To the Graduate Council:

I am submitting herewith a thesis written by Scott Allen Gordon entitled "Mating Systems In *Marasmius*." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Botany.

Ronald H. Petersen, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

# MATING SYSTEMS IN *MARASMIUS*

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Scott Allen Gordon

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## ABSTRACT

Fourteen species representing six sections in *Marasmius* were established in monokaryon cultures made from fresh material collected from the southern Appalachian Mountains. These monokaryons were used for self-crosses and intercollection crosses. By understanding mating systems (compatibility systems) in *Marasmius*, as well as morphological and cultural characteristics, data on which to base systematic concepts in this genus will increase.

Self-crossess of monokaryon isolates revealed a consistency of mating system types at the sectional level. Some sections were found to be predominately bipolar while other sections predominately tetrapolar. Descriptions of mating system types, macromorphologies of mated colonies, mating reactions, and unusual micromorphologies are provided.

In addition, intercollection crosses were made to compare morphological species concepts from this study area (Desjardin, 1989) to "biological species" data. Also, through intercollection crosses, distribution of mating type alleles were analysed.

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# CHAPTER I

## INTRODUCTION

The genus *Marasmius* (Tricholomataceae, Agaricales, Basidiomycotina) consists of litter-binding and litter-decomposing mushrooms found world-wide. Most species in this genus are saprophytic while few are parasitic (Seaver, 1944). Taxa may be substrate-specific or relatively non-specific as to preferred substrate (Desjardin, 1985, 1989). *Marasmius* may be distinguished from similar fungi by spores that are hyaline, smooth, inamyloid, acyanophilous, and thin-walled; monomitic tramal tissue; non-siderophilous basidia; and a pileipellis that is typically hymeniform, composed of either setulose (broom cells) or smooth cells. Diagnostic characters used in separation of infrageneric ranks within *Marasmius* include micromorphology of pileipellis cells; inamyloid vs. dextrinoid tissue; insititious vs. non-insititious stipe base; and presence or absence of pleurocystidia, setae, rhizomorphs, caulocystidia, and a collarium (Desjardin, 1985, 1989).

Although the genus name *Marasmius* is quite old (Fries, 1835), several recent taxonomic treatments have been published on North American taxa (Gilliam, 1973, 1975, 1976; Halling, 1983; Desjardin, 1985, 1986, 1989; Doyle and Sundberg, 1989). About 90 taxa are known to occur in North America with 38 of these taxa, representing eight sections, being reported from the southern Appalachian Mountains (Desjardin, 1989). While the majority of taxonomic works have treated only alpha-level characters (macro- and micromorphology), studies on

cultural characteristics (Arnold, 1935; Desjardin, 1989) and phenol-oxidase production (Marr, 1986; Desjardin, 1989) have also been produced. Culture differences, coupled with alpha-level taxonomic data, have revealed many interspecific differences within *Marasmius* (Desjardin, 1989), and these differences have served as criteria for circumscribing taxa. For example, production of extracellular enzymes such as laccase, tyrosinase, and peroxidase, is thought to aid the fungus in breakdown of lignin. Desjardin (1989) used spot tests developed by Marr (1986) as criteria for possible taxonomic diagnoses but found that phenol-oxidase production, by itself, was of limited infrageneric taxonomic importance.

By understanding mating systems (compatibility systems) in *Marasmius*, as well as morphological and culture characteristics, data on which to base systematic concepts in this genus will increase, bringing about a more coherent generic concept. The purpose of this study, therefore, was: 1) to elucidate mating systems of individual taxa within *Marasmius*; 2) to compare morphological species concepts to "biological species" data; 3) to assess for consistency of mating systems at infra-generic levels; and 4) to analyze distribution of biological species and mating type alleles.

# CHAPTER II

## REVIEW OF MATING STUDIES

The pioneering work on cross-matings in fungi was by Blakeslee (1904), who characterized various species in the Mucorales (bread mold; Zygomycetes) as either homothallic (self-compatible) or heterothallic (self-incompatible). A homothallic fungus could complete sexual reproduction without combining with another thallus, while a heterothallic fungus required union of two compatible thalli of different mating types in order for sexual structures to be formed. In the years following Blakeslee's work, the concept of mating systems was elucidated in various other groups of fungi (Esser, 1965).

Bensaude (1918) and Kniep (1920) were the discoverers of cross-mating concepts in the basidiomycetes (Raper, 1966). Both researchers, independently, reported on the lack of clamp connections in heterothallic monosporous mycelia, presence of clamp connections in polysporous (dikaryotic) mycelia, and establishment of clamp connections in various pairings of monosporous mycelia (Raper, 1966). Cytological investigations to explain these phenomena were sketchy until the middle of the twentieth century. With the advent of electron microscopy and later nuclear flourescence stains, methods of nuclear migration and dikaryotization were elucidated (Raper, 1966). Eventually, it became apparent how nuclear migration proceeded in compatible matings and how this was inter-related to the presence of clamp connections. In the majority of basidiomycetes, clamp connections became presumptive evidence of dikaryotization, and

therefore of compatible matings. In some basidiomycetes, clamp connections were not formed, so today, nuclear flourescent stains along with epiflourescent microscopy are necessary to see direct evidence of dikaryotization and therefore compatible matings.

Although cytological processes were not clearly understood, Bensuade and Kniep provided the foundations on which the concept of patterns of sexuality were formed as well as terminology of various phenomena used today.

**Bipolar (Unifactorial) Sexuality:**

Burgeff (1920), with his work on the smut *Ustilago violacea* (Ustilaginales; Basidiomycotina), introduced the term "bipolar sexuality" (Raper, 1966). Compatibility in a bipolar fungus is controlled by multiple alleles (1) and (2) of a single factor (gene) A. In a compatible mating, two thalli must carry different alleles at the A locus (i. e. $A_1$ X $A_2$: $A_2$ X $A_1$) while incompatible matings occur when identical alleles are present at the (A) locus (i. e. $A_1$ X $A_1$: $A_2$ X $A_2$). Therefore, from any spore population produced by a single mycelium, 50% of all matings should prove compatible and 50% incompatible.

**Tetrapolar (Bifactorial) Sexuality:**

Bauch (1930), with his work on the smut fungus *Ustilago longissima*, introduced the term "tetrapolar sexuality" (Raper, 1966). In this condition mating is dictated by multiple alleles of two factors (genes), A and B, which segregate independently during meiosis (Raper, 1966). From any spore population produced from a single thallus, four

different mating types can be produced ($A_1B_1$, $A_1B_2$, $A_2B_2$, and $A_2B_1$). In order for successful mating to occur, alleles at both the A and B loci must be dissimilar (i. e. $A_1B_1$ X $A_2B_2$: $A_2B_1$ X $A_1B_2$). Incompatible matings result between common mating factors (i. e. $A_1B_1$ X $A_1B_2$: $A_1B_1$ X $A_2B_1$: $A_1B_1$ X $A_1B_1$: and $A_2B_2$ X $A_2B_2$).

In tetrapolar mating systems, incompatible matings of common A or common B alleles often produce two distinct culture morphologies of mated monokaryons. The initial observations of culture morphologies of incompatible matings were made by researchers in the 1920's and 1930's (Vandendries, 1923, 1937; Vandedries and Brodie, 1933; Brodie, 1935, 1936; Smith and Brodie, 1935), who described a mutual aversion zone between two incompatible homokaryons. It was not until the 1950's that Fulton (1950) and Papazian (1950) initiated the concept of scoring matings by the use of culture morphologies (termed "flat" and "barrage") and assigned common mating factors to these morphologies (Raper, 1966).

This work set the stage for research on the distinction in function between the A and B genes. The A factor is thought to regulate formation of clamp connections while the B factor is thought to control nuclear migration and fusion of clamp connections to the incipient penultimate cell; therefore, an incompatible mating of common B factors should produce pseudo-clamp connections (false clamps) while a common A mating should remain clampless (Esser, 1965). Incompatible matings with common B factors produce a macro-morphological phenomenon in which confronted colonies form mutual "repulsive" aerial hyphae: The overall effect is termed "barrage."

Incompatible matings of common A factors produce a phenomenon known as a "flat", in which hyphae from two incompatible homokaryons form a "crevasse" with little or no hyphal growth between.

**Homothallism:**

Blakeslee (1904) introduced the term homothallism, which designated the ability of an individual to complete its life cycle without combining with a compatible thallus (Esser, 1965). Today, as a result of cytological research, two types of homothallism have been discovered: true (or primary) homothallism and secondary (or functional) homothallism.

True homothallism is a condition in which a single uninucleate haploid basidiospore can germinate and complete its entire sexual life cycle. In homothallic taxa that produce clamp connections, germination of a single uninucleate haploid basidiospore results in hyphae possessing clamp connections (Raper, 1966).

The concept of secondary homothallism was introduced by Sass (1929) who reported on various species of fungi which produced binucleate basidiospores. Upon germination, these basidiospores could produce dikaryon hyphae with or without clamp connections. If the nuclei in the basidiospore were compatible, clamp connections were evident even on germinating hyphae, but if the nuclei are incompatible, hyphae from germinated basidiospores would appear as monokaryotic (no clamp connections present), but would actually comprise binucleate cells. In this condition, mated mycelia were compatible with two independent mating types (i. e. a basidiospore and resultant hyphae

containing two incompatible nuclei $A_1B_1$ + $A_1B_2$ are compatible with $A_2B_2$ and $A_2B_1$ mating types).

# CHAPTER III

## APPLICATION OF MATING SYSTEMS TO FUNGAL SYSTEMATICS

For years, systematists in the higher fungi have used fruitbody morphology to determine taxonomic rank and phylogenetic relationships. Clear delimitation of species has proven difficult because of the variability of some unstable morphological characters (i. e. size, shape, and color of fruitbodies), and uniformity of other relatively stable characters (i. e. basidia and spore morphology and chemistry). According to Petersen (1976), taxonomists of the higher fungi have not "considered a 'species concept' at all, but utilize almost exclusively a single character field ('morphology'), exhibited by a single portion of the organism (the fruitbody), and the results often seem only coincidentally related to a 'natural' system reflecting phylogenetic relationships." By using only fruitbody morphology, investigation of the species concept has been set aside in favor of merely separating morphologically distinct taxa (morphological species).

Recently, there has been growing acceptance of the concept of "biological species" in the higher fungi. The definition of biological species in the heterothallic higher fungi is essentially identical to that which Mayr (1942) described for animal populations: "Biological species are groups of actual or potentially interbreeding natural populations that are reproductively isolated from other such groups." Therefore, if two populations of higher fungi are conspecific in the sense of biological species, they should share a common gene pool, be

sexually compatible, dikaryotize, exhibit karyogamy, and produce viable offspring (spores) when cross-mated. Many of the higher fungi have proven difficult or impossible to fruit in culture and therefore have not produced viable spores. Therefore compatible matings have, by convention, been considered conspecific even when fruitbodies and viable spores are not produced.

Morphological differences between taxa are often too subtle to discern easily, but, these difficulties may be overcome by the use of mating systems (compatibility systems) and intercollection matings to delineate distinct biological species. A number of ways to utilize mating tests in fungal systematics and species definition have been summarized by Boidin (1986):

a- Compatibility tests can be used to determine if morphologically similar species are reproductively isolated, and hence are distinct biological species.

b- "It has been possible to provide experimental evidence on the range of variation of various morphological characters to be expected within sympatric populations by correlating mating tests with morphological studies."

c- It is possible to demonstrate reproductive isolation between taxa which differ in their compatibility system.

d- Mating tests can define sibling species.

e- Strains of collections from geographically separated areas can be mated to show existence of identical or distinct biological species.

f- It is possible to obtain incomplete, or partial, intercompatibility, interpreted as taxa in the process of speciation.

Mating studies have been made in a number of taxa in higher fungi, usually in small groups or single species. Studies which have utilized one or more species within a genus for mating tests in the ways summarized by Boidin (1986) include those on *Armillaria* (Anderson, 1986; Anderson, *et. al.* 1980; Anderson and Ullrich, 1979, 1982; Berube and Dessureault, 1987; Hintikka, 1973; Korhonen, 1978; Lamoure and Guillaumin, 1985; Lung-Escarmant, *et. al.*, 1985; Roll-Hanson, 1985; Tommerup and Broadbent, 1975; Ullrich and Anderson, 1978; Watling *et. al.*, 1982), *Auricularia* (Banerjee, 1956; Duncan, 1972; Duncan and MacDonald, 1967; Wong, 1985), *Collybia* (Arnold, 1935; Vilgalys and Johnson, 1987; Vilgalys and Miller, 1983, 1987), *Coprinus* (Kemp, 1970, 1974, 1975), *Exidia* (Barnett, 1937), *Exidiopsis* (Wells, 1985; Wells and Wong, 1985, 1989), *Hericium* (Ginns, 1985), *Laccaria* (Fries, 1983; Fries and Mueller, 1984), *Lentinus* (Tokimoto, *et. al.*, 1973), *Marasmius* (Arnold, 1935; Lamoure, 1957; Burnett and Evans, 1966; Mallet and Harrison, 1988), *Panellus* (Macrae, 1942), *Panus* (Arita and Sakamoto, 1966), *Paxillus* (Fries, 1985), *Pleurotus* (Anderson, *et. al.*, 1973; Arita, 1974; Bresinsky, *et. al.*, 1987; Cailleux and Joly, 1987; Eger, *et. al.*, 1976, 1979; Eugenio and Anderson, 1968; Ohira, 1977; Terakawa, 1956), *Sistotrema* (Ullrich, 1973; Ullrich and Raper, 1974, 1975) and *Tremella* (Wong and Wells, 1985; Bandoni, 1963, 1965). The majority of these studies have used only one or a few taxa within a genus, yielding limited data on which to base systematic concepts. When large numbers of species within a genus are used for mating studies, more significant systematic data will be revealed, i. e. consistency of mating system types over larger systematic units. A few genera have been shown to possess

variability in mating systems at the subgeneric level (i. e. *Marasmius* (see above), *Sistotrema* (see above) and *Xeromphalina* (Petersen, pers. comm.).

**Mating Systems In *Marasmius***

The mating systems in *Marasmius* have have been described in only a few species, making useful systematic analysis difficult. Arnold (1935), in *Marasmius elongatipes* (= *M. pyrrhocephalus*), and Lamoure (1960), in *Marasmius limosus*, found these species to be tetrapolar. The most comprehensive examinations of mating systems in *Marasmius* has been made with *M. oreades* (the common "fairy ring" fungus). Burnett and Evans (1966) found that isolates of *M. oreades* from England were bipolar and basidiocarps from one "fairy ring" were homogeneous for mating factors. Mallet and Harrison (1988) studied collections of *M. oreades* from Canada and also found the fungus to be bipolar, and each "fairy ring" to be produced by a single dikaryotic mycelium. Lamoure (1989) published an extensive "checklist" of information on mating tests in the Agaricales. In this work, she cited previous authors' studies on mating systems of a variety of taxa in *Marasmius* (Table 1). Lamoure's (1989) publication must be considered a secondary source, compiled, as it was, from previous primary reports. In several cases (Armand, 1962; Bastouill, 1977; Viale, 1961) the primary sources are either obscure or unpublished, and data are not secured by discriminating taxonomical diagnosis or voucher specimens. Neither mating data nor taxonomic names may be accepted without question.

**TABLE 1:** Mating (sexuality) systems of Marasmius species as listed by Lamoure (1989).

| | SEXUALITY | REFERENCES |
|---|---|---|
| **SECTION *ANDROSACEI*** | | |
| *M. androsaceus* | tetrapolar | Piroard (1956)<br>Terra (1953)<br>Yen (1950a,b,c) |
| **SECTION *MARASMIUS*** | | |
| *M. rotula* | tetrapolar | Terra (1953)<br>Yen (1950a,c) |
| *M. bulliardii* | tetrapolar | Lamoure (1989) |
| *M. limosus* | tetrapolar | Lamoure (1989) |
| **SECTION *EPIPHYLLI*** | | |
| *M. epiphyllus* | tetrapolar | Terra (1953)<br>Yen (1950a,b,c) |
| *M. tremulae* | haploid parthenogenetic | Kühner (1947)<br>Lamoure (1958) |
| **SECTION *GLOBULARES*** | | |
| *M. collinus* | tetrapolar | Armand (1962)<br>Oddoux (1957)<br>Terra (1959) |
| **SECTION *ALLIACEI*** | | |
| *M. scorodonius* | tetrapolar | Kühner (1945)<br>Piroard (1956)<br>Terra (1959)<br>Yen (1950b,c) |
| *M. alliaceus* | tetrapolar | Piroard (1956)<br>Terra (1959)<br>Yen (1950a,b) |
| *M. epidryas* | tetrapolar | Lamoure (1989) |
| *M. prasiomus* | heterothallic | Bastouill (1977)<br>Viale (1961) |

Table 1 cont.:

| | SEXUALITY | REFERENCES |
|---|---|---|
| **SECTION *HYGROMETRICI*** | | |
| *M. buxi* | tetrapolar | Almandy (1958)<br>Lamoure (1989)<br>Piroard (1956) |
| **SECTION *SICCI* SERIES *SPINULOSI*** | | |
| *M. cohaerens* | bipolar | Armand (1962)<br>Vandendries (1936) |

These data confirm variability of mating systems within *Marasmius*, but with the mating systems of so few species described, the resultant data until now, have not been useful in systematic schemes.

# CHAPTER IV

# METHODS AND MATERIALS

## Field Methods:

A major part of this research was extensive fieldwork throughout the Great Smoky (GSMNP) and Blue Ridge Mountains to collect living basidiocarps from which single-spore isolates were obtained.

Fresh specimens were wrapped in wax paper and transported to the laboratory. Upon return to the lab, notes were immediately taken on phenetic characters of each specimen and photographs were made using a standard gray card and Ektachrome 200, 35-mm slide film. Particular attention was paid to color (Kornerup and Wanscher, 1978), taste, odor, and substrate. All collections were dried using an electric food drier, to allow for preservation of microstructure. All dried collections reside in the University of Tennessee Fungus Herbarium (TENN).

## Identification of Collections:

All collections were identified using the keys present in the Doctoral Dissertation "The Genus Marasmius From The Southern Appalachian Mountains" by Desjardin (1989). Dikaryon culture characters from this study were compared with culture descriptions by Desjardin (1989) to test consistency of characters.

## In-Lab Culture Preparation:

Collection of spores and subsequent single-spore isolation was achieved in two ways: 1) A spore-bearing portion of a fresh basidiome

was suspended from the inside cover (using petroleum jelly) of a sterile empty 35 X 10 mm Petri dish until a heavy spore deposit was obtained. The portion of the basidiome was then removed from the inside of the dish. Spores were collected with a bacteriological loop of sterile water and suspended in a test tube containing approximately 4 ml sterile water. A series of three dilutions were made and each dilution series was decanted onto Petri dishes containing malt extract agar [15 gm malt extract + 20 gm agar (Difco)/ 1000 ml distilled water]. These plates were allowed to stand overnight to permit excess water to evaporate from the agar surface. Resultant Petri dishes were wrapped in Parafilm and inspected daily for spore germination. 2) The spore-bearing portion of a fresh basidiome was suspended from the inside cover (using petroleum jelly) of a sterile 60 X 15 mm Petri dish containing malt extract agar. The Petri dish was placed at an angle of approximately 75°C to allow for wider spore dispersal. After a spore print became visible, the portion of basidiome was removed from the Petri dish. These plates were wrapped with Parafilm and inspected daily for spore germination.

**"In The Field" Culture Preparation:**

Many species in this genus have very delicate basidiocarps with thin-walled spores which desiccate very quickly (often within 10-15 minutes after collecting). When such basidiocarps were collected, the above methods of obtaining spore prints were performed directly in the field. Pre-prepared Petri dishes (both empty 35 X 10 mm dishes and 60 X 15 mm dishes with malt extract agar) and pre-cut laboratory parafilm were carried in the collecting basket for easy access. In order to

stack dishes and keep them stable in the collecting basket, a hollow cardboard tube was tied to the inside of the collection basket. This "in the field" preparation was very useful and produced good results when care was taken to prevent contamination of the dishes.

**Detection Of Spore Germination And Isolation of Spores:**

Germination was detected using a Wild stereo dissecting scope with substage illumination. When spores germinated, single germlings were cut out of the malt extract agar (while viewing through the microscope) using a sharpened dentist's explorer. These germlings (approx. 25) were transferred to a 100 X 15 mm Petri dish containing malt extract agar and monitored until colony growth was established. Colonies were transferred to glass test tube slants of malt extract agar, where monokaryon cultures were allowed to grow for several weeks and then stored at 5°C until mating tests were performed.

**Long Term Storage Of Cultures:**

Long-term storage was undertaken using the methods of Maekawa *et al.* (1988), whereby an agar block, with mycelium, was suspended in small vials (4 ml cap.) containing 10% glycerol (10 parts water: 1 part glycerol) and stored at -80°C. This method of storage results in a low mortality rate and high stability of stored cultures.

**Determination Of Mating Systems (Self-crosses):**

Each monospore stock culture was transferred to a 60 X 15 mm Petri dish and allowed to grow until colonies were of sufficient radius (approx. 3 mm) to obtain enough hyphae to perform mating tests.

Cultures were examined for presence or absence of clamp connections by removing a small portion of hyphae, staining with phloxine, and microscopic inspection. Absence of clamp connections suggested a monokaryotic culture while their presence indicated a dikaryotic condition. Subsequent monokaryons were used for mating experiments.

Monokaryons, usually 10-12 from a single collection, were crossed in all possible combinations. Isolates crossed against themselves served as controls. Matings were allowed to grow until hyphae from each donor came into contact. All matings were then examined microscopically for indication of nuclear condition (detected by the presence or absence of clamp connections). Compatible matings were evident in matings where clamp connections were present or, in taxa that did not form clamp connections, when two nuclei per cell were seen. Incompatible matings were evident when no clamp connections were formed or only one nucleus per cell was observed. In species where clamp connections were of sufficient size, microscopic observations were made directly at the zone of contact using a Wild compound light microscope equipped with a 25X ocular lens and a 10X objective. In species where clamp connections were not easily detected, a small portion of hyphae was removed, stained with phloxine, and viewed at 600X (15X ocular, 40X objective).

Compatible matings, as measured by the presence of clamp connections at the zone of confrontation, were termed (+). Compatible matings were also checked to determine the presence or absence of clamp connections on the peripheral hyphae of each isolate and denoted by a small (+) (with clamps) or a small (-) (without clamps) on the upper

right or lower left corner of each (+) (compatible mating denotation), corresponding to the isolate number on the upper or left side of the mating grid. In each individual species text, which contains matings which show unilateral nuclear migration, a (>) sign denotes the single-spore isolate that is dikaryotized. Detection of nuclear migration indicate strains which are able to dikaryotize or be dikaryotized. Approximately one week after mated colonies came into contact, each mating was observed for the presence or absence of "barrage" phenomena (common B pairings) termed (B), or a "flat" phenomenon (common A pairings) termed (F). Also, when appropriate, compatible matings which possessed few clamp connections were denoted ⊕, while matings which possessed abundant clamp connections were denoted ⊞. When all matings were read, including colony morphology, nuclear migration, and any other unusual characters, columns and rows from the resulting grid were adjusted to elucidate the mating system pattern and mating types assigned according to previously described methods and criteria. Tester strains (tester spores) of each mating type were chosen on the basis of mating types, relatively fast growth rates, and ability to form abundant clamp connections with compatible mating types.

Under individual taxa summarized below, tester strains were denoted by an (*) next to the strain number.

**Intercollection Matings:**

Tester strains from different collections of the same morphological species were paired in all possible combinations and results logged as described above. In bipolar mating systems, tester strains plus one other strain from each mating type (total = 4) were

chosen for intercollection matings. This procedure provided a more coherent indication of compatibility. By mating tester strains in all possible combinations, mating system determination (i.e. bipolarity or tetrapolarity) was rechecked and relationships between collections of geographically distinct areas were elucidated. Alleles at each mating type were then assigned to respective strains on basis of compatibility/incompatibility and macromorphology of mated colonies.

# CHAPTER V

# RESULTS OF

# SELF-CROSSES

## *MARASMIUS* sect. *ANDROSACEI*

1. ***MARASMIUS ANDROSACEUS*** (L.: Fr.) Fries

Specimen utilized: North Carolina, Macon Co., Blue Valley, vic. Forest Rd. 79, 9.VI.89, coll. SAG, det. SAG, field no. 2705 (TENN no. 48757).

Figure 1* illustrates that the mating system of *M. androsaceus* is tetrapolar (bifactorial). Of ten single-spore isolates crossed, nos. 5, 6*, and 10 represented $A_1B_1$, nos. 1*, 7, and 14 were $A_1B_2$, no. 2* was $A_2B_1$, and nos. 4*, 11, and 12 were $A_2B_2$.

In several compatible matings nuclear migration was mutual, but matings 14 X> 2, 5 X> 11, 5 X> 12, and 12 X> 10, showed unilateral nuclear migration. No matings exhibited abundant clamp connections, but matings 4 X 5, 5 X 12, 10 X 11, and 10 X 12 had few clamps scattered about the zone of contact.

No obvious macroscopic manifestation of dikaryotization was observed. Compatible matings exhibited white appressed to slightly raised hyphae with no differentiation at the zone of contact. Incompatible matings, however, showed three types of reactions: 1) overgrown, undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. Mating type assignments were made in accordance with interpretation of the above mating morphologies. Hyphae of incompatible matings were white, and appressed to slightly raised.

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*** All figures are placed in appendix**

## *MARASMIUS* sect. *MARASMIUS*

**2A. *MARASMIUS ROTULA*** (Scop.: Fr.) Fries

Specimen utilized: North Carolina, Macon Co., Bull Pen Rd., vic. Slick Rock, 21.VI.89, coll. RHP, det. RHP, field no. 1809 (TENN no. 48352).

As illustrated (fig. 2A), the mating system of *M. rotula* is tetrapolar (bifactorial). Of nine single-spore isolates crossed, nos. 1*, 3, and 6 represented $A_1B_1$, nos. 2* and 5 were $A_2B_2$, nos. 7* and 8 were $A_2B_1$, and nos. 4* and 9 were $A_1B_2$.

In several compatible matings nuclear migration was reciprocal, but in some seemed unilateral (6 X> 2, 3 X> 5, and 4 X> 7). Mating 4 X 8 showed clamp connections only at the zone of initial contact. As nuclear migration proceeded to the periphery of the mated mycelia, new growth often was aerial, fluffy, and cottony, but in other compatible matings no obvious macroscopic manifestation of dikaryotization was observed.

Several types of incompatible mating reactions were observed, namely: 1) overgrown, undifferentiated reactions; 2) "flat" reactions and 3) "barrage" reactions. Except for the absence of clamp connections, colony morphologies conform to the description by Desjardin (1989), namely white, appressed to slightly raised hyphae.

**Commentary:** In one mating (4 X 8), an extensive lethal reaction was noted, this reaction consisted of only a few clamp connections concentrated at the zone of contact and extensive hyphal evacuation occurring at that zone. Strain no. 8 formed a variety of reactions (including lethal reactions) in both compatible and incompatible matings.

**2B. *MARASMIUS ROTULA*** (Scop.: Fr.) Fries

Specimen utilized: North Carolina, Macon Co., Otto, vic. Coweeta Hydrologic Lab, Shope Creek Rd., 22.VI.89, coll. RHP, det. RHP, field no. 1816 (TENN no. 48535).

Figure 2B shows that the mating system of *M. rotula* is tetrapolar (bifactorial). Of eight single-spore isolates mated, nos. 1, 8*, and 10 represented $A_3B_3$, nos. 3* and 5 were $A_4B_4$, nos. 4, 7, and 9* were $A_4B_3$, and no single-spore isolates represented $A_3B_4$.

In most compatible matings, nuclear migration seemed restricted to the initial zone of contact, but matings 8 X> 3 and 10 X> 5 showed more extensive unilateral nuclear migration.

Incompatible matings showed three types of reactions; 1) overgrown undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. These reactions were not accurately noted nor independently plotted.

**Commentary:** Morphology of mated colonies was similar to matings of other collections of *M. rotula*. No cinnamon brown pigment was produced.

**2C. *MARASMIUS ROTULA*** (Scop.: Fr.) Fries

Specimen utilized: Georgia, Rabun Co., vic. Double Bridges, 1.5 mi. from Rt. 28, 24.VIII.89, coll. RHP, det. RHP, field no. 2080 (TENN no. 48461).

As illustrated (fig. 2C), the mating system of *M. rotula* is tetrapolar (bifactorial). Of twelve single-spore isolates crossed, nos. 1, 5*, and 10 represented $A_6B_6$, nos. 2, 8, 9*, and 11 were $A_6B_5$, nos. 3*, and 6 were $A_5B_5$, nos. 4 and 12* were $A_5B_6$, and no. 7 was designated $A_6B_6 + A_6B_5$ (see commentary).

In compatible matings, nuclear migration and abundance of clamp connections were not noted. Macromorphology of compatible and incompatible matings was similar to matings of other collections of *M. rotula*.

**Commentary:** Strain no. 7 was compatible with both $A_5B_5$ and $A_5B_6$ mating types, therefore, even though no false clamp connections were observed in single-spore isolate no. 7, an $A_6B_6 + A_5B_6$ mating type was assigned to this strain. It is believed that two incompatible spores were initially isolated. No cinnamon brown pigment was observed as in matings of collection # 2726.

**2D. *MARASMIUS ROTULA*** (Scop.:Fr.) Fries

Specimen utilized: Tennessee, Blount Co., GSMNP, vic. Chimney Tops trailhead, 27.VI.89, coll. SAG, det. SAG, field no. 2726 (TENN no. 48753).

As illustrated (fig. 2D), the mating system of *M. rotula* is tetrapolar (bifactorial). Of ten single-spore isolates crossed, nos. 2*,

8, and 10 represented $A_7B_7$, nos 1, 6*, and 7, were $A_8B_8$, nos. 4 and 11* were $A_8B_7$, no. 3* was $A_7B_8$, and no. 5 was designated $A_7B_7$ + $A_8B_7$ (see commentary).

Although not recorded on the furnished mating grid, nuclear migration in compatible matings seemed reciprocal. Peripheral hyphae of some compatible matings (2 X 7, 7 X 8, 1 X 5) was white , fluffy to cottony, and rarely appressed. A few compatible matings (6 X 10, 7 X 10, 5 X 7, 5 X 6, and 2 X 6) showed cinnamon brown pigments scattered throughout mated colonies. In general, no obvious macroscopic manifestation of dikaryotization was observed, but matings with fluffy to cottony periphery hyphae usually were indicative of compatibility. Numerous clamp connections were scattered throughout compatible mated colonies.

Incompatible matings showed three types of reactions: 1) overgrown undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. These reactions were distinctive and assignment of mating types was made in accordance with these reactions. Peripheral hyphae of "flat" reactions was thickly matted, white, and appressed while hyphae around the inoculum block were less congested, white, and arachnoid. The zone of contact in barrage reactions was slightly raised, white, and thickly matted, and few matings which exhibited the "barrage" phenomena (5 X 11, 4 X 5, 10 X 11) possessed a cinnamon brown pigment line on the hyphae at the zone of contact.

**Commentary:** Hyphae from strains 2 and 10 exhibited very fluffy white colonies. One aberrant double compatible mating was observed (3 X 5),

perhaps the result of two incompatible spores ($A_7B_7$ + $A_8B_7$) being isolated as spore no. 5.

**2E. *MARASMIUS ROTULA*** (Scop.: Fr.) Fries

Specimen utilized: North Carolina, Macon Co., vic. Forest Service Rd. 1.5 miles from Shortoff Baptist Church, 1.VII.89, coll. SAG, det. SAG, field no. 2760 (TENN no. 48751).

Figure 2E shows that the mating system of *M. rotula* is tetrapolar (bifactorial). Of ten single-spore isolates crossed, nos. 1 and 7* represented $A_9B_9$, nos. 2, 4, and 5* were $A_{10}B_{10}$, nos. 3, 6, and 8* were $A_{10}B_9$, and nos. 9 and 10* were $A_9B_{10}$.

In the majority of compatible matings, nuclear migration seemed reciprocal, with the exception of matings 2 X> 7, 1 X> 4, and 9 X> 6 where nuclear migration was unilateral and mating 9 X 3 where clamps were observed only at the zone of initial contact. No compatible matings exhibited abundant clamp connections, but matings 4 X 7, 5 X 7, and 3 X 9 had few clamps scattered about the zone of initial contact. Compatible matings exhibited white, appressed to slightly raised to rarely fluffy hyphae.

Incompatible matings showed three types of reactions; 1) overgrown undifferentiatied reactions; 2) "flat" reactions; and 3) "barrage" reactions. Except for the absence of clamp connections, colony morphology conformed to the description by Desjardin (1989) namely, white, appressed to slightly raised to rarely fluffy hyphae.

**Commentary:** "Flats" and "barrages" were not as distinctive as matings of other collections of *M. rotula*. Strains 4 and 8 produced

extremely fluffy colonies. No cinnamon brown pigments were produced as in collection # 2726.

### 3. *MARASMIUS SP.*

Specimen utilized: Japan, Tochigi Pref., 28.IX.89, coll. RHP, det. DED, field no. 2337 (TENN no. 48748).

Figure 3 shows that the mating system of this taxon is tetrapolar (bifactorial). Of twelve single-spore isolates crossed, nos. 1, 2, 3*, 7, and 10 represented $A_1B_1$, nos. 4 and 9* were $A_2B_2$, nos. 5* and 12 were $A_2B_1$, and nos. 6, 8, and 11* represented $A_1B_2$.

In the majority of compatible matings, nuclear migration was observed only at the zone of contact. Unilateral migration was observed in mating 2 X> 9, while mutual migration was seen in matings 3 X 9 and 5 X 11. Matings 3 X 4, 5 X 8, and 8 X 12 exhibited few clamp connections localized around the zone of contact while all other mated colonies possessed numerous scattered clamps.

Incompatible matings showed three types of reactions: 1) overgrown undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. These reactions were distinctive and mating type assignments were made in accordance with these morphologies. Matings 4 X 6, 4 X 8, 4 X 11, and 9 X 6 possessed very distinct "barrages" with a cinnamon brown to light tan pigment localized at the zone of initial contact.

**Commentary:** Matings 5 X 8 and 12 X 8 possessed clamp connections which were extremely small and inconspicuous. Most matings had many inflated intercalary cells which resembled clamp connections. Strain

no. 5 possessed a well-defined cinnamon brown to tan circumferential pigment line exuded into the agar medium. Many matings had a "mint-like" or "antiseptic" odor.

## *MARASMIUS* sect. *EPIPHYLLI*

### 4. *MARASMIUS FELIX* Morgan

Specimen utilized: Illinois, Jackson Co., vic. Touch of Nature Reserve, 20.X.90, coll. RHP, field no. 2427 (TENN no. 48761).

As illustrated (Fig. 4), the mating system of *M. felix* is tetrapolar (bifactorial). Of twelve single-spore isolates crossed, nos. 1, 4*, and 11 represented $A_1B_1$, nos. 2* and 5 were $A_2B_1$, nos. 3, 6*, 8, 9, and 10 were $A_1B_2$, and nos. 7 and 12* were $A_2B_2$.

In all compatible matings, nuclear migration was reciprocal. No obvious macroscopic manifestation of dikaryotization was observed, with most compatible matings exhibiting overgrown, undifferentiated contact zones. Compatible matings exhibited white, appressed hyphae with little or no aerial growth, and clamp connections were observed on both submerged and aerial hyphae. Many compatible matings showed abundant clamp connections at the initial contact zone (1 X 12, 4 X 12, 2 X 6) while other compatible matings had few clamps scattered about the zone of initial contact (7 X 11, 9 X 5, 8 X 2, 3 X 5).

Incompatible matings of common A or B factors showed "flat" and "barrage" reactions. These reactions were most apparent when viewing colony reverse. Interpretations of "flat" and "barrage" reactions were subjective but assignment of mating types was made in accordance with

interpretation of macroscopic mating reactions. Totally incompatible matings (both A and B factors in common) exhibited the same hyphal morphology as compatible matings, namely white, flat, hyphae with little or no aerial growth.

## *MARASMIUS* sect. *GLOBULARES*

**5A. *MARASMIUS DECIPIENS*** Halling, Desjardin, and Tish

Specimen utilized: Tennessee, Blount Co., GSMNP, vic. Chimney Tops trailhead, 27.VI.89, coll. SAG, det. DED, field no. 2722 (TENN no. 48755).

As illustrated (fig. 5A), the mating system of *M. decipiens* is bipolar (unifactorial). Of ten single-spore isolates crossed, nos. 1*, 2, 4, 5, 10, 12, and 13 were arbitrarily designated $A_1$ and nos. 7*, 9, and 11 were designated $A_2$.

Most compatible matings showed clamp connections only at the zone of contact while some matings showed reciprocal nuclear migration (7 X 4, 7 X 12, 7 X 13), and still other compatible matings showed unilateral nuclear migration (1 X> 7, 2 X> 7, 4 X> 11). Matings 7 X 10, 9 X 2, 9 X 12, 9 X 13, 11 X 4, 11 X 5, 11 X 10, 11 X 12, and 11 X 13, showed few clamps scattered about the zone of initial contact.

No obvious macroscopic manifestation of dikaryotization was observed, with both compatible and incompatible matings exhibiting white fluffy hyphae around inoculum block and white to pale yellow appressed hyphae at periphery of colonies.

**Commentary:** The above results were obtained when matings were

performed on 0.5% malt extract agar. When self-crosses were performed on 1.5% malt extract agar, 28% were compatible and then in no discernable pattern, compared to 42% compatibility and a discernable pattern with 0.5% malt extract agar.

**5B. *MARASMIUS DECIPIENS*** Halling, Desjardin, and Tish

Specimen utilized: North Carolina, Haywood Co., Cataloochee cove, 30.VI.89, coll. SAG, det. DED, field no. 2731 (TENN no. 48756).

As illustrated (fig. 5B), the mating system of *M. decipiens* no. 2731 appears to be bipolar (unifactorial). Of ten single-spore isolates crossed, nos. 1, 5, 8*, and 11 were arbitrarily designated $A_1$ and nos. 2, 6, 9, and 10* were designated $A_2$.

In compatible matings, clamp connections were observed only at the initial zone of contact with the exception of matings 5 X> 10 and 10 X> 11 where nuclear migration was unilateral. Matings 3 X 2, 6 X 8, 6 X 11, 2 X 8, 2 X 11, and 10 X 11 formed few scattered clamps in the zone of contact.

No obvious macroscopic manifestation of dikaryotization was observed, both compatible and incompatible matings exhibited white fluffy hyphae around inoculum block, and white to pale yellow appressed hyphae at the periphery of mated colonies.

**Commentary:** The above results were obtained when matings were performed on 0.5% and 1.5% malt extract agar. This collection has a 8.6% failure rate (percent of matings expected to be compatible but were not) which may be due to physiological factors affecting clamp formation caused by media used.

**6. *MARASMIUS NIGRODISCUS*** (Pk.) Halling

Specimen utilized: Tennessee, Knox Co., Knoxville, University of Tennessee campus, 21.VI.89., coll. DED, det. DED, field no. DED 4913 (TENN no. 00000).

As illustrated (fig. 6), the mating system of *M. nigrodiscus* is bipolar (unifactorial). Of twelve single-spore isolates crossed, nos. 1, 4*, 6, and 11 were arbitrarily designated $A_1$ and nos. 2*, 3, 5, 7, 8, 9, 10, and 12 were designated $A_2$.

Compatible matings showed the presence of clamp connections only at the initial zone of contact. Some compatible matings (1 X 3, 1 X 9, 6 X 7, 6 X 12, 11 X 3, 11 X 5, 11 X 9, 11 X 10, 11 X 12) formed few clamp connections scattered about the zone of initial contact. No matings showed abundant clamp connections, no obvious macroscopic manifestation of dikaryotization was observed, and all compatible matings showed white, appressed to slightly raised hyphae.

Incompatible matings were scored by the absence of clamp connections at the zone of initial contact as well as areas on each side of this zone. No obvious macroscopic morphologies (barrage, flat) of incompatibility were observed, and macromorphology of incompatible matings was indistinguishable from compatible matings.

**Commentary:** The above results were obtained when matings were performed on .5% malt extract agar. When matings were performed on 1.5% malt extract agar, compatible matings were unpatterned and less common than when mated on .5% malt extract agar (17% compatibility vs. 44% compatibility, respectively).

**7. *MARASMIUS CYSTIDIOSUS*** (Smith & Hesler) Gilliam

Specimen utilized: North Carolina, Macon Co., Coweeta Hydrologic Lab, vic. 1.5 mi. from lab on Shope Creek Rd., 1.VII.90, coll. SAG, det. DED, field no. 2756 (TENN no. 48754).

As illustrated (fig. 7), the mating system of *M. cystidiosus* is bipolar (unifactorial). Of twelve single-spore isolates crossed, nos. 1, 2*, 4, 5, 8, and 10 were arbitrarily designated $A_1$ and nos. 3, 6, 7, 9*, 11, and 12 were designated $A_2$.

In compatible matings, nuclear migration was variable. Most mated colonies exhibited clamp connections only in the zone of contact while some matings (9 X> 4, 9 X> 5, 11 X> 10, 12 X> 2, 10 X> 12, 2 X> 7) exhibited unilateral nuclear migration and others showed reciprocal nuclear migration (6 X 5, 9 X 1, 11 X 5). No obvious macroscopic manifestation of dikaryotization was observed, and hyphae of all mated colonies were white to pale yellow with little aerial growth. Some matings, both compatible and incompatible, produced a weak "barrage" zone at the site of initial contact.

Most matings formed numerous, scattered clamps, while some matings (3 X 4, 3 X 8, 1 X 12, 4 X 7) exhibited very few.

**Commentary:** Two aberrent matings (7 X 1 and 7 X 8) were incompatible but were expected to be compatible. *Marasmius cystidiosus* like some other species is in section *Globulares* and, may produce more patterned matings on .5% malt extract agar.

**8. *MARASMIUS OREADES*** (Bolt.: Fr.) Fries

Specimen utilized: New York, Cortland Co., Rt. 281, vic. St.

Mary's cemetary, 18.X.89, coll. TJB, det. TJB, field no. TJB 6314 (TENN no. 0000).

As illustrated (fig. 8), the mating system of *M. oreades* is bipolar (unifactorial). Of twelve single-spore isolates crossed, nos. 3, 6, 7*, 15, 16, and 17 were arbitrarily designated $A_1$ and nos. 2, 8, 11*, 12, 13, and 14 were designated $A_2$.

In all compatible matings, nuclear migration was reciprocal and numerous clamps were scattered throughout compatible mated colonies. No obvious macroscopic manifestation of dikaryotization was observed, all mated colonies exhibited white, fluffy, abundant aerial hyphae on and around inoculum plugs, and white, appressed hyphae at the periphery of mated colonies.

**9. *MARASMIUS STRICTIPES*** (Pk.) Singer

Specimen utilized: Illinois, Jackson Co., Touch of Nature Reserve, 21.X.89, coll. RHP, field no. 2427 (TENN no. 48761).

As illustrated (fig. 9), no mating system pattern for *M. strictipes* was discernable. No designation of mating types, therefore were made. Many flat and barrage reactions were observed in incompatible matings. Hyphae were white to tan to slightly dirt brown and appressed to rarely fluffy. Matings were checked one and four weeks after contact for presence or absence of clamp connections. Mating data was consistent at both readings.

## *MARASMIUS* sect. *ALLIACEI*

**10A. *MARASMIUS PYRRHOCEPHALUS*** Berk.

Specimen utilized: Illinois, Jackson Co., Touch of Nature Reserve, 20.X.89, coll. RHP, det. RHP, field no. 2419 (TENN no. (00000).

As illustrated (fig. 10A), the mating system of *M. pyrrhocephalus* is tetrapolar (bifactorial). Of twelve single-spore isolates crossed, nos. 1, 5, 8, 9, and 10* represented $A_2B_1$, nos. 2, 6, 7, and 13* were $A_2B_2$, nos. 3 and 14* were $A_1B_2$, and no. 11* was $A_1B_1$.

In compatible matings, nuclear migration seemed reciprocal, with the exception of matings 5 X> 3, 8 X> 3, and 9 X> 14 where nuclear migration was observed to be unilateral. Compatible matings exhibited colony morphologies similar to compatible matings of other collections of *M. pyrrhocephalus*. Matings 3 X 9, 3 X 10, 6 X 11, and 11 X 13 showed abundant clamp connections at the zone of contact while matings 3 X 5 and 3 X 8 had few clamps scattered about this zone.

Incompatible matings showed colony morphologies and reactions similar to matings of other collections of *M. pyrrhocephalus*.

**10B. *MARASMIUS PYRRHOCEPHALUS*** Berk.

Specimen utilized: North Carolina, Macon Co., Bull Pen Rd., vic. Slick Rock, 6.VI.89, coll. SAG, det. SAG, field no. 1992 (TENN no. 48759).

As illustrated (fig. 10B), the mating system of *M. pyrrhocephalus* is tetrapolar (bifactorial). Of ten single-spore isolates crossed,

nos. 5* and 6 represented $A_3B_3$, nos. 3* and 1 were $A_4B_4$, nos. 8, 4, 9*, and 2 were $A_4B_3$, and nos. 7 and 10* were $A_3B_4$.

In compatible matings, nuclear migration was reciprocal, with the exception of matings 7 X> 9 and 3 X> 6 where nuclear migration was unilateral. Compatible matings exhibited white to sometimes cinnamon brown hyphae appressed around inoculum plugs and fluffy, white to cinnamon brown hyphae at the periphery of mated colonies. Clamp connections were observed in both aerial and submerged hyphae, with the exception of mating 4 X 10 which exhibited clamps only on submerged hyphae. No compatible matings exhibited abundant clamp connections, but matings 1 X 5, 2 X 7, 7 X 8, and 4 X 10, had few clamps scattered about the zone of initial contact.

Incompatible matings showed three types of reactions: 1) overgrown, undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. These reactions were more graphic on reverse (underside), as opposed to obverse. Interpretations of "flat" and "barrage" reactions were subjective but mating type assignments were made in accordance with interpretation of mating reactions. Incompatible matings exhibited white to cinnamon brown hyphae, generally with less aerial growth when compared to compatible matings.

**Commentary:** A few matings possessed abnormal micromorphologies: 5 X 10 possessed many inflated intercalary and terminal cells; 3 X 10 had many areas within mated colonies which possessed tightly wound hyphae resembling a "triple helix". Two lethal reactions, in which extensive hyphal evacuation occurred in cells where clamps were attached, were seen in matings 9 X 10 and 3 X 5.

**10C. *MARASMIUS PYRRHOCEPHALUS*** Berk.

Specimen utilized: North Carolina, Swain Co., GSMNP, Kephart Prong Trail, 8.VI.89, coll. SAG, det. SAG, field no. 1999 (TENN no. 48760).

As illustrated (fig. 10C), the mating system of *M. pyrrhocephalus* is tetrapolar (bifactorial). Of ten single-spore isolates crossed, nos. 5 and 3* represented $A_5B_5$, nos. 9* and 2 represented $A_6B_6$, nos. 4 and 10* represented $A_6B_5$, and nos. 1, 6*, 7, and 8 represented $A_5B_6$.

Compatible matings exhibited overgrown undifferentiated reactions at the zone of contact. Hyphae of compatible matings were white to slightly cinnamon brown and appressed around inoculum plugs while peripheral hyphae was fluffy to cottony cinnamon brown to sometimes white. Colonies of compatible matings formed a very distinctive "heart-shaped" area of white appressed mycelium surrounded by cinnamon brown aerial hyphae. Clamp connections were observed in both areas. A few matings showed abundant clamp connections at the contact zone (2 X 3, 4 X 6, 4 X 7). Nuclear migration was not recorded.

Incompatible matings showed three types of reactions: 1) overgrown, undifferentiated reactions; 2) "flat" reactions; and 3) "barrage" reactions. These reactions were distinctive in both obverse and reverse views. Mating type assignments were made in accordance with interpretation of mating reactions. Incompatible matings exhibited appressed to slightly fluffy, white to cinnamon brown hyphae. Usually, peripheral hyphae of only one isolate of incompatible matings showed significant hyphal coloration.

**Commentary:** Morphology of mated colonies was similar to isolate no. 2711.

**10D. *MARASMIUS PYRRHOCEPHALUS*** Berk.

Specimen utilized: North Carolina, Macon Co., Highlands Biological Station, nature trail, 9.VI.89, coll. SAG, det. SAG, field no. 2711 (TENN no. 48752).

As illustrated (fig. 10D), the mating system of *M. pyrrhocephalus* is tetrapolar (bifactorial). Of ten single-spore isolates crossed, nos. 1*, 3, and 8 represented $A_6B_7$, nos. 2*, 4, 5, and 6 represented $A_8B_8$, nos. 7* and 10 represented $A_6B_8$, and no. 9* represented $A_8B_7$.

Compatible matings exhibited colony morphologies similar to those of collection no. 1999. Clamp connections were observed on both aerial and submerged hyphae. One compatible mating (9 X 7) showed few clamp connections at the contact zone while other compatible matings (3 X 4, 3 X 5, 3 X 6) had abundant clamps scattered about the zone of initial contact.

Incompatible matings showed colony reactions and macromorphology similar to matings of other collections of *M. pyrrhocephalus*.

**Commentary:** This isolate (no. 2711) was very similar to isolate no. 1999 with respect to culture morphologies. In particular, the "heart-shaped" appearance of compatible matings. Two matings (5 X 7, 4 X 5) exhibited many slender hyphae which wrapped around a single broader hypha in a manner consistent with parasitism. Upon further investigation, it was determined that all hyphae within these matings were those of *M. pyrrhocephalus*.

## *MARASMIUS* sect. *SICCI*

## series *HAEMATOCEPHALI*

### 11. *MARASMIUS FLORIDANUS* Murrill

Specimen utilized: field no. ASM 5707 (TENN no. 00000)

As illustrated (fig. 11), the mating system of *M. floridanus* is bipolar (unifactorial). Of twelve single-spore isolates crossed, nos. 1, 2*, 3, 4, 5, 6, 8, and 9 were arbitrarily designated $A_1$ and nos. 7, 10*, 11, and 12 were designated $A_2$.

In compatible matings, nuclear migration was variable. In some matings nuclear migration was reciprocal (1 X 7, 2 X 10, 2 X 7, 4 X 12, 5 X 10, 5 X 12, 6 X 10, 8 X 10, 8 X 7), some matings formed clamps only at the zone of contact (1 X 11, 1 X 12, 3 X 12, 3 X 7, 4 X 10, 4 X 11, 4 X 7, 5 X 11, 5 X 7, 6 X 11, 9 X 7), and some matings showed unilateral nuclear migration (10 X> 1, 11 X> 2, 2 X> 12, 10 X> 3, 11 X> 3, 12 X> 6, 7 X> 6, 11 X> 8, 8 X> 12, 10 X> 9, 11 X> 9, 12 X> 9). No obvious macroscopic manifestation of dikaryotization was observed, both compatible and incompatible matings exhibiting white, "stringy," fluffy, thick hyphae extending from inoculum to white, appressed, to slightly raised slender hyphae at the Petri dish periphery.

Some compatible matings (2 X 7, 3 X 11) possessed abundant clamp connections at the zone of contact while other matings (1 X 11, 3 X 12, 3 X 7, 4 X 11, 5 X 7, 6 X 11, 9 X 12) showed few clamp connections scattered about the zone of contact.

**Commentary:** Strain nos. 3, 4, 8, and 10 diffused a light pink

color into the agar, readily visible in reverse view, but less obvious from obverse.

**12A. *MARASMIUS SICCUS*** (Schw.) Fries

Specimen utilized: Japan, Tochigi Pref., 28.IX.89, coll. RHP, det. DED, field no. 2336 (TENN no. 48747).

As illustrated (fig. 12A), the mating system of *M. siccus* is bipolar (unifactorial). Of twelve single-spore isolates crossed, nos. 2, 3, 7*, 9, 10, and 12 were arbitrarily designated $A_1$ and nos. 4, 8*, 11, 13, and 14 were designated $A_2$.

In all compatible matings, nuclear migration, was measured three days after hyphae from mated single-spore isolates came in contact, clamp connections were seen only at the zone of contact with the exception of matings 4 X 12 and 10 X 11, which seemed to show mutual nuclear migration. At ten days after initial contact of hyphae from respective single-spore isolates, mutual nuclear migration was seen in compatible matings except the following in which matings showed unilateral nuclear migration: 2 X> 8, 7 X> 8, 8 X> 10, 13 X> 10, 5 X> 13, 14 X> 7, 9 X> 14, 10 X> 14, and 4 X> 7. No obvious macroscopic manifestation of dikaryotization was observed. All matings had white, submerged, hyphae, with little or no aerial growth.

No obvious macroscopic manifestation of incompatibility was observed, macromorphology of incompatible matings being indistinguishable from compatible matings.

**12B. *MARASMIUS SICCUS*** (Schw.) Fries

Specimen utilized: North Carolina, Haywood Co., Harmon Den, 18.IX.88, coll. DED, det. DED, field no. DED 4714 (TENN no. 0000).

As illustrated (fig. 12B), the mating system of *M. siccus* is bipolar (unifactorial). Of fifteen single-spore isolates crossed, nos. 1, 2*, 3, 7, 8, 13, and 15 were arbitrarily designated $A_1$ and nos. 4*, 5, 6, 9, 10, 11, 12, and 14 were designated $A_2$.

Both compatible and incompatible matings exhibited white, appressed hyphae with no obvious macroscopic manifestation of dikaryotization. Nuclear migration and abundance of clamp connections were not recorded.

**12C. *MARASMIUS SICCUS*** (Schw.) Fries

Specimen utilized: Ohio, Loraine Co., 8 mi. west of Oberlin, vic. Girl Scout Camp, 11.IX.89, coll. DED, det. DED, field no. DED 4956 (TENN no. 00000).

As illustrated (fig. 12C), the mating system of *M. siccus* is bipolar (unifactorial). Of ten single-spore isolates crossed, nos. 1, 4, 5*, 7, 9, and 10 were $A_3$ and nos. 2, 3*, 6, and 8 were $A_4$.

**Commentary:** Nuclear migration and abundance of clamp connections were not noted, but only a few well-developed clamps were observed and mycelial growth was slow, as was time to manifest compatibility. Many hooked diverticulate projections, which appeared like clamp connections, were observed along the length of hyphae, so analysis required high magnification observation.

**13A. *MARASMIUS PULCHERRIPES*** Peck

Specimen utilized: Tennessee, Blount Co., GSMNP, 1 mi. past Park Visitors' center, 1.VIII.89, coll. SAG, det. SAG, field no. 2127 (TENN no. 48758).

As illustrated (fig. 13A), the mating system of *M. pulcherripes* is bipolar (unifactorial). Of eight single-spore isolates crossed, nos. 1, 2, 3, 4, 5*, and 8 were arbitrarily designated $A_3$ and nos. 6 and 9* were designated $A_4$.

Analysis of nuclear migration was not undertaken because clamp connections were often inconspicuous and difficult to observe.

No obvious macroscopic manifestation of dikaryotization was observed. All matings had morphologies similar to collection no. 2779, specifically hyaline to pale white to dirt-brown submerged hyphae with little or no aerial growth.

**Commentary:** Unlike matings of collection no. 2779, no aberrant clamp connections were observed: all clamps were of normal medallion type. Matings 2 X 3 and 1 X 6 showed bent hyphal branches resembling false clamp connections, seen in both compatible and incompatible matings. Hyphae had many diverticulate branches and oil droplets which appeared much like clamp connections, so analysis required high magnification observation. Lethal reactions, where extensive hyphal evacuation occurred in cells which clamps attached, were seen in matings 1 X 6 and 8 X 9.

**13B. *MARASMIUS PULCHERRIPES*** Peck

Specimen utilized: Georgia, Rabun Co., vic. Warwoman Dell Picnic

Area, 18.VII.89, coll. SAG, det. SAG, field no. 2779 (TENN no. 48750).

As illustrated (fig. 13B), the mating system of *M. pulcherrripes* is bipolar (unifactorial). Of eleven single-spore isolates crossed, nos. 2*, 3, 4, 6, and 7 were arbitrarily designated $A_1$ and nos. 1, 5*, 8, 9, 10, and 11 were designated $A_2$.

Testing of nuclear migration was not undertaken, for reasons stated under no. 13A.

No obvious macroscopic manifestations of dikaryotization were observed. All matings had undifferentiated contact zones, consisting of hyaline to white to dirt-brown submerged hyphae with little or no aerial growth.

**Commentary:** Clamp connections were of various forms in this mating, ranging from typical medallion type to "loop-like" medallion clamps and abrupt assymetrical clamps (2 X 9, 4 X 9, 3 X 9) to normal medallion clamps with a hyphal branches extending off the apex of respective clamps (7 X 8, 4 X 8, 1 X 4). Many matings (6 X 3, 6 X 9, 6 X 10, 2 X 4, 4 X 7, 5 X 8, 8 X 10, 1 X 10) possessed bent hyphal branches resembling false clamp connections, seen in both compatible and incompatible matings. Hyphae had many diverticulate branches and oil droplets scattered throughout mated colonies, appearing much like clamp connections. A lethal reaction, where extensive hyphal evacuation occurred in cells which clamps attached, was seen in the compatible mating 6 X 11.

## *MARASMIUS* sect. *SICCI*

### ser. *LEONINI*

**14. *MARASMIUS FULVOFERRUGINEUS*** Gilliam

Specimen utilized: Georgia, Rabun Co., Warwoman Dell Picnic Area, 28.VIII.89, coll. RHP, det. RHP, field no. 2099 (TENN no. 48464).

As illustrated (fig. 14), the mating system of *M. fulvoferrugineus* is bipolar (unifactorial). Of ten single-spore isolates crossed nos. 2, 3, 5*, 7, 12, and 18 were arbitrarily designated $A_1$ and nos. 6, 9*, 10, and 19 were designated $A_2$.

In all compatible matings, nuclear migration was reciprocal. Numerous clamp connections were scattered throughout aerial hyphae with only a few clamps observed on submerged hyphae.

Incompatible matings were scored by the absence of clamp connections in the zone of contact as well as areas on each side of this zone. No obvious macroscopic manifestation of dikaryotization was observed, and macromorphology of incompatible matings was indistinguishable from compatible matings. All matings possessed hyaline to white, appressed to slightly raised hyphae.

# CHAPTER VI

# RESULTS OF

# INTERCOLLECTION MATINGS

## *MARASMIUS* sect. *MARASMIUS*

### *MARASMIUS ROTULA*

As illustrated (fig. 15), intercollection matings using tester strains from collections of *M. rotula* (field nos. 1809, NC; 1816, NC; 2080, GA; 2726, TN; 2760, NC) showed complete (100%) compatibility and mating types were assigned accordingly.

All matings showed overgrown undifferentiated mating reactions with white fluffy to cottony hyphae. Clamps were abundant in all matings. Nuclear migration was not analysed.

## *MARASMIUS* sect. *ALLIACEI*

### *MARASMIUS PYRRHOCEPHALUS*

As illustrated (fig. 16), intercollection matings using tester strains from collections of *M. pyrrhocephalus* (field nos. 2419, IL; 1992, NC; 1999, GSMNP; 2711 NC) showed universal compatibility with the exception of the following crosses from mating 1999 (GSMNP) X 2711 (NC): 1 X 10, 7 X 10, 1 X 9, and 7 X 9 (respectively). These matings showed macromorphologies consistent with the "flat" phenomenon and no clamp connections were observed, therefore, common A factors are presumed.

All compatible matings showed abundant clamp connections and mated colonies had overgrown, undifferentiated contact zones. All compatible

matings showed brown pigmented hyphae around the periphery of colonies while areas around inoculum blocks showed hyaline to white hyphae.

## *MARASMIUS* sect. *SICCI*

### series *HAEMATOCEPHALI*

#### *MARASMIUS SICCUS*

As illustrated (fig. 17,18), tester strain intercollection mating 4956 (OH) X 4714 (NC) showed universal compatibility while intercollection matings 2336 (Japan) X 4956 (OH) and 2336 (Japan) X 4714 (NC) showed partial compatibility.

When all available strains from collection nos. 4714 and 2336 were crossed, 33.3% compatibility was observed (fig. 17). These matings seemed to show a strain specific compatibility. Strains 2, 13, and 14 from collection no. 2336 formed abundant clamps with all strains from 4714. Most other compatible matings formed few clamps at the contact zone. When all spores from collection no. 2336 were mated with spores from collection no 4956, 36.6% compatibility was observed (fig. 18). These matings seemed to show a strain specific compatibility.
All matings had white, submerged hyphae with little or no aerial growth, and overgrown, undifferentiated contact zones. No obvious macroscopic manifestations of dikaryotization were observed.

**Commentary:** Matings were examined weekly for presence or absence of clamp connections. Clamp connections were not observed until about 21 days after contact. Approximately 28 days (4 weeks) were required before clamp connections were observed in matings 2336 (Japan) X 4714

(NC) and 2336 (Japan) X 4956 (NC). Matings 4956 (OH) X 4714 (NC) showed evidence of compatibility after seven days. It was evident that strains 2336/2, 13, and 14 produced abundant clamp connections in compatible matings with strains of collection 4714, while crosses involving strains 2336/4, 8, and 9 showed fewer clamps.

***MARASMIUS PULCHERRIPES***

As illustrated (fig. 19), intercollection crosses from collections of *M. pulcherripes* (field nos. 2127, GSMNP; 2779, GA) showed complete compatibility.

All matings showed overgrown, undifferentiated contact zones with hyaline, white, to dirt brown submerged hyphae with little to no aerial growth. Some matings (1 X 2, 9 X 2, 5 X 3, 9 X 5, 1 X 5, 1 X 8, 5 X 8) showed few clamps scattered over the contact zone while all other matings had numerous clamps scattered over this zone.

**Commentary:** Hyphae had many diverticulate branches and oil droplets easily mistaken for clamp connections. Clamps were often small and inconspicuous and high magnification was required to verify their presence.

# CHAPTER VII

# DISCUSSION

A total of fourteen species, representing six sections of *Marasmius* were studied in this project. Eight species are reported as bipolar, five tetrapolar, and one as inconclusive. Desjardin's (1989) regional flora of the genus outlined sectional concepts in *Marasmius* and when mating system data from my study, as well as data from previous researchers, are compared to Desjardin's (1989) work, sections appear consistent with regard to mating system type.

## SECTIONAL CONSISTENCY:

In section *Androsacei*, only one species, *M. androsaceus*, was obtained in single-spore culture, but was found to be tetrapolar, supporting the reports by Piroard (1956), Terra (1953), and Yen (1950a,b,d) cited by Lamoure (1989). It is the only species in the section whose mating system is known. Mating system analysis of other species in this section, therefore, is necessary in order to draw conclusions on sectional consistency of mating systems.

From limited data, section *Marasmius* seems to be predominately tetrapolar. In this study, *Marasmius SP.* (undetermined Japanese species in section *Marasmius*) and *M. rotula* (5 collections) were found to be tetrapolar. Lamoure (1989) reported that Terra (1953) and Yen (1950b,d) also found *M. rotula* to be tetrapolar. Moreover, Lamoure (1960, 1989) reported the European taxa *M. bulliardii* and *M. limosus* to have tetrapolar mating systems. *Marasmius graminum*, also a member of section *Androsacei* fruiting within the geographical range of my study,

has not yet been analyzed. Thus, the only four species analyzed in this section show tetrapolarity, indicating probable tetrapolar consistency.

In the southern Appalachians, section *Epiphylli* consists of three taxa, *M. epifagus*, *M. epiphyllus*, and *M. felix*. This study found that *M. felix* (from Illinois) is tetrapolar and Lamoure (1989) reported that Terra (1953) and Yen (1950a,b,d) found *M. epiphyllus* also to be tetrapolar. *Marasmius tremulae*, which does not fruit in this study area, has been reported as haploid parthenogenetic by Kühner (1947) and Lamoure (1958) (cf. Lamoure, 1989). So far, all taxa which occur in this study area have shown a tetrapolar mating system. The mating system of *M. epifagus* has yet to be elucidated.

The mating systems of five species in sect. *Globulares* were analyzed in this study. *Marasmius decipiens*, *M. nigrodiscus*, *M. cystidiosus*, and *M. oreades* were shown to be bipolar while *M. strictipes* remains unresolved at this time. In Lamoure's (1989) review, she cited reports by Armand (1962), Oddoux (1957), and Terra (1959) on a tetrapolar mating system for *M. collinus*. This species, not found in my study area is inconsistent with mating system data of this section. According to Desjardin (pers. comm.), this taxon produces clampless hyphae and probably is not be a member of *Marasmius*. Finally, Mallet and Harrisons (1988) and Burnett and Evans (1966) concluded that *M. oreades* was bipolar.

Taxa of section *Globulares* seem to differ physiologically from other sections in *Marasmius*. When self-crosses of some taxa of this section (*Marasmius dicipiens*, *M. nigrodiscus*, and *M. strictipes*) were

performed on 1.5% malt extract agar, compatible crosses were unpatterned and less common than in crosses on 0.5% malt extract agar. It seems that some otherwise compatible monokaryons were reluctant to dikaryotize on the higher nutrient medium but dikaryotized well on a weaker nutrient medium. Exceptions to these observations were *M. oreades* and *M. cystidiosus*, which dikaryotized in conclusive patterns on both media and *M. strictipes* which showed randomized mating data on both media. This section requires further research to determine which media support the best results, i. e. distinct patterns of compatibility and abundant clamps. With the exception of the problematic species *M. collinus*, this section seems predominately bipolar.

Section *Alliacei* includes three taxa found in the southern Appalachians; *M. pyrrhocephalus*, *M. scorodonius*, and *M. copelandii* var. *olidus*. In this study, *M. pyrrhocephalus* (4 collections) was found to be tetrapolar. Several other species in this section were listed in Lamoure's summary (1989) as tetrapolar. She noted that Kühner (1945), Piroard (1956), Terra (1953), and Yen (1950c,d) found *M. scorodonius* to be tetrapolar, Piroard (1956), Terra (1959), and Yen (1950 a,b) found *M. alliaceus* to be tetrapolar, Lamoure (1989) found *M. epidryas* to be tetrapolar, and Bastouill (1977) and Viale (1961) found *M. prasiomus* to be heterothallic with no indication of mating type listed. In my study, *M. copelandii* var. *olidus* was not collected, and its mating system remains unknown at this time. The tetrapolar mating system of the four taxa listed above indicate a consistency of mating systems in section *Alliacei*.

In section *Sicci*, mating systems of taxa from two series, *Haematocephali* and *Leonini*, have been elucidated. In series *Haematocephali*, *M. floridanus*, *M. siccus*, and *M. pulcherripes* were found to be bipolar.

*Marasmius sullivantii* was collected but subsequent "monospore" isolates were all clamped. Spores of dried specimens were examined using epiflourescence microscopy and the nuclear flourescent stain DAPI (4'-6-diamidino-2-phenylindole). Spores appeared to contain one nucleus, but, many spores seemed attached to one another. This adhesion of spores to one another may have resulted in multiple spores being harvested during single spore isolation attempts. If this is a bipolar species, the chance of harvesting two spores of opposite (compatible) mating type ($A_1 + A_2$) is 50%. Also, possible, however, is that the taxon may be homothallic. To test these hypotheses, fresh basidiocarps should be collected and spores plated out using a surfactant (i. e. "Tween 80") to increase dispersability, and spores from fresh basidiocarps should be observed with nuclear fluorescent stain to confirm nuclear condition.

In series *Leonini*, *M. fulvoferrugineus* was the only taxon tested and this species was found to be bipolar.

Lamoure (1989) reported that Armand (1962) and Vandendries (1936) found *M. cohaerens*, a member of section *Sicci* series *Spinulosi*, to be bipolar. All these data indicate section *Sicci* to be consistently bipolar section.

**INTERCOLLECTION MATINGS:**

Intercollection matings were made with collections of putatively conspecific morphological taxa to test morphological species concepts and analyze distribution of mating type alleles. Intercollection matings were possible in four species: *M. rotula*, *M. pyrrhocephalus*, *M. siccus*, and *M. pulcherripes*.

Tester strains of five collections of *M. rotula* were crossed in all combinations and results showed complete intercompatibility. These data indicate a heterothallic multi-allelic tetrapolar mating system. Ten alleles at the A and B loci were identified from these geographically separated collections. The presence of multiple alleles at each locus encourages outbreeding between populations and therefore increases genetic diversity. It is assumed that many more alleles exist at both the A and B loci. According to these data, understanding the high degree of error due to the extremely small sample size, the outbreeding efficiency is .80 [$(1-1/N_A+1/N_B)$ where $N_A$ is the number of alleles at the A locus and $N_B$ is the number of alleles at the B locus] (Raper, 1966). Because of a tetrapolar mating system in this taxon, inbreeding is reduced but outbreeding may also be reduced if an extensive series of alleles are not present at both the A and B loci (Raper, 1966). Because of the lack of study on spore dispersal in nature and inability to fruit many taxa in culture, it is nearly impossible to assess the detrimental effects of high levels of inbreeding (Raper, 1966).

Intercollection matings of *M. pyrrhocephalus* showed interesting results. A common A allele was observed in matings between collections

from western North Carolina and East Tennessee, separated by approximately 35 miles. All other collections showed complete compatibility with each other. These data indicate a multi-allelic tetrapolar mating system, but the number of alleles at each locus may be rather low. Although this is a very small sample size, these data indicate an outbreeding efficiency of .73 ($1-1/N_A + 1/N_B$) (Raper, 1966).

Intercollection matings of *M. siccus* (Ohio, North Carolina, Japan) indicate that this taxon may be in the process of speciation. According to Boidin (1986), incomplete compatibility between allopatric collections may be a result of climatic changes, division of land masses, adaptation to different host species and/or adaptation to different ecological habitats. The collections used for this study were determined by Desjardin (pers. comm.) to be the same morphological species. Even though it appears that genetic divergence has taken place, the taxon has not become completely sexually polarized. Duncan (1972), in his work with *Auricularia*, used the term "microevolutionary units" to describe these partially interincompatible units. Further research on this taxon is needed in order to determine if this morphological species concept contains isolated intersterility groups ("biological species"), the amount of genetic divergence that has taken place, what environmental influence (substrate specificity, geographic isolation etc.) has contributed to this speciation process, and what type of system, if any, is controlling intersterility. With the limited data contained here, it is apparent that genetic reproduction

barriers have been erected earlier in the speciation process than morphological differentiation (Kemp 1975).

The patterns of compatibility in these intercollection crosses (figs. 17, 18) seem to show strain-specific compatibility patterns. These data indicate that "factors controlling mating within a species are different from those which determine whether or not a hybrid mycelium between two strains will be established" (Bresinsky et. al., 1987). According to Chase and Ullrich (1990), ability to mate ("sterility/fertility" in their terminology) is under control of simple Mendelian factors and these factors (genes) are "distinct and separable from the mating-type (incompatibility) locus." As was seen in this study, some homokaryons were unable to dikaryotize even when compatibile mating type alleles were present. Analysis of the intercollection data for *M. siccus*, implied that a "sterility/fertility" system could be present. Chase and Ullrich (1990) elucidated a five-gene system determining "sterility/fertility" in *Heterobasidion annosum* and designated the two alleles at each locus "+" (the "positive" allele) and "-" (the "negative" allele). In crosses, when two + alleles were present at common genes, compatibility was allowed, but when - alleles or - and + alleles were present at a gene, no compatibility was permitted. Such a multi-factor system could operate in *M. siccus* to explain the results in figs. 17 and 18. In addition, a multi-factor system might provide an explanation for matings which exhibit only few clamps in the contact zone.

Intercollection matings with tester strains from two collections of *M. pulcherripes* (field nos. 2127, 2779) showed complete

compatibility. These data are typical of a multi-allelic bipolar mating system. The presence of multiple alleles at the mating type locus indicates an increased efficiency and chance of outbreeding, thereby maximizing genetic diversity.

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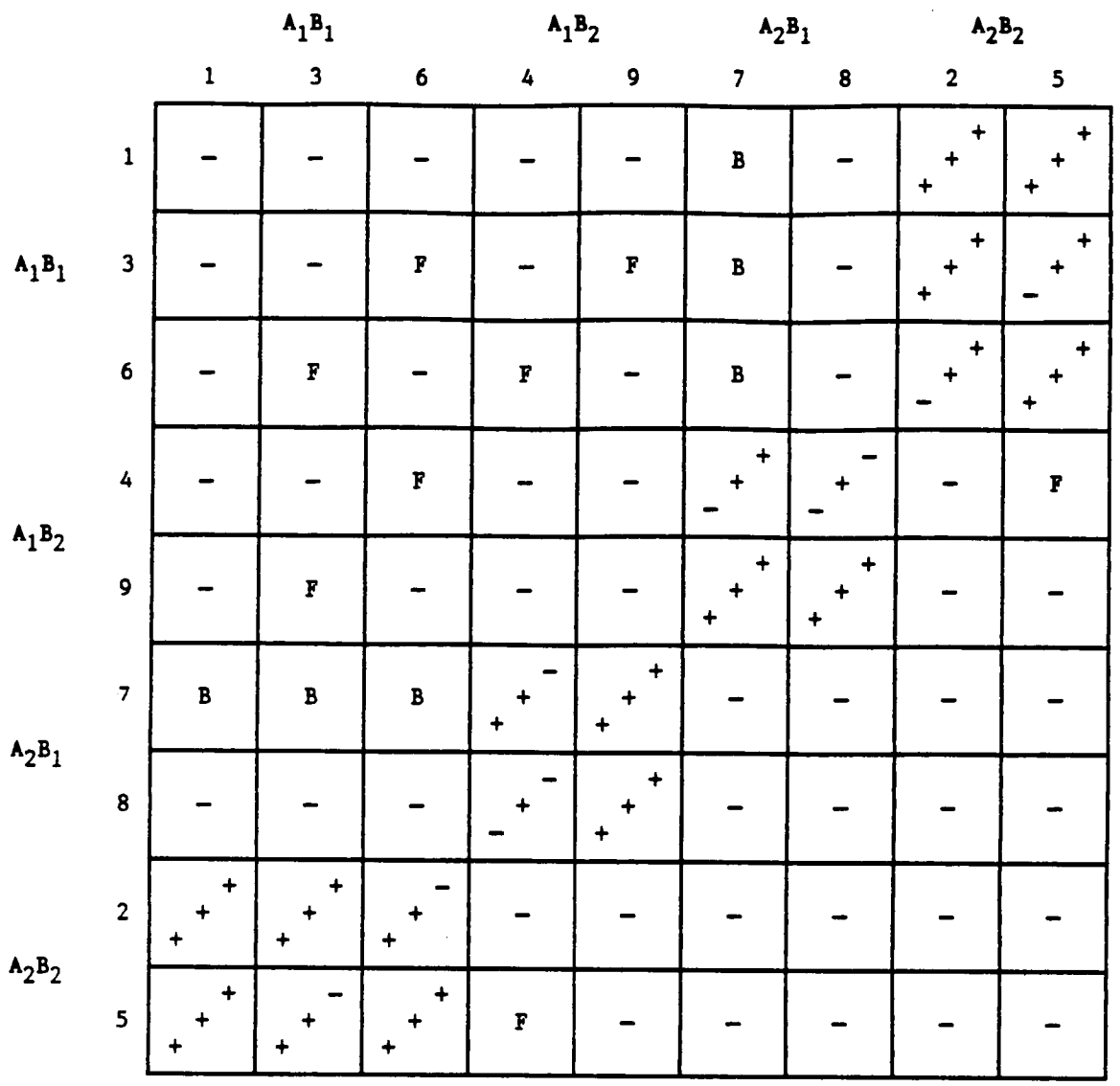
# APPENDIX

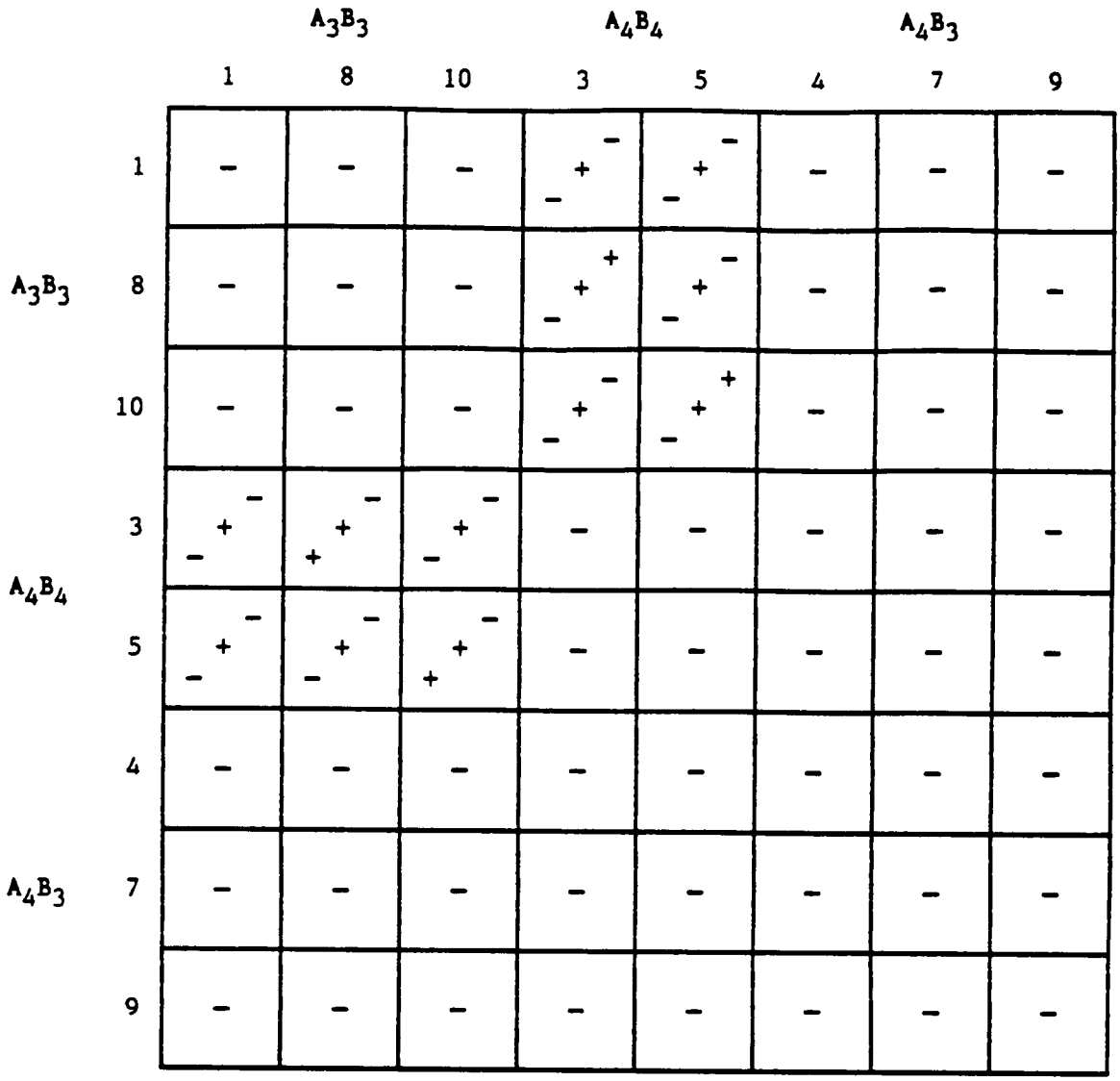
| | | $A_2B_2$ | | | $A_1B_1$ | | | $A_1B_2$ | | | $A_2B_1$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 4 | 11 | 12 | 5 | 6 | 10 | 1 | 7 | 14 | 2 |
| | 4 | − | − | − | +++ | +++ | +++ | − | − | − | − |
| $A_2B_2$ | 11 | − | − | − | +++ | +++ | +++ | − | B | − | − |
| | 12 | − | − | − | +++ | +++ | +++ | B | B | B | − |
| | 5 | +++ | +++ | +++ | − | − | − | − | − | − | B |
| $A_1B_1$ | 6 | +++ | +++ | +++ | − | − | − | − | − | − | B |
| | 10 | +++ | +++ | +++ | − | − | − | − | − | − | − |
| | 1 | − | − | B | − | − | − | − | − | − | +++ |
| $A_1B_2$ | 7 | − | B | B | − | − | − | − | − | − | +++ |
| | 14 | − | − | B | − | − | − | − | − | − | +++ |
| $A_2B_1$ | 2 | − | − | − | B | B | − | +++ | +++ | +++ | − |

**Figure 1.** Self-crosses of *Marasmius androsaceus*, no. 2705.




A. *Marasmius rotula*, no. 1809.

**Figure 2.** Self-crosses of *Marasmius rotula*.




B. *Marasmius rotula*, no. 1816.

**Figure 2.** (continued)

| | | $A_6B_6$ | | | | $A_6B_5$ | | | | $A_5B_5$ | | $A_5B_6$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 5 | 7 | 10 | 2 | 8 | 9 | 11 | 3 | 6 | 4 | 12 |
| $A_6B_6$ | 1 | - | F | - | - | - | - | - | - | + | + | B | - |
| | 5 | F | - | - | - | F | - | - | F | + | + | B | - |
| | 7 | - | - | - | - | - | - | - | - | + | + | + | + |
| | 10 | - | - | - | - | - | - | - | F | + | + | B | - |
| $A_6B_5$ | 2 | - | F | - | - | - | - | - | - | - | B | + | + |
| | 8 | - | - | - | - | - | - | - | - | - | B | + | + |
| | 9 | - | - | - | - | - | - | - | - | - | B | + | + |
| | 11 | - | F | - | F | - | - | - | - | - | B | + | + |
| $A_5B_5$ | 3 | + | + | + | + | - | - | - | - | - | - | F | - |
| | 6 | + | + | + | + | B | B | B | B | - | - | - | - |
| $A_5B_6$ | 4 | B | B | + | B | + | + | + | + | F | - | - | - |
| | 12 | - | - | + | - | + | + | + | + | - | - | - | - |

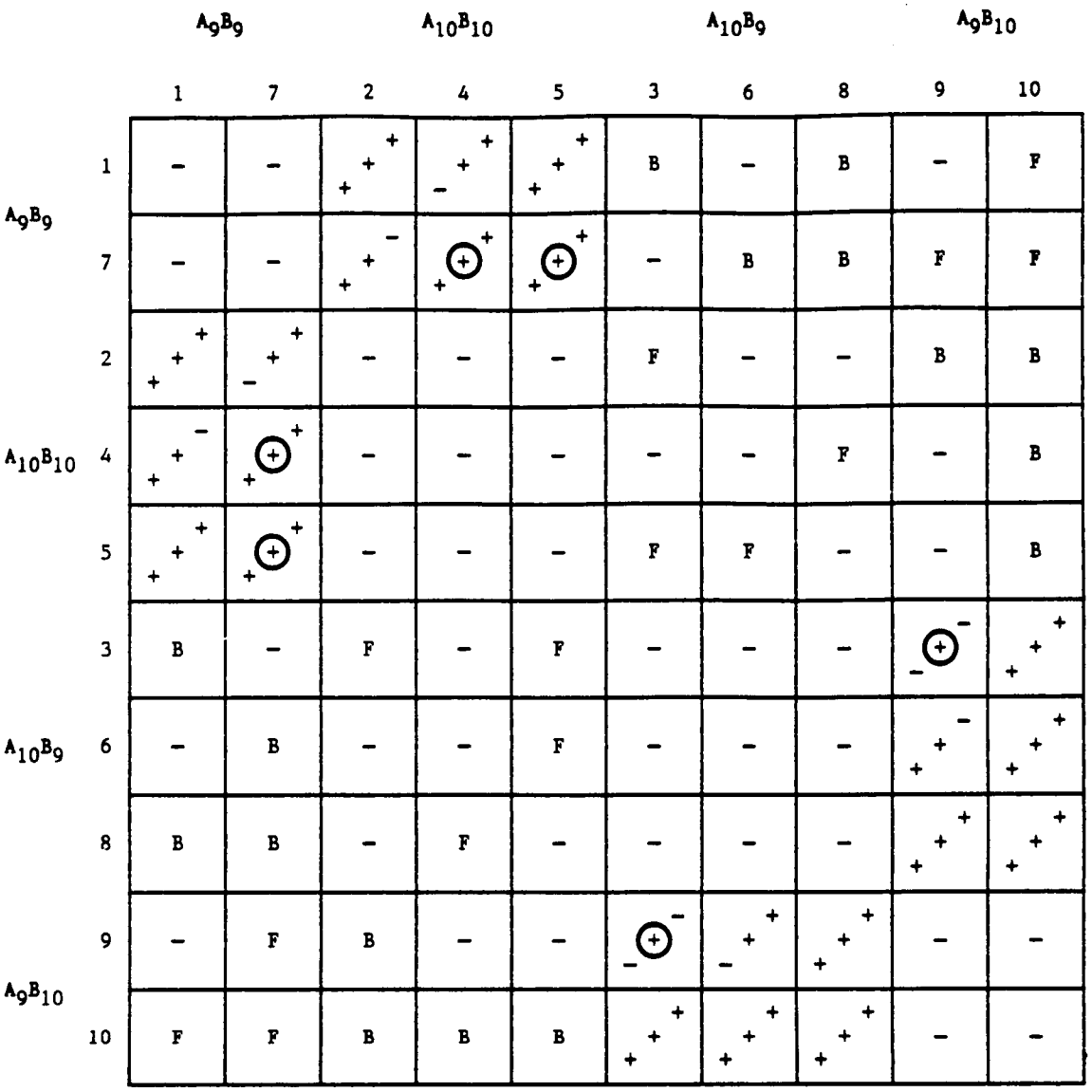
C. *Marasmius rotula*, no. 2080.

**Figure 2.** (continued)

| | | $A_7B_7$ | | | | $A_8B_8$ | | | $A_7B_8$ | | $A_8B_7$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 5 | 8 | 10 | 1 | 6 | 7 | 3 | 4 | 11 |
| $A_7B_7$ | 2 | - | - | - | - | + | + | + | F | - | B |
| | 5 | - | - | - | - | + | + | + | + | B | B |
| | 8 | - | - | - | - | + | + | + | F | B | - |
| | 10 | - | - | - | - | + | + | + | - | F | B |
| $A_8B_8$ | 1 | + | + | + | + | - | - | - | B | F | - |
| | 6 | + | + | + | + | - | - | - | B | F | F |
| | 7 | + | + | + | + | - | - | - | B | F | B |
| $A_7B_8$ | 3 | F | + | F | - | B | B | B | - | + | + |
| $A_8B_7$ | 4 | - | B | B | F | F | F | F | + | - | - |
| | 11 | B | B | - | B | - | F | B | + | - | - |

D. *Marasmius rotula*, no. 2726.

**Figure 2.** (continued)




E. *Marasmius rotula*, no. 2760.

**Figure 2.** (continued)

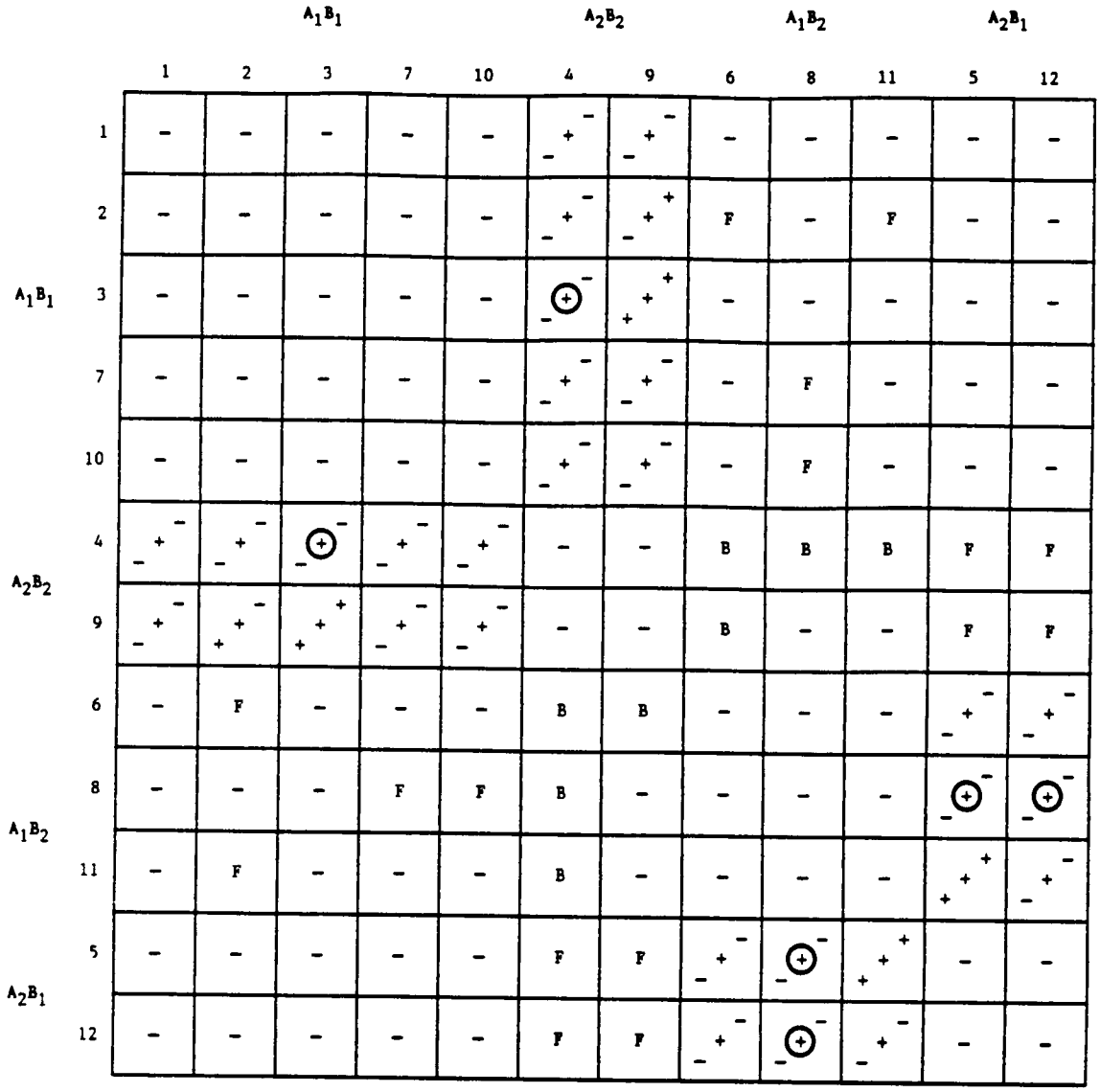



**Figure 3.** Self-crosses of *Marasmius SP.*, no. 2337.

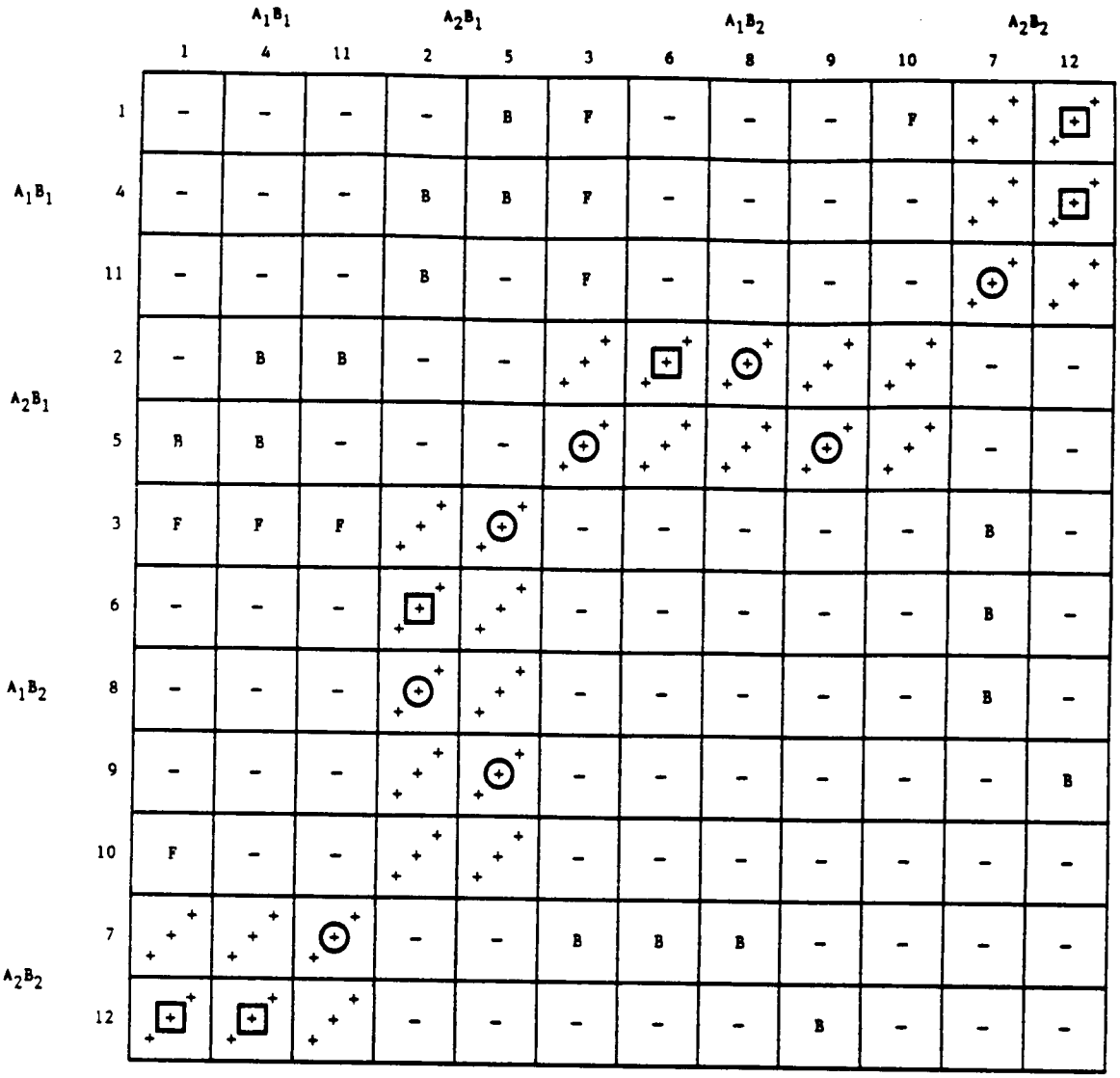
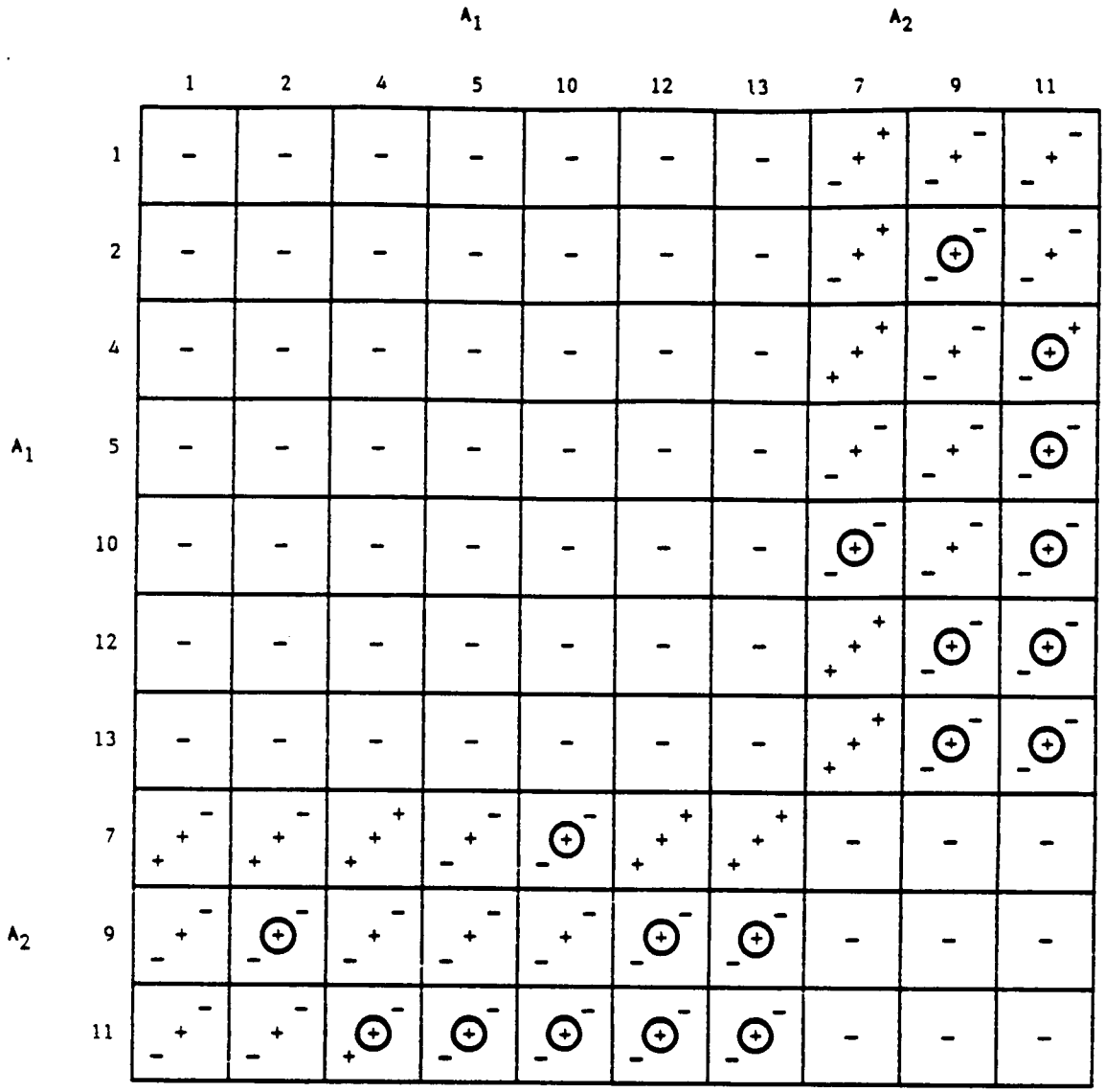
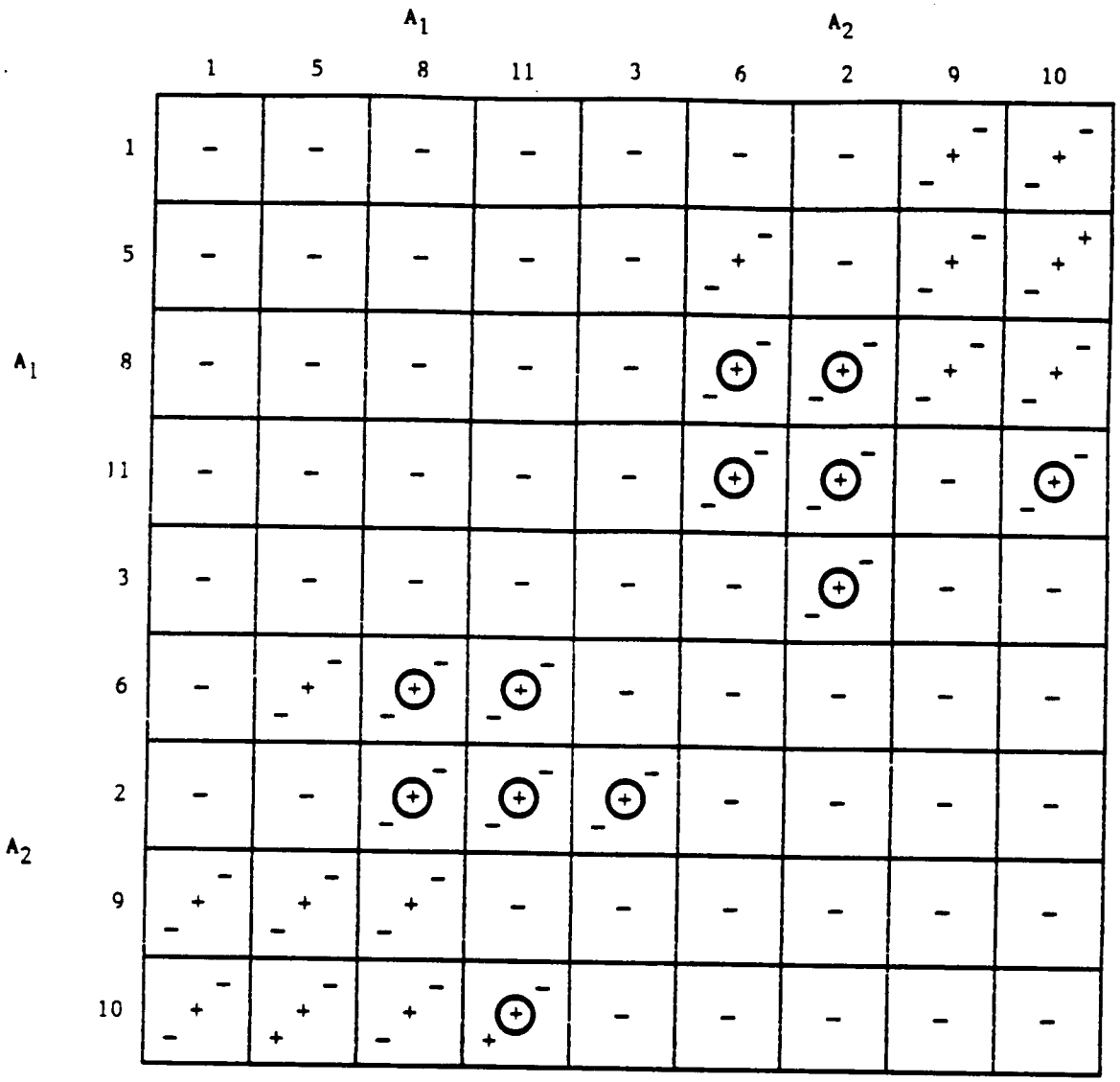



**Figure 4.** Self-crosses of *Marasmius felix*, s. n..




A. *Marasmius decipiens*, no. 2722.

**Figure 5.** Self-crosses of *Marasmius decipiens*.




B. *Marasmius decipiens*, no. 2731.

**Figure 5.** (continued)

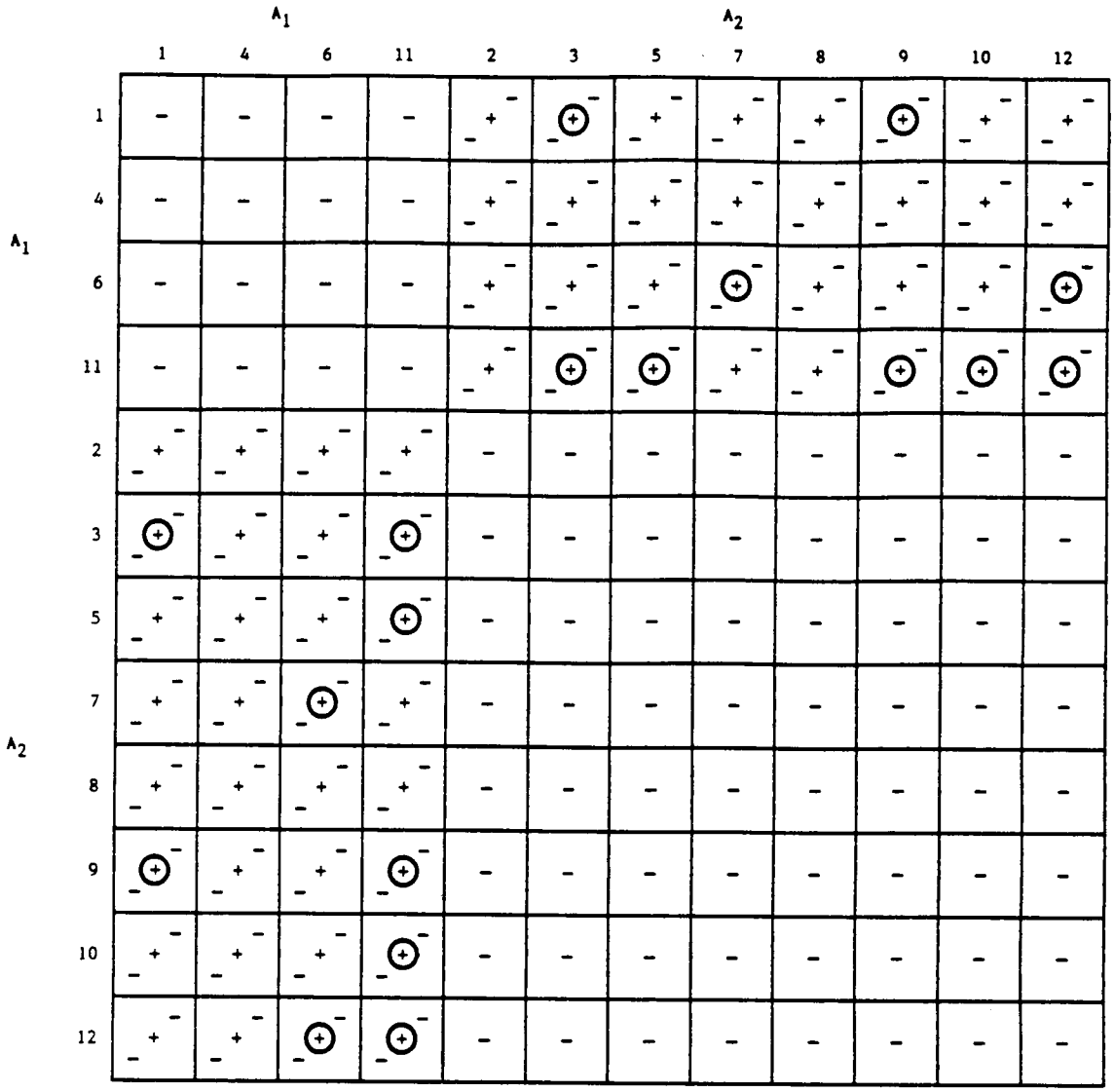



**Figure 6.** Self-crosses of *Marasmius nigrodiscus*, no. 4913.

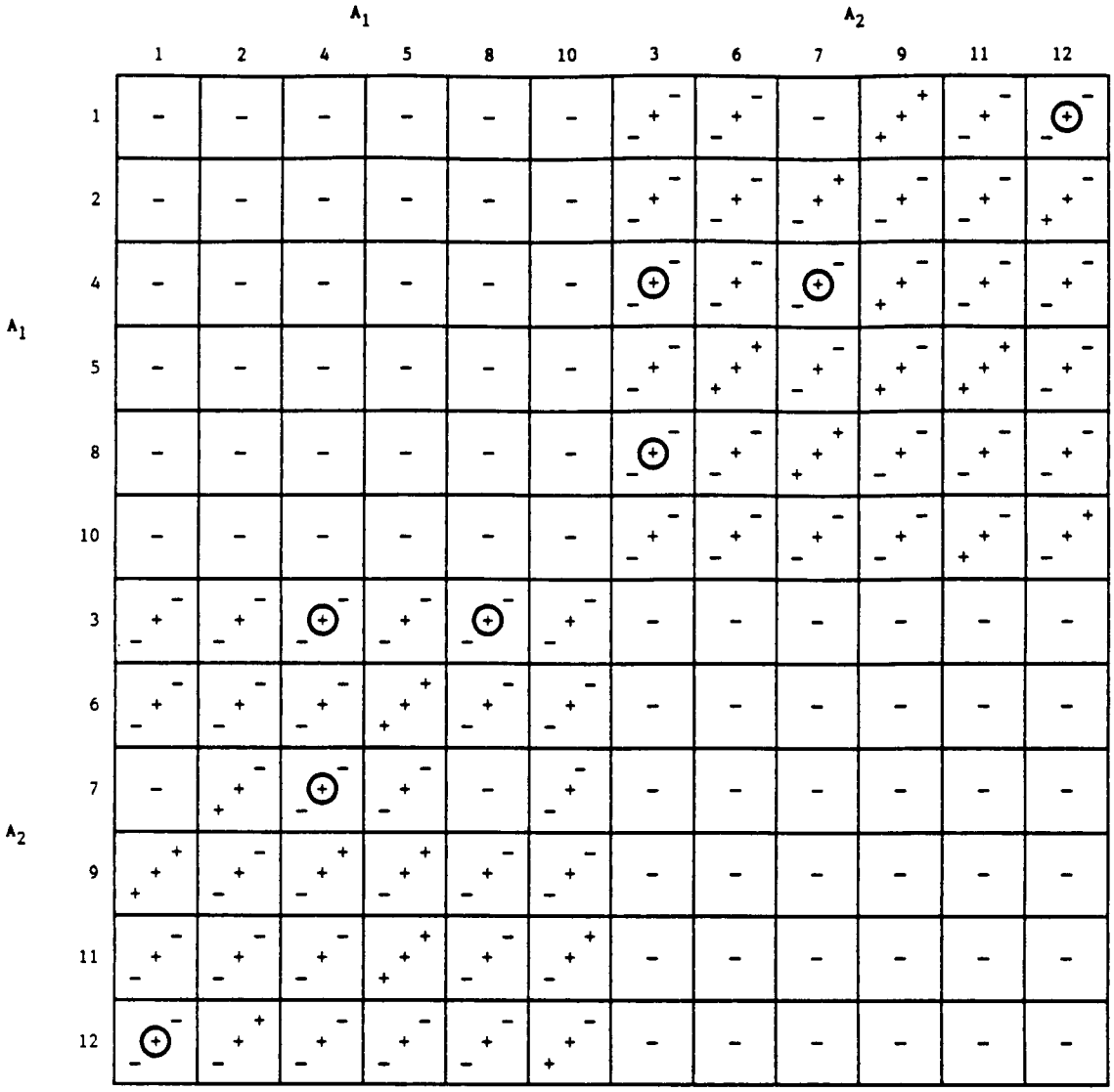



**Figure 7.** Self-crosses of *Marasmius cystidiosus*, no. 2756.

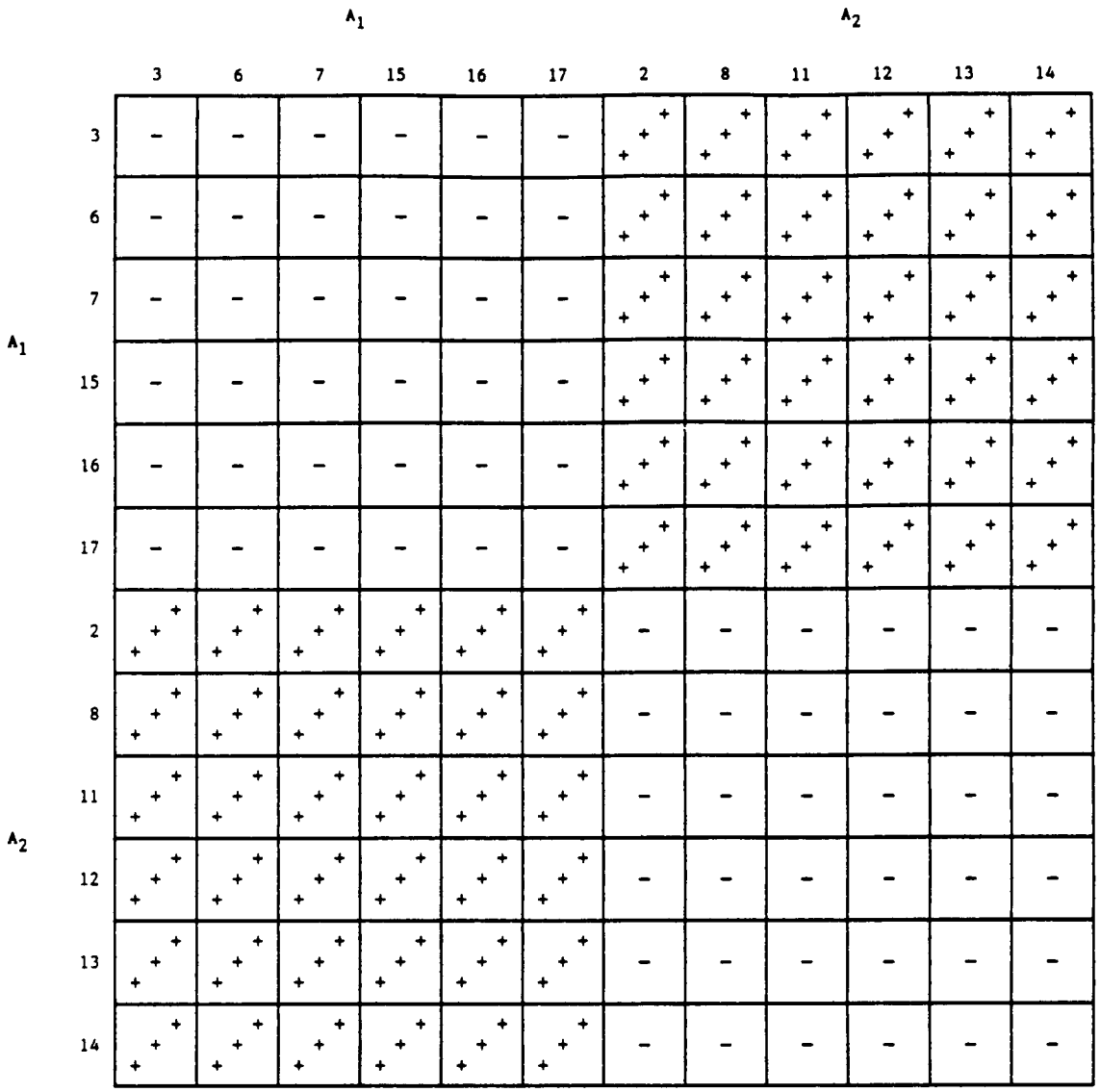
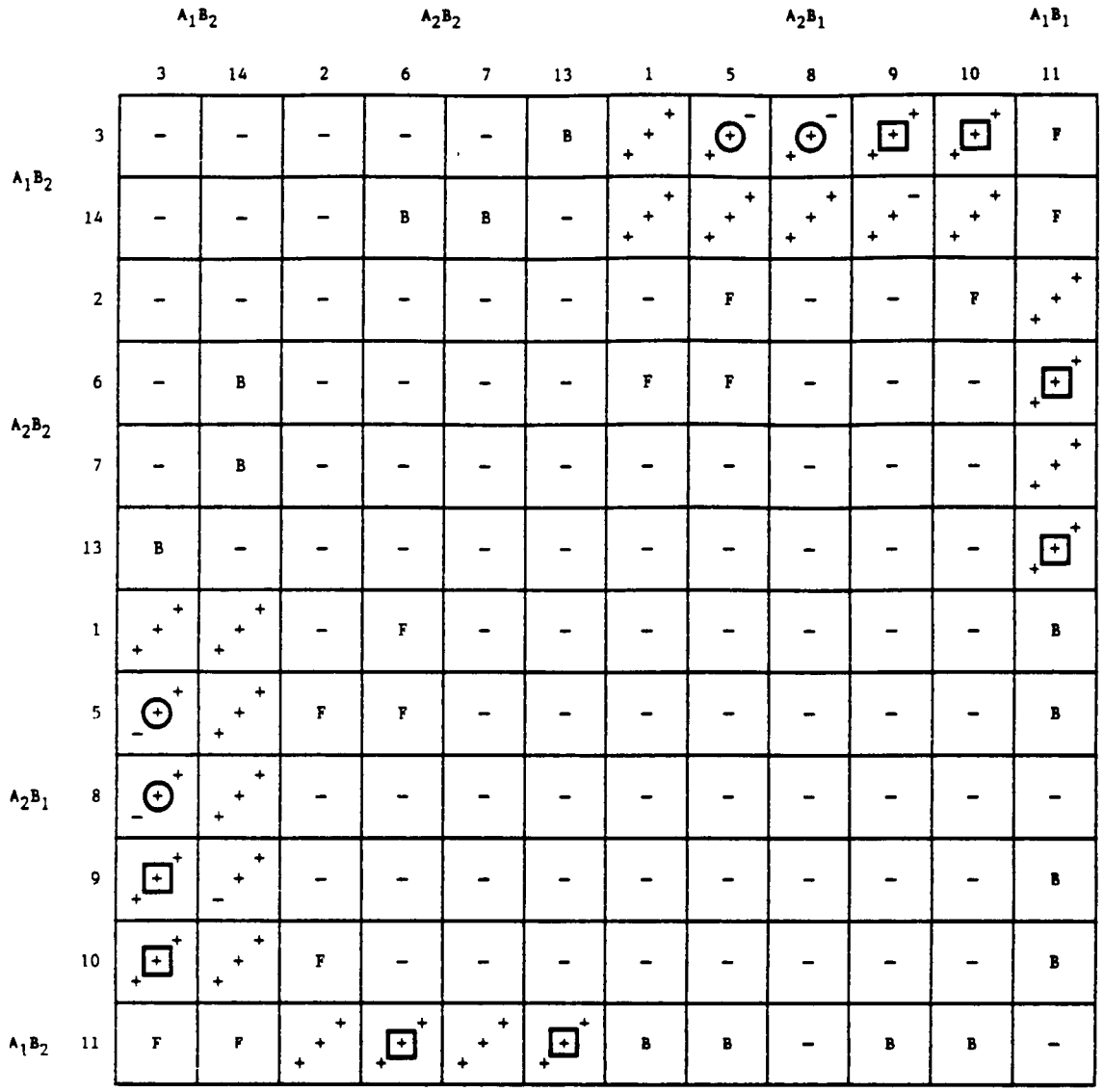



**Figure 8.** Self-crosses of *Marasmius oreades*, TJB no. 6314.

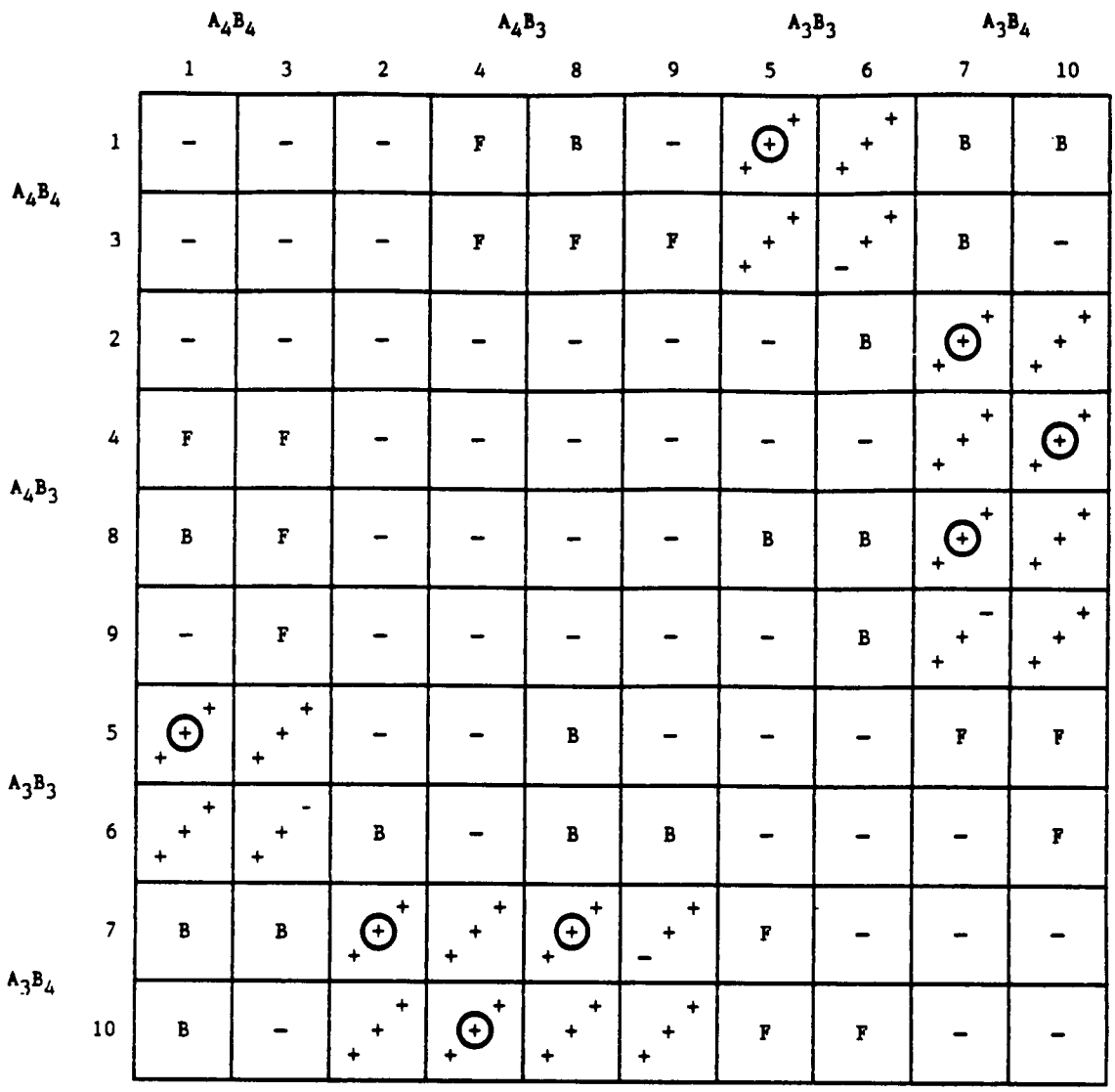
| | 1 | 2 | 11 | 3 | 12 | 15 | 17 | 9 | 4 | 10 | 8 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | - | - | B | - | - | - | - | - | - | + + + | + + + | + + + |
| 2 | - | - | - | - | - | - | B | B | - | + + + | + + + | + + + |
| 11 | B | - | F | F | - | - | - | - | - | + + + | + + + | + + + |
| 3 | - | - | F | - | - | - | - | - | B | B | + + + | + + + |
| 12 | - | - | - | - | - | - | - | - | - | - | + + + | + + + |
| 15 | - | - | - | - | - | - | B | - | - | B | + + + | + + + |
| 17 | - | B | - | - | - | B | - | - | - | + + + | - | - |
| 9 | - | B | - | - | - | - | - | - | - | + + + | - | B |
| 4 | - | - | - | B | - | - | - | - | - | + + + | B | - |
| 10 | + + + | + + + | + + + | B | - | B | + + + | + + + | + + + | - | - | - |
| 8 | + + + | + + + | + + + | + + + | + + + | + + + | - | - | B | - | - | - |
| 14 | + + + | + + + | + + + | + + + | + + + | + + + | - | B | - | - | - | - |

**Figure 9.** Self-crosses of *Marasmius strictipes*, no. 2427.




A. *Marasmius pyrrhocephalus*, no. 2419.

**Figure 10.** Self-crosses of *Marasmius pyrrhocephalus*.



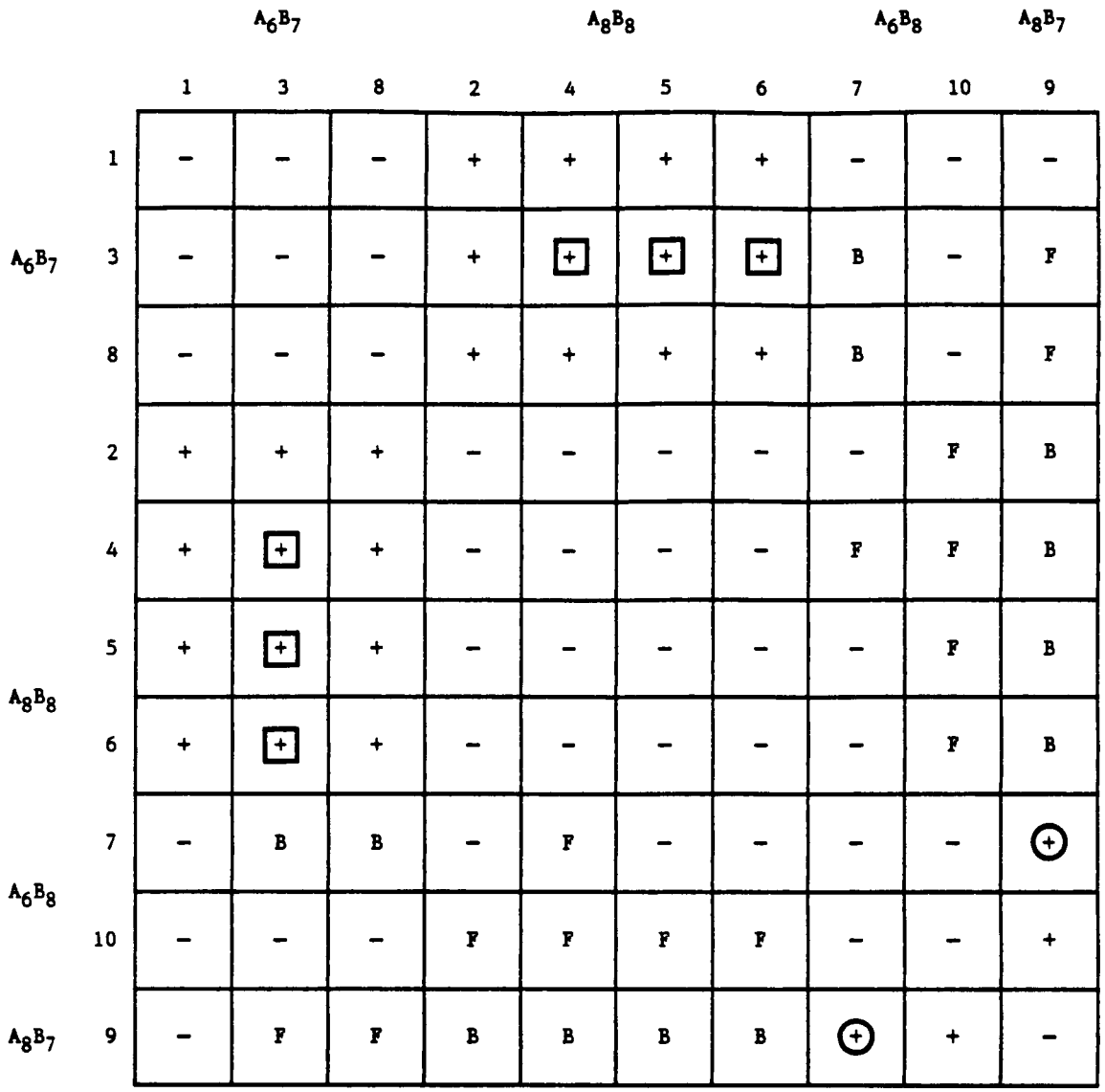

**B.** *Marasmius pyrrhocephalus*, no. 1992.

**Figure 10.** (continued)

| | | $A_5B_6$ | | | | $A_5B_5$ | | $A_6B_5$ | | $A_6B_6$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 6 | 7 | 8 | 3 | 5 | 4 | 10 | 2 | 9 |
| $A_5B_6$ | 1 | – | – | – | – | F | F | + | + | B | – |
| | 6 | – | – | – | – | – | – | + | + | – | – |
| | 7 | – | – | – | – | F | F | + | + | B | – |
| | 8 | – | – | – | – | F | F | + | + | – | – |
| $A_5B_5$ | 3 | F | – | F | F | – | – | B | B | + | + |
| | 5 | F | – | F | F | – | – | B | B | + | + |
| $A_6B_5$ | 4 | + | + | + | + | B | B | – | – | – | – |
| | 10 | + | + | + | + | B | B | – | – | – | – |
| $A_6B_6$ | 2 | B | – | B | – | + | + | – | – | – | – |
| | 9 | – | – | – | – | + | + | – | – | – | – |

C. *Marasmius pyrrhocephalus*, no. 1999.

**Figure 10.** (continued)




D. *Marasmius pyrrhocephalus*, no. 2711.

**Figure 10.** (continued)

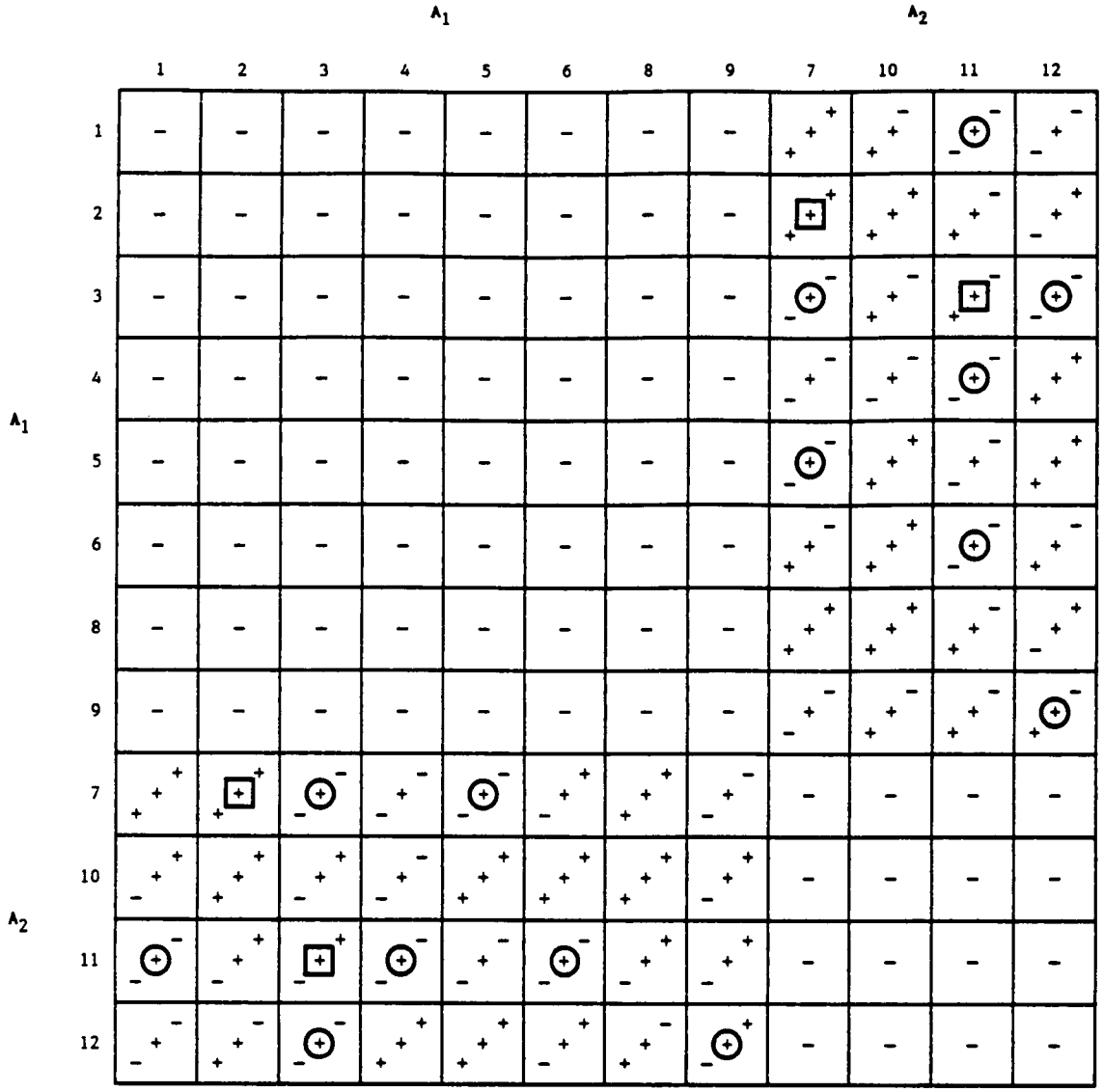
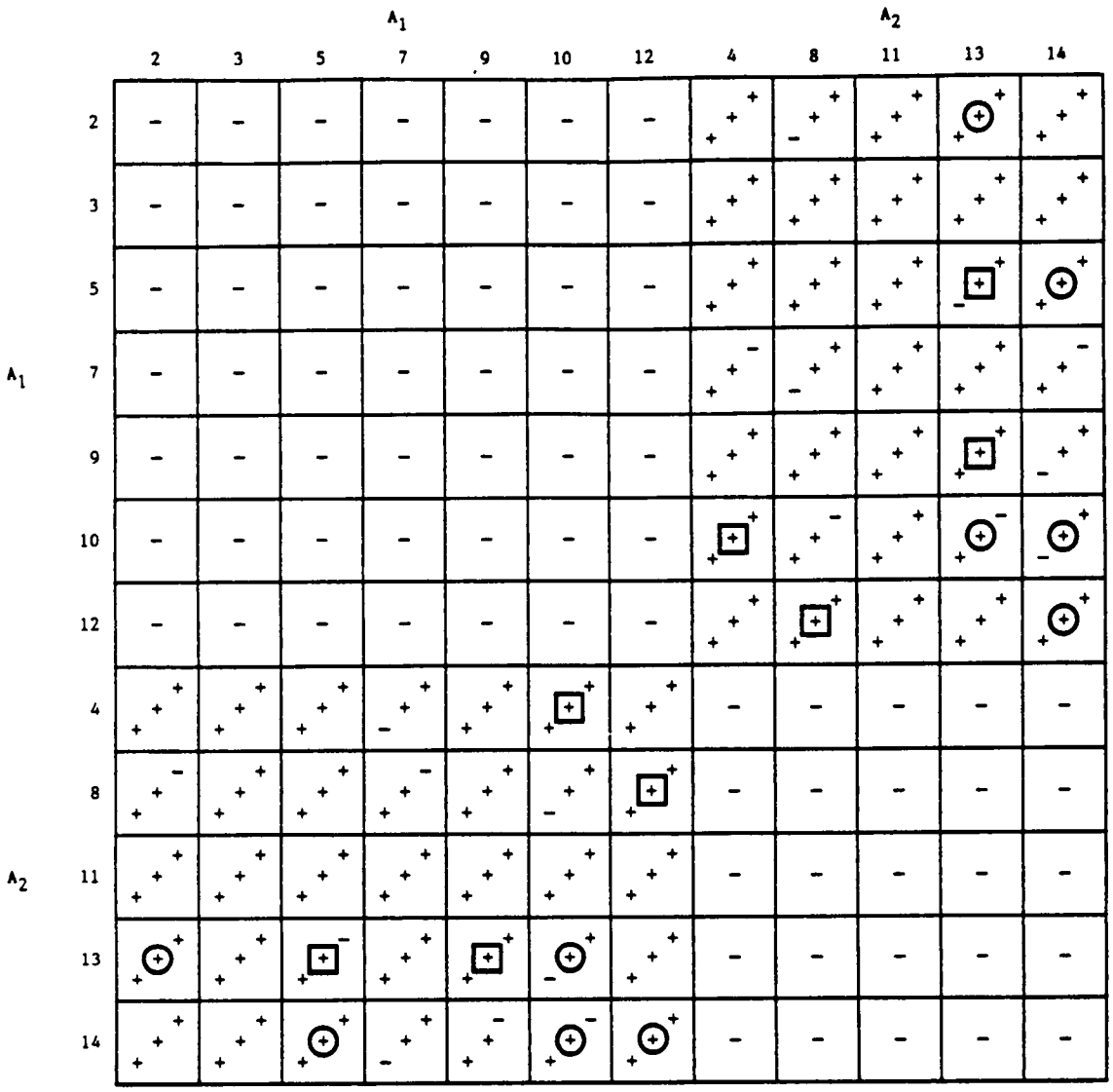



**Figure 11.** Self-crosses of *Marasmius floridanus*, no. ASM 5707.




A. *Marasmius siccus*, no. 2336.

**Figure 12.** Self-crosses of *Marasmius siccus*.

| | | $A_1$ | | | | | | | $A_2$ | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 7 | 8 | 13 | 15 | 4 | 5 | 6 | 9 | 10 | 11 | 12 | 14 |
| $A_1$ | 1 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 2 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 3 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 7 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 8 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 13 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| | 15 | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + |
| $A_2$ | 4 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 5 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 6 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 9 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 10 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 11 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 12 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |
| | 14 | + | + | + | + | + | + | + | - | - | - | - | - | - | - | - |

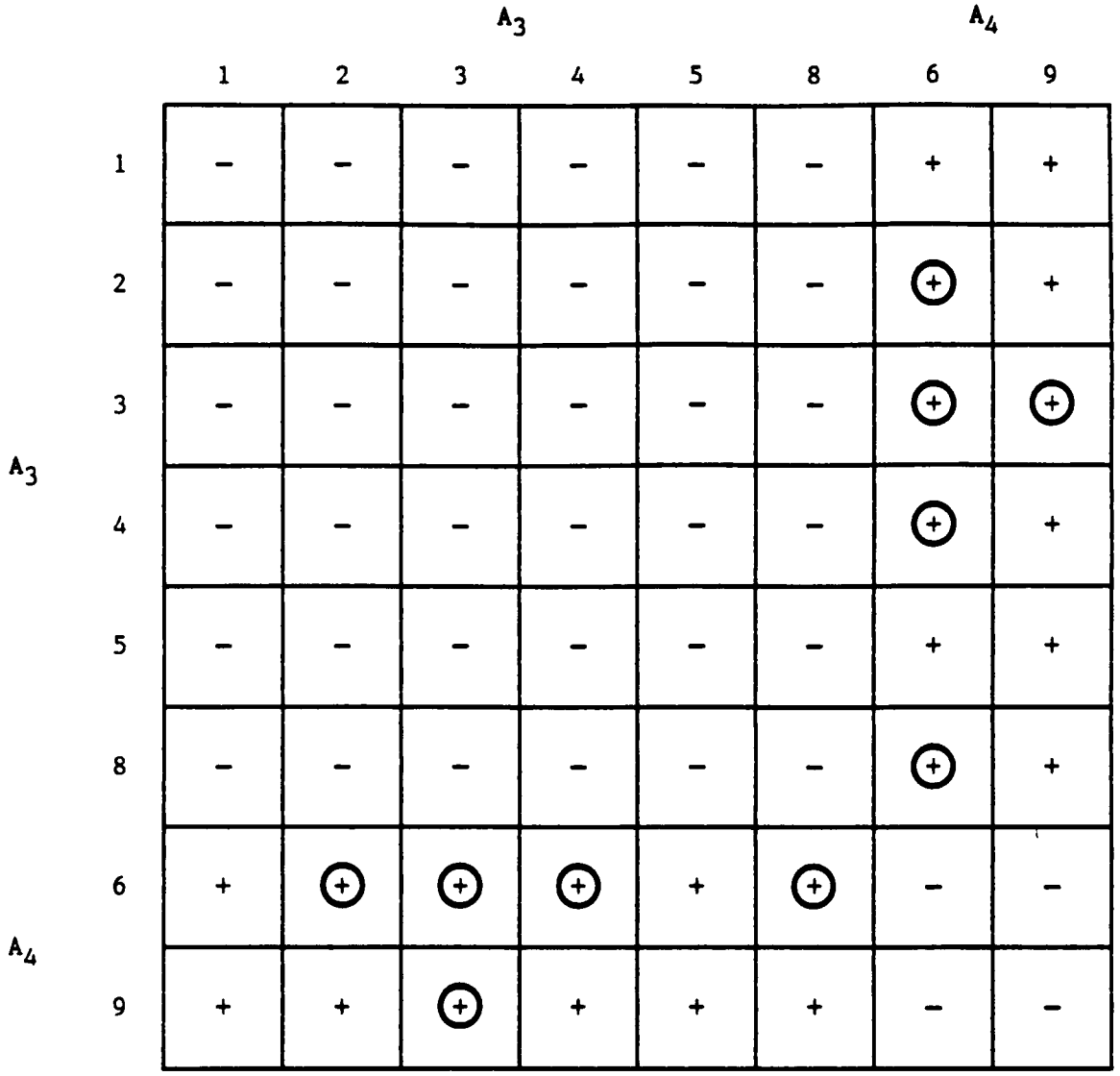
B. *Marasmius siccus*, no. DED 4714.

**Figure 12.** (continued)

| $A_3$ \ $A_4$ | 1 | 4 | 5 | 7 | 9 | 10 | 2 | 3 | 6 | 8 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | − | − | − | − | − | − | + | + | + | + |
| 4 | − | − | − | − | − | − | + | + | + | + |
| 5 | − | − | − | − | − | − | + | + | + | + |
| 7 | − | − | − | − | − | − | + | + | + | + |
| 9 | − | − | − | − | − | − | + | + | + | + |
| 10 | − | − | − | − | − | − | + | + | + | + |
| 2 | + | + | + | + | + | + | − | − | − | − |
| 3 | + | + | + | + | + | + | − | − | − | − |
| 6 | + | + | + | + | + | + | − | − | − | − |
| 8 | + | + | + | + | + | + | − | − | − | − |

C. *Marasmius siccus*, no. DED 4956.

**Figure 12.** (continued)




A. *Marasmius pulcherripes*, no. 2127.

**Figure 13.** Self-crosses of *Marasmius pulcherripes*

| | | $A_1$ | | | | | $A_2$ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 6 | 7 | 1 | 5 | 8 | 9 | 10 | 11 |
| $A_1$ | 2 | − | − | − | − | − | + | + | + | + | + | + |
| | 3 | − | − | − | − | − | + | + | + | + | + | + |
| | 4 | − | − | − | − | − | + | + | + | + | + | + |
| | 6 | − | − | − | − | − | + | + | + | + | + | + |
| | 7 | − | − | − | − | − | + | + | + | + | + | + |
| $A_2$ | 1 | + | + | + | + | + | − | − | − | − | − | − |
| | 5 | + | + | + | + | + | − | − | − | − | − | − |
| | 8 | + | + | + | + | + | − | − | − | − | − | − |
| | 9 | + | + | + | + | + | − | − | − | − | − | − |
| | 10 | + | + | + | + | + | − | − | − | − | − | − |
| | 11 | + | + | + | + | + | − | − | − | − | − | − |

B. *Marasmius pulcherripes*, no. 2779.

**Figure 13.** (continued)

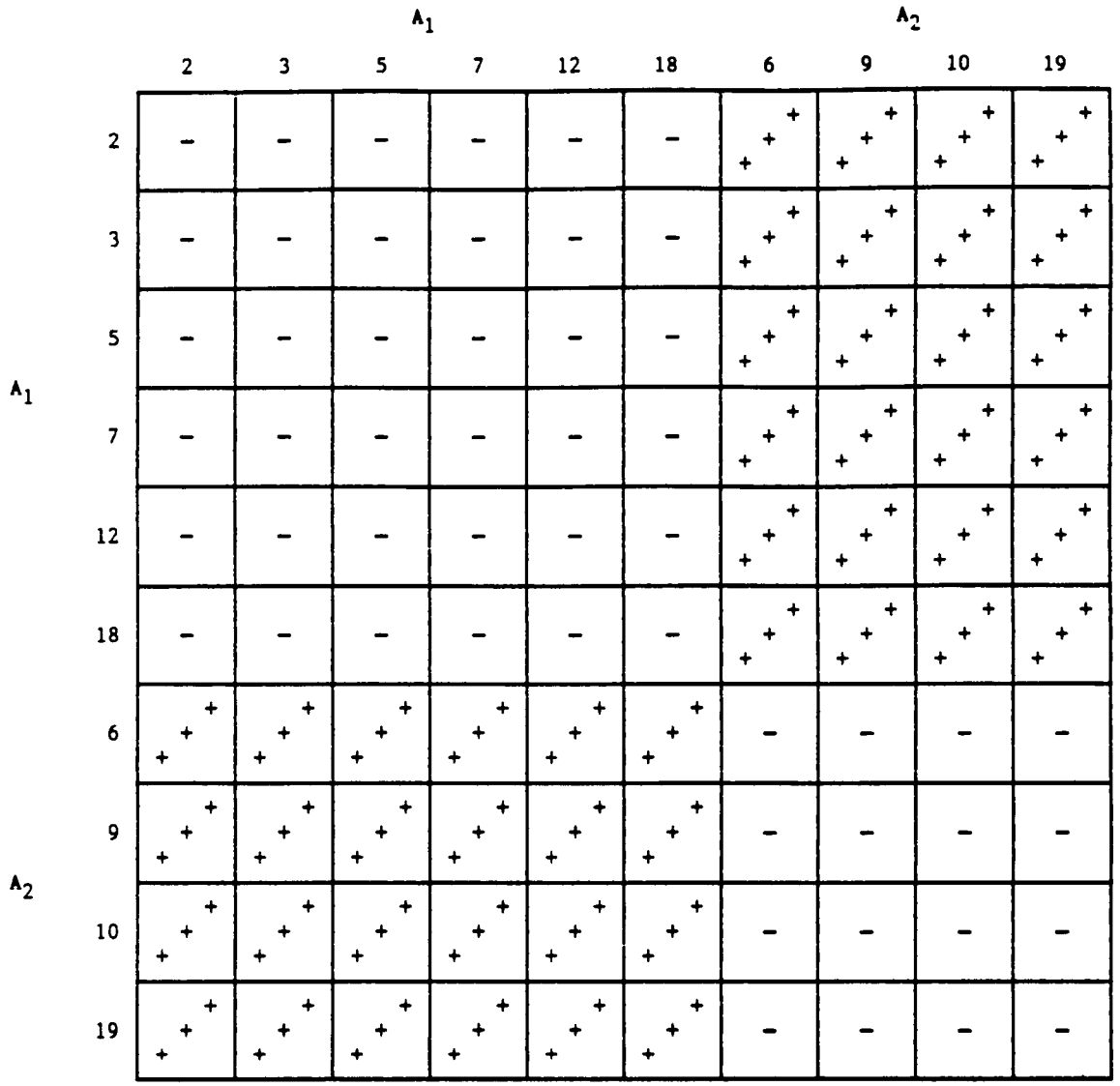



**Figure 14.** Self-crosses of *Marasmius fulvoferrugineus*, no. 2099.

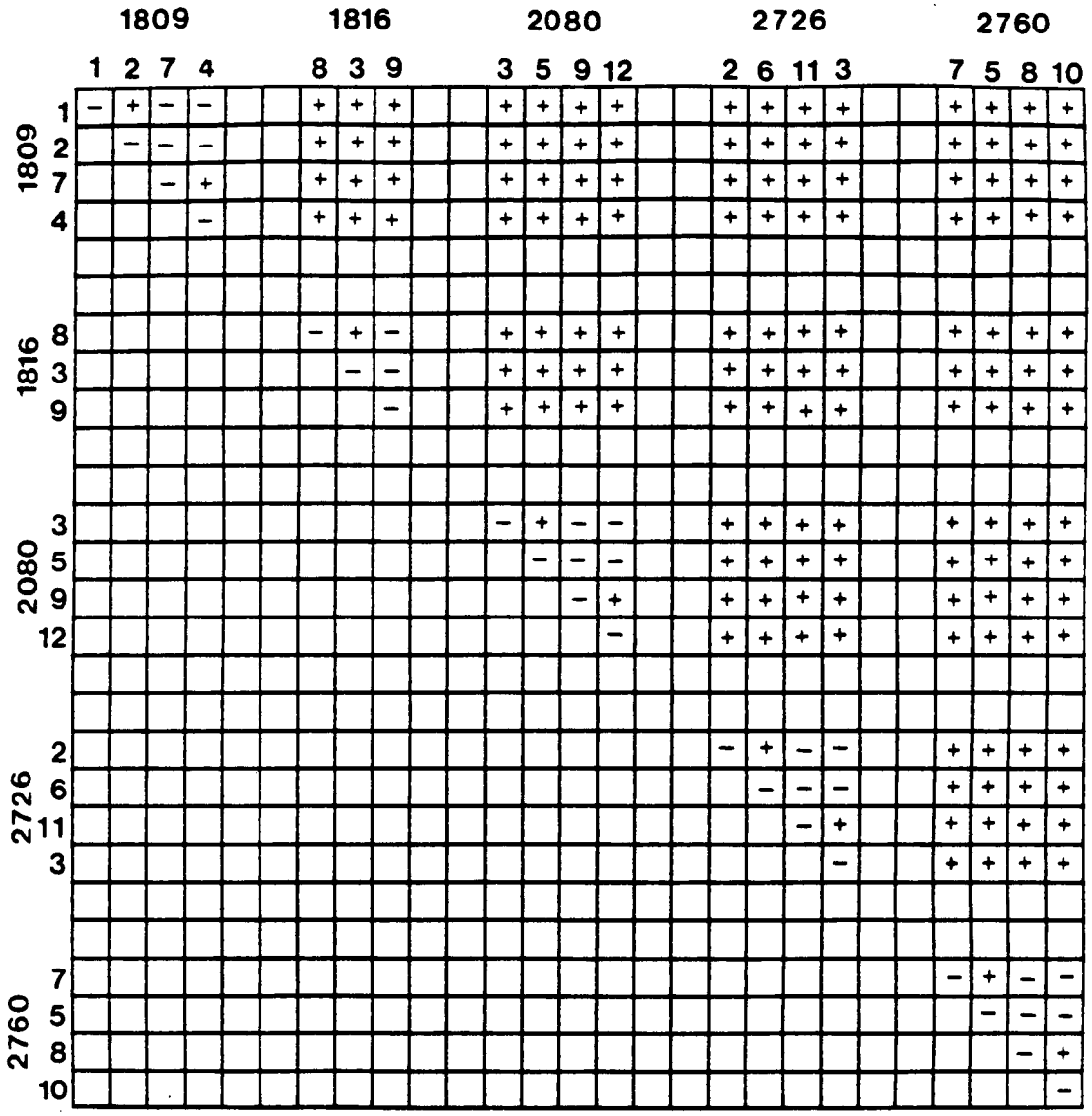



**Figure 15.** Intercollection crosses of five collections of *Marasmius rotula*. (nos. 1809, 1816, 2760-NC; 2726-TN; 2080-GA).

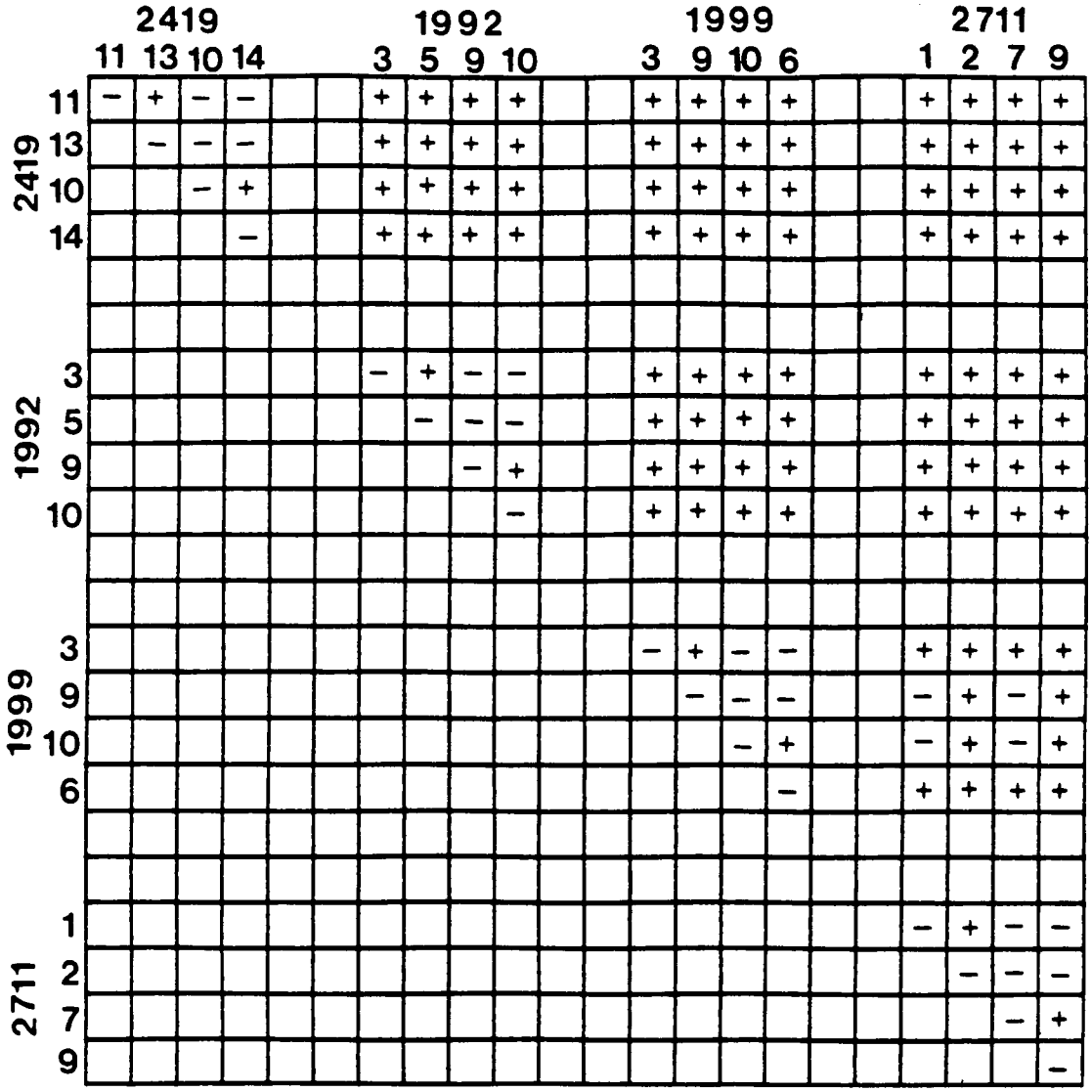



**Figure 16.** Intercollection crosses of four collections of *Marasmius pyrrhocephalus*. (nos. 1992, 1999, 2711-NC; 2419-IL).

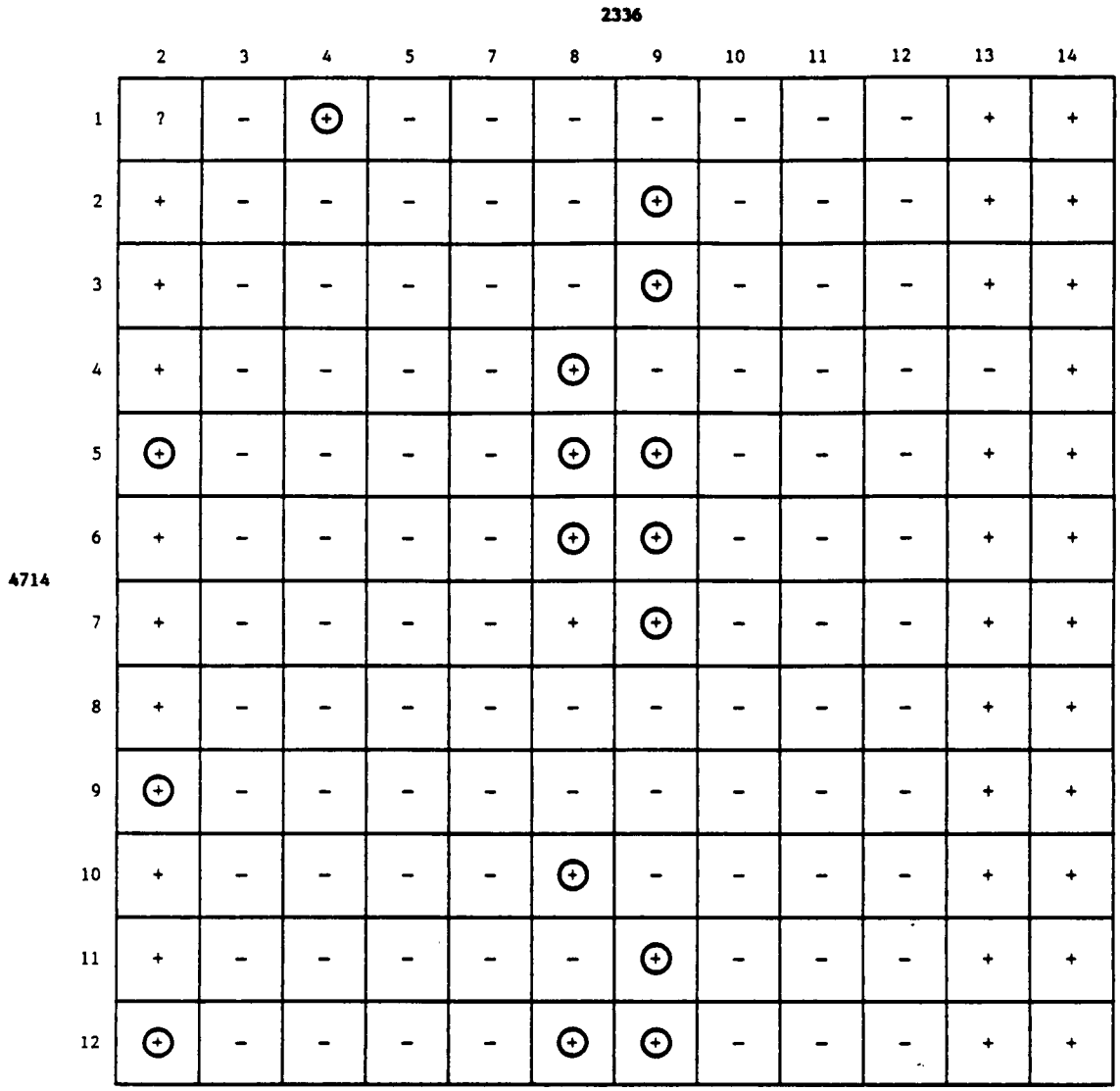



**Figure 17.** Intercollection crosses of *Marasmius siccus*. (2336-Japan; 4714-NC).

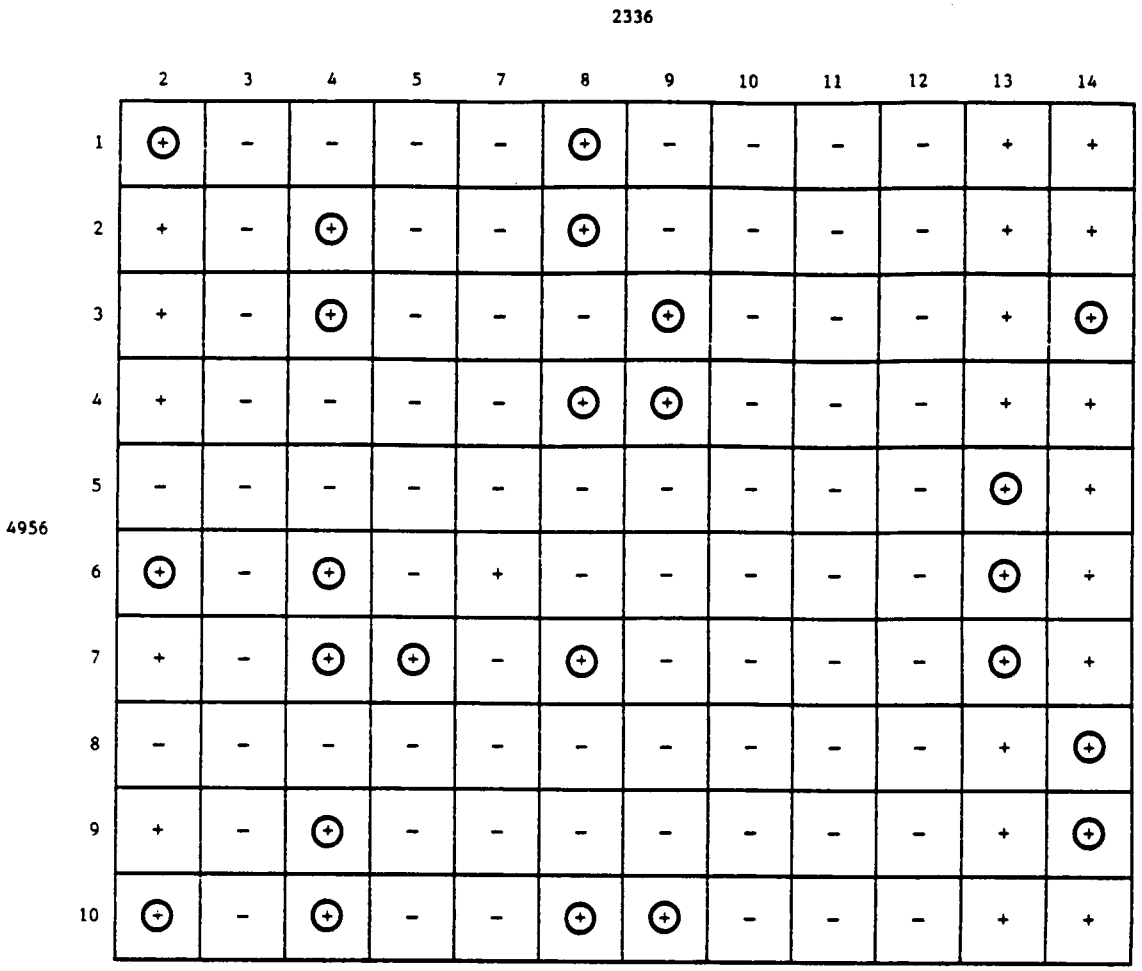



**Figure 18.** Intercollection crosses of *Marasmius siccus*. (2336-Japan; 4956-Ohio).

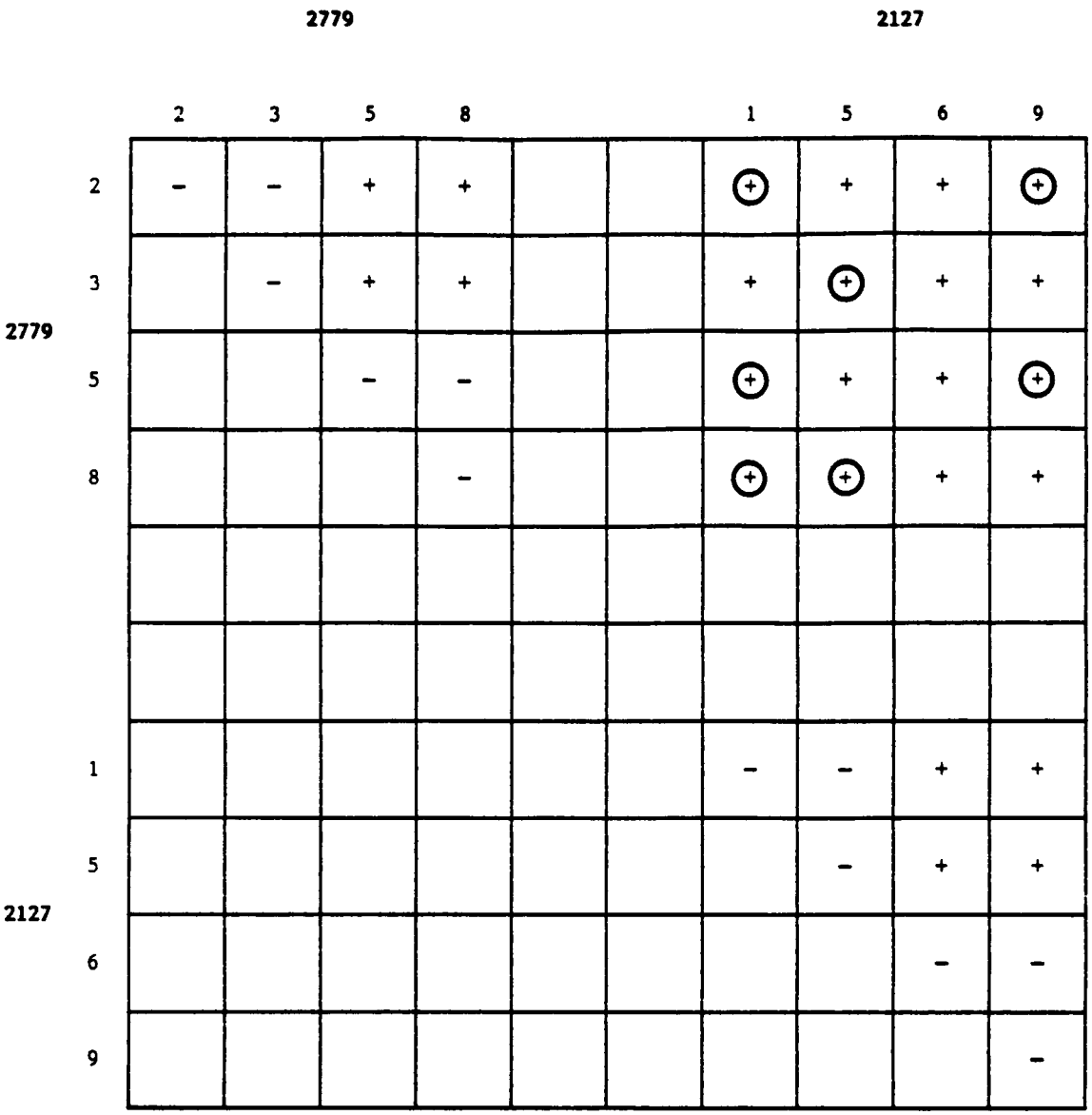



**Figure 19.** Intercollection crosses of *Marasmius pulcherripes*. (2127-TN; 2779-GA).

## VITA

Scott Allen Gordon was born on 31 October, 1967, in Malone, New York. He attended elementary schools in that city and was graduated with a Top Regents Diploma from Franklin Academy High School in June, 1985. While attending high school, he received numerous athletic and academic awards. The following August he entered the State University of New York at Cortland, where he was a member of the varsity swimming team and received numerous academic honors before graduating in May, 1988 with a Bachelor of Science degree in biology.

In August, 1988, Mr. Gordon accepted a teaching assistantship and enrolled at the University of Tennessee, Knoxville to pursue a Master of Science degree in botany, with research in mycology, under the tutelage of Dr. Ronald H. Petersen. While there he received two grants-in-aid from the Highlands Biological Station, North Carolina, a Science Alliance Summer Fellowship, Science Alliance Upgrade Award For Excellence In Teaching And Service, and presented his thesis work at the professional meeting of the Mycological Society of America. Mr. Gordon will receive his Master of Science in Botany in August, 1990.

After receiving his Master of Science degree, he plans to continue his studies with Dr. Petersen at the University of Tennessee, Knoxville to pursue a Doctor of Philosophy with a major in Botany.