Fields, W. G. An introduction to the genus Sordaria.

The genus Sordaria is closely related to Neurospora and Podospora. Of the several known species, three hove been the principal subjects in genetic studier. There include two homothallic species, S. fimicola and S. macrospora, and one heterothallic species, S. brevicollis. The natural habitat of all three species is dung of herbivorous animals. The homothallic species are common&d worldwide in distribution; S. brevicollir is less common but widely distributed. The specie of Sordoria ore similar morphologically, producing black perithecia containing asci with eight dork ascospores in a linear arrangement. Ascospore size and shape ore important taxonomic criteria for distinguishing species, although there is considerable variation within species. Ascospores of S. fimicolo ore about 12 x 20μ; those of S. macrospora are about 17 x 31μ. Ascospores of S. brevicollir are about 10 x 18μ, but the species is easily distinguished since it is heterothallic.

Life cycles and genetic peculiarities. Both S. fimicola and S. macrospora produce self-fertile thalli. That is, a culture derived from a single homokaryotic ascospore is capable of completing the life cycle. Unlike N. crassa, there is no homogenic incompatibility. Even though single spore cultures ore self-fertile, they may be crossed. For example, when two cultures of 2. macrospora ore paired in a petri dish, each mycelium will give rise to perithecio and homokaryotic asci. However, in the region where the two mycelia meet, heterokaryosis may occur, with the result that perithecio containing heterozygous asci are produced. A suitable marker (e.g., an ascospore color mutant) is usually employed to detect such crossed perithecia which may then be used in formal genetic studier. Similar crossing occurs between paired cultures of S. fimicolo. Not all such pairings ore successful. There is some evidence suggesting that a h&erogenic incompatibility mechanism operates in both species.

Another important aspect of the life cycles of these two homothallic species is that no macroconidia ore formed. The life cycle of S. brevicollir is essentially like that of N. crassa except that no macroconidia are formed. Microconidio ore produced, functioning as mole gametes in sexual reproduction. Germination of microconidio may occur, but is very poor. The mating behavior is controlled by a bipolar incompatibility system like that of N. crassa with the two mating types designated A and a. S. brevicollir displays one genetic feature not often seen in Neurospora. In the second meiotic division the spindles are partially overlapped, resulting in on excess of asymmetrical second-division asci. The degree to which this occurs varies from 0 to 78%. Second-division asci of the symmetrical type are unaffected by this phenomenon.

Details of the life cycle, cytology and formal genetics may be found in the following papers: S. fimicola - Olive, L. S. 1956 Am. J. Botany 43: 97, Carr, A. J. H. and L. S. Olive 1958 Am. J. Botany 45: 142, El-ani, A. S., L. S. Olive and Y. Kitani 1961 Am. J. Botany 48: 716. S. brevicollir - Olive, L. S. and A. A. Fantini 1961 Am. J. Botany 48: 124, Chen, K. S. 1965 Genetics 51: 509, Chen, K. S. and L. S. Olive 1965 Genetics 51: 761. S. macrospora - Heslot, H. 1958 Rev. Cytol. Biol. Veg. 19 (Suppl.): 1, Esser, K. and J. Straub 1958 Z. Vererbungsl. 89: 729, Esser, K. and R. Kuenen 1967 Genetics of Fungi, Springer, New York.

Cultural methods and techniques. The species of Sordoria grow and reproduce easily on many kinds of agar. Routine solid media for cultivation and crossing ore as follows:

S. fimicolo: (1) Difco corn meal agar 17 g., glucose 2 g., yeast extract 1 g., 1 liter water.
(2) Difco corn meal agar 17 g., glucose 7 g., sucrose IO g., yeast extract 1 g., KH_2PO_4 0. 1 g., 1 liter water.

S. macrospora: Corn meal extract 1 liter, malt extract 1.5 g., agar 20 g. Commercial corn meal agar may be used

S. brevicollir: Difco corn meal agar 17 g., glucose 2 g., sucrose 3 g., yeast extract 1 g., 1 liter water.

Spore germination medium: consists of crossing media supplemented with 0.7% sodium acetate. Ammonium acetate or potassium acetate may also be used.

Dissecting agar medium: Difco corn meal agar 4 g., Difco Bocto agar 30 g., sodium acetate 7 g., 1 liter water. This medium is used for ascus dissections by hand or with a micromanipulator.

Mature spores of Sordoria may be germinated immediately. Almost complete germination is obtained with any medium, solid or liquid, supplemented with acetate. Some of the ascospore color mutants do not require acetate for germination. Spore germination begins about 4-5 hrs. after inoculation at 23-25°C. Cultures of S. fimicola and S. brevicollis are cultivated at 23-25°C. with completion of the life cycle in 7-9 days for S. fimicola and 9-12 days for S. brevicollir. S. macrospora is cultivated at 26-27°C, with completion of the life cycle in 7-9 days.

Crosses of S. fimicola and S. macrospora are made by confrontation of mycelia. Inocula ore often placed close to one another, a technique which g&rally increases the number of crossed perithecia. Crosser of S. brevicollir are made by confrontation of compatible mycelia, or by microconidiation. In the latter technique a suspension of microconidia from a 3-4 day old culture is Poured over a compatible culture of the same age.

Spores may be isolated by hand under a dissecting microscope. Mature asci are transferred to dissecting agar and dissection performed with hand-drawn gloss needler or small steel needles. Foster and more exact dissections may be mode with a micromanipulator.

Mass spore isolations may be made by inverting mature crosses over dissecting agar or spore germination agar. The ascospores ore ejected from the asci, often in groups of eight. Light is not necessary for this process in freshly mature crosses, but moy enhance the process in older crosses. Freshly mature crosses discharge the ascospores in large numbers within a matter of minutes. Older crosses may require longer.

Stock cultures may be kept on any kind of solid media (except agar containing acetate) in the refrigerator at 4-6°C. Cultures of S. brevicollis tend to become less fertile after long periods of storage and fresh isolates from spores should be made periodically.

Strains and linkage groups. Most of the genetic studier with S. fimicola hove utilized three different geographical isolates, Cl, C7 and Al, described by Olive (1956 Am. J. Botany 43:97). The most extensive work has utilized only the Al strain. Seven chromosomes hove been detected cytologically but only one linkage group has been mapped (El-ani, A. S., L. S. Olive and V. Kitani 1961 Am. J. Botany 48:716). Most of the localized mutants are ascospore color mutants, restricted growth mutants, and sterile mutants. The latter group consists of various types of mutations which affect the normal self-fertile condition in sexual reproduction. Similar types of mutants have been isolated and used in genetic studier in S. macrospora. A fragmentary map has been established.

Seven linkage groups of S. brevicollis have been identified (Chen, K. C. 1965 Genetics 51:509). A large number of ascospore color mutants have been mopped and are distributed among the seven linkage groups. For most rites, a large number of alleles is known. In addition a number of morphological mutants affecting growth of the mycelium have been isolated.

Some of the mutant strains of S. fimicola and S. brevicollis are deposited in the American Type Culture Collection. All of the mutants of S. fimicola are maintained in L. S. Olive's laboratory (Department of Botany, University of North Carolina, Chapel Hill, North Carolina 27514). All of the mutants of S. brevicollis are kept in our laboratory (Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48823). Cultures of S. macrospora ore maintained in K. Esser's laboratory (Institut für Allgemeine Botanik, Ruhr-Universität, 463 Bochum, Postfach 2148, Germany).

S. fimicola

Linkage group I*

Locus and mop units	Characteristics
rt-64	Partially fertile; ascospores of variable color with slow maturation.
14.2	
st-52	Partially fertile; few perithecia with asci and ascospores.
16.4	
st-9	Partially fertile, with protoperithecia and a few perithecia.
13.5	
st-60	Normal growth, but completely sterile.
15.4	
r	Restricted growth
3.6	
sp (spotty)	Slow growth, perithecia produced in spotted pattern
9.1	
mi (milky)	Creamy, mottled mycelium, gray-brown ascorporer.
0.6	
mot	Slow growth, compact hyphae
0.4	
g (gray)	Ascospore color mutants; 1 gray, 3 hyaline.
3.4	
cor (corona)	Slow growth, reduced fertility, halo-like zone around inoculum.
19.5	
rt-22	Complete sterility.

* A second linkage group has been identified, but not mopped (El-ani, A. S. and L. S. Olive 1959 Proc. 9th Intern. Botan. Congr.; El-ani, A. S. 1964 Science 245: 1067).

S. brevicollis

Linkage Group	Locus	Number of mutant alleles	Centromere-gene distance	Characteristics
I	col-1	1	1.5	Slow growth; forms limited colony.
	yl	22	0.4-1.4	Spores yellow or green.
	A		1.8	Mating type.
	or-2	1	3.2	Orange color accumulating in mycelium, homozygous cross sterile.
	y12	5	7-8	spores yellow or green.
	dk	1	15.5	Mycelium dark.
II	b1	16	1.5-2.5	Spores beige or green.
	R111	1	5.0	Restricted growth.
	R286	1	5.5	Restricted growth.
	R344	1	8.9	Restricted growth.
	R339	1	12	Restricted growth.
	Y9	14	12-13	Spores yellow or gray-green.
	R318	1	16.5	Restricted growth.
	g4	9	33.3	spores gray
III				
	g2	8	2.8	Spores gray-green or beige.
	Y7	1	9.6	Spores yellow.
IV				
	g6	4	2.1	Spores gray-green.
	g5	4	12.6	Spores gray-green.
V				
	y4	15	o-o. 7	Spores yellow, beige, hyoline or green.
	df-2	1	1.0	Very slow growth.
	R34	1	1.5	
	df-1	1	5.6	Very slow growth.
	R112	1	6.0	Restricted growth.
	R97	1	9.0	Restricted growth.
VI				
	hl	24	4.6-6.0	Spores hyoline
	b3	1	6.6	Spores beige.
	gl	4	7.4	Spores gray-green.
	R155	1	9.3	Restricted growth.
	R83	1	11.5	Restricted growth.
VII				
	g7	2	2.2	Spores gray-green.

Genetic problems. The following problems have been studied or are currently under investigation:

S. fimicola -
Mechanism of intragenic recombination using ascospore color mutants (Kitani, Olive).
Cytology of meiosis and ascospore formation (Carr, Olive).
Analysis of cross compatibility of self-fertile and self-sterile cultures (Carr, Olive).
Analysis of self-sterile mutants with special reference to origin of heterothallism (El-ani, Olive)
Construction of chromosome mops (El-ani, Olive, Kitoni).
Genetic analysis of incompatibility involving geographical races (Olive, Fields).
Conversion ond recombination frequencies with relation to temperature (Lamb).

S. macrospora:
-Genetic analysis of mutants affecting development (Heslot, Esser, Stroub).
Construction of chromosome maps (Heslot, Kemper).
Analysis of crossing-over and interference (Kemper).

S. brevicollis:
-Mechanism of intragenic recombination using ascospore color mutants (Fields, Olive).
Construction of chromosome maps (Chen, Fields).
Genetic analysis of spindle overlap (Chen).
Biased distribution and polarized segregation (Berg).

Advantages of species of Sordaria for use in genetic studies. The three species mentioned above hove been used often in genetic studier, but other species have also received some attention. Generally, Sordaria species have many things in common:

(1) Short life cycles. Of the three discussed above, this varies from 7-12 days, depending on the strains and the species
(2) Since the homothallic species are self-fertile, each strain is isogenic.
(3) The homothallic species ore particularly suitable for studier of sexuality and morphogenesis.
(4) The heterothallic species above (and others) ore similar to Neurospora except that no conidia are produced.
(5) Mutants ore easily obtained for all species, even though no conidia are produced by any species, by treating mycelium or small hyphal fragments (or microconidia in the heterothallic species).
(6) All kinds of mutants are obtainable, in particular ascospore color mutants. Such visual mutants aid in tetrad analysis, especially in analysis of intragenic recombination.

The aim of this short review has been to acquaint geneticists with the work going on with Sordaria and to convey some of the potentialities of the genus as an object of study. The citations I have made are not inclusive. If any should desire a complete reference list, I would be glad to furnish it.

Many thanks ore due to Prof. Olive and Prof. Esser for their comments and cooperation. - - - Deportment of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48823.