laws of physics and chemistry. Thus it may be seen that organization is a legitimate field for scientific inquiry and not an “affair of the reflective judgment.”