

SPECIATION BY ANEUPLOIDY AND POLYPLOIDY IN *MIMULUS* (SCROPHULARIACEAE)¹

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Speciation by aneuploid and polyploid changes in chromosome numbers is so common in flowering plants as to be almost a characteristic of the angiosperms. Elegant examples of these patterns of evolution are exhibited by monkey flowers of the genus *Mimulus* (Scrophulariaceae).

The genus *Mimulus* contains some 150 species occurring in western North and South America with a few outlying species in eastern North America, Japan, Vietnam, the Himalayas, New Zealand, Australia, and South Africa. The center of diversity is California, with a secondary center in Chile. Some species are annuals of deserts, grasslands, or forests; some are biennials of marshy places; some are herbaceous perennials from springs, streamsides, or lake-shore habitats; and others are woody shrubs of the dry California chaparral. The species form clusters reflecting these various life forms. There are 8–10 such clusters commonly recognized as sections of the genus *Mimulus* (Grant 1924, Pennell 1951, Chuang and Heckard personal communication).

Chromosome numbers of over 50 species (Table 1), that is, approximately one-third of the *Mimulus* species, have been ascertained by Vickery and his co-workers (Vickery 1978, Vickery, Chu et al. 1981, Vickery, Simpson et al. 1981, Vickery et al. 1982, 1985, 1986, 1990, unpublished) and by Chuang and Heckard (personal communication). Chromosome numbers reveal intriguing patterns of evolution by aneuploidy and polyploidy.

First, let us consider the base chromosome numbers of the eight main sections of the genus. Section *Mimulastrum* has a base number of $x = 7$; *Eumanus* and *Erythranthe* have base numbers of $x = 8$; *Paradanthus* 8, 9, 10; *Eumimulus* 8, 11, 12; *Oenoe* 9; *Diplacus* 10;

and *Simiolus* 14, 15, 16, 30. Base numbers of the sections suggest extensive evolution by both aneuploidy and polyploidy. For the genus as a whole, the base number appears to be $x = 8$, inasmuch as the other plausible base number, $x = 7$, is found only in one, apparently derived, desert species, *M. mohavensis* Lemmon (Table 1).

Next, let us consider the chromosome numbers by individual species. All species counted thus far are the same in each of several sections, specifically, in *Mimulastrum*, *Erythranthe*, *Oenoe*, and *Diplacus*. The other sections are polymorphic for their species' chromosome numbers and frequently exhibit speciation by aneuploidy and/or polyploidy, often in complex combinations. For example, the various species of section *Eumimulus* exhibit $n = 8$, 11, and 12; species of section *Eumanus* exhibit $n = 8$, 10, and 16; species of section *Paradanthus* exhibit $n = 8$, 9, 16, 17, 18, and 30; and species of section *Simiolus* exhibit $n = 13$, 14, 15, 16, 24, 28, 30, 31, 32, 46, and 48 (Table 1).

Section *Simiolus*, which shows by far the most speciation by aneuploidy and/or polyploidy of all sections of the genus, consists of six species groups, that is, complexes of related species and varieties. First is the *M. guttatus* complex, centered in California; it has as its base number $x = 14$, with aneuploid forms at $n = 13$ and $n = 15$ (Table 1), as well as tetraploid forms with $n = 28$. Second is the alpine (western United States) *M. tilingii* complex with its base number of $x = 14$ and aneuploid forms at $n = 15$, $n = 16$, and an unusual polyploid form at $n = 24$. The third species group is the *M. dentilobus* complex of southwestern United States and northwestern Mexico with its base number of $x = 16$ and an aneuploid form at $n = 15$. Fourth is the *M. luteus* complex

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TABLE 1. Chromosome numbers in the genus *Mimulus* by sections (counts by Chuang and Heckard and by Vickery and co-workers; see text for references).

Taxon	n =
<i>Mimulastrum</i> Gray (x = 7)	
<i>M. mohavensis</i> Lemmon	7
<i>Eumimulus</i> Gray (x = 8, 11, 12)	
<i>M. alatus</i> Aiton	11
<i>M. gracilis</i> R. Br.	8
<i>M. ringens</i> L.	8, 12
<i>Eunanus</i> Gray (x = 8)	
<i>M. bolanderi</i> Gray	8
<i>M. layneae</i> (Greene) Jepson	8
<i>M. brevipes</i> Bentham	8
<i>M. cusickii</i> (Greene) Piper	8
<i>M. nanus</i> Hook. & Arn.	8
<i>M. torreyi</i> Gray	10
<i>M. biglovii</i> Gray	16
<i>Paradanthus</i> Grant (x = 8, 9, 10)	
<i>M. bicolor</i> Hartweg ex Bentham	8
<i>M. filicaulis</i> Watson	8
<i>M. breweri</i> (Greene) Coville	16
<i>M. floribundus</i> Douglas	16
<i>M. moschatus</i> Douglas	16
<i>M. latidens</i> (Gray) Greene	16
<i>M. arenarius</i> Grant	16
<i>M. primuloides</i> Rydb.	9, 17, 18
<i>M. repens</i> R. Br.	10
<i>M. nepalensis</i> Bentham	16, 30
<i>Erythranthe</i> Greene (x = 8)	
<i>M. cardinalis</i> Douglas	8
<i>M. eastwoodiae</i> Rydb.	8
<i>M. lewisii</i> Pursh	8
<i>M. nelsonii</i> Grant	8
<i>M. rupestris</i> Greene	8
<i>M. verbenaceus</i> Greene	8
<i>Oenoe</i> Gray (x = 9)	
<i>M. pictus</i> (Curran) Gray	9
<i>M. tricolor</i> Lindl.	9
<i>M. pygmaeus</i> Grant	9 (or 10?)
<i>M. pilosellus</i> Greene	9
<i>Diplacus</i> Gray (x = 10)	
<i>M. aridus</i> (Abrams) Grant	10
<i>M. aurantiacus</i> Curt.	10
<i>M. calycinus</i> Eastw.	10
<i>M. clevelandii</i> Brandg.	10
<i>M. fasciculatus</i> (Pennell) McMinn	10
<i>M. longiflorus</i> (Nutt.) Grant	10
<i>M. puniceus</i> (Nutt.) Steud.	10
<i>Simiolus</i> Greene (x = 14, 15, 16)	
<i>M. gutatus</i> Fischer ex DC.	14, 15, 28
<i>M. laciniatus</i> Gray	14
<i>M. nasutus</i> Greene	13, 14
<i>M. glaucescens</i> Greene	14
<i>M. platycalyx</i> Pennell	15
<i>M. tilingii</i> Regel	14, 15, 24, 28
<i>M. gemniparus</i> Weber	16
<i>M. dentilobus</i> Rob. & Fern.	15, 16
<i>M. wiensii</i> Vickery	16
<i>M. glabratus</i> HBK	15, 30, 31
<i>M. andicolus</i> HBK	46
<i>M. pilosiusculus</i> HBK	46
<i>M. externus</i> (Skotts.) Skotts	46
<i>M. luteus</i> L.	30, 31, 32
<i>M. cupreus</i> Dombrain	31
Undescribed	
n. sp #A	16
n. sp #B	32
n. sp #C	32, 48 ± 1-4

from the central and southern Andes of South America. Its base number is $x = 30$, but there are $n = 31$ and $n = 32$ forms as well. Fifth, there is the *M. glabratus* complex that ranges from Canada to Patagonia. Its varieties in central North America exhibit the base number of the complex, $x = 15$. In the Rio Grande drainage we find tetraploids with $n = 30$. From northern Mexico to southern Colombia we find the aneuploid tetraploid $n = 31$ varieties of the complex. From Ecuador south to southern Argentina and including the Juan Fernandez Islands off the coast of Chile, we find the aneuploid hexaploid species and varieties with $n = 46$ chromosomes. Apparently, each change in chromosome number facilitated an adaptive radiation further south. Last is the *M. wiensii* complex of the mountains of western Mexico with its base number of $x = 16$ and three apparent new species that are morphologically distinct and reproductively isolated (Vickery et al. unpublished). One has $n = 16$ chromosomes, one has $n = 32$ chromosomes, and the third has two forms—one with $n = 32$ chromosomes and the other with $n = 48 \pm 1-4$ chromosomes (incipient aneuploidy?).

How does speciation by aneuploidy and polyploidy occur? We carefully examined meiosis in *M. glabratus* var. *utahensis* and *M. glabratus* var. *fremontii*, two of the widespread diploid varieties of the *M. glabratus* complex, and their intervarietal F_1 hybrids. First, of 1317 cells examined in diakinesis or metaphase of first meiosis (Tai and Vickery 1970, 1972), 1090 exhibited regular 15 bivalent chromosomes. Another 23 cells, or 1.7%, had aneuploid numbers of chromosome pairs ranging from only 6 to as many as 13, plus 4-18 univalents. These cells presumably could produce aneuploid gametes, at least in some cases. A sizeable minority, 204 cells, exhibited 14 II and 2 I, or 13 II and 1 IV, or complement fractionation with its uneven groupings of chromosomes. These cells might produce aneuploid gametes also. Second, of 782 additional cells observed in Anaphase I, 294 (37.5%) exhibited unequal disjunction, laggard chromosomes, or chromatin bridges. These cells also could result in aneuploid gametes. Some 47 of these abnormalities occurred in *M. glabratus* var. *fremontii*, only 18 occurred in *M. glabratus* var. *utahensis*, but most, 229, occurred in the intervarietal hybrids. Thus, varieties differ in their potential for producing aneuploid gametes,



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