CHROMOSOME COUNTS IN SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). IX. POLYPLOID AND ANEUPLOID PATTERNS OF EVOLUTION

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This cytological investigation clearly documents the presence of the unusual north to south polyploid-aneuploid-polyploid series in the *Mimulus glabratus* complex (table 1) adumbrated in our earlier reports (Mukherjee and Vickery, 1962; Mia, et al., 1964; Vickery, et al., 1968). The new chromosome counts—obtained by essentially the same aceto-carmine squash technique previously employed (Vickery, et al., 1968)—confirm the presence of diploid ($\mathbf{n} = \mathbf{15}$), tetraploid ($\mathbf{n} = \mathbf{30}$), aneuploid tetraploid ($\mathbf{n} = \mathbf{31}$), and hexaploid ($\mathbf{n} = \mathbf{46}$) members of the complex. The distribution of the 69 cytologically known populations (table 1 and Vickery, 1955; Mukherjee, et al., 1957; Mukherjee and Vickery, 1959, 1960; Mia, et al., 1964; Vickery, et al., 1968) reveals that the diploids occur in the Great Basin of the western United States, in the Great Plains region of the central United States, in southwestern Texas and New Mexico, and in the Sierra Madre Oriental of northeastern Mexico. The tetraploids are found along the southern limit of the diploids, from west Texas to southeastern California. The aneuploid tetraploids occur further south in the highlands of western and central Mexico and in the mountains of Chiapas and Guatemala. The hexaploids are found in South America along both flanks of the Andean Cordillera from Columbia to southern Patagonia and in the Juan Fernandez Islands 500 km off the coast of Chile. Both the geographic extent and the north to south direction of this polyploid series appear to be exceptional, if not unique in the Western Hemisphere.

Several of the populations of the *M. glabratus* complex were observed to have one pair of chromosomes which was late condensing during prophase I, late in separating at anaphase I, and generally light staining (fig. 1). Aside from causing several errors in chromosome counts here corrected (table 1), this behavior suggests the interesting possibility that the genes controlling meiosis may be concentrated on that pair of chromosomes.

The new chromosome counts obtained in this investigation (table 1) for *M. guttatus* taken in conjunction with those previously reported (Calder and Taylor, 1968b; Vickery, 1955; Mukherjee, et al., 1957; Mukherjee and Vickery, 1959, 1960; Mia, et al., 1964; Vickery, et al., 1968) show that *M. guttatus* ($\mathbf{n} = \mathbf{14}$) appears to be evolving tetraploid ($\mathbf{n} = \mathbf{28}$) populations along the periphery of its range. Its range extends from the Aleutian Islands to Chihuahua and from the Pacific Coast to the Rocky Mountains. The tetraploid populations are found,

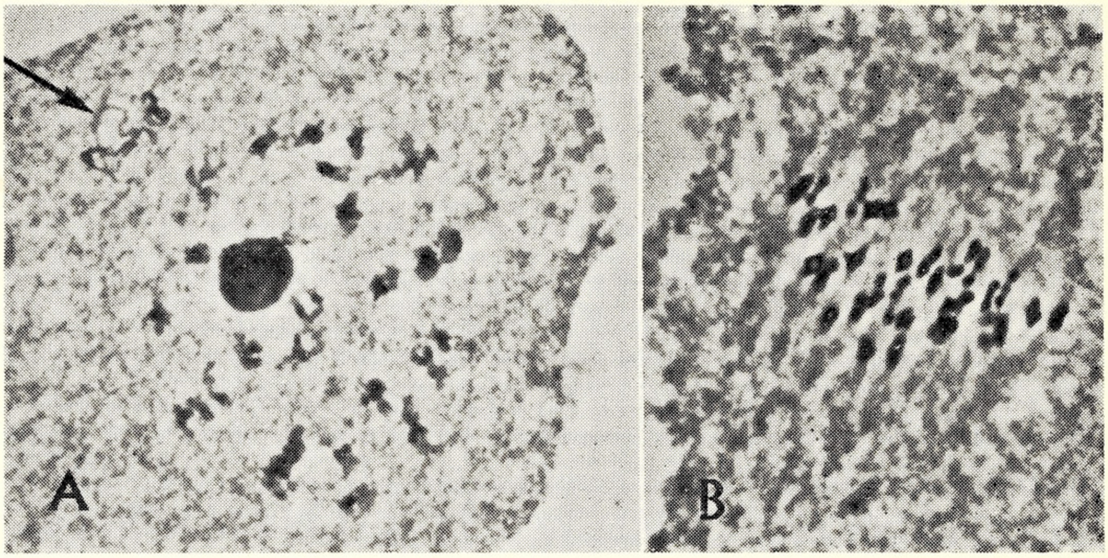

FIG. 1. Chromosomes of *Mimulus glabratus* var. *glabratus*. A. Late condensing bivalent, culture 7304, mag. ca. 1110×. B. First metaphase, culture 7299, 31 II, mag. ca 1345×.

typically at higher elevations, along the northwestern and southern edges of the range. The northern tetroploids are sufficiently morphologically distinct to suggest that they originated by alloploidy. In fact, the tetraploids of the Queen Charlotte Islands have been recognized as a separate subspecies, *M. guttatus* subsp. *haidensis,* by Calder and Taylor (1965, 1968a). Probably that name should be applied to all the northern tetraploids. The southern tetraploids are not distinct morphologically from the diploids and may have originated by autoploidy. For example, two populations consist of mixed diploid and tetraploid plants. No triploids were observed. The diploids show a consistent 14 II's, whereas the tetraploids exhibit an average of 6 IV's (range 3 IV to 9 IV) which suggests that these populations are now in the process of evolving auto-tetraploid forms.

The new counts for *M. nasutus* Greene and *M. tilingii* Regel confirm the presence of aneuploidy at the diploid level in both species (table 1). *Mimulus nasutus* has $n = 14$ and $n = 13$ populations (table 1; Mukherjee and Vickery, 1960; Mia, et al., 1964). *Mimulus tilingii* has $n = 14$ and $n = 15$ populations primarily (table 1; Vickery, 1955; Mukherjee and Vickery, 1959, 1960), with some $n = 24$ and $n = 28$ populations as well (Mukherjee and Vickery, 1959; Vickery, et al., 1968). However, for neither species are enough counts available to clarify its pattern of evolution.

In summary, this investigation indicates the presence of two distinctive patterns of evolution in section *Simiolus*. In the *M. glabratus* complex the pattern consists of a north to south series of increasing polyploid-aneploid-polyploid levels. In the common yellow monkey flower, *M. guttatus,* the pattern consists of an extensive, western North American area of diploid populations with occasional, apparently allo-tetra-

TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS.[1]

M. glabratus var. *externus* (Skottsb.) Skottsberg. **n = 46:** Chile, Islas Juan Fernández, Isla Más-a-Tierra, 30 m, *7325* (*Meyer,* 1965).

M. glabratus var. *fremontii* (Benth.) Grant. **n = 15**: U.S.A., Kan., Reno, Arlington, 472 m, *7648;* Neb., Custer, Victoria Sprs., 885 m, *7135;* Thomas, Middle Loup R., 930 m, *7136;* N. M., Catron, Allegros Pk. rd., 2135 m, *6610* so. of Reserve, 1770 m, *6612;* Grant, Gila R., 1340 m, *6616;* Rio Arriba, Abiquiu, 1770 m, *6621;* San Miguel, Tecolote Cr., 1800 m, *6620;* Socorro, Dripping Sprs., 1677 m, *6608;* Tex., Brewster, Calamity Cr., 1400 m, *6619;* Wis., Dane, Wingra Sprs., 262 m, *7701;* Mexico, Coahuila, Saltillo, 1677 m, *7308.* **n = 30**: U.S.A., Tex., Culberson, near Van Horn, 1357 m, *6296, (McVaugh 8002);* Jeff Davis, Limpia Cr. Canyon, 1525 m, *6617;* and 1523 m, *6618;* Presidio, Fresno Cr., 823 m, *6294 (Johnson and Warnock 3682);* Gillespie, Enchanted Rock, 457 m, *6278.*

M. glabratus var. *glabratus.* **n = 31**: Guatemala, Huehuetenango, El Tapon Canyon, 1982 m, *7299;* near Huehuetenango, 1951 m, *7300;* Quezaltenango, 35 km so. of Huehuetenango, 2440 m, *7301;* Totonicapán, near San Cristóbal, 2440 m, *7303;* near Totonicapán at km 104 no. of Guatemala City, 2287 m, *7304;* Mexico, Chiapas, near Santo Tomás, 2195 m, *7296;* near San Cristóbal de las Casas, 2165 m, *7297;* D. F., Miguel Hidalgo Nat. Park, 2744 m, *7305;* Durango, Papasquiaro, 2287 m, *6647*[2]; e. of El Salto, 2440 m, *7286;* Llano Grande, 2440 m, *7287;* Mex., Acambay, 2592 m, *7307.*

M. glabratus var. *michiganensis* (Pennell) Fassett. **n = 15:** U.S.A., Mich., Cheboygan, Little Carp Lake R., 214 m, *7703;* Mackinac, Epoufette, 180 m, *6629.*

M. glabratus var. *parviflorus* (Lindl.) Grant. **n = 46:** Argentina, Río Negro, Cerro Catedral, 1200 m, *9546;* Chile, Bío-Bío, Salta del Laja, 400 m, *6683;* Aconcagua, no. of La Laguna, 1 m, *7658;* Aisen, near Ibáñez, ca. 1220 m, *6327;* Bahia Jaras, 220 m, *6328;* Atacama, Quebrada, 1525 m, *9092;* Río Cholloy, 1400 m, *9093;* Coquimbo, near Illapel, 1300 m, *5041*[2]; U.S.D.A.P.I.S. *144534;* Concepción, Pen. de Tumbes, 1 m, *6317, (Moore 285);* Valparaiso, near Viña del Mar, 8 m, *9544;* Talco, Los Cipreces, 1050 m, *9098.*

M. glabratus subsp. *utahensis* Pennell. **n = 15:** U.S.A., Calif., Mono, Mono Lake, 1964 m, *(Stebbins 714) 5048*[2]*;* Nev., Elko, Cherry Cr., 1982 m, *5972;* Mineral, Pilot Pk., 1677 m, *5747*[2]; White Pine, Ely, 1957 m, *7681;* Utah, Davis, Antelope Is., 1311 m, *5996;* Tooele, Wendover, 1311 m, *5852*[2].

M. guttatus Fischer ex DC. **n = 14:** U.S.A., Ariz., Coconino, Oak Cr. Canyon, 1510 m, *7793;* Calif., Riverside, Hurkey Cr., 1326 m, *7561;* Calif., San Bernardino, Mill Cr., 915 m, *9109 (Mathews,* 1968) ; Utah, Salt Lake, west fork of Lambs Canyon, 1890 m, *7709;* Butterfield Cr., 1740 m, *9550;* Tooele, Middle Canyon, 2073 m, *9549;* Utah, Mt. Nebo, Salt Cr., 2317 m, *7711;* Loop Spr., 2561 m, *7712;* Mt. Timpanogas, 2256 m, *7713;* Washington, Blake Gubler Ranch, Pine Valley Mtns., 2135 m, *9548;* Sevier, in tributary of Fish Lake, 2881 m, *7625;* Utah, Summit, Lily Lake, 3065 m, *7495;* Beaver Cr. campground, 2256 m, *9653.***n = 14, 28:** Ariz., Mohave, Moccasin, 1525 m, *7555;* Utah, Kane, Three Lakes, 1646 m, *9555.* **n = 28:** Ariz., Cochise, Ramsey Canyon, 1646 m, *7558;* Colo., Grand, Rollins Pass, 3354 m, *7693* (*Foreman,* 1967) ; Ore., Multnomah, at the base of Multnomah Falls, 85 m, *9562.*

M. nasutus Greene. **n = 14:** U.S.A., Calif., Sonoma, near Stewarts Point, 15 m, *5865 (Holme,* 1951).

M. tilingii Regel. **n = 14:** U.S.A., Calif., Mono, below Saddlebag Lake, 3018 m, *7684;* Utah, Duchesne, Lovenia Cirque, Uinta Mtns., 3,475 m, *7679 (Hall).* **n = 15:** Utah, Mt. Timpanogas Trail, 1968, 2560 m, *7714* and 2745 m, *7717;* Emerald Lake, 3050 m, *7716.*

[1] The taxonomic treatment is based on Fassett, 1939; Grant, 1924; Pennell, 1935; and Skottsberg, 1951. Collectors' names are not given for specimens collected by or for the authors and, hence, clearly identified by the culture number.

[2] Corrected counts.

ploid populations on the northern periphery and scattered, probably auto-tetraploid populations on the southern periphery of the range.

Many of the chromosome counts here reported are included in the dissertations of McArthur, Tai, and Alam submitted to the faculty of the University of Utah in partial fulfillment of the Ph.D. degree. Some of the counts are from the thesis of Eldredge submitted to the faculty of the University of Utah in partial fulfillment of the requirements for the M.S. degree. The project was supported by grants from the University of Utah Research Fund and the National Science Foundation (GB7318, GB18139). Traineeship support for varrying lengths of time for McArthur, Eldredge, and Tai by an N.I.H. Genetics Training Grant (GM 1374) and fellowship support of McArthur by the N.D.E.A. Title IV program are gratefully acknowledged. M. T. Alam is now Cytogeneticist, Quebec Ministry of Health, Laval, Canada. W. Tai is Assistant Professor of Botany, Michigan State University, East Lansing. E. D. McArthur is Rearch Fellow, Department of Agricultural Sciences, The University, Leeds, England.

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