Cytological Investigations in the Genus Weissia in Southeastern United States.

Betty Ann elberson Lemmon

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Louisiana State University and Agricultural and
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CYTOLOGICAL INVESTIGATIONS IN THE GENUS WEISSIA
IN SOUTHEASTERN UNITED STATES

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Botany and Plant Pathology

by

Betty Ann Elberson Lemmon
B. S., University of Southwestern Louisiana, 1945
M. S., University of Southwestern Louisiana, 1965
August, 1968
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ABSTRACT

Cytological study of the three species and hybrids of Weissia that occur in southeastern United States was undertaken in an attempt to determine their traditionally disputed relationships to each other. When it became apparent that cytological races exist within the species, the scope was broadened, with the collaboration of Dr. Lewis E. Anderson, to include cytological sampling of Weissia throughout southeastern United States.

The three species, W. controversa Hedw., W. ludoviciana (Sull.) Reese & Lemmon, and W. muhlenbergiana (Sw.) Reese & Lemmon, were found to have a 13-, 14-, and a 26-chromosome race. The small, distinct m-chromosome was the additional chromosome in all of the 14-chromosome race populations. It was consistently absent in the 13-chromosome race populations. The karyotypes of comparable chromosome races in different species are indistinguishable.

W. controversa was selected for a distribution study and chromosome counts were made from 460 populations: 82% were of the 13-chromosome race, 16% were of the 14-chromosome race, and 2% were of the 26-chromosome race. The distribution of the 13-chromosome race, based upon 378 populations, was 47% in the Coastal Plain, 17% in the Piedmont, 31% in the Appalachian System, 4% in the Ozarkian System, and 1% in the Central Lowlands. The distribution of the 14-chromosome race, based upon 73 populations, was 66% in the Coastal Plain, 32% in the Piedmont, 1% in the Appalachian System, and 1% in the Ozarkian System. The
distribution of the 26-chromosome race is 11% in the Appalachian System, and 89% in the Ozarkian System.

Detailed comparisons of plants of the chromosome races of the three species revealed no significant morphological or ecological differences, except in the 26-chromosome race of *W. controversa*. This taxon has been called *W. tortilis* (Schwaegr.) C. Mueller, but its taxonomic position is uncertain.

Three hybrid populations, each of which belonged to a separate chromosome race, were discovered. The 13- and 14-chromosome race hybrids were growing in the same colony as their presumed parents, and were intermediate in all sporophyte characteristics. The morphologically similar genomes were compatible at meiosis. The 26-chromosome race population, suspected to be of hybrid origin but different in aspect, was sampled by comparing all of the plants (38) in a sq cm. The plants consisted of an uninterrupted series of forms, from typical *W. ludoviciana* to typical hybrids; no *W. controversa* was present. It is assumed that genetic imbalance and faulty cytokinesis are responsible for the large percentage of sterile and deformed spores in hybrids because meiosis is completely regular.

The genomes of each chromosome race are morphologically and behaviorally alike in all the species. The genomes of each species, regardless of chromosome number, are genetically different enough to produce a phenotype that is recognizable within the specific description. Genetic isolation barriers apparently exist because genetic integrity in the species is maintained, with few exceptions, in spite of the fact that cytologically similar populations grow in mixed
colonies and sometimes fruit simultaneously. There is no evidence of hybridization between chromosome races either interspecifically or intraspecifically.
INTRODUCTION

The moss genus *Weissia* includes a group of widely distributed species whose relationships have been much disputed. Whether the species in this complex should be included in one, two, three or even more genera has been discussed by Lindberg (1879), Andrews (1920, 1922, 1924), Hilpert (1933), Grout (1938), Jensen (1939), Chen (1941), Steere, Anderson & Bryan (1954), Podpera (1954), Nyholm (1956), Wijk, et al (1959-1962), Demeret & Castagne (1964), and Reese & Lemmon (1965).

Attempts to answer this question by traditional taxonomic means have been notably unsuccessful, mainly because taxonomists differ in their evaluation of the relative importance of gametophyte and sporophyte characteristics. In all of the species in question, the gametophyte characters of leaf length, width, and degree of involution are remarkably uniform, while the sporophyte characters of seta length, operculum, and peristome teeth development, are strikingly variable.

In the first part of this century Nicholson (1905) reported hybridization between the stegocarpous *Weissia crispata* Ldb. and the cleistocarpous *rispa* Mitt. in England. During the 1920's Andrews suspected *Astomum muhlenbergianum* (Sw.) Grout and *Weissia controve* Hedw. hybridize. During the course of an investigation of the *hsp* of Lafayette Parish, La. (Lemmon, 1966) Dr. W. D. Reese and I encountered a collection which we strongly suspected might be a hybrid between *Weissia* and *Astomum*. After careful morphological analyses and spore germination tests we concluded that the intermediate
form was a hybrid between *Weissia controversa* Hedw. and *Astromum ludoviciana* Sull. (Reese & Lemmon, 1965).

Because of the fact that the low fertility rate of the hybrid spores suggested meiotic irregularities a chromosome study of the hybrid was begun by the writer. Surprisingly, no meiotic irregularities were found, and the chromosome number of the hybrid, $n = 14$, was at variance with the published chromosome numbers of the putative parents, both of which were reported to have the number, $n = 13$ (Sannomiya, 1955; Steere, Anderson & Bryan, 1954; Steere, 1954; Khanna, 1960a; 1960b; Al-Aish & Anderson, 1961; Bryan, 1956; and Gyroffy, 1964). Chromosome studies of the putative parents in the vicinity of the hybrid verified that they also had the number, $n = 14$.

The difference in chromosome number between the Louisiana population and the North Carolina populations was reported to Dr. L. E. Anderson of Duke University, who kindly restudied the North Carolina populations of *W. controversa* and substantiated the validity of earlier counts. After considerable discussion, and with assurances of collaboration and cooperation from Dr. Anderson the present investigation was undertaken.

The purpose of the present investigation was to study as many populations as feasible of *Weissia controversa* in an attempt to determine its relationship to *Astromum muhlenbergianum* and *Astromum ludovicianum*, as well as to determine what relationship, if any, exists between chromosome races and morphological and ecological variants.
TAXONOMY

Taxonomic History

The generic name Weissia, honoring the German botanist Fredrich Wilhelm Weiss, has been coined twice. Its current application is valid because the earlier use predates the starting point for moss nomenclature, Hedwig's Species Muscorum (1801). Ehrhard used the name in 1787 to apply to what is now known as Ulota, a genus in the Orthotrichaceae. Grout's (1938) usage of another spelling, "Weisia," is an attempt to avoid confusion with the earlier Weissia of Ehrhart, but the correct spelling is that used by Hedwig, Weissia.

The genus Weissia Hedw. belongs to the large and somewhat unwieldy moss family, Pottiaceae, which consists of about 80 genera and nearly 1500 species. The members are mostly rather small acrocarpous plants which are adapted to xeric, calcareous substrates. The somewhat glaucous gametophytes consist of simple or branched stems bearing several ranked leaves with cells that are frequently thin-walled and hyaline at the base and thick-walled and papillose, often strongly so, at the tips. The leaf margins are frequently inrolled and the leaves, when dry, are tightly crisped. Capsules are exserted on long setae, operculate, with a single peristome of 16 or 32 straight or twisted teeth in some species, and immersed, cleistocarpous, and gymnostomous in others.

While the operculate members of the genus Weissia have maintained a fairly stable taxonomic position, the inoperculate species
have been variously classified, usually under the generic name Astomum. The inoperculate mosses were set apart from the more complex operculate species by early bryologists. Although the "cleistocarpi" was recognized as a convenient but artificial category as early as 1823, this view was not generally accepted until the latter part of that century.

Prior to the publication of *Species Muscorum Frondosorum* by Hedwig (1801) only five species of inoperculate mosses had been described. Dillenius (1741) included the three inoperculates that he knew in Sphagnum and Linnaeus (1753, 1764) transferred them to the genus Phascum. Two additional inoperculates were described by Schreber in *De Phasco Observationes* (1770).

Hedwig (1801) treated all the inoperculate mosses known to him, 11 species, in the genus Phascum, which he separated from other genera by "Sporangio astomo," and it was in this work that the first Astomum species was described, Phascum crispum /Astomum crispum (Hedw.) Hampe/.* The genus Weissia was quite distantly located in his generic key on the basis of characters of the peristome and position of the "flore mascule."

In the first volume (1797) of *Muscologia Recentiorum*, Bridel presented a synopsis of this classification of mosses and expanded it in the second volume (1798) to include species authorities and descriptions. He divided the mosses into four classes, Aperistomati (the modern genus Phascum), Gymnoperistomati /Sphagnum, Hedwigia, and

---

*In this section the older nomenclature is followed by the current names in brackets.*
Gymnostomum, Aploperistomati (15 genera), and Diploperistomati (14 genera). Bridel's later work, *Bryologia Universe* (1826-1827) reflects a radically different concept of moss nomenclature. In this work he distributed the inoperculate genera among three of the six classes of Section I, Musci Calyptrati, olocarpi.

Hooker and Taylor (1827), following a basic concept similar to Bridel's, established four divisions of mosses: Schistocarpi (*Andreaea*), Astomi (*Phascum*), Gymnostomi (*Sphagnum* and *Gymnostomum*), and Peristomi which was further divided into Aploperistomi and Diploperistomi.

The first attempt to incorporate inoperculate mosses with the operculate species to which they are gametophytically similar was made by Nees von Esenbeck, Hornschuch and Sturn in *Bryologica Germanica* published between 1823 and 1831. At about the same time Furnrohr (1829), although using the family Phascoideae to contain the inoperculates, expressed the opinion that the inoperculates should eventually be distributed among the other families.

Hampe, writing in *Flora* (1837), divided *Phascum* into genera which he placed in separate families; among them was *Astomum* (including *Pleuridium*) which he designated as a genus of the Dicranaceae. He later repudiated his stand, according to Loeske (1910, p. 70) and in 1873 included all the inoperculate mosses, except *Archidium*, in the Cleistocarpi, a division of the acrocarpous Stegomitria within Musci Genuini (cf. Roth, 1904, p. 85).

Although the convenience of consolidating inoperculate mosses was utilized in part by Bruch, Schimper, and Gümbel in *Bryologia Europeae* (1836-56), they placed *Astomum* Hampe in Weissiaceae along
with *Hymenostomum*, *Weissia*, *Gymnostomum*, *Anoectangium*, and *Eucladium*. They noted that except for the absence of a dehiscent operculum *Astromum* corresponds almost completely to *Hymenostomum*. However, in the *Corollarium* (1855) of *Bryologia Europeae*, Schimper placed *Astromum* (*Astromaceae*) in the Cleistocarpi with only a brief comment on its similarity to *Hymenostomum*.

Carl Mueller (1849) proposed the class Cleistocarpi to contain the inoperculate mosses, and divided the remaining mosses into the Schistocarpi (*Andreaea*) and Stegocarpi, in which he placed acrocarpous and pleurocarpous groups. He divided Cleistocarpi into three tribes: *Astromum* (including *Pleuridium* species) was placed in Tribe I (*Bruchiacae*) along with *Archidium* and *Bruchia*.

Wilson (1855) retained the inoperculate mosses within the Phasceae, a suborder of Acrocarpi, dividing it into *Archidium* and *Phascum*. *Phascum* was further divided into six sections; of the final one, *Astromum*, Wilson noted that in a strictly natural arrangement it should not be separated from *Gymnostomum*.

Sullivant (1856) treated all of the inoperculates, except *Aphanorhegma*, as a single group for which he chose Mueller's nomenclature, the Cleistocarpi. Although he used the two genera *Archidium* and *Phascum* he recognized that in the latter group several sections ("genera") are necessary to receive the species in a natural arrangement. The four species of *Astromum* were recognized as being close to *Weissieae* in the Stegocarpi.

Mitten (1851) distributed inoperculate species among families of stegocarps and in 1859 stated, "The cleistocarpus order has been suppressed because its component parts are readily referrable to
families of higher development." Following Mitten, both Jaeger (1869) and Milde (1869) propounded the distribution of the cleistocarpous mosses.

Although the recognition of the relationship of the inoperculates to more complex groups was completely acceptable to many bryologists by this time, not all were ready to abandon the Cleistocarpi classification. Schimper's *Synopsis Muscorum Europaeorum* (1876) was greatly influential and no doubt led to the retention of the Cleistocarpe by later workers. He divided the mosses into two series, the Acrocarpae and Pleurocarpae, and separated the Acrocarpae into the orders Cleistocarpe and Stegocarpe. *Astomum* was, however, placed in the first tribe of the Stegocarpe, Weissiceae, because of its relationship to *Hymenostomum*.

In the same year (1876) Limpricht, viewing the disbandment of the Cleistocarpi as impractical, split the mosses into four major groups, Bryinae, Phascaceae (Musci Cleistocarpi), Andreaeaceae and Sphagnaceae. All of the inoperculates were placed in four tribes of Cleistocarpe except *Systegium*/*Astomum* which, because of its indehiscent, sometimes imperfectly formed operculum was included in the Weissieae (of Musci Acrocarpe) along with *Weissia, Anoectangium* and *Gymnostomum*.

A work influential in the general acceptance of the denial of the Cleistocarpi as a legitimate natural group was that of Lindberg (1879). He placed the inoperculates in the Acrocarpi among the families where they were most naturally disposed. He was the first to formally recognize the close phylogenetic relationship between *Astomum*,
Hymenostomum and Weissia by uniting them in a single genus. For this genus he chose Mollia in the Tortuleae of the family Tortulaceae.

Lesquereux and James (1884) in *The Manual of Mosses of North America* placed all of the mosses without separable opercula in the Phasceae, except Astomum which they assigned to the tribe Weissiaceae.

Following Lindberg's arrangement of distributing the inoperculates was Braithwaite (1887-1905) who included Astomum in the genus Mollia. Kindberg (1883) also followed Lindberg's system of inoperculate distribution, but by 1897 he had assumed the use of stegocarpous, schizocarpous and cleistocarpous tribes as divisions of the acrocarpous mosses according to Schimper's arrangement.

Roth (1904) first followed Limpricht but in 1911 changed his arrangement of the Cleistocarpaceae by recognizing "Unterfamilien" for the inoperculates. Astomum appears in the Trichostomeae cleistocarpaceae.

An important system of classification by Fleischer (1915-1922) was a revision of previously published arrangements. Brotherus, who wrote the section on Bryales in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (1924-1925), acknowledged the value and influence of Fleischer's work and used the same major divisions. Astomum appears in his scheme as one of the ten genera of inoperculate mosses in the Pottiaceae.

Dixon (1924) and Monkemeyer (1927) both used a classification of mosses in accordance with Fleischer and Brotherus. Dixon placed the species of Astomum in the genus Weissia, subgenus Systegium.

Andrews in a series of papers (1920-1933) discussed the North American species of the Astomum-Hymenostomum-Weissia complex which he
united under the generic name *Hymenostomum*. Among his reasons for considering them congeneric were basic similarity of the gametophyte, intergrading forms of sporophyte development and suspected hybridity between the cleistocarpous and stegocarpous species.

Hilpert (1933), in a study of the systematics of the "Trichostomaceen," merged the European species of *Weissia*, *Hymenostomum* and *Astromum* into the genus *Weissia*, the oldest valid name of the three. He suggested that the original independent genera may naturally become sections.

Jensen (1939) treated *Astromum* in *Skandinaviens Bladmossflora* as a subgenus of *Weissia* in *Trichostomeae, Pottiaceae*.

The *Moss Flora of North America*, published between 1933 and 1940, by Abel Joel Grout, is the most comprehensive treatment of the mosses of this continent, north of Mexico. In it Grout described two orders, Andreales and Bryales, and arranged families in an order somewhat similar to that proposed by Brotherus. He treated *Hymenostomum* as a subgenus of *Weissia* and recognized *Astromum* as a separate genus. The following couplet appears in his generic key:

Capsules immersed or barely exserted, dehiscing irregularly... *Astromum*

Capsules exserted on a long seta, operculate; peristome often present... *Weissia*

Grout commented on the Pottiaceae, "A large and polymorphous family, difficult to define satisfactorily by reason of the degenerate sporophytes of some of its genera." His classification of the family and the pertinent species is as follows:
1. Pleuroweissiiae

   *Anoectangium*  
   6 spp.

2. Trichostomeae

   *Aschisma*  
   1 sp.
   *Astomum*  
   6 spp.
   *A. muhlenbergianum*  
   *A. phascoides*  
   *A. ludovicianum*

   *Weisia*  
   *Subgenus Hymenostomum*
   *W. microstoma*  
   *W. ligulaefolia*  
   *W. tortilis*  

   *Subgenus Euweisia*
   *W. viridula (W. controversa)*  
   *W. viridula var. australis*  
   *W. viridula var. Wolfii*  
   *W. andrewsii*  
   *W. glauca*  
   *W. jamaicensis*  
   *Gymnostomum*  
   4 spp.
   *Eucladium*  
   1 sp.
   *Rhamphidium*  
   1 sp.
   *Trichostomum*  
   3 spp.
   *Timmiella*  
   2 spp.
   *Pleurochaete*  
   1 sp.
   *Tortella*  
   6 spp.
   *Triquetrella*  
   1 sp.
   *Leptodontium*  
   2 spp.
   *Hyophila*  
   1 sp.
   *Barbula*  
   19 spp.
Rhizophyllum 1 sp.
Didymodon 7 spp.

3. Pottiaceae

Acaulon 4 spp.
Phascum 2 spp.
Pottia 11 spp.
Pterigoneurum 3 spp.
Aloina 3 spp.
Crossidium 6 spp.
Husnotiella 3 spp.
Desmatodon 12 spp.
Trichostomopsis 3 spp.
Tortula 23 spp.
Merceya 2 spp.
Bryobrittonia 1 sp.

4. Cinclidoteae

Cinclidotus 1 sp.

The most recent taxonomic treatment of the Pottiaceae is a study by Chen (1941). He followed Hilpert in uniting the Astomum-Hymenostomum-Weissia complex in the genus Weissia, and in his concept of the phylo-
genetic relationships of the former genera. His classification for the family is as follows:

Pottiaceae

1. Trichostomoideae

Tortelleae

Oxystegus
Tortella

Pseudosymblepharis

Pleurochaete

Trichostomeae

Weisia (including Astomum and Hymenostomum)

Trichostomum

Timmiella

2. Barbuloideae

Hyophileae

Barbuleae

3. Pottioideae

Merceyae

Pottieae

4. Leptodontioideae

Recent European bryological works are variable in their treatments. Podpera (1954) and Wijk et al (1959-1962) recognize all three genera, Astomum, Hymenostomum and Weissia. Nyholm (1956) recognizes two genera, Weissia (including Hymenostomum) and Astomum. Demaret and Castagne (1964) recognize only Weissia (including Astomum and Hymenostomum).


For purposes of the present investigation the following generic treatment is used:
Generic Treatment in This Investigation

**Weissia** Hedw. Sp. Musc. 64. 1801.

Plants small cespitose, branching freely, usually growing on rather dry calcareous or sandy soil, crevices of rocks, bricks, or on damp clay; upper leaves usually much the larger, erect spreading, strongly crisped when dry, elongate-lanceolate, margins strongly involuted above or almost flat; costa usually short excurrent; basal leaf cells rectangular and hyaline, the upper cells small, rounded and thickly papillose. Seta much longer than the perichaetial leaves or short, almost lacking; capsule erect and symmetric, spherical to ovoid-cylindric; operculum long rostrate to absent; peristome teeth well developed, short and irregular or lacking. Type species, *W. controversa*. Fig. 1.

*Subgenus Weissia* Hedw.

Capsule well exserted on a seta 3-10 mm long, ovoid to ovoid-cylindric; operculum long rostrate, dehiscing at maturity; peristome teeth most often well developed, of 3-10 segments; exothecial cell walls thickened.

**Weissia controversa** Hedw. Sp. Musc. 68. 1801.

Plants in thin or dense sods, up to 5 mm or more in height; leaves gradually increasing in size from the bottom up, lanceolate, erect-spreading when moist, crisped when dry; margins entire and strongly involute, plane near the widened base; basal cells elongated, rectangular, hyaline, smooth, upper leaf cells small, roundish-hexagonal and strongly papillose; monoicous; seta erect, yellowish, 3-10 mm long; capsules ovoid to ovoid-cylindric, brown, shining as if varnished; operculum obliquely long-rostrate; peristome teeth various, of few to
Figure 1. 

*Weissia controversa* Hedw. A reproduction of the illustration of this species as *Bryum viridulum* in *Flora Londinensis* published by William Curtis, 1777-1798.
Bryum viridulum.
several sections, lanceolate and sometimes perforate to narrowly linear, smooth or strongly papillose; spores 15-22µ, coarsely papillose.

Type locality: Germany.

Distribution: almost cosmopoliton; in North America common east of the Rockies, apparently less so west of them.

Various varietal names have appeared in the literature. The variety longiseta (Lesq. & James) C. S. A. (var. australis Aust.) and var. wolfii (Lesq. & James) C. S. A. are sometimes recognized but they intergrade with the species in every respect. Andrews (1933) pointed out that var. longiseta was recognizable only in its extreme form.

In addition to W. controversa Andrews recognized only one other stegocarpous Weissia for North America, W. andrewsii Bartr., known from Arizona. Grout (1938), however, regarded W. andrewsii as, at best, a variety of W. controversa.

Two additional species were listed by Grout (1938), neither of which were collected in the present investigation. W. glauca Bartr., characterized by long, branched papillae on the leaf cells, is known from Jeff Davis Co. Texas, where it was collected at an altitude of about 5200 feet. W. jamaicensis (Mitt.) Grout is a species of tropical affinities that has been collected infrequently in the United States, where it apparently does not fruit. Originally described as a Tortula it was removed to Trichostomum by Jaeger and Sauerbeck, and finally to Weissia by Grout. Further study of this species is required before the problem of its phylogenetic position can be settled.
Subgenus Astomum Hampe

Capsules immersed, borne on short seta 0.2-1.5 mm long, spherical to ovoid; operculum with short apiculation, marked with an annulus only, not dehiscing, or lacking completely; peristome teeth lacking; exothecial cell walls thin.


Plants cespitose, unbranched or branched; leaves spreading, strongly crisped when dry, the upper leaves longest, up to 10 mm, lanceolate, with involute or often almost plane margins; costa strong, excurrent in a short mucro; basal cells rectangular, hyaline, smooth; upper cells quadrate to hexagonal 7-12 mm, densely papillose; seta very short, about the length of the vaginula, both together shorter than the capsule; capsule spherical to elongate-spherical, + 0.4 mm in diameter with a small apiculation; spores 20-30μ, strongly papillose.

Type locality: eastern United States, probably Pennsylvania.

Distribution: eastern North America, from Saskatchewan to the Gulf of Mexico and Arizona.


Plants up to 7 mm high, becoming much branched; leaves lanceolate, margins entire and involute; costa strong, excurrent in a short mucro; seta short, 1.0-1.5 mm long, occasionally more than one from a perichaetium; capsules ovoid to oblong-ovoid, apiculate to sub-rostellate, often showing a line of demarcation between urn and indehiscent lid; spores 20-30μ.

Type locality: New Orleans, Louisiana.

Distribution: southeastern United States, most common in the Gulf States.
Andrews (1922) concluded that this species is the American plant closest to the European species, *Weissia (Astomum) crispum* (Hedwig) Hampe. It is, however, distinct enough to be treated as a separate species.

Much confusion has existed concerning the two species of the subgenus *Astomum*. They are very much alike, but can be distinguished by the characteristics of the capsule and seta. In *W. muhlenbergiana* the capsule is spherical with a small apiculation and no line of demarcation, and the seta is consistently short, no longer than the vaginula. In *W. ludoviciana* the capsule is more elongated, ovoid with a longer apiculation (sub-rostrate), a distinct line of demarcation, and the seta is longer than the vaginula.

A third species of the subgenus *Astomum* is listed by Crum, Steere, and Anderson (1965) as *Astomum phasoides* (Hook. ex Drumm.) Grout. This species, with setae nearly as long as the perichaetal leaves, is of doubtful status. Andrews, quoted by Grout (1938), first thought it to be a hybrid but later was less inclined to this view because of its rather wide distribution.
HYBRIDIZATION

The first report of natural hybridization (in this group) was published by Nicholson in 1905. He described plants intermediate in characters between the stegocarpous Weissia crispata Ldb. and the cleistocarpous Weissia crispa (Hedw.) Mitt. from several localities in England. Andrews (1922) suspected hybridization between W. controversa and W. muhlenbergiana in North America. Khanna (1960a) interpreted an Asian species, Weissia exserta (Broth.) Chen, as being a stabilized amphidiploid hybrid between Weissia crispa and Weissia controversa Hedw. (W. virdula Hedw.).

A natural hybrid from Louisiana was reported by Reese & Lemmon in 1965. Its putative parents, with which it was growing, were W. controversa and W. ludoviciana. The original description of the sporophyte is as follows:

Weissia ludoviciana X W. controversa. Seta yellowish or reddish, 2.5 mm long; capsules erect, ovate, brown, 1.5-2 mm long with the operculum, bearing a few stomates at the base; operculum short to long-rostrate, well differentiated from the urn by small, thick-walled cells, but not dehiscing; exothecial cells with walls thin or moderately thickened, mostly ca 25-33 µ wide and 50-90 µ long; peristome absent or imperfectly formed within the operculum; spores mostly 19.5-22 µ in diameter, irregularly roughened, many deformed and remaining in tetrads; calyptra cucullate. Louisiana, Lafayette Parish; Low, wet woods, vicinity of Pont Brule, 18 March, 1965. Reese 7925 (Laf).
A series of pictures (Fig. 2) reproduced here to allow comparison of significant sporophytic characters in the hybrid and two presumed parents was first published in the Bryologist 68: 278 (Reese & Lemmon, 1965).
Figure 2. *Weissia ludoviciana*, *W. ludoviciana X W. controversa*, and *W. controversa*.  
2-1. Capsule of *W. ludoviciana*, X38.  
ECOLOGY AND PHENOLOGY

Southeastern United States is well within the range for all three of the members of Weissia studied in this investigation. Given a suitable substrate they thrive, producing extensive vegetative growth and fruiting freely. One of the cleistocarpous species, W. ludoviciana, is restricted to this area; the other, W. muhlenbergiana is more widely distributed, but is nowhere more common than here. Both share the old field, roadside and ditchbank habitats with the weedy W. controversa, but are far less common and are less alkaline tolerant.

W. controversa has an extremely wide ecological amplitude which allows it to exploit a variety of substrates. It grows on rock, and occasionally on old concrete and brickwork, in addition to the clay and light sandy loam substrates in the habitats previously mentioned. Apparently a considerable amount of weathering is required to bring these substrates within its tolerance range, the upper limits of which overlap the lower range limits of true calcophiles such as Barbula crugeri Sond. ex C. Mueller.

Observations of the development of Weissia sporophytes over a three-year period in Southeastern United States indicate that temperature, day length and moisture are factors that influence fruiting. Fruiting has, during the observation period never been observed earlier than November or later than March. Adequate moisture must be present for gametophytes to accumulate sufficient growth to produce sex organs, and rain or at least heavy dew is necessary at the critical time for fertilization to occur.

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Fruiting was delayed for two months in the Baton Rouge area of Louisiana by a severe autumn drought in 1967, despite the fact that temperature patterns were normal. Gametophyte growth, which is dependent primarily on moisture, was delayed until late December, and the young sporophytes appeared in late January.

Sex Organs: Clusters of four to eight archegonia are produced in apical perichaetia. The perichaetial leaves are modified slightly, having wide bases that surround the archegonial clusters and being considerably longer than the other leaves. Apparently the archegonia are produced continuously in a perichaetium until fertilization occurs in one of them. I have frequently observed old, shriveled archegonia, mature archegonia ready for sperm entry and archegonial initials all in the same perichaetium. This capacity for continuous production of archegonia is no doubt responsible for the prodigious crop of sporophytes that is routinely produced. Although the members of the genus are clearly monoicous, only about ten percent of the plants bear antheridia; all bear archegonia. The number of antheridia in an antheridial bud may vary from two to twenty or more. They, together with slender paraphyses, are clasped by a pair of short perigonial leaves which have wide bases. Other, smaller leaves may subtend the modified pair and the branch may be very short, the bud being almost sessile, or it may attain considerable length.

The position of the perigonial bud on the plant varies as does the relative abundance of antheridia. Some positions that I have frequently observed are: buds sessile at the apex of an old plant, together with archegonial buds which are often quite elongated; buds
on branches of medium length arising on a stem that bears archegonia at its apex; buds arising from the base of a new plant and becoming independent plants at maturity. Occasionally, I have seen perigonia right next to the perichaetia down in the leaves in the apex of a new shoot. The branch of an antheridial bud does not elongate, but occasionally new shoots arise from inside perigonal leaves. Apparently they give rise to male plants as no archegonia have been observed on them.
HISTORY OF CHROMOSOME INVESTIGATIONS

Historical accounts of cytological investigations in the Musci have been published by Steere, Anderson and Bryan (1954), and discussed in detail by Anderson (1964). Some of the early workers who pioneered in the field of bryophyte cytology were the Marchais (Elie & Emile Marchal, 1906, 1907, 1909, 1911), Wettstein (1923, 1924a, 1924b, 1924c, 1926, 1928a, 1928b, 1930, 1932, 1937, 1940), and Heitz (1926, 1928). Their investigations marked a brilliant period of discoveries that included polyploidy, hybridization, sex determination, heteropycnosis, and heteromorphism.

The first survey of chromosome numbers in the Musci was published by Heitz (1928), although chromosome numbers were sometimes reported by the early workers incidental to their investigation. Since then numerous investigators (see Anderson, 1964) have added to the knowledge of chromosome numbers, but few have attempted to correlate chromosome information with the taxonomy of mosses. The first to do so was Lowry (1948) who constructed a cytological classification for the genus Mnium. He was followed by Bryan, who published on the chromosomes of Sphagnum (1955) and later a series of articles (1956a, 1956b, 1957) on her extensive chromosome studies of cleistocarpous and gymnom stomous mosses compared to some of the peristomate genera within the same families. In addition, contributions have been made to the cytotaxonomy of Sphagnum (Holmen, 1955), Fissidens (Anderson & Bryan, 1956), Ditrichum (Anderson & Bryan, 1958b) and Atrichum (Tatuno, 1960; Noguchi & Osada, 1960).
The only important cytological study of the family Pottiaceae was one made by Steere, Anderson & Bryan as part of a chromosome study on California mosses in 1954. Chromosome numbers for 8 genera, including 14 taxa were reported; the most common basic chromosome number was 12, with a range from 11 through 14, complicated throughout by ploidy. The authors remarked, "In general, the meiotic chromosomes of this family seem to present less morphological distinctiveness and greater numbers than elsewhere among mosses, at least within our experience." In addition, they noted a disproportionate amount of anomalous behavior of chromosomes, aneuploidy, polyploidy and widespread presence of small chromosomes. They found that the members of the subfamily Trichostomeae (Barbula, Timmiella and Weissia) tend to have smaller chromosome numbers than the members of the Pottieae (Aloina, Desmatodon, Phascum, Pottia, and Tortula).

Since then additional chromosome numbers in the Pottiaceae have been reported; a total of 24 genera including 70 species are listed in a survey of chromosome numbers by Anderson (1962).

The chromosomes of the three members of the genus Weissia studied in the present investigation have been studied by Bryan (1956a). She studied two inoperculate species, W. ludoviciana and W. muhlenbergiana, and the stegocarpous W. controversa as a part of a cytotaxonomic study undertaken to find corroborating evidence for the systematic position of the operculates. She compared the chromosomes of the three species and found them similar, the main difference being in numbers due to the ploidy she encountered in W. muhlenbergiana.
Bryan's counts are included with those of other investigators in Table 1.

Table 1. Chromosome numbers of three species of *Weissia* reported prior to the present investigation.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Chromosome number</th>
<th>Locality</th>
<th>Investigator</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>W. controversa</em></td>
<td>n = 14</td>
<td>Finland</td>
<td>Vaarama (1950a)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>California</td>
<td>Steere, et al. (1954)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>California</td>
<td>Steere (1954)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>Japan</td>
<td>Sannomiya (1955)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>North Carolina</td>
<td>Bryan (1956a)</td>
</tr>
<tr>
<td></td>
<td>n = 13; n = 14</td>
<td>India</td>
<td>Khanna (1960a &amp; 1960b)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>North Carolina</td>
<td>Al-Aish &amp; Anderson (1961)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>Hungary</td>
<td>Györfi (1964)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>Britain</td>
<td>Smith &amp; Newton (1967)</td>
</tr>
<tr>
<td></td>
<td>n = 13</td>
<td>Russia</td>
<td>Lazarenko, A. S., O. I. Visotska, &amp; E. M. Lesnyak (1967)</td>
</tr>
<tr>
<td>var. densifolia</td>
<td>n = 13</td>
<td>Britain</td>
<td>Smith &amp; Newton (1967)</td>
</tr>
<tr>
<td><em>W. ludoviciana</em></td>
<td>n = 13</td>
<td>North Carolina</td>
<td>Bryan (1956a)</td>
</tr>
<tr>
<td><em>W. muhlenbergiana</em></td>
<td>n = 13</td>
<td>North Carolina</td>
<td>Bryan (1956a)</td>
</tr>
</tbody>
</table>
METHODS AND MATERIALS

Cytological Technique

Each sample collected in the field was immediately placed in an individual plastic bag and labeled with location and habitat data, and the date of collection. The living mosses were taken directly to the laboratory for immediate study whenever possible. Often it was necessary to store material for varying periods at low temperature. Anderson & Crum (1958) found that the only noticeable effect of low temperature on meiotic chromosomes is to extend the period of time that they remain in metaphase I. They found no differences in behavior, morphology, or number of chromosomes between plants of the same population held at normal temperature versus those stored from 20 to 26 C.

Chromosomes were observed in meiotic figures in sporocytes which had been fixed in Carnoy's solution (3:1), stained in acetic-orecin, and squashed. The exact procedure, essentially that of Steere et al. (1954) is as follows: the population is surveyed under a dissecting microscope and a capsule that appears to be in the correct stage is selected. Meiosis usually occurs when the capsule is mature in size but is still green. A fairly reliable indicator of the onset of meiosis is the color of the annulus, which is usually faintly reddish at meiosis.

The practice of placing cytological material directly in vials of fixative is satisfactory for flowering plants, but is impractical for mosses. Size may be used as a criterion for estimating the cytological condition of a flower bud but it is useless for predicting
meiosis in mosses because the capsule reaches full size prior to the onset of meiosis. The fixative bleaches the color of the annulus, thereby causing the loss of the only guide to judging the capsule age.

After removal of the operculum, or top of the inoperculate capsules, the sporocytes are squeezed into a drop of fixative. The fixative is prepared by combining 3 parts of absolute alcohol and 1 part glacial acetic acid (Darlington & LaCour, 1962). When the fixative has almost completely evaporated, a drop of acetic-orcein is added. The acetic-orcein stain is prepared by placing 1 gram of orcein in 50 cc of 45% acetic acid. After several days, during which time the vessel containing the stain is shaken frequently, but not heated, the solution is filtered through a fine grain filter paper. Filtration must be repeated periodically as a fine precipitate forms, but otherwise the stain solution remains usable for years. A cover slip is placed over the drop of stain and gently tapped with a scalpel to distribute the sporocytes in a single layer. Pressure is then applied to the cover glass either by tapping or by continuous force until the chromosomes are spread apart.

Observations were made using a Zeiss binocular, compound microscope with a 100 X planapochromat oil immersion objective, N. A. = 1.3; an achromatic-aplanatic condenser, N. A. = 1.4; and 12.5 X paired, widefield, compensating eyepieces. A green filter, as nearly monochromic as possible was used to improve contrast.

Observations, measurements, sketches, photographs, and interpretations were always made immediately, and no attempt was made to make slides permanent. Slides may be kept in usable condition for a
day or two by sealing the edges of the cover slip to the slide with warm vaseline or paraffin. Although desiccation is avoided by this procedure the slides gradually become useless because the cytoplasm takes up stain.

An appropriately numbered voucher specimen for each population was preserved immediately when a chromosome count was achieved. Vouchers are on deposit either in the Biology Herbarium of the University of Southwestern Louisiana (Laf) or The Herbarium of Duke University (D).

Morphological Comparisons

Careful morphological comparisons were made of the different chromosome races of each of the three species as well as of hybrid populations. Each plant studied was washed carefully in water and mounted on a slide in Hoyer's semi-permanent mounting medium. In addition to the scoring of features of individual plants, several plants from each population were examined to determine the position of antheridia, and the manner in which new growth arises from old plants, rhizoids, and protonema.

W. controversa: Forty populations of the 14-chromosome* race and an equal number of populations of the 13-chromosome race were sampled for morphological comparisons. The selection of the 13-chromosome populations was determined by their proximity to the location of the 14-chromosome populations. In many cases it was possible to study both

*In all further discussion "14-chromosome" will be used to refer to the gametophytic number, n = 14, and "13-chromosome" to the gametophytic number, n = 13, etc.
races from collections made at the same site. In other cases both races were at least from the same county, and in only a few were they less closely matched.

A randomly selected plant from each population was scored for the following (Fig. 3): total length of plant (gametophyte and sporophyte), length of old gametophyte, length of new gametophyte, length of leaf, width of leaf, length of the flattened leaf base, average cell size near the leaf tip, leaf apex, degree of involution of leaf margin, total length of sporophyte, length of seta, length of vaginule, total length of capsule, length of urn, width of urn, length of operculum, annulus, peristome teeth, average size of exothecial cells, degree of thickening of exothecial cells, and size of mature spores if present.

W. muhlenbergiana: Since only a single population of the 14-chromosome race was available, five plants from it and five from a 13-chromosome race were scored. The same observations were made as for W. controversa, except that the apiculation of the capsule was substituted for the absent operculum. Five plants of a 26-chromosome race were scored in the same way.

W. ludoviciana: Three plants each from a 14-chromosome race, a 13-chromosome race, and the 26-chromosome race population were examined and scored for the same features as used in W. muhlenbergiana.

W. controversa X W. ludovidiana: Nine plants of a single population of 14-chromosome hybrids were examined as well as three plants of a 13-chromosome population. One population of a suspected hybrid with the
Figure 3. *Weissia*, with measurements made for taxonomic comparisons indicated.

A. 1. total plant height.
   2. old gametophyte
   3. new gametophyte

B. 1. leaf length
   2. leaf width at base
   3. length of leaf base
   4. average cell size

C. 1. total sporophyte height
   2. seta length
   3. vaginule
   4. capsule length
   5. urn length
   6. urn width
   7. operculum
   7a. apiculation
chromosome number n = 26, because of its unusual chromosome comple-
ment and appearance, was sampled differently. One sq cm was cut from
the population, and all of the plants (38) contained in it were measured.
OBSERVATIONS

Cytological

The chromosome number of the first populations I studied from Louisiana was n = 14, which was in disagreement with the number n = 13 reported from southeastern United States by Bryan (1956a), and Anderson and Bryan (1958a).

The chromosome number n = 14 had been reported for Weissia controversa from Finland (Vaarama 1950a) and from India by Khanna (1960b). It was suggested by Steere, et al. (1954) that the precocious disjunction of a large bivalent, which they found in California populations of the number n = 13, would result in univalents that could easily be mistaken for bivalents because of comparable size. Bryan (1956a) offered the same explanation to account for the conflict of Vaarama's count with her counts in W. controversa from North Carolina.

This explanation did not appear to be applicable to the Louisiana population because the extra chromosome was a very small but distinct bivalent in addition to 13 bivalents similar to the ones illustrated by the previous investigators. Being unable to reconcile my observations with available interpretations, I sought the aid of Dr. L. E. Anderson. Through his courtesy I went to North Carolina with some of the Weissia from Louisiana, from which we both made cytological preparations in his laboratory at Duke University. Dr. Anderson immediately recognized the small, extra chromosome as an m-chromosome, a regular member of the chromosome complement of many species of mosses.
The 13-chromosome complement (Fig. 4) is characterized by having one large bivalent (ca 2μ long) and 12 medium bivalents (ca 1μ long). The dual nature of the bivalents may be apparent toward the end of metaphase I (Fig. 4A). Disjunction is not always completely synchronous; both precocious disjunction of bivalents into univalents at metaphase I and delayed disjunction in anaphase I (Fig. 4C, D) have been observed.

The 14-chromosome complement consists of 13 bivalents that look and behave like those of the 13-chromosome complement just described, plus a very small (ca. 0.25μ) bivalent, the m-chromosome (Fig. 5A). The behavior of the m-chromosome is highly variable. It sometimes separates quite normally into univalents at anaphase I and into chromatids at anaphase II, but it frequently disjoins prematurely at metaphase I. It may separate into two univalents (Fig. 5B), one univalent and two chromatids (Fig. 5C), or into four chromatids (Fig. 5D), while the other chromosomes are still tightly synapsed.

W. controversa

No striking differences were revealed by cursory examination of the plants of the 13-chromosome and the 14-chromosome races. The question arose as to the geographic distribution of the two chromosome races. Since they cannot be distinguished in the field, cytological sampling over a wide geographic area was necessary.

Because Dr. Anderson's interest was aroused by the possibility that the 13-chromosome race might occur in the southeastern United States and the 14-chromosome race only in the southcentral United States, he agreed to collaborate in determining the distribution. He kindly placed
Figure 4. The 13-chromosome race complement of W. controversa.
X1900.
A. metaphase I, polar view
B. metaphase I, side view
C. D. anaphase I
Figure 5. The 14-chromosome race complement of W. controversa. X2700.

A. metaphase I; the m-chromosome is completely synapsed.
B. metaphase I; the m-chromosome has separated into two univalents.
C. metaphase I; the m-chromosome has separated into one univalent and two chromatids.
D. metaphase I; the m-chromosome has separated into four chromatids. Two chromatids are still connected by a thin strand, and the other pair have moved farther apart.
at my disposal the data that he gathered in the Appalachians, Ozarks and in the southeastern states. Thus the value and scope of the present study has been greatly extended.

It soon became obvious that the 13-chromosome race and the 14-chromosome race both occurred throughout the Atlantic and Gulf Coastal Plain. Furthermore, preliminary investigations indicated that the 14-chromosome race was restricted to the Coastal Plain. Subsequent work revealed, however, that the 14-chromosome race does occur in the lower Piedmont, but so far only two populations have been found outside the Coastal Plain and Piedmont.

A collection made from a limestone habitat in the Appalachian Mountains of eastern Tennessee in the spring of 1967 proved to be sporophytically tetraploid. In the following year collections made in similar limestone-cedar glade habitats in the Ozark Mountains of Arkansas yielded additional tetraploid populations. These 26-chromosome race populations, recognizable by subtle but reliable differences, have been found only in this restricted habitat.

Cytologically, the 26-chromosome complement appears to behave normally at meiosis. No multivalents (Fig. 6A, B, C) are formed and separation at anaphase is without mishap (Fig. 6D).

During the three seasons of field work (1966, 1967, 1968) a total of 460 populations of _W. controversa_ was studied cytologically. Of these, 378 were of the 13-chromosome race, 73 were of the 14-chromosome race, and 9 were of the 26-chromosome race. The percentage of each race in the total number of chromosome counts (frequency) is as follows:
Figure 6. The 26-chromosome race complement of W. controversa.
X1900.
A. metaphase I, polar view
B, C. metaphase I, side view
D. anaphase I

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n = 13 82%
n = 14 16%
n = 26 2%

The distribution of the 14-chromosome race is shown in Fig. 7, the 13-chromosome race in Fig. 8, and the 26-chromosome race in Fig. 9. A single dot is used for each county regardless of the actual number of populations counted from it.

Collection data for each population counted appear in the Appendix and may be consulted for exact numbers. The data are arranged by taxon, and chromosome race, and are listed by state and county in alphabetical order.

The distribution of the three chromosome races is shown on Table 2.

The three chromosome races of *W. controversa* were represented in each of the physiographic regions by the following frequencies (Table 3).

Sixty-six percent of the 14-chromosome race populations were found on the Coastal Plain; of these 77 percent were of the Gulf Coastal Plain, and 23 percent were on the Atlantic Coastal Plain.

*W. muhlenbergiana*

The chromosome number of n = 26 published by Bryan (1956a) was substantiated by Anderson for North Carolina populations, but was not found elsewhere. Populations of the 13-chromosome race and the 14-chromosome race were found in Lafayette Parish, Louisiana, and a population of the 13-chromosome race was found in Sullivan Co., Tennessee. The distribution in physiographic regions is as follows:
Figure 7. The distribution of the 13-chromosome race in southeastern United States.
Figure 8. The distribution of the 14-chromosome race in southeastern United States.
Figure 9. The distribution of the 26-chromosome race in southeastern United States.
Table 2. The distribution of the chromosome races of *W. controversa* in each of the physiographic regions in southeastern United States, based on the total number of chromosome counts of each race.

<table>
<thead>
<tr>
<th>Region</th>
<th>Coastal Plain</th>
<th>Piedmont</th>
<th>Appalachian System</th>
<th>Ozarkian System</th>
<th>Central Lowlands</th>
</tr>
</thead>
<tbody>
<tr>
<td>n = 13</td>
<td>47%</td>
<td>17%</td>
<td>31%</td>
<td>4%</td>
<td>1%</td>
</tr>
<tr>
<td>n = 14</td>
<td>66%</td>
<td>32%</td>
<td>1%</td>
<td>1%</td>
<td>0%</td>
</tr>
<tr>
<td>n = 26</td>
<td>0%</td>
<td>0%</td>
<td>11%</td>
<td>89%</td>
<td>0%</td>
</tr>
</tbody>
</table>

Table 3. The frequencies of three chromosome races of *W. controversa* in each of the physiographic regions in southeastern United States, based on the total number of chromosome counts from each region.

<table>
<thead>
<tr>
<th>Region</th>
<th>n = 13</th>
<th>n = 14</th>
<th>n = 26</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal Plain</td>
<td>79%</td>
<td>21%</td>
<td>0%</td>
</tr>
<tr>
<td>Piedmont</td>
<td>73%</td>
<td>27%</td>
<td>0%</td>
</tr>
<tr>
<td>Appalachian System</td>
<td>98%</td>
<td>1%</td>
<td>1%</td>
</tr>
<tr>
<td>Ozarkian System</td>
<td>63%</td>
<td>4%</td>
<td>33%</td>
</tr>
<tr>
<td>Central Lowlands</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
</tbody>
</table>
n = 13 Coastal Plain and Appalachian System
n = 14 Coastal Plain
n = 26 Piedmont

Cytological data, however, are insufficient to allow further analysis. The collection data are in the Appendix.

The chromosome complements of the chromosome races are like the comparable races in *W. controversa* in size, shape, and behavior. The only cytological difference was in the staining reaction. The chromosomes required a much longer time to stain adequately and the cytoplasm, which was full of oil globules, stained rather quickly.

*W. ludoviciana*

Populations of 13-, 14- and 26-chromosome races were discovered. All were on the Coastal Plain: 13- and 14-chromosome race populations were from Louisiana, and the 26-chromosome race populations were from Mississippi. The collection data are in the Appendix.

The chromosome complement is like *W. controversa* in morphology (Fig. 10B) and behavior. The staining reaction is somewhat intermediate; some populations had chromosomes which stained easily, like those of *W. controversa*, while others exhibited a staining reaction almost as slow as in *W. muhlenbergiana*.

**Hybrids**

Two hybrid populations from Louisiana were studied cytologically. The first was found in Lafayette Parish about 8 miles from the originally described hybrid population (Reese & Lemmon, 1965), which had been destroyed before it could be studied cytologically. It had the chromosome number n = 14 (Fig. 10C). Both of the presumed parents,
Figure 10. The 14-chromosome complements of *W. controversa*, *W. ludoviciana*, and *W. controversa* × *W. ludoviciana*. X1900.

A. *W. controversa*, metaphase I
B. *W. ludoviciana*, metaphase I
C. *W. controversa* × *W. ludoviciana*, metaphase I
D. *W. controversa* × *W. ludoviciana*, anaphase I

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W. controversa (Fig. 10A) and W. ludovici (Fig. 10B) had the same number, n = 14. The chromosomes, paired normally in prophase I (Fig. 10C) and separated regularly at anaphase I (10D). The second hybrid population found about 30 miles away in Vermilion Parish had the chromosome number n = 13, as did both of its putative parents, W. controversa and W. ludovici. The chromosomes of these hybrids differed in no apparent way from their putative parents; meiosis was completely normal, with no difficulties in pairing and no anaphasic irregularities noted.

A third population suspected of being the result of hybridization was collected in Perry County, Alabama. It was, however, quite different from the other hybrid populations in that it was a large, well-established colony, the sporophytes of which seemed to range from typical W. ludovici to typical hybrids. However, no W. controversa was present. The population proved to be sporophytically tetraploid with the chromosome number n = 26. The only W. controversa plants in the area, and they were unusually few, had the chromosome number n = 14.

The collection data are in the Appendix.

The constancy of the chromosome number within a population was tested by sampling several capsules from each of several populations in various states. In every test the results showed constancy of chromosome number within the colony.

In order to determine whether or not the chromosome number remained constant in a population from year to year, two colonies in Durham, North Carolina and two in Lafayette, Louisiana were studied in
two successive years. The two colonies in North Carolina, one a 13-chromosome race and the other a 14-chromosome race, showed no variance in the chromosome number from year to year. The 13- and 14-chromosome populations in Louisiana likewise remained constant.

Morphological

Detailed morphological comparisons of the gametophytes of all the chromosome races of Weissia investigated in this study failed to show any significant differences, except for the 26-chromosome race of one species, W. controversa. In growth habit, this race is softer, less compact, and can be more easily removed from the substrate than the colonies of the 13-chromosome race growing with it in the same habitat. The leaves are different: they are as wide as those of the other race but are considerably shorter. Although the margins are involute, the upper portion of the leaf is not tubular because of the wide, flat area between the inrolled margins. The costa is very strong, orange-brown in color, and ends in a short mucro point that extends abruptly from the more rounded leaf tips.

Comparison of the sporophytes revealed only one minor but interesting difference. The sporophytic characteristics, seta length, capsule shape, apiculation, development of annulus and peristome teeth, of the 26-chromosome races in all three species fell within the lower limits of the individual species. Seta length, because it was found to be most consistently correlated with the other characteristics that separate the species and because it can be measured quantitatively, was chosen to be presented graphically. The
measurements are plotted against number of individuals counted for each species and coded to indicate chromosome race (Fig. 11). Analysis of the other measurements and observations of various features showed no significant differences between members of the chromosome races.

The range of seta length of the 13- and 14-chromosome race hybrid populations, and of their presumed parents, are represented on the same graph (Fig. 12) as well as those of the 26-chromosome race population suspected, because of its characteristics, to be of hybrid origin. The other characteristics, shape of capsule, length of spiculation, development of annulus and peristome teeth, as with the 13- and 14-chromosome race populations, were intermediate between W. controversa and W. ludoviciana, but closer in this case to the latter species.

Table 4 is a summation of sporophyte characteristics of the taxa. The arbitrarily assigned values were based on numerous measurements of samples of the available populations of 13-, 14- and 26-chromosome races.

A characteristic that had not previously been compared in the species is the presence and nature of the stomates, which occur at the base of the capsule. They were observed to be very well developed and obvious in W. muhlenbergiana, due to the large, orange guard cells, and fewer and much less conspicuous in W. controversa. Those of W. ludoviciana and the hybrids are intermediate in this respect.

Examination and measurements of the spores of all the taxa showed that they are consistently rough-papillose, approximately spherical, and that the diameter is variable, from 18-33u. Overlapping
Figure 11. Seta length in mm versus number of individuals for three species and three hybrid populations of Weissia.
Figure 12. Seta length in mm for hybrids and presumed parents in two chromosome races, and for a hybrid populations in a third chromosome race. a. Hybrid; b. *W. ludoviciana*; c. *W. controversa*.
Table 4. Comparison of values arbitrarily assigned to six characteristics of three species and a hybrid of *Weissia*.

<table>
<thead>
<tr>
<th></th>
<th>Seta</th>
<th>Peristome teeth</th>
<th>Exothecial cell walls</th>
<th>Annulus</th>
<th>Apiculation</th>
<th>Shape of capsule</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>W. muhlenbergiana</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>W. ludoviciana</em></td>
<td>0+</td>
<td>0</td>
<td>0+</td>
<td>1</td>
<td>0+</td>
<td>1</td>
</tr>
<tr>
<td><em>W. ludoviciana X</em></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1+</td>
<td>1</td>
<td>1+</td>
</tr>
<tr>
<td><em>W. controversa</em></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

Seta:  
0 = .00 - .20 mm  
0+ = .21 - 1.0 mm  
1 = 1.01 - 2.5 mm  
2 = 3.5 - 8.0 mm

Peristome teeth:  
0 = none  
1 = fragmentary  
2 = well developed

Exothecial cell walls:  
0 = no thickening  
1 = slight thickening  
2 = thickened

Annulus:  
0 = none  
1 = line, not dehiscing  
2 = dehiscing at maturity

Apiculation:  
0 = .05 - .15 mm  
1 = .16 - .18 mm  
2 = .5 - .9 mm

Shape of capsule:  
0 = spherical  
1 = ovoid  
2 = ovoid-cylindric
range in spore size in chromosome races and in species makes this character an unreliable criterion.

Germination of spores was attempted only for the 26-chromosome race of suspected hybrid origin. No germination occurred from the first attempt. Spores from a second set of capsules which had matured for a few weeks before being sown on agar plates were from 10-20% viable. Previous germination tests (Reese & Lemmon, 1965) showed that approximately 98% of the *W. controversa* and 93% of the *W. ludoviciana* spores produced protonema. The spores from a hybrid between them were from 0-2% viable.

The gametophytes frequently appear to be identical, but can sometimes be distinguished on the basis of leaf size. The perichaetal leaves of *W. muhlenbergiana* may be longer, up to 4 mm, and may be quite flat. Those of *W. controversa* are consistently smaller, about 2 to 3 mm, and strongly involute, while those of *W. ludoviciana* are intermediate, usually about 3 mm in length. This characteristic may be due in large part to environment and vigor and age of the colony, and is a criterion of doubtful taxonomic value.
DISCUSSION

Two types of cytological variation, aneuploidy and polyploidy, exist in members of the genus Weissia studied.

Aneuploidy

The m-chromosome was consistently found to be responsible for aneuploidy in Weissia; it was present in all of the 14-chromosome race populations and absent from all of the 13-chromosome race populations. The behavior of the m-bivalent in Weissia parallels the behavior of comparable bivalents in Sphagnum described by Bryan (1955), and in other mosses as reported by numerous workers (see Anderson, 1964). The m-bivalent was seen completely synapsed (Fig. 5A), or as separated univalents (Fig. 5B), as a univalent and two chromatids (Fig. 5C), or as four chromatids (Fig. 5D). Although disjunction was frequently precocious at metaphase I (Fig. 5), anaphasic behavior was quite regular. There is no indication that the eventual distribution of the four chromatids of the m-bivalent is anything other than one chromatid into each of the four incipient spores.

It was apparent that the size of the m-bivalent varied from population to population. The size in all cases, however, was considerably less than the other bivalents. The m-bivalent always presented itself as a discrete body or bodies, never attached to or close to another bivalent, so that there is no suspicion of its being a satellite.
The number of the 14-chromosome race is appropriately expressed as \( n = 13 + m \). The practice of indicating a small bivalent in a genome by a number \((13 + 1)\), first used by Heitz (1927), is confusing because it is at present widely used to denote the presence of an accessory chromosome in a genome. Although the \( m \)-chromosomes are comparable in morphology to the accessory or supernumary chromosomes of some flowering plants, they differ in meiotic behavior. The accessory chromosomes are unstable members of the genome, segregating irregularly at meiosis and undergoing somatic non-disjunction and elimination, frequently fragmenting (Hokansson, 1945; Swanson, 1957). The \( m \)-bivalents are constant from individual to individual and, as pointed out by Bryan (1955), should be considered as regular members of the meiotic complement. Chromosome counts from \textit{Weissia} populations in Louisiana and North Carolina over two successive years revealed that the \( m \)-chromosome is not eliminated or generated at random. All populations were constant in chromosome number.

Standard taxonomic studies of the taxa indicate that the presence of the \( m \)-bivalent in the genome is not accompanied by any distinctive morphological differences. The only feature that varied significantly between the two races is total gametophyte height. This characteristic, of no taxonomic value, varies in direct relationship to the yearly increments of gametophore growth, a characteristic that indicates genetic response to environment. Routine ecological observations have failed to reveal a correlation between the microhabitat occupied by the moss and the presence or absence of an \( m \)-bivalent in its genome.
Two conclusions may be drawn from an analysis of the distribution of the two chromosome races in southeastern United States. First, the 13-chromosome race is much more common, comprising 82% of the total population of W. controversa. Second, the 14-chromosome race is most common on the Coastal Plain, where 66% of the populations of that race occur.

Whether or not the m-chromosome is of recent or of ancient origin is a matter of speculation. A recent origin could be due to the spontaneous production of an m-chromosome from one of the other chromosomes. At the beginning of this study I was aware that the size of the large chromosome, termed the H-chromosome by Yano (1957a, 1957b, 1957c), varied considerably from population to population. Measurements and careful observations, however, soon indicated that a reduction in size of the large bivalent cannot be correlated with the presence of the m-bivalent. It may be that more sophisticated techniques of measuring somatic chromosomes will make it possible to construct an accurate ideogram in which minute differences could be detected. However, many diminutive chromosomes of mosses are heterochromosomal and are not always visible in somatic mitosis.

There is slightly more reason to suppose that the origin of the m-chromosome is ancient rather than recent. The theory that the m-chromosome is primitive has been suggested by Yano (l. c.), who believes that all mosses have both a large chromosome, the H-chromosome, and a small one, the h-chromosome (m-chromosome). Populations of W. controversa which have an m-chromosome as part of their karyotype have been also reported from Europe (Vaarama, 1950a).
and India (Khanna, 1960b). Although data are insufficient to speculate upon the geographic distribution, the occurrence of the 14-chromosome race in such widespread locations strongly supports the idea of an ancient origin of the m-chromosome.

The m-chromosome is present in the genome of 35% of the genera of the Pottiaceae and at least one member of 30% of the families of mosses for which chromosome counts are published (Anderson, 1962). This general occurrence of the m-chromosome in mosses is further evidence that it is of ancient rather than recent origin.

Polyploidy

No meiotic irregularities or multivalents were observed in any of the tetraploid races of the taxa of Weissia studied. There is ample evidence, dating from the early 1920's when Wettstein began his long series of experiments, to allow the assumption that meiotic regularity is an indication of stability in a spontaneous tetraploid race. Wettstein (1923, 1924a, 1924b) found that an induced tetraploid race of Funaria hygrometrica Hedw. gradually became completely "diploidized" over an 11 year period. All of the gigas characters, increased spore size, increased cell size and meiotic irregularities, which were noted when the tetraploid race was first produced were eventually lost, the tetraploid race finally resembling quite closely the diploid race.

Vaarama (1955) investigated a spontaneous tetraploid race of E. hygrometrica using Wettstein's criteria and techniques. He found that his plants resembled the diploid race of Wettstein more closely than they did the artificial tetraploid race that Wettstein had
produced experimentally. His data reinforced the hypothesis that a tetraploid race may lose gigas characteristics over a period of time and eventually become stabilized as a perfectly fertile taxon. Whether or not it is morphologically distinct from the race which gave rise to it depends upon genetic diversity and selection, and not upon polyploidy per se (Wettstein & Straub, 1942).

Stebbins (1950), in discussing the role of polyploidy in evolution, maintains that variation is a function of genetic diversity and that polyploidy can only produce additional variations on an already established theme. Thus, during times of great climatic change polyploidy can supply the variety of gene combinations that may allow the species to exploit new environments, but in times of stable ecological conditions, polyploidy limits the chances for variability by isolating the polyploid from gene exchange with plants at lower levels of ploidy.

A difference between the tetraploid and diploid races was apparent only in _W. controversa_; in the other species the equivalent forms are indistinguishable. It is interesting that all of the characteristics of the tetraploid races are at the most conservative end of the limits for the individual species. Polyploidy in these species tends to limit rather than extend variation. Karyotypic balance is evidently maintained through the levels of ploidy and phenotypic expression remains limited by genetic potential.

Data on distribution and habitat are sufficient only in the tetraploid race of _W. controversa_. This race is known only from very distinctive and restricted mountain habitats of junipers and flat, terraced limestone, where the moss grows on the edges of the rocks. It was first discovered in the Appalachian System and later, when
similar habitats were searched, in several locations in the Ozarkian System (Fig. 9). The distribution figures (8 locations in the Ozarks, 1 in the Appalachians) are not the result of random collections, and the bias must be considered when interpreting the significance of the distribution of this race in the two areas.

The distribution pattern of the tetraploid race is unique among the three chromosome races of *W. controversa* in southeastern United States in that it is restricted to two physiographic areas which both served as plant refugia during the last glacial period. The 13-chromosome race that is found growing with the tetraploid race appears to be the same cytological race that is widespread in the Coastal Plain and Piedmont.

The tetraploid race under discussion is the same taxon that Crum, Steere and Anderson (1965) list as *W. tortilis* (Schwaegr.) C. Mueller. Sharp called it *Hymenostomum tortilis* in a publication (1941) on historical factors and the distribution of southern Appalachian bryophytes. He cited it as an example of a xeric species that probably arrived in its eastern outpost, Tennessee, during a dry geological period.

*W. tortilis* is most like *W. andrewsii* Bartr., a species recognized by Andrews (1933) as distinct from *W. viridula* (*controversa*). It is known from the Santa Cataline Mountains of Arizona and also from Texas. The chromosome number is not known. Both the tetraploid race of this investigation (recognized as *W. tortilis* by Sharp) and *W. andrewsii* have wider leaves, more broadly pointed tips, a very strong,
wide costa and strongly papillose peristome teeth that are often only rudimentary.

The taxonomic level at which this taxon is most agreeably situated is still problematical. Polyploidy, although considered by some cytotaxonomists to be sufficient for separating species, has been shown for the other two species of *Weissia* to be unrelated to any taxonomic criteria by which the tetraploid race may be recognized. Lewis (1967) who considers polyploidy an important step toward speciation, would avoid the "tagging of morphologically similar individuals with formal Latin designations." He suggests recognition of chromosome races, not yet evolved into distinct species, by the use of a numerical designation of the level of ploidy (2X, 4X, etc.) after the scientific name. In respect to the tetraploid race of *W. controversa* it seems appropriate to recognize the morphological and ecological differences that perhaps were selected for over long periods of spatial and genetic isolation. The occupancy of two areas of common historical significance strongly suggests a common, ancient origin for the taxon.

One way in which doubling of a chromosome complement, syndiploidy, can occur in nature is by the failure of the sporocyte to undergo cytokinesis following the last mitotic division prior to the onset of meiosis. The subsequent fusion of nuclei in the "double" sporocyte or of the meiotic prophase spindles after the onset of meiosis may result in the chromosomes of both sets being deployed on a single spindle (Fig. 13B). Syndiploidy was observed in a sporocyte of a 13-chromosome race (Fig. 13A) population from Greene County,
Figure 13. Syndiploidy in *W. controversa*. X2700.
A. a normal sporocyte, metaphase I.
B. a "double" sporocyte in which the 13-chromosomes from each of the two nuclei are deployed on a single spindle at metaphase I.
Ohio (not included in the distribution study because it is outside the area delimited for this investigation). It was also observed in a sporocyte of a 14-chromosome race population from Choctaw Co., Alabama. Presumably there were 28 chromosomes but it was impossible to determine whether or not the m-bivalent was duplicated because the chromosomes of both sets were crowded on a spindle located in the narrow isthmus of the dumbbell shaped sporocyte. It is unfortunate that an accurate count was not possible in view of the fact that no 28-chromosome race was found during the study. In other mosses, Orthotrichum for example, an m-bivalent is present in the diploid race but is not represented proportionately in each additional genome in the polyploids.

Syndiploidy does not always occur in "double" sporocytes; several incompletely divided sporocytes from a 13-chromosome race from Liberty Co. Florida each had only 13 chromosomes on a spindle in one of the lobes of cytoplasm. Two explanations are offered; either the faulty cytokinesis occurred in a cell that had failed to undergo mitosis, or if two sets of chromosomes were present, one of them aborted.

Syntetraploidy was observed in imperfectly divided, "double" sporocytes of a 26-chromosome race of W. controversa from Tennessee. At metaphase I the 52 bivalents were observed crowded on the spindle (Fig. 14A) and at late anaphase I (Fig. 14B) the 52 univalents were equally distributed at each of the two poles. Each of the spores produced in this manner would, if viable, give rise to tetraploid gametophytes, but no such plants have been found.
Figure 14. Syntetraploidy in *W. controversa*. X1900.

A. a "double" sporocyte in which the 26 bivalents from each of the two nuclei are crowded on a single spindle at metaphase I

B. anaphase II; 52 chromosomes at each pole
The process of cytoplasmic division that accompanies the meiotic division of the chromosomes appears to be independent of the events of meiosis. The cytoplasm becomes distorted into four lobes during prophase I, clearly anticipating the disposition of the four sets of chromosomes at telophase II. Malformation of the spores in the hybrid populations is presumed to be the result of faulty cytokinesis because meiosis is normal. The underlying cause may be the disruption of a delicate balance that normally exists between meiosis and cytokinesis. It cannot be denied that such a balance may be under genetic control, but it seems that the mechanism of control is something other than meiotic events.

Reduced fertility in polyploids was once attributed to the formation and irregular segregation of multivalent associations of chromosomes (Darlington, 1937). In recent years, however, this theory has been revised and it is now generally considered that sterility is frequently physiological in nature. Sterility in autotetraploid maize is largely controlled by specific genes or gene combinations (Randolph, 1941). Sterility in allopolyploids is likewise frequently best explained in genetic terms rather than on a cytological basis (Stebbins, 1950).

Spore fertility in the genus Weissia has been investigated only superficially. Reese and Lemmon (1965) tested germination in W. controversa, W. ludoviciana, and a presumed hybrid between them by sowing spores from each of several capsules onto sterile Benecke's agar in petri plates. They found that germination occurred in approximately 98% of the spores of W. controversa, and in 93% of the spores.
of *W. ludoviciana*. Spores from the capsules of a presumed hybrid were from 0-2% viable. This extremely low fertility rate might best be explained as the result of a series of disharmonies created by the presence of the morphologically similar, but physiologically different paternal chromosomes.

The spore fertility of a tetraploid race of *Weissia* from Perry Co., Alabama was determined in order to understand better its uncertain taxonomic position. The spores, tested for viability in the same way as previously described, proved to be 10-20% viable. Numerous colonies of this unusual taxon were found growing on wet, flat terraces about a foot across which had eroded between clumps of grass that had been planted on a road cut. Many of the capsules were exserted just beyond the perichaetial leaves, and some were immersed as in typical *W. ludoviciana*. One sq cm from one of these populations contained 38 plants, which when compared morphologically proved to consist of an uninterrupted series of types which graded from typical *W. ludoviciana* plants into one typical of the previously described hybrid between *W. controversa* and *W. ludoviciana*. There was no *W. controversa* growing in these populations and a careful search of the area (approximately 50 ft x 110 ft) revealed only a few depauperate plants of this species. These proved to be of the 14-chromosome race, and therefore not closely related cytologically to the 26-chromosome race population.

Chromosome doubling following back crossing of a hybrid might produce a stable tetraploid population that could be expected to be reasonably fertile. Although the viability of the spores of this population was low (10-20%) by the standards set by *W. controversa* and
W. ludoviciana, it was nonetheless high enough to account for the numerous similar populations which were found in the area. The fertility rate does not, however, prove anything about the origin of the genome. None of the protonemata were grown to maturity so no further analysis of the possible types, nor speculations about the progenitors can be made at this time.

Those plants with the capsules exerted beyond the tips of the perichaetal leaves resemble a species of dubious status which is listed by Crum, Steere and Anderson (1965) as Astocum phascoides (Hook. ex Drumm.) Grout. The taxon in question is prevented from being settled in this species by the fact that the populations consist of an uninterrupted series of forms, only about half of which resemble A. phascoides.

The possibility that A. phascoides populations also consist of a series of plants is not dismissed. The chromosome number is unknown. Grout (1938) states that it often grows with W. muhlenbergiana or with W. controversa and that Andrews suspected it to be a hybrid, but he adds that its wide distribution (Saskatchewan, Minnesota, Ohio, Arizona, Texas) makes this seem unlikely.

A tetraploid species in Asia, W. exserta, that is morphologically intermediate between the stegocarpous W. crispata and the cleistocarpous W. crispum was declared by Khanna (1960a) to be the result of hybridization followed by chromosome doubling. He interpreted the achievement of this species in successfully occupying an intermediate habitat as a function of the amphidiploidy. W. exserta is clearly morphologically intermediate but proof of its presumed cytological history is lacking.
Evaluation of the Genus

The question arises as to how genetic integrity is maintained in the species of *Weissia*. The three species studied are morphologically distinct entities whose characteristics, although variable in two species, nevertheless fall within the defined specific framework for each. *W. muhlenbergiana* is remarkably uniform; *W. controversa* is strikingly variable, but still easily recognizable. *W. ludoviciana*, slightly variable but distinct, is much closer to *W. muhlenbergiana* than to *W. controversa*, and is suspected to have its origin in the backcrossing of a hybrid (*W. controversa* x *W. muhlenbergiana*) to *W. muhlenbergiana*. This speculation is based on an analysis of the morphological characteristics of *W. ludoviciana* in relation to those of the other two species, the presence of deformed spores (Reese & Lemmon, 1965), cytology, and its ability to hybridize with *W. controversa*.

A natural hybrid between *W. muhlenbergiana* and *W. controversa*, apparently similar to the hybrids studied during this investigation, was reported by Williams (1966) from Ontario, Canada. All of the hybrids of my observation, however, seemed to involve *W. ludoviciana* as the cleistocarpous parent. The hybrids reported by Nicholson (1905) and Khanna (1960a) involved the cleistocarpous *W. crispa*, which Andrews (1922) found to be the European species most closely related to *W. ludoviciana*.

The species of *Weissia* are cytologically similar; the genomes are morphologically alike, are meiotically compatible and share the following parallels. A 13-, a 14- and a 26-chromosome race is known in all three species; no 27- or 28-chromosome tetraploids are known to
occur in any of the species, and no diploid race is known in which the m-chromosome occurs as a univalent. The species are sympatric and frequently grow mixed in the same colony. Barriers to hybridization certainly exist because intermediate forms are produced only rarely. Maturation of gametes is not usually coincidental; *W. mucilaginosum* frequently fruits two weeks or more before *W. ludoviciana*, and both fruit about a month earlier than *W. controversa*. This temporal isolation could, if it was consistent, account for the prevention of hybridization. However, *W. ludoviciana* and *W. controversa* have been observed to fruit simultaneously with no hybrids being produced. In all the presumed hybrid populations the situation was ideal for hybridization; the two parents and the hybrids were growing together in the same stage of development and all were growing on flat, heavy clay on which a thin film of water was standing.

The mechanism by which the sperm locate the archegonia and fertilize the eggs inside is apparently very effective in *Weissia*. Sporophytes develop in almost every perichaetium in all of the species, even though antheridia are borne in small clusters and occur on only about one in ten plants. Whether or not any selectivity for fertilization is operative at the specific level is not known.

None of the thousands of sporophytes examined appeared to be abortive, except for a few that had obviously succumbed to fungal invasion. It seems unlikely that the incompatibility of the genomes in the diploid cells is responsible for the paucity of hybrids. However, embryos that abort while very young would be undetected by routine examination, and this possibility must be considered. Several
archegonia are usually produced in a single perichaetium and the egg in a second archegonium would likely be fertilized and produce a sporophyte if the first egg to be fertilized should abort.

It is more difficult to determine what factors prevent hybridization than it is to predict that few hybrids are likely to be perpetuated. The sporophyte is short-lived and dependent on the gametophyte. The haploid spores, produced by meiosis, no longer contain the two sets of chromosomes that were brought together in hybridization. Very few of them are likely to be viable, and those that do germinate are probably the few that received either a complete maternal or a complete paternal set of chromosomes at meiosis. For a diploid sporophyte to give rise to a completely hybrid gametophyte, meiosis must be circumvented and the gametophyte will be diploid. Unreduced spores would give rise to diploid gametophytes with all the advantages or hazards of an allopolyploid. The doubling of chromosomes by the failure of the sporocyte to undergo cytokinesis, as previously described, would result in diploid spores with any of the possible combinations of chromosomes from one maternal set and one paternal set to two sets of one or the other.

Aneuploidy and polyploidy were evidently not operative as isolating mechanisms leading to speciation of the members of the genus Weissia studied, since the same chromosome races occur in all the species. It is possible that the chromosome races are isolated from each other within the species, however, because there is no evidence of interbreeding between chromosome races either intraspecifically or interspecifically. The genomes of each chromosome race are alike in
all the species, both morphologically and behaviorally. The genomes of each species, regardless of the chromosome number, are genetically different enough, however, to produce a phenotype that is recognizable within the specific description. Several hybrids between a cleistocarpous and a stegocarpous species have been reported, and three such hybrids were studied cytologically. The facile manner in which the two chromosome complements pair and proceed through the intricacies of meiosis is further evidence of the close genotypic relationship. It is assumed that genetic barriers exist because genetic integrity is maintained, with few exceptions, at the specific level in spite of the fact that cytologically similar populations grow in mixed colonies and sometimes fruit simultaneously.
SUMMARY

1. Three species of Weissia occur in southeastern United States; one stegocarpous species, W. controversa, and two cleistocarpous species, W. ludoviciana and W. muhlenbergiana.

2. Each of the three species studied had a 13-, a 14- and a 26-chromosome race.

3. Aneuploidy in the sporophytically diploid races was due to the presence of the small m-bivalent. The m-chromosome never occurred as a univalent at meiosis, and was absent in all of the tetraploid races.

4. Comparison of the morphology and ecology of all the chromosome races in each of the species revealed no differences except in the 26-chromosome race of W. controversa. This taxon has been called W. tortilis, but its taxonomic position is questionable.

5. Frequencies and distribution of W. controversa chromosome races were based on chromosome counts from 460 populations. The frequency of the 13-chromosome race was 82%; its distribution was 47% in the Coastal Plain, 17% in the Piedmont, 31% in the Appalachian System, 4% in the Ozarkian System, and 1% in the Central Lowlands. The frequency of the 14-chromosome race was 16%; its distribution was 66% in the Coastal Plain, 32% in the Piedmont, 1% in the Appalachian System, and 1% in the Ozarkian System. The frequency of the 26-chromosome race was 2%; its distribution was 11% in the Appalachian System, and 89% in the Ozarkian System.

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6. There is evidence of interspecific hybridity in all three of the chromosome races. There is no evidence of hybridization between different chromosome races either intraspecifically or inter- specifically.

7. Genetic integrity is maintained in spite of biotic sympatry, mixed populations, occasional coincidental gamete maturation, morphological similarity of karyotypes, and meiotic compatibility of chromosomes.
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1-75.


APPENDIX

**Weissia controversa** n = 13

**ALABAMA**

**Blount Co.:**
- 4 miles NW of Brooksville, clay soil, roadbank
  - Nov. 24, 1967
  - L. E. Anderson 20184 (D)
- 4 miles SE of Brooksville, clay soil, roadbank
  - Nov. 24, 1967
  - L. E. Anderson 20186 (D)

**Butler Co.:**
- 10 miles NE of Greenville, roadside
  - Feb. 4, 1967
  - L. E. Anderson 25023 (Laf)

**Calhoun Co.:**
- 4 miles W of Piedmont, gravelly, clayey soil, roadbank
  - Nov. 25, 1967
  - L. E. Anderson 20144 (D)
- Same, another colony
  - L. E. Anderson 20145 (D)
- Same, another colony
  - L. E. Anderson 20146 (D)

**Cherokee, Co.:**
- 8 miles E of Spring Garden, rocks, exposed road cut
  - Nov. 25, 1967
  - L. E. Anderson 20148 (D)
- Same, another clump
  - L. E. Anderson 20149 (D)
- 6 miles E of Spring Garden, roadbank
  - Nov. 25, 1967
  - L. E. Anderson 20156 (D)
- Same, another clump
  - L. E. Anderson 20157 (D)

**Choctaw, Co.:**
- 4 miles N of Butler, soil, roadside
  - Dec. 30, 1967
  - B. E. Lemmon 1831 (Laf)
- .5 mile S of Ararat, roadbank
  - Dec. 30, 1967
  - B. E. Lemmon 1825 (Laf)
- 1 mile S of Gilbertown, roadside
  - Dec. 30, 1967
  - B. E. Lemmon 1835 (Laf)
- 1 mile S of Gilbertown, roadside
  - Dec. 30, 1967
  - B. E. Lemmon 1834 (Laf)
- 8 miles SE of Butler, roadside
  - Dec. 30, 1967
  - B. E. Lemmon 1838 (Laf)

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**W. controversa** n = 13 Alabama

**Choctaw Co.**
8 miles SE of Butler, roadside
Dec. 30, 1967 B. E. Lemmon 1837 (Laf)

8 miles SE of Butler, roadside
Dec. 30, 1967 B. E. Lemmon 1841 (Laf)

4 miles N of Butler, roadside
Dec. 30, 1967 B. E. Lemmon 1845 (Laf)

**Cleburne Co.**
1 mile from State line, E of Borden Springs,
soil among weeds, roadside
Nov. 25, 1967 L. E. Anderson 20150 (D)

Same, another clump L. E. Anderson 30151 (D)

**Conecuh Co.**
7 miles NE of Evergreen
Feb. 4, 1967 L. E. Anderson 35013 (Laf)

**Cullman Co.**
1 mile SW of Joppa, soil, roadbank
Nov. 24, 1967 L. E. Anderson 20201 (D)

2 miles E of Balleyton, soil, roadbank
Nov. 24, 1967 L. E. Anderson 20207 (D)

**Dale Co.**
2 miles NW of Midland City, roadside
Dec. 29, 1967 B. E. Lemmon 1839 (Laf)

**Dekalb Co.**
1.5 miles W of Ider, soil under pines, eroded field
Nov. 24, 1967 L. E. Anderson 20206 (D)

2.2 miles S of Ider, clay soil, roadbank
Nov. 24, 1967 L. E. Anderson 20205 (D)

**Escambia Co.**
7 miles W of Wallace
Feb. 4, 1967 L. E. Anderson 25020 (Laf)

**Etowa Co.**
1 mile E of Walnut Grove, soil among grasses
Nov. 24, 1967 L. E. Anderson 20193 (D)

**Hale Co.**
Praireville, roadside
Dec. 30, 1967 B. E. Lemmon 1829 (Laf)

**Houston Co.**
9 miles S of Dothan, ditchbank
Dec. 29, 1967 B. E. Lemmon 1840 (Laf)

**Jackson Co.**
Higdon, soil, roadside
Nov. 24, 1967 L. E. Anderson 20187 (D)
<table>
<thead>
<tr>
<th>County</th>
<th>Location Details</th>
<th>Collector</th>
<th>Specimen Code</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jackson Co.</td>
<td>1 mile SE of Flat Rock, soil, roadside</td>
<td>L. E. Anderson</td>
<td>20188 (D)</td>
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<tr>
<td></td>
<td>Nov. 24, 1967</td>
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<tr>
<td></td>
<td>Same, another clump</td>
<td>L. E. Anderson</td>
<td>20189 (D)</td>
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<tr>
<td>Lee Co.</td>
<td>11 miles NE of Opelika</td>
<td>L. E. Anderson</td>
<td>25007 (Laf)</td>
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<td>Feb. 4, 1967</td>
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<tr>
<td>Lowndes Co.</td>
<td>5 miles N of Sandy Ridge</td>
<td>L. E. Anderson</td>
<td>25010 (Laf)</td>
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<td>Feb. 4, 1967</td>
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<tr>
<td></td>
<td>6.8 miles E of Lowdensboro, roadside</td>
<td>B. E. Lemmon</td>
<td>1803 (Laf)</td>
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<td>Dec. 26, 1967</td>
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<tr>
<td>Macon Co.</td>
<td>Tuskegee</td>
<td>L. E. Anderson</td>
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<tr>
<td>Marengo Co.</td>
<td>11.3 miles W of Demopolis, roadside</td>
<td>B. E. Lemmon</td>
<td>1823 (Laf)</td>
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<td>Dec. 30, 1967</td>
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<tr>
<td></td>
<td>Faunsdale, steep RR cut, under trees</td>
<td>B. E. Lemmon</td>
<td>1857 (Laf)</td>
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<td>Dec. 30, 1967</td>
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<tr>
<td>Marshall Co.</td>
<td>6 miles NE of Albertville, soil among grasses, roadside</td>
<td>L. E. Anderson</td>
<td>20202 (D)</td>
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<td>Nov. 24, 1967</td>
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<tr>
<td></td>
<td>Warrenton, soil among grasses, roadside</td>
<td>L. E. Anderson</td>
<td>20199 (D)</td>
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<td>Nov. 24, 1967</td>
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<tr>
<td>Montgomery Co.</td>
<td>4 miles N of Davenport</td>
<td>L. E. Anderson</td>
<td>25016 (Laf)</td>
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<td>Feb. 4, 1967</td>
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<tr>
<td>Morgan Co.</td>
<td>Hulaco, clay soil, roadbank</td>
<td>L. E. Anderson</td>
<td>20200 (D)</td>
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<td>Nov. 24, 1967</td>
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<tr>
<td>Perry Co.</td>
<td>.7 miles E of Uniontown, roadcut, heavy yellow clay, flat, wet places among grasses</td>
<td>B. E. Lemmon</td>
<td>1801 (Laf)</td>
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<td></td>
<td>Dec. 30, 1967</td>
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<tr>
<td>Pike Co.</td>
<td>1.5 miles S of Brundridge, roadside</td>
<td>B. E. Lemmon</td>
<td>1827 (Laf)</td>
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<td></td>
<td>Dec. 29, 1967</td>
<td></td>
<td></td>
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<tr>
<td>Sumter Co.</td>
<td>4.5 miles S of York, roadside</td>
<td>B. E. Lemmon</td>
<td>1828 (Laf)</td>
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<tr>
<td></td>
<td>Dec. 30, 1967</td>
<td></td>
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**W. controversa**  \( n = 13 \)

**ARKANSAS**

<table>
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<tr>
<th>County</th>
<th>Location Description</th>
<th>Date</th>
<th>Collector</th>
<th>Specimen Number</th>
<th>Notes</th>
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</thead>
<tbody>
<tr>
<td>Baxter Co.</td>
<td>1 mile S of Clarkridge, limestone in open glade</td>
<td>March 8, 1968</td>
<td>(collected by Paul Redfern, Jr.)</td>
<td>B. E. Lemmon 1870</td>
<td>(Laf)</td>
</tr>
<tr>
<td>Calhoun Co.</td>
<td>13.2 miles N of Hampton, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1562</td>
<td>(Laf)</td>
</tr>
<tr>
<td>Clark Co.</td>
<td>18 miles SW of Arkadelphia, bank, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1558</td>
<td>(Laf)</td>
</tr>
<tr>
<td>Dallas Co.</td>
<td>3.3 miles N of Fordyce, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1580</td>
<td>(Laf)</td>
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<tr>
<td>Grant Co.</td>
<td>2 miles W of Poyen, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1568</td>
<td>(Laf)</td>
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<tr>
<td>Hempstead Co.</td>
<td>.5 mile N of Hope, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1578</td>
<td>(Laf)</td>
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<tr>
<td>Hot Springs Co.</td>
<td>1 mile W of Donaldson, roadside</td>
<td>Feb. 26, 1967</td>
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<td>B. E. Lemmon 1552</td>
<td>(Laf)</td>
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<tr>
<td>Izard Co.</td>
<td>4 miles NW of Calico Rock, sandstone outcrop</td>
<td>March 9, 1968</td>
<td>L. E. Anderson 20275</td>
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<td>(D)</td>
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<td></td>
<td>Melbourne, sandstone</td>
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<td>L. E. Anderson 20276</td>
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<td></td>
<td>Same</td>
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<td>L. E. Anderson 20277</td>
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<td></td>
<td>Near Mt. Pleasant, sandstone</td>
<td>March 9, 1968</td>
<td>L. E. Anderson 20278</td>
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<td>(D)</td>
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<td>Miller Co.</td>
<td>2 miles S of Doddridge, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1572</td>
<td>(Laf)</td>
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<tr>
<td>Pike Co.</td>
<td>1 mile SE of Delight, roadside</td>
<td>Feb. 26, 1967</td>
<td></td>
<td>B. E. Lemmon 1566</td>
<td>(Laf)</td>
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</tbody>
</table>
**W. controversa**  
*n = 13*

**FLORIDA**

**Calhoun Co.:**  
Blounston, sandy soil, roadside  
Dec. 29, 1967  
B. E. Lemmon 1859 (Laf)

**Columbia Co.:**  
4 miles SE of Fort White, roadside  
Dec. 27, 1967  
B. E. Lemmon 1816 (Laf)

**Gadsen Co.:**  
9 miles W of Tallahassee, roadside  
Dec. 29, 1967  
B. E. Lemmon 1842 (Laf)

**Holmes Co.:**  
4.5 miles W of Ponce de Leon, concrete culverts in ditch  
Dec. 26, 1967  
B. E. Lemmon 1806 (Laf)

**Jackson Co.:**  
6 miles SW of Marianna, eroded road cut, under trees  
Dec. 29, 1967  
B. E. Lemmon 1858 (Laf)

Marianna State Park, roadside, edge of woods  
Dec. 39, 1967  
B. E. Lemmon 1818 (Laf)

6 miles SW of Marianna, eroded road cut, under trees  
Dec. 29, 1967  
B. E. Lemmon 1854 (Laf)

6 miles SW of Marianna, eroded road cut, under trees  
Dec. 29, 1967  
B. E. Lemmon 1854a (Laf)

Marianna State Park, flat roadside, edge of woods  
Dec. 29, 1967  
B. E. Lemmon 1819 (Laf)

**Jefferson Co.:**  
.5 mile W of Waukeenah, ditchbank  
Dec. 27, 1967  
B. E. Lemmon 1812 (Laf)

**Lafayette Co.:**  
2 miles W of Mayo, sandy soil, roadside  
Dec. 29, 1967  
B. E. Lemmon 1852 (Laf)

**Leon Co.:**  
.5 miles E of Tallahassee, ditchbank  
Dec. 27, 1967  
B. E. Lemmon 1830 (Laf)

Tallahassee, soil and concrete banks of ditches near 1806 Croyden Drive, collected by Ruth Breen  
Feb. 22, 1967  
B. E. Lemmon 1574 (Laf)

Tallahassee, sandy soil, collected by Ruth Breen  
Jan., 1967  
B. E. Lemmon 1447 (Laf)
**W. controversa**  n = 13  Florida

**Liberty Co.**
- 7 miles S of Rock Bluff, roadside
  - Dec. 29, 1967  B. E. Lemmon 1832 (Laf)
- Torryea State Park, flat ground under trees
  - Dec. 29, 1967  B. E. Lemmon 1851 (Laf)
- Torryea State Park, flat ground under trees
  - Dec. 29, 1967  B. E. Lemmon 1855 (Laf)
- Torryea State Park, flat ground under trees
  - Dec. 29, 1967  B. E. Lemmon 1852 (Laf)
- Torryea State Park, roadside
  - Dec. 29, 1967  B. E. Lemmon 1821 (Laf)

**Madison Co.:**
- 17.7 miles NW of Perry, sandy soil, roadside
  - Dec. 27, 1967  B. E. Lemmon 1814 (Laf)

**Okaloosa Co.:**
- 6.3 miles W of Crestview, roadside
  - Dec. 26, 1967  B. E. Lemmon 1804 (Laf)

**Santa Rosas Co.:**
- 1 mile E of Milton, old bank under trees
  - Dec. 26, 1967  B. E. Lemmon 1805 (Laf)

**Suwannee Co.:**
- 8 miles W of Fort White, edge of woods
  - Dec. 27, 1967  B. E. Lemmon 1815 (Laf)

**Taylor Co.:**
- 4.2 miles E of Perry, roadside
  - Dec. 27, 1967  B. E. Lemmon 1813 (Laf)
- 3.5 miles W of Perry, sandy soil, roadside
  - Dec. 27, 1967  B. E. Lemmon 1856 (Laf)

**Walton Co.:**
- 1.4 miles W of Mossy Head, sandy soil, roadside
  - Dec. 26, 1967  B. E. Lemmon 1854 (Laf)

**Washington Co.:**
- 3 miles W of Chipley, roadside
  - Dec. 27, 1967  B. E. Lemmon 1807 (Laf)

**GEORGIA**

**Banks Co.:**
- 7 miles SE of Homer
  - Feb. 3, 1967  L. E. Anderson 25082 (Laf)

**Bartow Co.:**
- 6 miles N of Rydal, clay soil, rocky bank
  - Nov. 23, 1967  L. E. Anderson 20174 (D)
W. controversa  n = 13  Georgia

Calhoun Co.:
4 miles N of Piedmont, clay soil, eroded bank
Nov. 25, 1967  L. E. Anderson 20154 (D)
Same, another clump  L. E. Anderson 20155 (D)

Carroll Co.:
Carrolton, lawn at Lampton residence (collected by Robert Lampton)
Dec. 7, 1967  B. E. Lemmon 1626 (Laf)

Catoosa Co.:
3 miles W of Ringold, clay soil, roadside
Nov. 24, 1967  L. E. Anderson 20196 (D)
3 miles SE of Ringold, soil, roadside
Nov. 24, 1967  L. E. Anderson 20192 (D)

Cherokee Co.:
Woodstock, clay soil, bank
Nov. 25, 1967  L. E. Anderson 20127 (D)
1 mile E of Canton
Nov. 25, 1967  L. E. Anderson 20160 (D)
Same, another clump  L. E. Anderson 20161 (D)

Clayton Co.:
2 miles N of Riverdale
Feb. 4, 1967  L. E. Anderson 25017 (Laf)

Cobb Co.:
Kennesaw, soil, roadbank
Nov. 25, 1967  L. E. Anderson 20208 (D)

Coweta Co.:
12 miles NE of Newman
Feb. 4, 1967  L. E. Anderson 25009 (Laf)

Dade Co.:
3 miles W of Trenton, rocky soil, edge of woods
Nov. 24, 1967  L. E. Anderson 20191 (D)
Trenton, soil, edge of oak woods
Nov. 24, 1967  L. E. Anderson 20198 (D)

Dawson Co.:
9 miles SE of Dawsonville, soil, edge of hardwood forest
Nov. 25, 1967  L. E. Anderson 20164 (D)
Same, another clump  L. E. Anderson 20165 (D)

DeKalb Co.:
Atlanta
Feb. 3, 1967  L. E. Anderson 25015 (Laf)
W. controversa  n = 13  Georgia

Fanin Co.:  2 miles W of Marganton, soil, rock crevices
            Nov. 23, 1957   L. E. Anderson 20176 (D)
            2.6 miles E of Marganton, soil, roadbank
            Nov. 23, 1967   L. E. Anderson 20175 (D)

Forsyth Co.:  7 miles W of Cumming, clay soil, road bank
              Nov. 25, 1967   L. E. Anderson 20158 (D)
              Same, another clump   L. E. Anderson 20159 (D)

Fulton Co.:  10 miles SE of Atlanta
              Feb. 4, 1967   L. E. Anderson 25021 (Laf)

Gordon Co.:  3 miles N of Ranger, soil, roadbank
              Nov. 23, 1967   L. E. Anderson 20131 (D)
              2 miles E of Fairmont, soil, roadside
              Nov. 23, 1967   L. E. Anderson 20172 (D)
              Same, another clump   L. E. Anderson 20173 (D)

Glynn Co.:  St. Simon Island, Brickwork, under spreading live
            oaks, cemetery, Christ Church
            Dec. 24, 1967   L. E. Anderson 20228 (D)
            Same, another clump   L. E. Anderson 20229 (D)

Gwinnett Co.:  5 miles NW of Laurensville
              Feb. 3, 1967   L. E. Anderson 25029 (Laf)

Habersham Co.:  Baldwin, soil, edge of woods
                Nov. 26, 1967   L. E. Anderson 20171 (D)
                8 miles NE of Clarksville, clay soil, roadbank
                Nov. 26, 1967   L. E. Anderson 20169 (D)
                8 miles NE of Clarksville, clay soil, roadbank
                Nov. 26, 1967   L. E. Anderson 20170 (D)

Hall Co.:  5 miles N of Gainsville
            Nov. 26, 1967   L. E. Anderson 20162 (D)
            Same, another clump   L. E. Anderson 20163 (D)
            2 miles NE of Lula, clay soil, roadbank
            Nov. 26, 1967   L. E. Anderson 20166 (D)
            Same, another clump   L. E. Anderson 20167 (D)
W. controversa  n = 13  Georgia

Haralson Co.:  2 miles NW of Buchanan, clay soil, among
  lichens, scrub pine
  Nov. 25, 1967  L. E. Anderson 20129 (D)

  Same, short distance away  L. E. Anderson 20130 (D)

Harris Co.:  Callaway Gardens
  Feb. 4, 1967  L. E. Anderson 25019 (Laf)

Hart Co.:  NE of Hartwell on I 15
  Feb. 3, 1967  L. E. Anderson 25022 (Laf)

Jackson Co.:  3 miles W of Commerce
  Feb. 3, 1967  L. E. Anderson 25040 (Laf)

Liberty Co.:  Midway, concrete wall, around old cemetery
  Dec. 24, 1967  L. E. Anderson 20235 (D)

Meriwether Co.:  Luthersville
  Feb. 4, 1967  L. E. Anderson 25014 (Laf)

Murray Co.:  8 miles S of Chatsworth, soil, roadside, old
  roadbank, oak woods
  Nov. 23, 1967  L. E. Anderson 20203 (D)

Paulding Co.:  4.5 miles SW of Dallas, pebbly clay soil,
  eroded field
  Nov. 25, 1967  L. E. Anderson 20128 (D)

Pickens Co.:  4 miles NE of Hinton, concrete culverts
  Nov. 23, 1967  L. E. Anderson 20181 (D)

  6 miles NE of Hinton, soil, roadside
  Nov. 23, 1967  L. E. Anderson 20177 (D)

Polk Co.:  6 miles W of Cedartown, clay soil, edge of oak-
  pine woods
  Nov. 25, 1967  L. E. Anderson 20153 (D)

  3 miles N of Cedartown, clay soil, roadbank
  Nov. 25, 1967  L. E. Anderson 20125 (D)

  Same, short distance away  L. E. Anderson 20126 (D)
W. controversa  n = 13  Georgia

Rabun Co.:  Tallulah Falls, bank of gorge  Nov. 26, 1967  L. E. Anderson 20142 (D)
            Same, short distance away  L. E. Anderson 20143 (D)
            1 mile NE of Dillard, soil among rocks, deep road cut  Nov. 26, 1967  L. E. Anderson 20147 (D)

Stephens Co.:  5 miles N of Toccoa, clay soil, roadside  Nov. 26, 1967  L. E. Anderson 20211 (D)

Towns Co.:  2 miles S of Young Harris  Nov. 23, 1967  L. E. Anderson 20140 (D)
            Same, short distance away  L. E. Anderson 20141 (D)

Troup Co.:  11 miles S of LaGrange  Feb. 4, 1967  L. E. Anderson 25008 (Laf)

Union Co.:  2.2 miles NE of Blairsville, soil among lichens, eroded pine field  Nov. 23, 1967  L. E. Anderson 20136 (D)
            Same, different clump  L. E. Anderson 20137 (D)
            Same, different clump  L. E. Anderson 20138 (D)
            Same, different clump  L. E. Anderson 20139 (D)

Walker Co.:  14 miles SW of Chickamanga, soil eroded bank  Nov. 24, 1967  L. E. Anderson 20197 (D)
            8 miles SW of Chickamanga, soil among grasses, edge of field  Nov. 24, 1967  L. E. Anderson 20180 (D)

Whitefield Co.:  2 miles NW of Dalton, clayey soil, edge of woods, roadside  Nov. 24, 1967  L. E. Anderson 20195 (D)
            7 miles NW of Dalton, clayey soil, roadbank  Nov. 24, 1967  L. E. Anderson 20194 (D)
W. controversa n = 13

LOUISIANA

Acadia Parish: 2.6 miles E of Egan exit of I 10, disturbed soil, roadside
Jan. 19, 1967 B. E. Lemmon 1435 (Laf)

Allen Parish: 6.4 miles S of Oakdale, roadside
Jan. 29, 1967 B. E. Lemmon 1503 (Laf)

Ascension Parish: 4.8 miles E of Donaldsonville, disturbed soil, roadside
Feb. 5, 1967 B. E. Lemmon 1513 (Laf)

Bienville Parish: 1 mile E of Arcadia, roadside
Feb. 19, 1967 B. E. Lemmon 1531 (Laf)

Bossier Parish: 1 mile S of Filmore, steep bank by road
Feb. 19, 1967 B. E. Lemmon 1536 (Laf)

Caddo Parish: 5 miles S of Ida, roadside
Feb. 26, 1967 B. E. Lemmon 1556 (Laf)

Calcasieu Parish: 4 miles N of Moss Bluff, edge of woods, ditchbank
Feb. 25, 1967 B. E. Lemmon 1550 (Lfa)

Claiborne Parish: 4 miles S of Athens, roadside
Feb. 19, 1967 B. E. Lemmon 1532 (Laf)

East Baton Rouge Parish: L. S. U. campus, along side Audubon Hall
Jan. 30, 1968 B. E. Lemmon 1864 (Laf)

Evangeline Parish: 4.8 miles E of Oakdale, ditchbank
Jan. 28, 1967 B. E. Lemmon 1499 (Laf)

Grant Parish: 9 miles N of Pollack, soil, base of tree, oak-pine woods
Feb. 13, 1967 L. E. Anderson 25050 (Laf)

Same, another clump
L. E. Anderson 25051 (Laf)

Iberville Parish: 2 miles SE of White Castle, roadside
Feb. 5, 1967 B. E. Lemmon 1515 (Laf)

Rosedale, W corp. limits, bank near road
Feb. 5, 1967 B. E. Lemmon 1517 (Laf)
**W. controversa**  \( n = 13 \)  Louisiana

**Iberia Parish:**
- New Iberia, old nursery, N end of town, under pine trees
  - Jan. 23, 1967  B. E. Lemmon 1457 (Laf)

**Jackson Parish:**
- 1.8 miles N of North Hodge, disturbed soil, roadside
  - Feb. 19, 1967  B. E. Lemmon 1527 (Laf)

**Jefferson Davis Parish:**
- Roanoke, grassy bank, under live oak
  - Jan. 19, 1967  B. E. Lemmon 1445 (Laf)

**Lafayette Parish:**
- U. S. L. campus, near Judice Hall
  - Jan. 24, 1967  B. E. Lemmon 1459 (Laf)
- 3 miles S of Youngsville, steep, eroded roadbank
  - Jan. 22, 1967  B. E. Lemmon 1455 (Laf)
- E bank of Vermilion River at Lafayette, bayou bank near Condee
  - Jan. 21, 1967  B. E. Lemmon 1451 (Laf)
- 6 miles S of Lafayette, soil at base of uprooted tree
  - Jan. 15, 1967  B. E. Lemmon 1432 (Laf)
- E bank of Vermilion River at Lafayette, bare soil under tree
  - Dec. 16, 1967  B. E. Lemmon 1350 (Laf)
- E bank of Vermilion River at Lafayette, old field, moist
  - Jan. 4, 1967  B. E. Lemmon 1405 (Laf)
- 5 miles S of Lafayette, ditchbank near Flanders Bridge
  - Jan. 12, 1967  B. E. Lemmon 1413 (Laf)
- Lafayette, bare soil, Protestant cemetery
  - Dec. 29, 1966  B. E. Lemmon 1358 (Laf)
- E bank of Vermilion River, back yard of E. T. Lemmon
  - Dec. 22, 1967  B. E. Lemmon 1351 (Laf)
- E bank of Vermilion River at Lafayette, front yard of E. T. Lemmon
  - Dec. 18, 1966  B. E. Lemmon 1350-2 (Laf)
<table>
<thead>
<tr>
<th>Parish</th>
<th>Location Details</th>
<th>Specimen Details</th>
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<tbody>
<tr>
<td>Madison Parish:</td>
<td>2 miles W of Waverly, flat, moist soil area under trees along road</td>
<td>Feb. 13, 1967 L. E. Anderson 25060 (Laf)</td>
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<td>L. E. Anderson 25061 (Laf)</td>
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<td>L. E. Anderson 25066 (Laf)</td>
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<td>L. E. Anderson 25067 (Laf)</td>
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<tr>
<td>Natchitoches Parish:</td>
<td>1 mile N of Natchitoches, top of 6 ft high eroded bank, under trees</td>
<td>Feb. 19, 1967 B. E. Lemmon 1523 (Laf)</td>
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<td></td>
<td></td>
<td>Derry, steep, clay bank roadside</td>
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<td>Feb. 19, 1967 B. E. Lemmon 1521 (Laf)</td>
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<tr>
<td>Pointe Coupee Parish:</td>
<td>4 miles NE of Livonia, ditchbank</td>
<td>Jan. 25, 1967 B. E. Lemmon 1475 (Laf)</td>
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<td>Richland Parish:</td>
<td>Rayville, soil, moist roadbank</td>
<td>Feb. 13, 1967 L. E. Anderson 25056 (Laf)</td>
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<td>-Rayville, soil, moist roadbank</td>
<td>Feb. 13, 1967 L. E. Anderson 25058 (Laf)</td>
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<td>St. James Parish:</td>
<td>2 miles NW of Vacherie, old Valcour Amie homesite, bank of dry pond in woods</td>
<td>Feb. 5, 1967 B. E. Lemmon 1511 (Laf)</td>
</tr>
<tr>
<td></td>
<td>2 miles S of Vacherie, ditchbank in cane field</td>
<td>Feb. 5, 1967 B. E. Lemmon 1509 (Laf)</td>
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</tbody>
</table>
W. controversa  n = 13  Louisiana

St. Landry Parish:  1 mile N of Grand Coteau, open field near Oak Alley
Jan. 15, 1967  B. E. Lemmon 1421 (Laf)
Grand Coteau, ditchbank in town
Jan. 15, 1967  B. E. Lemmon 1424 (Laf)
1 mile W of Arnaudville, ditchbank
Jan. 15, 1967  B. E. Lemmon 1427 (Laf)

Rapides Parish:  12 miles W of Alexandria, grassy roadside
Feb. 19, 1967  B. E. Lemmon 1519 (Laf)

St. Martin Parish:  1.1 miles W of Cecelia, roadside
Jan. 15, 1967  B. E. Lemmon 1429 (Laf)

St. Tammany Parish:  Slidell
Feb. 7, 1967  L. E. Anderson 25001 (Laf)
11 miles SE of Slidell
Feb. 7, 1967  L. E. Anderson 25000 (Laf)

Terreborne Parish:  1.2 miles W of Gibson, old field
Feb. 5, 1967  B. E. Lemmon 1507 (Laf)

Union Parish:  6.7 miles NE of Lillie, steep bank
Feb. 26, 1967  B. E. Lemmon 1576 (Laf)

Vermilion Parish:  3.1 miles S of Banker, disturbed soil in low woods
Jan. 24, 1967  B. E. Lemmon 1469 (Laf)
4 miles SW of Perry, grassy roadside
Jan. 24, 1967  B. E. Lemmon 1461 (Laf)

Webster Parish:  .5 mile N of Dubberly, disturbed soil
Feb. 19, 1967  B. E. Lemmon 1534 (Laf)

West Feliciana Parish:  1 mile S of Weyanoke, roadbank
Jan. 25, 1967  B. E. Lemmon 1477 (Laf)

Winn Parish:  11.6 miles SW of Winnfield, roadbank
Feb. 19, 1967  B. E. Lemmon 1525 (Laf)
Gum Springs Recreation Area, S of Winnfield, tree base, ravine in woods
Feb. 19, 1967  B. E. Lemmon 1540 (Laf)
**Mississippi**

<table>
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<th>County</th>
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<th>Collector</th>
<th>Date</th>
<th>Specimen Number</th>
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<tr>
<td>Carroll Co.</td>
<td>2 miles S of Vaiden, clay soil among clumps of <em>Andropogon</em>, road bank</td>
<td>L. E. Anderson</td>
<td>Feb. 17, 1967</td>
<td>25088 (Laf)</td>
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<tr>
<td></td>
<td>Same, another clump</td>
<td>L. E. Anderson</td>
<td></td>
<td>25089 (Laf)</td>
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<tr>
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<td>Same, another clump</td>
<td>L. E. Anderson</td>
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<td>25090 (Laf)</td>
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<td>Forrest Co.</td>
<td>3 miles N of Hattiesburg, ditchbank</td>
<td>B. E. Lemmon</td>
<td>Dec. 30, 1967</td>
<td>1822 (Laf)</td>
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<tr>
<td>Hancock Co.</td>
<td>Pearlington</td>
<td>L. E. Anderson</td>
<td>Feb. 7, 1967</td>
<td>25002 (Laf)</td>
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<td>Same</td>
<td>L. E. Anderson</td>
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<td>25006 (Laf)</td>
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<tr>
<td>Hinds Co.</td>
<td>4 miles W of Clinton, clayey soil, road bank</td>
<td>L. E. Anderson</td>
<td>Feb. 14, 1967</td>
<td>25074 (Laf)</td>
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<td>4 miles W of Clinton, clayey soil, road bank</td>
<td>L. E. Anderson</td>
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<td>25076 (Laf)</td>
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<tr>
<td>Holmes Co.</td>
<td>Durant</td>
<td>L. E. Anderson</td>
<td>Feb. 17, 1967</td>
<td>25087 (Laf)</td>
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<tr>
<td></td>
<td>3 miles N of Durant, clayey soil among <em>Andropogon</em> clumps</td>
<td>L. E. Anderson</td>
<td>Feb. 14, 1967</td>
<td>25086 (Laf)</td>
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<tr>
<td></td>
<td>4 miles W of Clinton, clayey soil, road bank</td>
<td>L. E. Anderson</td>
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<td>25081 (Laf)</td>
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<td></td>
<td>6 miles N of Canton, old road cut in pasture</td>
<td>L. E. Anderson</td>
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<td>25082 (Laf)</td>
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<tr>
<td></td>
<td>6 miles N of Canton, old road cut in pasture</td>
<td>L. E. Anderson</td>
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<td>25084 (Laf)</td>
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<tr>
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<td>6 miles N of Canton, old road cut in pasture</td>
<td>L. E. Anderson</td>
<td></td>
<td>25088 (Laf)</td>
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</table>

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**W. controversa** n = 13 Mississippi

**Marshall Co.:**
- 4 miles S of Holly Springs, soil, open ground, sparse oak-hickory
  - Feb. 16, 1967
  - L. E. Anderson 25119 (Laf)
- 1 mile E of Chulahoma, road bank, shaded
  - Feb. 16, 1967
  - L. E. Anderson 25116 (Laf)

**Montgomery Co.:**
- 6 miles N of Winona, soil, among clumps of **Andropogon**, soil bank
  - Feb. 14, 1967
  - L. E. Anderson 25094 (Laf)
- 4 miles N of Winona
  - Feb. 14, 1967
  - L. E. Anderson 25092 (Laf)

**Panola Co.:**
- 1 mile S of Sarois, soil, clumps of **Andropogon**
  - Feb. 15, 1967
  - L. E. Anderson 25095 (Laf)
- 2 miles SW of Batesville, soil base of oak, oak-hickory forest
  - Feb. 15, 1967
  - L. E. Anderson 25109 (Laf)
- 8 miles SW of Batesville, soil base of oak, oak-hickory forest
  - Feb. 15, 1967
  - L. E. Anderson 25108 (Laf)
- 8 miles SW of Batesville, soil base of oak, oak-hickory forest
  - Feb. 15, 1967
  - L. E. Anderson 25107 (Laf)

**Tallahatchie Co.:**
- 12 miles SE of Charleston, soil, base of oak, oak-pine woods
  - Feb. 15, 1967
  - L. E. Anderson 25104 (Laf)
- 12 miles SE of Charleston, soil among clumps of grasses, open cedar grove
  - Feb. 15, 1967
  - L. E. Anderson 25101 (Laf)

**Warren Co.:**
- 3 miles E of Vicksburg, soil in oak woods, N facing bluff
  - Feb. 14, 1967
  - L. E. Anderson 35073 (Laf)
- Vicksburg Battlefield
  - Feb. 13, 1967
  - L. E. Anderson 25069 (Laf)

**Wayne Co.:**
- 2 miles NE of Waynesboro, roadside
  - Dec. 30, 1967
  - B. E. Lemmon 1850 (Laf)

**Yalobusha Co.:**
- 3 miles N of Oakland, soil, bases of oak, pine-oak slope
  - Feb. 15, 1967
  - L. E. Anderson 25098 (Laf)
W. controversa  n = 13

MISSOURI

Barry Co.: 7 miles E of Cassville, soil, cedar glade (collected by Paul Redfern)  March 2, 1968. L. E. Anderson 20270 (D)
Oregon Co.: 1.5 miles SW of Thomasville, soil, under scrub oaks, among scattered small boulders of sandy dolomite  March 8, 1968 L. E. Anderson 20285b (D)
          2 miles N of Howards Ridge, in crevices, side of flat limestone boulder, cedar glade  March 9, 1968 L. E. Anderson 20287 (D)
Shannon Co.: Rocky Falls, soil, oak woods near waterfalls  March 8, 1968 L. E. Anderson 20284 (D)
Greene Co.: (collected by Paul Redfern)  B. E. Lemmon 1433 (Laf)

NORTH CAROLINA

Alleghany Co.: 3 miles NE of Piney Creek, clayey soil, road bank  Nov. 3, 1967 L. E. Anderson 20097 (D)
Ashe Co.: 12 miles NE of Jefferson, clay bank, roadside  Nov. 3, 1967 L. E. Anderson 20099 (D)
Beaufort Co.: Washington, sandy soil, ditchbank, roadside  Feb. 18, 1968 L. E. Anderson 20263 (D)
          Ransomville, clay soil among grasses  Feb. 18, 1968 L. E. Anderson 20266 (D)
Burke Co.: Linville Falls, Stone wall, upper falls  April 10, 1966 L. E. Anderson 19040 (D)
          Same, upper lookout  L. E. Anderson 19041 (D)
          Hildebran, clay soil, road bank  Oct. 18, 1967 L. E. Anderson 20090 (D)
Cabarrus Co.: 6 miles E of Concord  Feb. 2, 1967 L. E. Anderson 25047 (Laf)
**W. controversa** n = 13 North Carolina

**Chatham Co.**
10 miles S of Pittsboro, clayey soil
March 13, 1966 L. E. Anderson 19020 (D)

**Clay Co.:**
7.4 miles NE of Shooting Creek, rock crevices, road cut
Nov. 23, 1967 L. E. Anderson 20134 (D)
Same bank, another clump
L. E. Anderson 20135 (D)

3.2 miles NE of Shooting Creek, soil between rocks, roadcut
Nov. 23, 1967 L. E. Anderson 20178 (D)
Same, another clump
L. E. Anderson 20179 (D)

**Cleveland Co.:**
King's Mt.
Feb. 3, 1967 L. E. Anderson 25025 (Laf)

**Davidson Co.:**
4 miles S of Jackson Hill on N. C. 49
Feb. 2, 1967 L. E. Anderson 25035 (Laf)

4 miles S of Jackson Hill on N. C. 49
Feb. 2, 1967 L. E. Anderson 25041 (Laf)

**Durham Co.:**
Duke University campus, clayey soil, edge of oak-hickory woods, roadside Science Drive, across from BSB
Dec. 7, 1967 L. E. Anderson 20190 (D)

Duke University campus, W side dormitory complex, gravelly soil, lawn under scattered oaks
Station B L. E. Anderson 20212 (D)
Same, Station D L. E. Anderson 20214 (D)
Same, Station E L. E. Anderson 20215 (D)
Same, Station F L. E. Anderson 20216 (D)

Lake Miche, soil, roadbank
March 3, 1966 L. E. Anderson 19002 (D)

Duke Forest, Gate 9, Soil, base of tree
March 11, 1966 L. E. Anderson 19006 (D)

10 miles N of Durham, Eno River, near Oxford Road, soil among grasses
March 12, 1966 L. E. Anderson 19017 (D)

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W. controversa  \( n = 13 \) North Carolina

Forsyth Co.: 3 miles N of Walkertown, sandy soil, RR embankment
Nov. 1, 1967  L. E. Anderson 20103 (D)

Same, short distance away
L. E. Anderson 20104 (D)

Same, short distance away
L. E. Anderson 20105 (D)

Gaston Co.: Lowell
Feb. 3, 1967  L. E. Anderson 25042 (Laf)

Graham Co.: 7 miles E of Fontana, rock crevices
Oct. 15, 1967  L. E. Anderson 20076 (D)

Same, short distance away
L. E. Anderson 20077 (D)

Same, short distance away
L. E. Anderson 20078 (D)

Henderson Co.: 1 mile SW of Mells River, soil, roadside shoulder
Nov. 26, 1967  L. E. Anderson 20209 (D)

Hyde Co.: Alligator Pungo R. canal, north of Fairfield, sandy soil, among grasses
Feb. 18, 1968  L. E. Anderson 20267 (D)

Jackson Co.: 6 miles E of Cashiers, roadside, gravelly soil
Nov. 26, 1967  L. E. Anderson 20210 (D)

Lee Co.: 11 miles S of Sanford, clayey soil
March 13, 1966  L. E. Anderson 19021 (D)

Macon Co.: 6 miles E of Highlands, on micaceous soil, roadside
Oct. 15, 1967  L. E. Anderson 20081 (D)

3 miles NW of Highlands, Cullasaja Gorge, soil, roadside, near Dry Falls
Oct. 15, 1967  L. E. Anderson 20079 (D)

3 miles E of Highlands, on micaceous soil, roadside
Oct. 14, 1967  L. E. Anderson 20071 (D)

3 miles E of Highlands, on micaceous soil, roadside
Oct. 14, 1967  L. E. Anderson 20072 (D)

Same, short distance away
L. E. Anderson 20073 (D)
**W. controversa** n = 13 North Carolina

<table>
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<th>Date</th>
<th>Collector</th>
<th>Collection Code</th>
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<tr>
<td></td>
<td>1.5 miles S of Aberdeen, sandy soil</td>
<td>March 13, 1966</td>
<td>L. E. Anderson</td>
<td>19022 (D)</td>
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<td>Same</td>
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<td>L. E. Anderson</td>
<td>19023 (D)</td>
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<td>Moore Co.</td>
<td>7 miles E of Middlesex, sandy soil among grasses</td>
<td>Feb. 17, 1968</td>
<td>L. E. Anderson</td>
<td>20264 (D)</td>
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<td>1 mile E of Hertford, on rock, along roadside</td>
<td>Feb. 19, 1968</td>
<td>L. E. Anderson</td>
<td>20265 (D)</td>
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<td>Randolph Co.</td>
<td>2 miles W of Asheboro</td>
<td>Feb. 2, 1967</td>
<td>L. E. Anderson</td>
<td>25038 (Laf)</td>
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<td>Richmond Co.</td>
<td>5 miles NE of Hamlet, sandy soil, edge of stone hill</td>
<td>Dec. 26, 1967</td>
<td>L. E. Anderson</td>
<td>20237 (D)</td>
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<td>Sampson Co.</td>
<td>5 miles NE of Faison</td>
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<td>L. E. Anderson</td>
<td>19033 (D)</td>
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<td>Stokes Co.</td>
<td>3 miles N of Danbury, shaded bank, clayey soil</td>
<td>Nov. 1, 1967</td>
<td>L. E. Anderson</td>
<td>20115 (D)</td>
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<tr>
<td>Surry Co.</td>
<td>Mt. Airy, city street, clayey bank</td>
<td>Nov. 1, 1967</td>
<td>L. E. Anderson</td>
<td>20116 (D)</td>
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<tr>
<td>Swain Co.</td>
<td>7 miles S of Lauada, soil among boulders, steep roadbank</td>
<td>Oct. 15, 1967</td>
<td>L. E. Anderson</td>
<td>20080 (D)</td>
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<td>6 miles S of Lauada, steep road cut, micaceous soil, crevices of rocks</td>
<td>Oct. 15, 1967</td>
<td>L. E. Anderson</td>
<td>20075 (D)</td>
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<tr>
<td>Wilkes Co.</td>
<td>18 miles NW of North Wilkesboro, rock crevices, road bank</td>
<td>Nov. 3, 1967</td>
<td>L. E. Anderson</td>
<td>20091 (D)</td>
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<td>Same</td>
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<td>L. E. Anderson</td>
<td>20092 (D)</td>
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<td>Same</td>
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<td>L. E. Anderson</td>
<td>20093 (D)</td>
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</table>
**W. controversa**  n = 13  North Carolina

Wilson Co.:  6 miles E of Wilson, clayey soil, steep roadside bank, among grasses  
             Feb. 17, 1968  L. E. Anderson 20262 (D)

Yadkin Co.:  6 miles W of Brooks Cross Roads, clayey soil, road bank  
             Nov. 3, 1967  L. E. Anderson 20119 (D)

**OKLAHOMA**

Cherokee Co.:  1 mile E of Cherokee-Muskogee Co. line on Hwy 10, collected by Paul Redfern, Jr.  
               May, 1966  B. E. Lemmon (Laf)

**SOUTH CAROLINA**

Anderson Co.:  12 miles NW of Anderson  
               Feb. 3, 1967  L. E. Anderson 25049 (Laf)

                 12 miles NW of Anderson  
                 Feb. 3, 1967  L. E. Anderson 25034 (Laf)

                 4 miles W of Piedmont  
                 Feb. 3, 1967  L. E. Anderson 25018 (Laf)

Bamberg Co.:  1.5 miles SW of Bamberg, sandy soil, roadbank  
              Dec. 26, 1967  L. E. Anderson 20247 (Laf)

Cherokee Co.:  2 miles N of Blacksburg  
               Feb. 3, 1967  L. E. Anderson 25026 (Laf)

                 2 miles N of Cowpens  
                 Feb. 3, 1967  L. E. Anderson 25045 (Laf)

Chesterfield Co.:  Middeldorf, garden loam, street bank  
                   Dec. 26, 1967  L. E. Anderson 20240 (D)

Darlington Co.:  4 miles SE of Darlington, sandy soil among grasses, RR embankment  
                 Dec. 22, 1967  L. E. Anderson 20253 (D)

Dillon Co.:  5 miles NE of Little Rock, sandy soil  
            March 14, 1966  L. E. Anderson 19024 (D)

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W. controversa  n = 13  South Carolina

Florence Co.: Florence, packed sandy soil, park
Dec. 22, 1967  L. E. Anderson 20248 (D)
Same, another clump  L. E. Anderson 20249 (D)
Same, another clump  L. E. Anderson 20250 (D)

Georgetown Co.: Belle Isle, Kinloch Plantation, sandy soil, rock bank
Dec. 23, 1967  L. E. Anderson 20251 (D)
Belle Isle, Kinloch Plantation, thin soil on concrete
Dec. 23, 1967  L. E. Anderson 20252 (D)

Hampton Co.: Yemassee, sandy soil among honeysuckle, roadbank
Dec. 23, 1967  L. E. Anderson 20226 (D)
Same, another clump  L. E. Anderson 20227 (D)

Horry Co.: 7 miles SE of Loris, sandy soil
March 14, 1966  L. E. Anderson 19026 (D)
Same, another clump  L. E. Anderson 19027 (D)

Kershaw Co.: 4 miles SW of Bethune, sandy soil, RR embankment
Dec. 26, 1967  L. E. Anderson 20236 (D)

Mareboro Co.: 1 mile SW of Brownsville, sandy soil among grasses, roadbank
Dec. 22, 1967  L. E. Anderson 20254 (D)
Same, short distance away
L. E. Anderson 20255 (D)

Marion Co.: 3 miles SE of Mullins, sandy soil
March 14, 1966  L. E. Anderson 19025 (D)

Oconee Co.: 6 miles E of Fairplay
Feb. 3, 1967  L. E. Anderson 25044 (Laf)

Spartanburg Co.: Duncan
Feb. 3, 1967  L. E. Anderson 25033 (Laf)
1 mile E of Wellford
Feb. 3, 1967  L. E. Anderson 25024 (Laf)
W. controversa n = 13

TENNESSEE

Carroll Co.: 6 miles S of Yuma, soil, wooded bluff
Feb. 16, 1967 L. E. Anderson 25140 (Laf)

Cumberland Co.: Mayland, soil and cinders along RR embankment
Feb. 19, 1967 L. E. Anderson 25164 (Laf)

Cumberland Co.: Mayland, soil and cinders along RR embankment
Feb. 19, 1967 L. E. Anderson 25163 (Laf)

Davidson Co.: 10 miles E of Nashville, soil base of tree, oak woods
Feb. 18, 1967 L. E. Anderson 25152 (Laf)

Decatur Co.: 18 miles N of Parsons, soil, open woods
Feb. 16, 1967 L. E. Anderson 25143 (Laf)

Dickson Co.: 1 mile E of Dickson, soil, base of oaks in oak woods
Feb. 16, 1967 L. E. Anderson 25147 (Laf)

Fayette Co.: 3 miles SE of LaGrange, soil, base of oak, sparse oak woods
Feb. 16, 1967 L. E. Anderson 25127 (Laf)

Hardeman Co.: 4 miles N of Bolivar, soil, open woods
Feb. 16, 1967 L. E. Anderson 25130 (Laf)

Henderson Co.: 2 miles N of Wildersville, soil, oak-hickory woods
Feb. 16, 1967 L. E. Anderson 25138 (Laf)

Jackson Co.: 9 miles NE of Gainesboro, soil among clumps of Andropogon
Feb. 18, 1967 L. E. Anderson 25158 (Laf)

Johnson Co.: Shadey Valley, clayey soil, edge of woods, roadside
Nov. 3, 1967 L. E. Anderson 20095 (D)

Johnson Co.: Same, short distance away
L. E. Anderson 20096 (D)

Knox Co.: Near New Hopewell, acid soil, ridge top, mixed oak woods
Nov. 12, 1967 L. E. Anderson 20122 (D)
**W. controversa**  
\( n = 13 \)  
Tennessee

**Knox Co.:**

Near Mascot, crevices of dolomitic rocks, roadbank  
Oct. 16, 1967  
L. E. Anderson 25086 (D)

Same, some distance away  
L. E. Anderson 20087 (D)

Same, some distance away  
L. E. Anderson 20088 (D)

**Madison Co.:**

10 miles S of Jackson, soil margin of hardwood grove  
Feb. 16, 1967  
L. E. Anderson 25131 (Laf)

12 miles NE of Jackson, grassy roadbank  
Feb. 16, 1967  
L. E. Anderson 25135 (Laf)

**Morgan Co.:**

2 miles S of Oakdale  
Feb. 19, 1967  
L. E. Anderson 25169 (Laf)

2 miles S of Oakdale  
Feb. 19, 1967  
L. E. Anderson 25168 (Laf)

**Overton Co.:**

S of Hilham, roadside, among clumps of *Andropogon*  
Feb. 18, 1967  
L. E. Anderson 25156 (Laf)

**Putnam Co.:**

7 miles N of Cooksville, soil, base of cedar, oak-cedar glade  
Feb. 18, 1967  
L. E. Anderson 25154 (Laf)

4 miles N of Cooksville, among clumps of *Andropogon*  
Feb. 18, 1967  
L. E. Anderson 25153 (Laf)

**Roane Co.:**

3 miles SW of Harriman, soil among clumps of grasses, RR embankment  
Feb. 19, 1967  
L. E. Anderson 25175 (Laf)

Rockwood, soil base of oak, scrub-oak stand  
Feb. 19, 1967  
L. E. Anderson 25167 (Laf)

**Sevier Co.:**

Newfoundland Gap, Great Smokey Mt. Nat. Park, rock crevices  
March 30, 1966  
L. E. Anderson 19037 (D)

7 miles S of Gatlinburg, rocks  
March 30, 1966  
L. E. Anderson 19038 (D)
W. controversa  n = 13  Tennessee

Sullivan Co.:  2 miles SE of Bristol, clay bank, edge of hardwood forest
Nov. 3, 1967  L. E. Anderson 20100 (D)

Same, short distance away
L. E. Anderson 20101 (D)

TEXAS

Jasper Co.:  2 miles W of Holly Springs, roadside, among grass
Feb. 25, 1967  B. E. Lemmon 1560 (Laf)

VIRGINIA

Carroll Co.:  1 mile SE of Cana, clayey soil, roadside
Nov. 1, 1967  L. E. Anderson 20112 (D)

Same, short distance away
L. E. Anderson 20113 (D)

Grayson Co.:  11 miles W of Volney, clayey soil, roadbank
Nov. 3, 1967  L. E. Anderson 20118 (D)

Patrick Co.:  6 miles S of Stuart, clay soil, among clumps of Andropogon
Nov. 1, 1967  L. E. Anderson 20106 (D)

8 miles SW of Stuart, hard clay, roadside
Nov. 1, 1967  L. E. Anderson 20117 (D)

Scott Co.:  4 miles E of Bruno, bare soil, roadside
Nov. 3, 1967  L. E. Anderson 20108 (D)

Smyth Co.:  4 miles N of Marion, rock crevices, high vertical road cut
Nov. 2, 1967  L. E. Anderson 20107 (D)

Tazewell Co.:  12 miles S of Scales, sandy soil, edge of woods
Nov. 2, 1967  L. E. Anderson 20110 (D)
W. controversa  n = 13  Virginia

Washington Co.:  4 miles E of Damascus, soil among boulders, roadbank  
Nov. 3, 1967  L. E. Anderson 20120 (D)  
3 miles E of Damascus, moist crevices, vertical rock cliff, shaded  
Nov. 3, 1967  L. E. Anderson 20094 (D)  
Wise Co.:  St. Paul, clay soil, roadside  
Nov. 2, 1967  L. E. Anderson 20109 (D)  

W. controversa  n = 14  

ALABAMA

Baldwin Co.:  3.3 miles W of Malbis, ditchbank with grass  
Dec. 26, 1967  B. E. Lemmon 1810 (Laf)  
3 miles W of Seminole, roadside  
Dec. 26, 1967  B. E. Lemmon 1843 (Laf)  
Chambers Co.:  3 miles S of Lanett  
Feb. 4, 1967  L. E. Anderson 25031 (Laf)  
Choctow Co.:  1 mile S of Gilbertown, hard, red clay bank  
Dec. 30, 1967  B. E. Lemmon 1834 (Laf)  
.5 mile S of Ararat, ditchbank  
Dec. 30, 1967  B. E. Lemmon 1824 (Laf)  
.5 mile S of Ararat, ditchbank  
Dec. 30, 1967  B. E. Lemmon 1826 (Laf)  
Dallas Co.:  8 miles W of Selma, soil, roadside  
Dec. 30, 1967  B. E. Lemmon 1844 (Laf)  
DeKalb Co.:  2 miles SW of Tyffe, soil, roadbank  
Nov. 24, 1967  L. E. Anderson 20185 (D)  
Houston Co.:  9 miles S of Dothan, ditchbank  
Dec. 29, 1967  B. E. Lemmon 1841 (Laf)  
Mobile Co.:  Bellingrath Gardens near Mobile  
Feb. 5, 1967  B. E. Lemmon 25011 (Laf)  
Sumter Co.:  4.5 miles S of York, roadside  
Dec. 30, 1967  B. E. Lemmon 1846 (Laf)  

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**W. controversa**  \( n = 14 \)

### ARKANSAS

<table>
<thead>
<tr>
<th>County</th>
<th>Location Details</th>
<th>Collector</th>
<th>Date</th>
<th>Accession Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cleveland Co.</td>
<td>13.5 miles N of Fordyce, roadside</td>
<td>B. E. Lemmon</td>
<td>Feb. 26, 1967</td>
<td>1582 (Laf)</td>
</tr>
<tr>
<td>Union Co.</td>
<td>3 miles S of Eldorado, on bark, base of tree in woods</td>
<td>B. E. Lemmon</td>
<td>Feb. 26, 1967</td>
<td>1564 (Laf)</td>
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### FLORIDA

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<tr>
<th>County</th>
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<th>Collector</th>
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<th>Accession Number</th>
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<tbody>
<tr>
<td>Alachua Co.</td>
<td>2 miles SE of Alachua, roadside</td>
<td>B. E. Lemmon</td>
<td>Dec. 27, 1967</td>
<td>1863 (Laf)</td>
</tr>
<tr>
<td>Escambia Co.</td>
<td>9 miles N of Pensacola, roadside grassy</td>
<td>B. E. Lemmon</td>
<td>Dec. 26, 1967</td>
<td>1811 (Laf)</td>
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<tr>
<td>Lafayette Co.</td>
<td>.5 miles W of Mayo, sandy soil</td>
<td>B. E. Lemmon</td>
<td>Dec. 27, 1967</td>
<td>1817 (Laf)</td>
</tr>
<tr>
<td>Liberty Co.</td>
<td>Torryea State Park, flat ground, edge of woods</td>
<td>B. E. Lemmon</td>
<td>Dec. 29, 1967</td>
<td>1820 (Laf)</td>
</tr>
<tr>
<td>Walton Co.</td>
<td>1.9 miles W of Mossy Head, roadside</td>
<td>B. E. Lemmon</td>
<td>Dec. 26, 1967</td>
<td>1808 (Laf)</td>
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### GEORGIA

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<th>Collector</th>
<th>Date</th>
<th>Accession Number</th>
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<tbody>
<tr>
<td>Glynn Co.</td>
<td>9 miles SW of Brunswick, on dirt pile, roadside</td>
<td>L. E. Anderson</td>
<td>Dec. 25, 1967</td>
<td>20231 (D)</td>
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<tr>
<td>Franklin Co.</td>
<td>Lavonia</td>
<td>L. E. Anderson</td>
<td>Feb. 3, 1967</td>
<td>25030 (Laf)</td>
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<tr>
<td>Franklin Co.</td>
<td>Same, another clump</td>
<td>L. E. Anderson</td>
<td></td>
<td>20323 (D)</td>
</tr>
<tr>
<td>Franklin Co.</td>
<td>Same, another clump</td>
<td>L. E. Anderson</td>
<td></td>
<td>20223 (D)</td>
</tr>
<tr>
<td>Franklin Co.</td>
<td>North end of Jekyll Island, on sand, among grasses, disturbed soil, edge of maritime forest</td>
<td>L. E. Anderson</td>
<td>Dec. 25, 1967</td>
<td>20234 (D)</td>
</tr>
</tbody>
</table>
**W. controversa** n = 14

**LOUISIANA**

**Beauregard Parish:** Ragley, roadside, grassy  
Feb. 25, 1967  B. E. Lemmon 1554 (Laf)

**Evangeline Parish:** Hawkin's Place, S of Chicot, bare soil under tree  
Jan. 29, 1967  B. E. Lemmon 1497 (Laf)

**Lafayette Parish:** E bank of Vermilion River at Lafayette, disturbed soil  
Jan. 24, 1967  B. E. Lemmon 1460 (Laf)

E bank of Vermilion River at Lafayette, disturbed soil  
Dec. 28, 1967  B. E. Lemmon 1401 (Laf)

**LaSalle Parish:** Tullos, soil, base of tree in oak-pine woods  
Feb. 13, 1967  L. E. Anderson 25055 (Laf)

**Madison Parish:** 2 miles W of Waverly, flat, moist soil under trees along road  
Feb. 14, 1967  L. E. Anderson 25063 (Laf)

**Red River Parish:** 15 miles N of Coushatta, eroded slope, roadside  
Feb. 11, 1967  B. E. Lemmon 1538 (Laf)

**St. Mary Parish:** Centerville, bare soil under oak tree  
Feb. 5, 1967  B. E. Lemmon 1505 (Laf)

**West Feliciana Parish:** 5.8 miles NE of Tunica, roadside, edge of woods  
Jan. 25, 1967  B. E. Lemmon 1479 (Laf)

5.8 miles NE of Tunica, roadside, edge of woods  
Jan. 25, 1967  B. E. Lemmon 1481 (Laf)

6.2 miles NE of Tunica, roadside, edge of woods  
Jan. 25, 1967  B. E. Lemmon 1482 (Laf)

**MISSISSIPPI**

**Adams Co.:** .9 miles S of Sibley, roadside  
Jan. 25, 1967  B. E. Lemmon 1483 (Laf)

2.6 miles W of Woodville, roadside  
Jan. 25, 1967  B. E. Lemmon 1489 (Laf)
**W. controversa**  \( n = 14 \)  Mississippi

**Harrison Co.:**  
Gulfport  
Feb. 7, 1967  
L. E. Anderson 25005 (Laf)

Pass Christian  
Feb. 7, 1967  
L. E. Anderson 25004 (Laf)

Pass Christian  
Feb. 7, 1967  
L. E. Anderson 25003 (Laf)

**Montgomery Co.:**  
4 miles S of Winona  
Feb. 14, 1967  
L. E. Anderson 25091 (Laf)

**Warren Co.:**  
3 miles E of Vicksburg  
Feb. 13, 1967  
L. E. Anderson 25071 (Laf)

3 miles E of Vicksburg  
Feb. 13, 1967  
L. E. Anderson 25072 (Laf)

**Wayne Co.:**  
8.1 miles NE of Waynesboro, edge of road, sandy soil  
Dec. 30, 1967  
B. E. Lemmon 1861 (Laf)

**MISSOURI**

**Oregon Co.:**  
1.5 miles SW of Thomasville, soil, under scrub oaks, among scattered small boulders of sandy dolomite  
March 8, 1968  
L. E. Anderson 20285a (D)

**NORTH CAROLINA**

**Bladen Co.:**  
2 miles W of White Oak, sandy soil, roadside  
March 1, 1966  
L. E. Anderson 19001 (D)

**Brunswick Co.:**  
5 miles NE of Shallotte, sandy soil  
1966  
L. E. Anderson 19031 (D)

**Cabarrus Co.:**  
6 miles E of Concord  
Feb. 2, 1967  
L. E. Anderson 25046 (Laf)

**Clay Co.:**  
7.4 miles NE of Shooting Creek, rock crevices, road cut  
Nov. 23, 1967  
L. E. Anderson 20132 (D)

Same, end of the same clump  
L. E. Anderson 20133 (D)
W. controversa n = 14 North Carolina

Durham Co.: Duke University W campus, west side of dormitory complex, gravelly soil, lawn under scattered oaks. Station C. L. E. Anderson 20213 (D)

Same, Station G L. E. Anderson 20217 (D)
Same, Station Q L. E. Anderson 20218 (D)
Same, Station L L. E. Anderson 20219 (D)
Same, Station N L. E. Anderson 20220 (D)
Same, Station P L. E. Anderson 20221 (D)
Same, Station J L. E. Anderson 20222 (D)
Same, Station O L. E. Anderson 20223 (D)
Same, Station M L. E. Anderson 20224 (D)
Same, Station H L. E. Anderson 20225 (D)

Duke University campus, Biological Science Bldg. March 8, 1966 L. E. Anderson 19005 (D)

Harnell Co.: 5 miles E of Pineview, sandy soil, roadside March 1, 1966 L. E. Anderson 19000 (D)

Johnston Co.: 4 miles W of Princeton, soil March 6, 1966 L. E. Anderson 19004 (D)

Pender Co.: 9 miles N of Burgan, sandy soil L. E. Anderson 19032 (D)

SOUTH CAROLINA

Chesterfield Co.: Middendorf, garden loam, street bank Dec. 26, 1967 L. E. Anderson 20238 (D)

Same, another clump L. E. Anderson 20239 (D)
Same, another clump L. E. Anderson 20241 (D)
Same, another clump L. E. Anderson 20242 (D)
W. controversa  n = 14  South Carolina

Chesterfield Co.:  
- Same, another clump  
  L. E. Anderson 20243 (D)
- Same, another clump  
  L. E. Anderson 20244 (D)
- Same, another clump  
  L. E. Anderson 20246 (D)

Horry Co.:  
- Little River, Palmetto shores  
  March 14, 1966  
  L. E. Anderson 19029 (D)
- Same, another clump  
  L. E. Anderson 19030 (D)

Spartanburg Co.:  
- 5 miles S of Duncan  
  Feb. 3, 1967  
  L. E. Anderson 25032 (Laf)

W. controversa  n = 26  

ARKANSAS

Baxter Co.:  
- Norfolk, North Fork River, near junction with White River, high bluffs, limestone (or sandstone)  
  March 9, 1968  
  L. E. Anderson 20286 (D)

Izzard Co.:  
- 1 mile S of Mt. Pleasant, in loose tufts on flat limestone outcroppings, cedar glade  
  March 9, 1968  
  L. E. Anderson 20272 (D)
- Same, another clump  
  L. E. Anderson 20273 (D)
- Same, another clump  
  L. E. Anderson 20274 (D)

Lawrence Co.:  
- 1 mile W of Black Rock, limestone  
  March 7, 1968  
  L. E. Anderson 20283 (D)
**W. controversa**  n = 26

**MISSOURI**

Barry Co.: Ca. 3 miles S of Eagle Rock, soil, edge of limestone, Table Rock Lake (collected by Paul Redfern, Jr.)
March 2, 1968  L. E. Anderson 20268 (D)

Same  L. E. Anderson 20269 (D).

**TENNESSEE**

Knox Co.: French Broad River, on dolomite boulders at Gov. John Sevier Highway
Oct. 16, 1967  L. E. Anderson 20168 (D)

**W. muhlenbergiana**  n = 13

**LOUISIANA**

Lafayette Parish: 3 miles S of Youngsville, eroded roadbank
Jan. 22, 1967  B. E. Lemmon 1455 (Laf)

E. bank of Vermilion River at Lafayette, C. T.
Montgomery property, flat, moist meadow
Jan. 24, 1967  B. E. Lemmon 1453 (Laf)

**TENNESSEE**

Sullivan Co.: 2 miles SE of Bristol, clay bank, edge of hardwood forest
Nov. 3, 1967  L. E. Anderson 20102 (D)
W. *muhlenbergiana* n = 14

**LOUISIANA**

Lafayette Parish: Pont Brule (hybrid location), N of Lafayette, heavy clay, disturbed soil in low woods
Dec. 21, 1967 B. E. Lemmon 1352 (Laf)

W. *ludovidiana* n = 13

**LOUISIANA**

Concordia Parish: 2 miles W of Ferriday, flat, wet ditchbank
Jan. 24, 1967 B. E. Lemmon 1491 (Laf)

Jackson Parish: 1.8 miles N of North Hodge, disturbed soil, roadside
Feb. 19, 1967 B. E. Lemmon 1528 (Laf)

Lafayette Parish: E bank of the Vermilion Rover at Lafayette, Wallis property, wet, flat meadow
Jan. 4, 1967 B. E. Lemmon 1405 (Laf)

St. Martin Parish: 1.1 miles W of Cecilia, ditchbank
Jan. 15, 1967 B. E. Lemmon 1429 (Laf)

St. James Parish: 2 miles W of Vacherie, old Valcour Amie homesite, edge of dry pond, woods
Feb. 5, 1967 B. E. Lemmon 1511 (Laf)

Tangipahoa Parish: 6 miles E of Ponchatoula, lower portion of roadside bank in mowed area, collected by W. D. Reese (10233)
Nov. 11, 1967 B. E. Lemmon (Laf)

Vermilion Parish: 4 miles SW of Perry, moist, flat, grassy roadside
Jan. 24, 1967 B. E. Lemmon 1461 (Laf)

**NORTH CAROLINA**

Johnston Co.: 4 miles W of Princeton, U. S. #70, sandy soil
March 6, 1966 L. E. Anderson 19003 (D)
W. ludoviciana  n = 14

LOUISIANA

Lafayette Parish:  E. bank of Vermilion River at Lafayette,  
Lemmon property, back yard, among grass  
Jan. 8, 1967  B. E. Lemmon 1407 (Laf)  
E. bank of Vermilion River at Lafayette,  
Lemmon property, soil at base of tree near slip  
Jan. 8, 1967  B. E. Lemmon 1406 (Laf)  
E. bank of Vermilion River at Lafayette,  
Lemmon property, bare soil under tree, front yard  
Dec. 27, 1967  B. E. Lemmon 1402 (Laf)  

W. ludovidianna  n = 26

MISSISSIPPI

Wayne Co.:  2 miles W of Wayesboro, edge of road, sandy soil,  
among pea gravel  
Dec. 30, 1967  B. E. Lemmon 1849 (Laf)
HYBRIDS

W. controversa x W. ludoviciana  n = 14

Lafayette Parish, La.: E bank of Vermilion River at Lafayette, clayey soil, poorly drained, area had been filled and leveled about 5 years ago. Many clumps of both putative parents growing among scattered blackberry bushes; several with hybrids.
Feb. 15, 1966 B. E. Lemmon 1340 (Laf)

n = 13

Vermilion Parish, La.: 4 miles SW of Perry, La., clayey, poorly drained soil, roadside, among grasses, many plants of W. controversa and W. ludoviciana but few hybrids
Jan. 24, 1967 B. E. Lemmon 1461 (Laf)

Hybrid of unknown origin  n = 26

Perry Co., Ala.: .75 miles E of Uniontown, Ala., yellow clay soil, road cut, eroded but held by clumps of grass in small, flat terraces, many clumps of hybrids, and W. muhlenbergiana, but not many of W. controversa.
Dec. 30, 1967 B. E. Lemmon 1800 (Laf)
B. E. Lemmon 1847 (Laf)
B. E. Lemmon 1848 (Laf)
VITA

Betty Ann Elberson Lemmon was born in New Orleans, Louisiana on December 22, 1925. In 1927 she moved with her family to Lafayette, Louisiana where she attended Mt. Carmel Convent. She was graduated from Lafayette High School in 1942, and received a Bachelor of Science degree from the University of Southwestern Louisiana in 1945.

She joined the faculty of the Department of Biology of the University of Southwestern Louisiana in 1946. In 1947 she married Edmund Thomas Lemmon. She resigned from the faculty in 1949 and rejoined the faculty in 1959. She received a Master of Science degree from the University of Southwestern Louisiana in 1965.

She was granted a leave from the University of Southwestern Louisiana where she held the position of Instructor in Biology, in September, 1967 to complete graduate work begun at Louisiana State University in 1966. She is a candidate for the degree of Doctor of Philosophy in August, 1968.
EXAMINATION AND THESIS REPORT

Candidate: Betty Ann Elberson Lemmon

Major Field: Botany

Title of Thesis: Cytological Investigations in the Genus Weissia in Southeastern United States

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination: July 12, 1968

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