CHROMOSOME COUNTS IN THE SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). VI. NEW NUMBERS IN M. GUTTATUS, M. TIGRINUS, AND M. GLABRATUS[1]

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The new chromosome numbers found in this investigation significantly enlarge the cytogenetic concept of *M. guttatus* DC. and amplify the knowledge of such other species of the section as *M. nasutus* Greene, *M. tigrinus* Hort. ex Sieb. & Voss, *M. luteus* L., and *M. glabratus* H.B.K. (figs. 1, 2). The cytological techniques employed were slightly modified from those previously used (Mukherjee and Vickery, 1962). The fixative was strengthened from 2 to 3 parts glacial acetic acid mixed with the usual 1 part absolute ethanol saturated with ferric acetate. The length of fixation was reduced from 24 to 4 hours. The slides were made permanent by first, dehydrating them in an ethanol vapor chamber for 3 to 4 days. Next, the cover slips were ringed with diaphane and the slides were left in the vapor chamber for an additional 2 to 3 days. Representative chromosome configurations were recorded either photographically or by drawings made with the aid of a camera lucida. Vouchers of each culture will be deposited in the University of Utah herbarium.

Among the *M. guttatus* populations ten, in addition to the 34 previously sampled (Vickery, 1955; Mukherjee et al., 1957; Mukherjee and Vickery, 1959; 1960), were found to have n=14 chromosomes (table 1). Two others had n = 16 and genetic tests now in progress may well indicate that these populations belong to a new species that should be segregated from *M. guttatus*. The final *M. guttatus* population had n=28 chromosomes.

This tetraploid, n = 28 population was studied cytologically and genetically. In meiosis, its chromsomes formed regular bivalent associations with no indications of tri- or tetravalent configurations. Several plants of this population were crossed with a highly fertile diploid *M. guttatus* (5052). The F_1 hybrids were vigorous but sterile. Of 31 pollen mother cells observed at or near first metaphase of meisosis 23 had 14_{II} and 14_{I}, three had 12_{II} and 18_{I}, and five had 9_{II} and 24_{I}. This pairing behavior and that of the tetraploid plants themselves indicate that if the Verde Valley population is an autotetraploid as its close morphological similarity to diploid *M. guttatus* suggests, and not an allotetraploid, then it must have arisen long enough ago to permit the accumulation of sufficient gene differences in its chromsomes to prevent autosyndesis. Even though this tetraploid population will not produce fertile hybrids with

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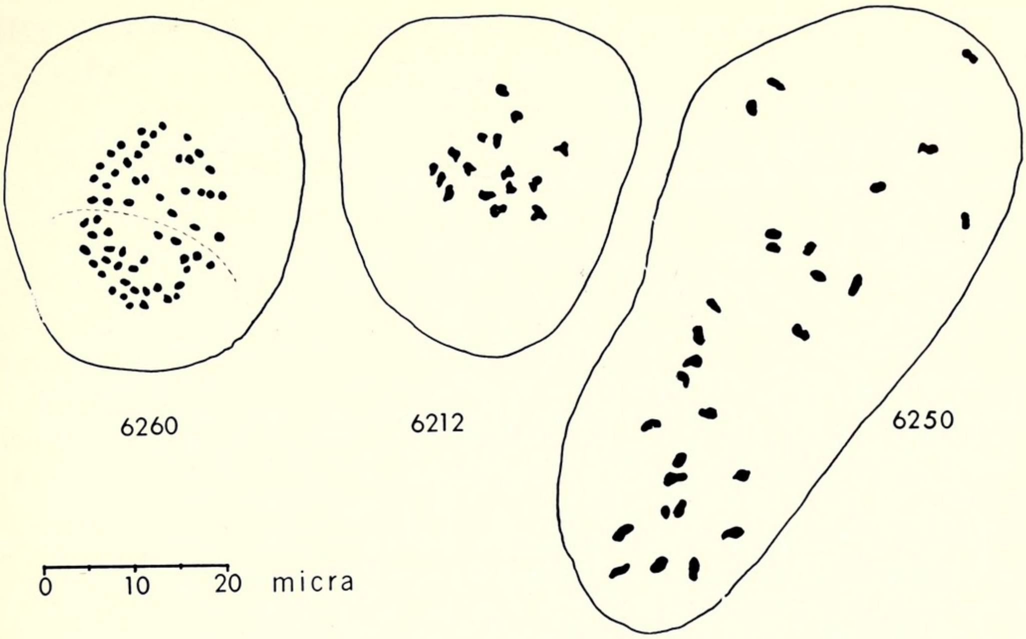

FIG. 1. Meiotic chromosomes of *Mimulus: M. tigrinus*, 6260, has n = 30 chromosomes, *M. guttatus*, 6212 and 6250, has n = 16 and n = 28, respectively. The first cell is in first anaphase whereas the latter two are in first metaphase. The dotted line delimits the two planes of focus in the cell of 6260. The camera lucida drawings were at an original magnification of × 2,720, reduced to approx. × 900 in reproduction.

diploid populations, we hesitate to suggest that it is a separate species. Probably other such tetraploid populations have arisen or will arise here and there throughout the extensive range of *M. guttatus* (Grant, 1924). Possibly, as in *Galium* (Ehrendorfer, 1955) such polyploid populations would be able to exchange genes. If such a situation proved to be the case, a restricted gene flow would still be potentially possible from the diploids to the tetraploids and amongst the latter. This gene flow would hold the tetraploid and diploid forms together, at least loosely, in a common evolutionary pathway.

The chromosome counts for *M. nasutus, M. tigrinus*, and *M. luteus* (table 1) include a new number, n=30, for *M. tigrinus*. Previous reports (Brozek, 1932; Mukherjee and Vickery, 1959; 1960) are for n=32 populations. The latter number is also characteristic of *M. luteus* (table 1; Mukherjee and Vickery, 1959; 1960) from which the horticultural species *M. tigrinus* was derived. However, one *M. luteus* culture (Mukherjee and Vickery, 1960) was found to have n=30 + 0, 1, or 2 chromosomes. In view of this variable population, the discovery of a consistently n=30 *M. tigrinus* population is not surprising, but interesting.

Mimulus glabratus H.B.K. is a highly polymorphic, widespread complex of related varieties (Grant, 1924). It occurs as scattered populations that range from the north woods of Michigan (Fassett, 1939) and the Great Basin of the Western States (Pennell, 1947), south through Mexico to Guatemala and then from Peru on south to Argentina and the Juan Fernandez Islands (Skottsberg, 1953). The striking diversity and scatter of the members of the complex raise a question as to the closeness of their relationship.

The most outstanding result of the investigation was the demonstration of aneuploidy at each of the three polyploid levels in the complex,

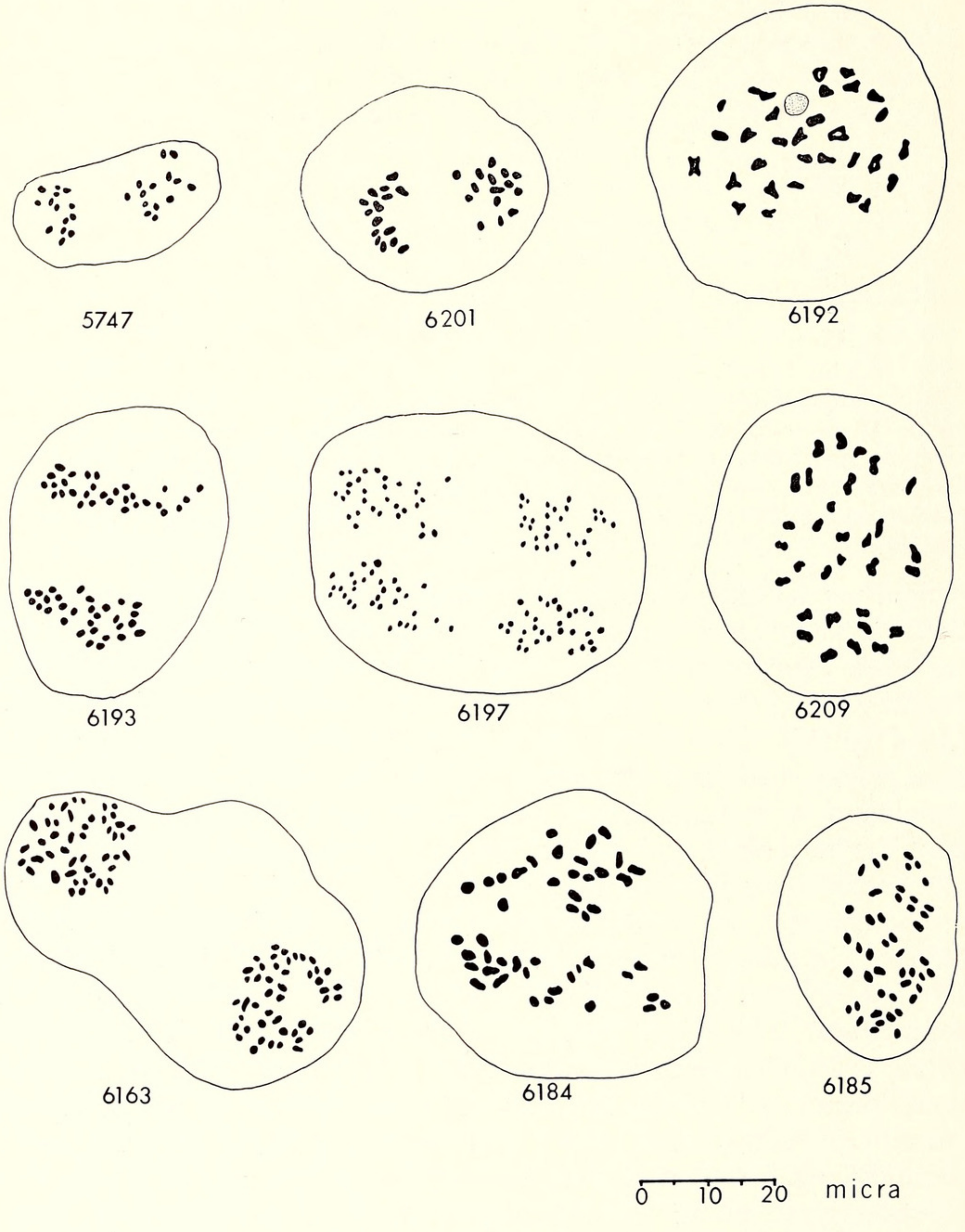

FIG. 2. Meiotic chromosomes of *Mimulus*: *M. glabratus* var. *utahensis*, 5747 (n = 14), 6201 (n = 15); *M. glabratus* var. *glabratus*, 6192, 6193 (n = 30), 6197, 6209 (n = 31); *M. glabratus* var. *parviflorus*, 6163, 6184, 6185 (n = 46). The figures were selected to illustrate the appearance of the chromosomes in several stages of meiosis, diakenesis, 6192; metaphase I, 6209, 6184, and 6185; metaphase II, 5747, 6201, 6193, and 6163; anaphase II, 6197. The camera lucida drawings were at an original magnification of × 2,100, reduced to approx. × 700 in reproduction.

TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS

M. glabratus var. *glabratus*. **n = 30:** e of Morelia along route 15, Michoacan, Mexico, 8300 ft., *Wiens 2519* (6192); Hidalgo, along route 15, Michoacan, Mexico, 8300 ft, *Wiens 2520* (6193); El Salto, km 1104 on Durango-El Salto rd, Durango, Mexico, 8500 ft, *Wiens 2639* (6210). **n = 31:** Santa Rosa, along route 15, Michoacan, Mexico, *ca* 8500 ft, *Wiens* 2521 (6194); n of Tehuacan along route 150, Puebla, Mexico, 7200 ft, *Wiens 2552* (6197); Ciudad Mendoza, along route 150, Vera Cruz, Mexico, 4800 ft, *Wiens 2555* (6198); Cofre de Perote, Vera Cruz, Mexico, 9500 ft, *Wiens 2575* (6199); n of Puebla along route 119, Tlaxcala, Mexico, 6700 ft, *Wiens 2588* (6200); El Salto, km 1050 on Durango-El Salto rd, Durango, Mexico, 8000 ft, *Wiens 2635* (6209).

M. glabratus var. *parviflorus*. **n = 46:** Auetrihue, Argentina, *Diem,* in 1959 (6162); Lumaco-Puente del Cina, Malleco, Chile, 660 ft, *Kunkel*, Nov. 29, 1958 (6163); Tafi del Valle, La Quebradita, Tucuman, Argentina, 7300 ft, *de la Sota,* Feb. 7, 1959 (6184); e of La Divisiona, in the Cordillera Azul, Loreto, Peru, 6600 ft, *Mathias 5151* (6185).

M. glabratus var. *utahensis*. **n = 14:** Telephone Canyon, Pilot Cone, Mineral Co., Nevada, 5500 ft, *Figg-Hoblyn*, July 4, 1950 (5747). **n = 15:** Geneva Steel Plant, Utah Co., Utah, 4490 ft, *Lindsay*, Apr. 4, 1959 (6156); Rio Tierra Quemada and route 57, Guanajuato, Mexico, 5700 ft, *Wiens 2598* (6201); Saltillo, route 57, Coahuila, Mexico, 5500 ft, *Wiens 2509* (6203).

M. guttatus. **n = 14:** Lewiston grade, Nez Perce Co., Idaho, 840 ft, *Preece, Murdoch, & Rumely 2167* (5262); Botanic Garden, Wageningen, Netherlands, *Venema 1949* (5306); Mutica, Sonora, Mexico, *Gentry 2194* (5321); Mono Lake, Mono Co., California, 6440 ft, *Vickery 200* (5397); Holberg's, Lake Co., California 3000 ft, *Vickery 2043* (6138); near Cache Creek, Lake Co., California, 1300 ft, *Vickery 2044* (6139); West Thumb, Yellowstone Park, Wyoming, 7000 ft, *Mia*, July 25, 1959 (6186); Cache Creek, Lake Co, California, 1250 ft, *Campbell*, June 18, 1948 (6288), seeds from 131652 (TFX); Atlantic City, Wind River Mtns., Fremont Co., Wyoming, 7680 ft, *Edmunds*, Aug. 18, 1960 (6303); Lobdel Lake, Sweetwater Mtns., Mono Co., California, 9400 ft, *Beaman 957* (5257). **n = 16:** km 1155, Durango-Mazatlan rd, Durango, Mexico, 8500 ft, *Wiens 2643* (6212); w of crest of Durango-Mazatlan rd, Durango, Mexico, 8300 ft, *Vickery 2616* (6273). **n = 28:** Verde Valley, Yavapi Co., Arizona, 3010 ft, *Vickery 2593* (6250).

M. luteus. **n = 32:** Auetrihue, Aregntina, *Diem*, in 1959 (6161).

M. nasutus. **n = 14:** Alabama Hills, Inyo Co., California, 500 ft, *Dedecker*, May 30, 1956 (6060).

M. tigrinus. **n = 30:** Cultivated in gardens, Kathmandu, Nepal, 4500 ft, *Brydon*, May, 1960 (6260).

as follows: *M. glabratus* var. *utahensis* Penn., n = 14 and n = 15; *M. glabratus* var. *glabratus,* n = 30 and n = 31; and *M. glabratus* var. *parviflorus* (Lindl.) Grant, n = 45 and n = 46 (table 1). For *M. glabratus* var. *utahensis,* the additional determinations verified the previous reports (Vickery, 1955; Mukherjee, *et al.,* 1957; Mukherjee and Vickery, 1960). The counts now available suggest a generally central and western Great Basin distribution for the n = 14 form and an eastern Great Basin and Mexican Plateau distribution for the n = 15 form. At first, culture 5852 from the Wendover, Utah population was thought to be *M. guttatus* (Vickery, 1955), but further study has shown it to belong to *M. glabratus* var. *utahensis.* It is the most eastern n = 14 population found thus far.

The new counts show *M. glabratus* var. *glabratus* to be a tetraploid as is *M. glabratus* var. *fremontii* (Benth.) Grant (Mukherjee and Vickery, 1960). However, morphologically var. *glabratus* is far closer to var. *utahensis* than it is to var. *fremontii.* The few n = 30 populations of var. *glabratus* found to date occur only in Michoacan and Durango, Mexico whereas the n = 31 populations are more common and more widespread (table 1).

The new counts for *M. glabratus* var. *parviflorus* plus the previous n = 45 report (Mukherjee and Vickery, 1959) reveal that this variety aslo has two chromosome forms. Morphologically and cytologically *M. pilosiusculus* H.B.K. (Mukherjee and Vickery, 1959) belongs to this taxon. In contrast, the Tafi del Valle population (6184) is very distinct from the other n = 46 or n = 45 populations. It is erect and the others are prostrate.

Cytologically, the *M. glabratus* complex presents a most interesting picture of a polyploid series with aneuploidy at each level. The polyploid levels increase from north to south in a striking manner. However, while these counts clearly indicate the complexity of the group, an improved taxonomic treatment of it must await a cytological study of the other varieties (Fassett, 1939; Skottsberg, 1951, p. 784) and a genetic investigation of the whole complex.

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