

type in that some had long trichomes on the stem, the leaves were ashy grey, more heavily pubescent, and they apparently flowered earlier. Hybridization between *H. crenatus* and *H. ciliaris* may have been responsible for some of these variations, but generally they represent combinations not present in either species. Furthermore, Heiser and Smith (1955) have reported the chromosome number of *H. ciliaris* as  $n=51$  (also  $n=34$ , Heiser unpublished) while the writer has found  $n=17$  in *H. crenatus*. It may well be that these variations resulted from past hybridization with an unknown or now extinct species.

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### CHROMOSOME COUNTS IN THE SECTION *SIMIOLUS* OF THE GENUS *MIMULUS* (SCROPHULARIACEAE). III.

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This report<sup>1</sup> on the determination of chromosome numbers in the section *Simiolus* of the genus *Mimulus* is an integral part of a long range investigation into the taxonomy, genetics, and evolution of species in *Mimulus* (Vickery, 1951). Taken in conjunction with the previous counts (Vickery, 1955 and Mukherjee, Wiens, and Vickery, 1957), the counts reported here reveal a pattern of evolution in section *Simiolus* that involves both polyploidy and aneuploidy.

A slightly modified version of the technical method of Swaminathan, Magoon, and Mehra (1954) was found to produce better results than the methods previously used (Vickery, 1955 and Mukherjee, Wiens, and Vickery, 1957). Buds expected to contain anthers at the desired stages of microsporogenesis were killed and fixed for 24 hours in a mixture of two parts absolute ethanol and one part glacial acetic acid saturated with ferric acetate. Acetic acid was substituted for the propionic acid called

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for in Swaminathan, Magoon, and Mehra's schedule. Also, the buds were transferred after 24 hours to 70 per cent ethanol whereas their schedule called for leaving the buds in the fixative until used. The anthers were dissected out of the buds, smeared and stained in iron-aceto-carmin. Camera lucida drawings were made for each count and, in addition, photomicrographs were taken of the more intricate configurations. Each chromosome number reported is based on counts from an average of approximately ten microsporocytes. Herbarium specimens were prepared for each of the cultures studied. They will be deposited for future reference in the Garrett Herbarium of the University of Utah.

A total of eleven cultures was studied during the present investigation (table 1). The cultures include representatives of seven species and varieties of the section *Simiolus*: *M. guttatus* DC., *M. tilingii* Regel var. *tilingii*, *M. tilingii* var. *corallinus* (Greene) Grant, *M. glaucescens* Greene, *M. glabratus* var. *parviflorus* (Lindl.) Grant, *M. pilosiusculus* HBK., and *M. tigrinus* hort.

Of the five cultures of *M. guttatus* examined, three, (5003, 5007, and 5839) showed  $n=14$  chromosomes. The configurations were regular and similar to those observed previously for other cultures of *M. guttatus* (Vickery, 1955, Mukherjee, Wiens, and Vickery, 1957). However, the two cultures of *M. guttatus* from Mather, California, exhibited frequent lagging chromosomes during the anaphase stage of the first meiotic division. Eight cells from three different plants of culture 5009 were observed at this stage of division. Two pairs of lagging chromosomes were found in each of two cells, one pair in each of three cells and no lagging chromosomes in the remaining three cells. In addition, two cells from two different plants of the other Mather culture, 5010, were observed at the first anaphase stage of meiosis. These cells each contained a single pair of lagging chromosomes. The cause of the lagging chromosomes was not clear from the configurations studied. Observations of five cells in the first telophase stage of division revealed that in one case the lagging pair of chromosomes was not being included in either nucleus whereas in the other four cases, both members of the pair were being included in one nucleus producing 15 to 13 segregations of the chromosomes. Observations of cells in the second metaphase stage of division confirmed the reality of these irregular segregations and indicated that, apparently, in a few cases, two pairs of lagging chromosomes had been included in the same daughter nucleus. Of such 16 to 12 segregations, only cells with 16 chromosomes were actually observed. Perhaps the number of cells studied was too small a sample to detect cells with 12 chromosomes which may be less viable than cells with 13 or more chromosomes. Of the 22 configurations of second metaphase chromosomes observed in microsporocytes of three plants of culture 5009, three contained 14 chromosomes, twelve contained 15, five contained 13, and two contained 16. Of twelve configurations of second metaphase chromosomes observed in microsporocytes of plants of culture 5010 five contained the normal number of 14 chromosomes, four



TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS

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n = 14	<i>M. guttatus</i> DC. Pescadero, San Mateo County, California, altitude 20 feet, <i>Clausen</i> 2083 (5003). Yosemite Junction (marsh), Tuolumne County, California, altitude 1,350 feet, <i>Hiesey</i> 559 (5007). Big Cottonwood Canyon, Salt Lake County, Utah, altitude 7,100 feet, <i>Vickery</i> 334 (5839). <i>M. glaucescens</i> Greene Richardson Springs, Butte County, California, altitude 600 feet, <i>F. W. Pennell &amp; A. A. Heller</i> 25667 (5653).
n = 14 ± 1 or 2	<i>M. guttatus</i> DC. Mather (meadow), Tuolumne County, California, altitude 4,600 feet, <i>Hiesey</i> 571 (5009). Mather (spring area), Tuolumne County, California, altitude 4,800 feet, <i>Hiesey</i> 569 (5010).
n = 15	<i>M. tilingii</i> Regel <i>tilingii</i> Mount Timpanogos, Utah County, Utah, elevation 7,800 feet, <i>Del Wiens</i> , Aug. 6, 1956 (5967).
n = 24	<i>M. tilingii</i> var. <i>corallinus</i> (Greene) Grant Porcupine Flat, Mariposa County, California, altitude 8,000 feet, <i>Hiesey</i> 576 (5011).
n = 32	<i>M. tigrinus</i> hort. Commercial seeds from F. Kirchhoff and Co., Johannesburg, South Africa (5056).
n = 45	<i>M. glabratus</i> var. <i>parviflorus</i> (Lindl.) Grant Illapel, Coquimbo, Chile, altitude 4,000 feet; Plant Introduction Service no. 144534, USDA (5041).
n = 46	<i>M. pilosiusculus</i> HBK. Botanic Garden, Copenhagen, Denmark (wild in Argentina, Chile, and Peru); Plant Introduction Service no. 181130, USDA (5320).

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contained 15, one contained 13 and two contained 16. Thus, in the Mather cultures irregular meioses occurred in more than 50 per cent of the microsporocytes and a comparable proportion of aneuploid microspores was produced. If the resulting aneuploid gametes are functional, even occasionally, they might lead to the formation of aneuploid plants or populations. If such gametes are generally non-functional, they might help to explain the marked self and cross sterility observed in the Mather cultures in comparison to the relatively high self and cross fertility of other cultures of *M. guttatus* (Vickery, in press).

*Mimulus glaucescens* (5653) is morphologically closely related to *M. guttatus* (Pennell, 1951). It has  $n=14$  chromosomes which are indistinguishable in appearance from those of *M. guttatus* (fig. 1). This investigation revealed no cytological basis for the strong crossing barrier (Vickery, 1956) that separates *M. glaucescens* from *M. guttatus* and its related species.

*Mimulus tilingii* var. *tilingii* (culture 5967) from a population growing on Mount Timpanogos of the Wasatch Mountains, Utah, generally has  $n=15$  chromosomes in contrast to other Utah and California populations

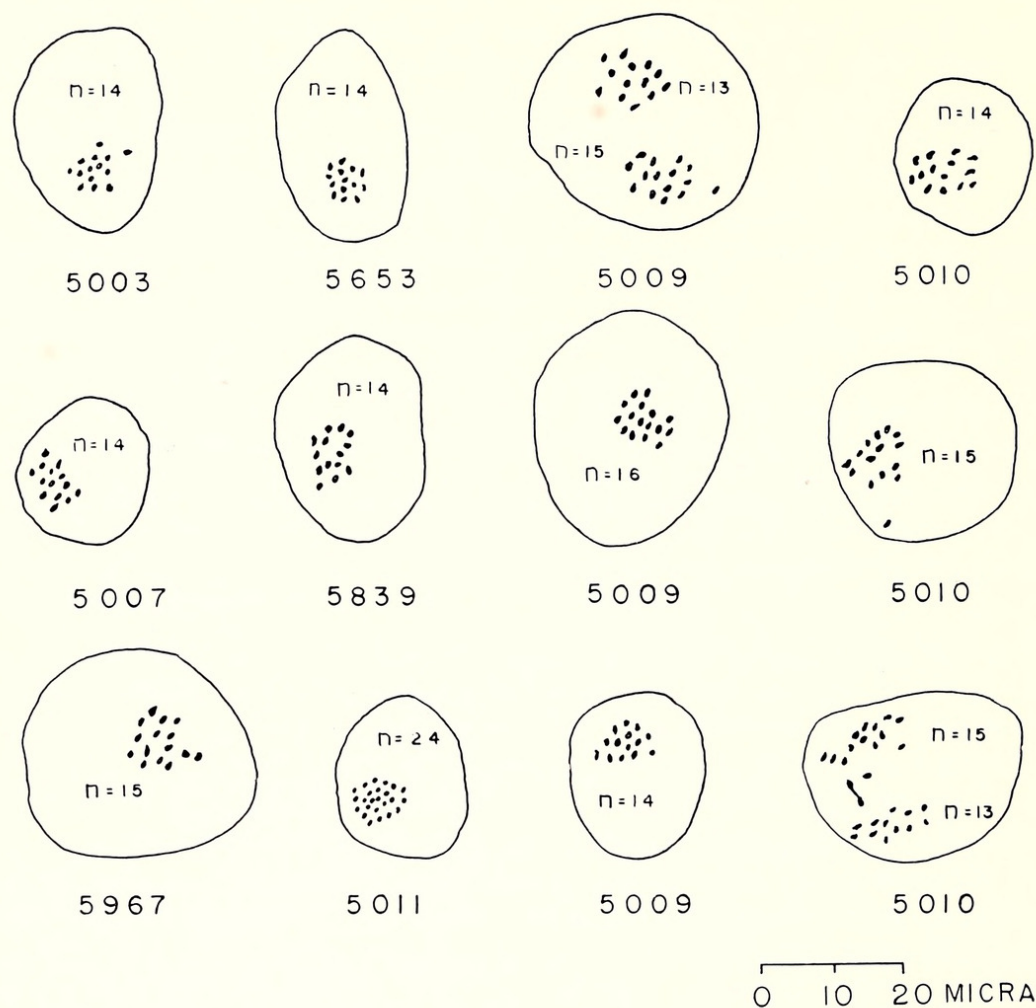


FIG. 1. Meiotic chromosomes of North American *Mimulus*: *M. guttatus*, 5003, 5007, 5009, 5010, 5839; *M. glaucescens*, 5653; *M. tilingii* var. *tilingii*, 5967, var. *corallinus*, 5011. All cells are in or near second metaphase except 5007, 5011, and 5967 which are in first metaphase. (Camera lucida drawings,  $\times 645$ .)

of that variety which have  $n=14$  (Vickery, 1955 and unpublished). Various stages of meiosis were examined in 16 microsporocytes from three different plants of culture 5967. Two of the cells contained 13 and 14 chromosomes instead of the more prevalent 15. However, *M. tilingii* var. *tilingii* did not show irregular numbers nearly as frequently as did the Mather populations of *M. guttatus*.

*Mimulus tilingii* var. *corallinus* (culture 5011) is closely related morphologically to *M. guttatus* and to *M. tilingii* var. *tilingii* (Grant, 1924) but is effectively separated from them by genetic barriers (Vickery, 1956). Culture 5011 forms sterile hybrids with *M. guttatus* and will not hybridize, despite numerous attempts, with *M. tilingii* var. *tilingii*. *Mimulus tilingii* var. *corallinus* has  $n=24$  chromosomes in contrast to the  $n=14$  of *M. guttatus* and the  $n=14$  and  $n=15$  of *M. tilingii* var. *tilingii*. Further work is in progress to try to establish the chromosome homologies



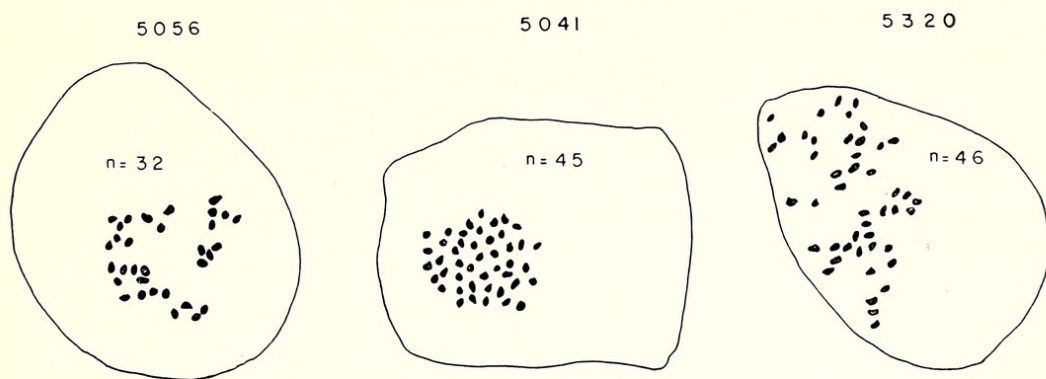


FIG. 2. Meiotic chromosomes of South American *Mimulus*: *M. tigrinus*, 5056 (first metaphase); *M. glabratus* var. *parviflorus*, 5041 (second metaphase); *M. pilosiusculus*, 5320 (second metaphase). (Camera lucida drawings,  $\times 1134$ .)

and the genetic relationships of the various entities within the *Mimulus tilingii* complex.

The three species from South America used in this study have higher chromosome numbers than any of the North American forms determined thus far. *Mimulus glabratus* var. *parviflorus* (culture 5041) from the Andes Mountains of Chile has  $n=45$  chromosomes and *M. pilosiusculus* (culture 5320), originally from southern South America, has  $n=46$  (fig. 2). *Mimulus tigrinus* hort., a cultivated derivative of *M. luteus* L. (Miller and Bailey, 1947) has  $n=32$  chromosomes (fig. 2) which agrees with the report of Brozek (1932).

In conclusion, this survey of chromosome numbers and behavior in section *Simiolus* indicates that in general the chromosome number for *M. guttatus* is  $n=14$ . However, aneuploid microspores are produced with a frequency of greater than 50 per cent in the two cultures of *M. guttatus* from Mather. Such microspores, if functional even occasionally, might lead to the production of aneuploid plants or populations of *M. guttatus* similar to the aneuploid populations found in *M. tilingii* var. *tilingii*, *M. glabratus* var. *utahensis* and in the *M. glabratus* var. *parviflorus*—*M. pilosiusculus* group. The high chromosome numbers found in the South American species indicate that polyploidy, as well as aneuploidy, plays an important role in the evolution of species in section *Simiolus*. Further work is in progress to elucidate the questions of the cytogenetic relationships and taxonomic status of several entities in section *Simiolus* which have been raised by the results of this investigation.

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#### REVIEW

*Pollen and Spore Morphology/Plant Taxonomy*. Gymnospermae, Pteridophyta, Bryophyta (Illustrations). (An Introduction to Palynology. II). By GUNNAR ERDTMAN. 151 pp., frontispiece, 5 plates, 265 figs. Almquist & Wilsell, Stockholm. 1957. \$8.00.

Over a period of more than 13 years, Gunnar Erdtman has undertaken the voluminous task of describing and illustrating representative pollen and spores of the world's plants. His contribution toward better understanding of the fundamentals of microspore morphology has given world-wide impetus to the development of this aspect of plant morphology and to palynology.

Erdtman's earlier publications were largely concerned with the pollen morphology of the more common angiosperms and gymnosperms in the experience of the Pleistocene pollen-analyst. Pollen workers, 10-15 years ago, were generally satisfied with knowing the gross morphologic features and key characteristics of pollen of the common wind-pollinated genera. Within the past few years, however, the boundaries of pollen work have been vastly expanded. The need for a thorough understanding of the pollen morphology of living plants has become increasingly apparent in identification and interpretation of fossil pollen, as well as a basis for the application of pollen morphology to systematic studies. Need for clarification of many of the details of microspore morphology and knowledge of pollen and spores of increasing numbers of plants has been answered in part by two volumes recently published by Erdtman. "An Introduction to Palynology. I. Pollen Morphology and Plant Taxonomy. Angiosperms" appeared in 1952. The volume being reviewed, "An Introduction to Palynology. II.", comprises the illustrations to the text of a treatise (Vol. III) on the morphology of microspores of the gymnosperms, pteridophytes and bryophytes which will be published at a later date.

Volume II includes "palynograms" (diagrammatic drawings showing the gross morphology of the grains as well as details of the surface pattern and exine stratification), a few photomicrographs and some electron micrographs of thin sections through spore walls of representatives of 12 gymnosperm families, 29 pteridophytic and 63 bryophytic families (23 Hepaticae and 40 Musci). Also included are similar illustrations for the surface pattern of, and optical sections through, the megaspore



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