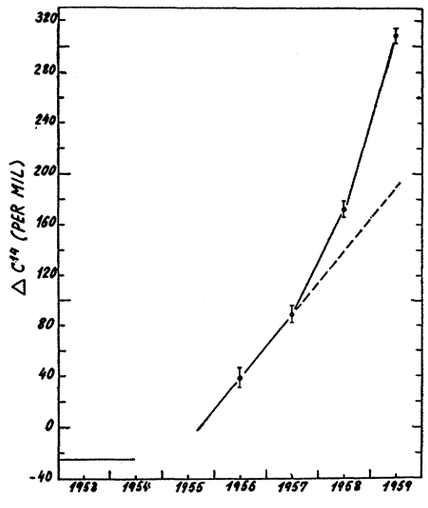

Fig. 1. Rise in C^{14} activity in Danish cereals. The dotted line agrees closely with the rise found by Broecker and Walton (*4*).

United States, at about 40°N, and from North Atlantic air at 25° to 34°N. Their results undoubtedly are more representative for the Northern Hemisphere than those in this study. Although some additional increase above that predicted by them was to have been expected for 1959, it seems almost impossible that the average activity for the hemisphere could have risen to the values measured in Denmark. This would require that the total admixture of C^{14} to the northern troposphere should have been more than three times as great in 1959 as in 1958. In Denmark the ratio was only 1.6.

The high values for tropospheric C^{14} levels in Denmark in the summers of 1958 and 1959 most probably stem from the large increase in high-yield nuclear detonations during 1957 and 1958 in northern latitudes and in areas not far from Scandinavia. Almost all bomb-generated C^{14} is injected into the stratosphere; the high C^{14} values are in keeping with the findings that stratospheric debris released in northern latitudes (where the U.S.S.R. testing grounds are located) is brought down more rapidly than fallout injected into the stratosphere in the tropics (*9*). Hence, the reported levels of C^{14} in Denmark, all of which are summer values, may constitute an equivalent, for C^{14}, to the spring peaks for Sr^{90} fallout found during the same years in northern latitudes (*9*, *10*).

Table 1. Carbon-14 content of Danish cereals.

Year	Sample No. (Copenhagen)	Material	ΔC^{14}
1956	K-612	Barley, ears (Frederiksdal)	39 ± 8
1957	K-611	Barley, ears (Sorgenfri)	89 ± 7
1958	K-613	Wheat, grains (Virum)	172 ± 7
1959	K-610	Rye, ears (Frederiksdal)	308 ± 7
1959	K-614	Oats, straw (Naerum)	308 ± 9
1959	K-615	Rye, ears (Vedbaek)	309 ± 9

For lack of more geographically spaced samples, it is not possible to decide whether the higher C^{14} concentrations in Denmark, as compared to the measurements by Broecker and Walton, are due to latitudinal variations or to different distances from the test sites. However, particulate fallout and CO_2 are brought down from the stratosphere by the same circulation mechanism; the strong latitudinal dependence for fallout, which is presumably caused by a selective downward mixing from the stratosphere in middle latitudes via the gap in the tropopause (*11*, *12*), therefore suggests that similar variations occur for bomb-produced C^{14} in CO_2.

Stratospheric CO_2 which descends to the troposphere is not washed down with the rain, like particulate fallout, but is mixed throughout the hemisphere, with a mixing time of the order of 1 month. By this mixing, the stratospheric CO_2 is rapidly diluted with less active CO_2, and a general rise in C^{14} level is produced. Only additional increase above this level is discernible as latitudinal variation. If the downward mixing from the stratosphere continues at nearly the same latitudes, and at an approximately constant rate throughout the year, a more or less permanent latitudinal gradient in C^{14} concentration will be established. If the mixing from the stratosphere shows seasonal variations (*11*, *13*), the gradient will grow up in the periods of descent and vanish again at other times. In the case of such seasonal variations, plant material will only exhibit latitudinal variations if the periods of descent coincide with periods of assimilation. Further, in certain areas latitudinal variations may be masked by local Suess effects, the two effects being of comparable size and of opposite direction. More measurements of the C^{14} variations in tropospheric CO_2 from latitudinally spaced locations may provide further information on the mechanism of the stratosphere-troposphere exchange processes.

If C^{14} from cosmic rays likewise comes down from the stratosphere dominantly in the North and South Temperate zones, slight latitudinal differences in natural radiocarbon activities may be present. The size of such an effect will depend on the circulation pattern in the stratosphere, which is not well understood at the moment. The effect will be more marked if the transport from stratosphere to troposphere shows definite seasonal variations, so that most C^{14} comes down in the springtime, when the rate of assimilation is highest. However, with changing climates the latitudes of dominant descent of stratospheric carbon dioxide, and consequently the zones of the highest C^{14} concentrations, may have varied in the past.

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23 November 1959

Heterocaryotic Nature of Ring Formation in the Predaceous Fungus Dactylella doedycoides

Abstract. Morphologically indistinguishable conidia of the predaceous nematode-attacking hyphomycete *Dactylella doedycoides* Drechsler vary in their ability to produce constricting rings, depending upon their heterocaryotic state. Three types are noted: those producing rings with or without stimulation, those never producing rings, and a mixed or wild type, made up of a mixture of the first two types.

The genetic mechanisms controlling constricting ring formation in the nematode-attacking predaceous fungi are poorly understood. In the present work information concerning these mechanisms was obtained by studying ring formation in single conidial isolates derived from a monoconidial culture of *Dactylella doedycoides* Drechsler (*1*) found in garden soil in Teddington, Middlesex, England.

The initial monoconidial culture was isolated and multiplied on Difco corn meal agar at room temperature. The fungus grew readily on this medium, forming profuse numbers of erect coni-

diophores, each bearing a single terminal conidium and an occasional subterminally borne conidium. Single conidia were readily removed from the cultures with a solid glass rod with a finely drawn tip (*2*). Conidia were transferred singly to the upper surface of small corn meal agar cylinders 6.0 mm in diameter and of uniform depth. These cylinders were arranged in rows inside the top cover of a large, inverted, plastic cheese dish. A piece of filter paper moistened with sterile water was forced into the dish bottom, and the dish was closed bottom side up. Such cultures could be kept moist and free of contamination for about 5 weeks, which was long enough to provide the necessary data.

Spores planted on the agar cylinders germinated, usually after 2 or 3 days, and their subsequent development was observed under the microscope at frequent intervals for about 3 weeks. Observations made within a week after spore germination indicated that certain spores derived from the original wild-type culture spontaneously produced constricting rings (that is, rings with no nematodes or other exogenous stimulant present) while other spores did not spontaneously produce rings. Observations continued over 3 weeks showed that, in the germlings that produced rings spontaneously, only 3 to 12 spontaneous rings were produced per spore, and then ring production ceased. In the non-ring-producing germlings no rings appeared, even after 5 weeks. Observations made on a large number of spores indicated that about 30 percent of the spores from the wild type spontaneously produced rings (Table 1, *a*). Hereafter, spores spontaneously producing rings are designated A, those producing no spontaneous rings B, and the original wild type A/B. Single conidia were taken from mycelia derived from A- and B-type spores and tested for spontaneous ring formation. In Table 1, parts *b* and *c* show that 83 percent of the spores descended from the A type spontaneously produced rings while 13 percent of those spores derived from the B type spontaneously produced rings.

It was commonly supposed that hyphal strands of a ring-forming predaceous fungus were uniformly capable of being stimulated to form constricting rings, given an appropriate stimulus (*3*). It seemed advisable to test the validity of this supposition in view of the unsuspected apparent heterogeneity in spore populations derived from a single conidium.

Saprophytic nematodes of the genera *Panagrellus* and *Rhabditis,* reared according to the method of Taylor *et al.* (*4*), were found to stimulate ring structure formation in *Dactylella doedycoides* after they had been air-dried until dead and then rehydrated in a small drop of water. Single adult female nematodes, killed in this fashion, were rehydrated in a small drop of sterile distilled water, picked out of the water by a nylon bristle, and deposited in the center of the agar cylinders upon which the conidia were germinating. The fungus was stimulated to form rings within 3 to 5 days after the dead nematode was placed on the cylinder.

Table 1. Summary of spontaneous ring formation in single-spore culture from strain A/B.

Generation and type	Cultures (No.)	Ring formation		No ring formation	
		No.	%	No.	%
a. Parent (wild type), A/B	183	45	25	138	75
	58	25	43	33	57
	36	5	14	31	86
	21	1	4	20	96
	67	26	39	41	61
Total	365	102		263	
Mean			28		72
b. Progeny of A	75	68	80	7	20
	25	15	60	10	40
Total	100	83		17	
Mean			83		17
c. Progeny of B or A/B	82	16	20	66	80
	59	3	5	56	95
Total	141	19		122	
Mean			13		87
d. Progeny of (A + B)	60	15	25	45	75
	83	9	11	74	89
Total	143	24		119	
Mean			17		83

The effect of adding ring stimulatory material to the various types of spores was then studied by this technique. Sixty percent of the A/B type spores produced rings after stimulation. Eighty-seven percent of the A type spores produced rings after stimulation while only 30 percent of the B type spores produced rings after stimulation (Table 2, *a*, *b*, and *c*). Thus it became quite clear that, even though stimulation did cause an increase in the percentage of ring production by all three spore types, spore populations were not homogenous for this character, and in reality three types of conidia exist side by side in nature but are readily separable by simple laboratory procedures.

Single spore cultures of A and B spores were grown together on the same plates. After the mycelium had mingled long enough for possible hypal fusions to take place, single spores were taken from the mutual margin of the two cultures and tested for ring-producing ability. These spores were found to exhibit the three types of ring producing potential originally observed—that is, the wild A/B type was produced and also the A and B types (Table 1, *d*).

Thus it would appear that among conidia of *D. doedycoides* a wild type designated A/B is present. From the individual conidia of this type three types of ring-producing potential can be observed: the A type which produces constricting rings spontaneously and always produces more rings upon stimulation with nematodes; type B which never produces constricting rings spontaneously and does not produce rings upon stimulation with nematodes; and type A/B which is a mixture of A and

Table 2. Summary of ring formation after stimulation in single-spore cultures from strain A/B.

Generation and type	Cultures (No.)	Ring formation		No ring formation	
		No.	%	No.	%
a. Parent (wild type) A/B	30	20	67	10	33
	24	18	75	6	25
	33	14	42	19	58
Total	87	52		35	
Mean			60		40
b. Progeny of A	39	34	87	5	13
Total	39	34		5	
Mean			87		13
c. Progeny of B or A/B	50	18	36	32	64
	56	14	25	42	75
Total	106	32		74	
Mean			30		70

B and produces some rings spontaneously. The conidia of these three types are morphologically indistinguishable and can only be separated according to their ability to form rings spontaneously. Thus a certain percentage of apparently B type conidia are actually A/B type conidia which will produce both A and B type responses when germinated.

These data indicate that the genetic control of ring formation in the predaceous hyphomycete *Dactylella doedycoides* Drechsler is a heterocaryotic phenomenon. The ability of this fungus to produce constricting rings in the presence of free-living nematodes may be quite variable because of the nuclear heterogeneity indicated by the data presented here. These data explain many of the anomalous observations which have been recorded in the literature concerning ring formation in the predaceous nematode-trapping hyphomycetes (*5*).

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10 November 1959

Sexuality and Mating in Salmonella

Abstract. Another criterion for the presence of the agent (F) promoting genetic exchange in *Escherichia coli* was found. It involves a staining reaction of Hfr and F+ coli, but not F– coli, when mixed with strains of *Salmonella typhimurium*. This reaction was used as a guide in following the transfer of the F agent to *Salmonella* and back to *E. coli*. The F agent in *Salmonella* seems to promote the same kinds of events that it promotes in *E. coli*.

The mating type system in the bacteria *Escherichia coli* has been shown to be under the control of an agent called F (*1, 2*). Those bacterial strains that lack F act as recipients for genetic material, while strains that have F act as donors of genetic material. It has been concluded from the work of Wollman and Jacob (*3*) that the genetic material of the donor passes into recipient bacteria in a linear fashion. There is no evidence for the reciprocal transfer of genetic material from recipient bacteria to donor bacteria (*4, 5*).

The F agent can exist in at least two states in donor strains. One state confers upon donor bacteria the ability to pass the F agent to recipients at high frequency, but the chromosome at low frequency (F+ bacteria). The other confers the ability to donor bacteria of passing their chromosome (or part) at high frequency, while the F agent is transferred at low frequency (Hfr bacteria). The transmission of the F agent in the former case results in an F+ bacterium, while in the latter it results in an Hfr bacterium. It has therefore been inferred that the difference between these two kinds of bacteria depends upon the localization of the F agent: F+ bacteria have the agent in a free state, while Hfr bacteria have the agent at a particular one of a number of possible chromosomal sites. It has also been inferred that all effective transfers of genetic material from F+ to F– bacteria involve either a transient or permanent fixation of the F agent to the chromosome (*6*).

One other bacterial property might be ascribed to the F agent. Since, for an effective mating, the two mating types must make a sufficient cell-by-cell bridge, some differences in the surface properties might be expected. Differences in the staining and agglutinating properties have been observed (*7*). Thus, it would seem that F– bacteria change their surface when "infected" with the F agent. In this respect the action is analogous to that produced by some temperate bacteriophages, a process called lysogenic conversion (*8, 9*). Loeb (*10*) reports a bacteriophage which will differentiate F+ and Hfr bacteria from F– bacteria.

Baron *et al.* (*11*) and Miyake and Demerec (*12*) have shown that some strains of salmonella will act as recipients for genetic material from Hfr coli. Since Zinder and Lederberg (*13*) tested many of these same salmonella strains for mating *inter se* and failed to find any evidence for this, it might be assumed that salmonella is, as is the average coli, F–. Therefore, if the F agent could be transferred to salmonella, they too might mate. This report describes the successful transfer of the F agent to salmonella and the properties of the resulting F+ organisms.

The preparation of mutant lines of bacteria was accomplished as described by Lederberg (*14*). The abbreviations used to describe the genotypes are as follows. The fermentation mutants are designated "lac" for lactose, "gal" for galactose, "arab" for arabinose, "mal" for maltose, and "mtl" for mannitol.

Drug resistance mutations are as Az^r for resistance to sodium azide. Auxotrophic mutations and notations used are "meth" for methionine, "pro" for proline, "thr" for threonine, "leu" for leucine, "try" for tryptophan, and "his" for histidine.

The derivatives of *E. coli* K-12 that were employed were Hfr (Cavalli) (*1*) of genotype meth–; Hfr (Hayes) (*15*) of genotype meth– Az^r; F+ and F– with genotypes for both of meth– and thr–, leu–, lac–, gal–.

The salmonella strains were all derivatives of *S. typhimurium* LT2 (*13*). Their genotypes are described in the text.

The special media for the study of bacterial genetic processes were the same as those described by Lederberg (*14*). Of special use in this study was eosin methylene blue agar without any sugar supplementation (EMB 0).

In *E. coli* F– organisms become F+ during mixed culture with F+ organisms. This can be demonstrated by reisolating the orginally F– organisms on the basis of some differentiating marker and testing their mating behavior. Since coli are lactose fermenters and salmonella are nonfermenters, the reisolation of the salmonella type after mixed culture with coli is readily accomplished. However, the recognition of any transfers of the F agent is more difficult. It would involve the testing of a large number of independent isolates either for ability to transfer back to *E. coli* F–, the F agent, or for mating with other salmonella strains. Both of these are contingent properties, in that F might be transferred to salmonella with very low frequency and similarly have a low, if existent, frequency of back transfer, or that it might not, in salmonella, confer mating ability. Of some use in this and other problems would be some other criterion for the F state of bacteria.

In the course of some experiments, it was noted that when an F+ or an Hfr coli was cross-streaked with LT2, or some other salmonella, on EMB 0, there would be a straining of the bacteria in the area of their intersection: a red spot. Such reddenings are characteristic of the cross-streaks of lysogenic and nonlysogenic bacteria. The lysis of the nonlysogenic bacteria after attack by the phage released from the lysogenic bacteria releases some acid, thereby lowering the *p*H and allowing eosin to stain. Eosin stains bacteria at *p*H below 5.5 and hence is used in the EMB medium to determine fermentative responses. However, no evidence for any propagable entity such as phage was found.

An effort was made to correlate in detail the staining reaction and the F status of the coli. An F+ and an F– coli were grown in mixed culture, and on the basis of some independent marker, such as lactose fermentation,