CHROMOSOME NUMBERS IN XYLORHIZA NUTTALL (ASTERACEAE - ASTEREAE)

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Xylorhiza is a genus of eight species of the western United States and Mexico. The plants are suffruticose perennials or small shrubs that grow and flower in early spring. Most of the taxa have limited distributions in remote areas. Previously, the genus has been studied largely from the few specimens available in herbaria. Chromosomal data presented in this paper were obtained during the course of a biosystematic investigation of the genus (Watson, 1977).

Chromosome counts have been reported previously for only four species of the genus: *X. tortifolia* (Raven et al., 1960); as *Machaeranthera tortifolia*), *X. wrightii* (Turner, 1964; Powell and Sikes, 1970; as *M. wrightii;* Urbatsch, 1974), *X. glabriuscula* (Solbrig et al., 1969; as *M. glabriuscula*) and *X. frutescens* (Anderson et al., 1974; as *M. frutescens*). All plants counted previously were diploids with $2n = 12$.

MATERIALS AND METHODS

Achenes and/or immature capitula for chromosome counts were collected from populations throughout the range of each species of *Xylorhiza*. Fruits and/or inflorescences were taken from one to five plants at each site. Immature heads were fixed in modified Carnoy's solution (4 chloroform: 3 ethanol: 1 glacial acetic acid; v/v/v). Aceto-carmine squashes of anthers were obtained by the method of Turner and Johnston (1961).

Seeds were germinated on moist filter paper in petri dishes. Emerging root tips were pretreated for four hours in a saturated solution of paradichlorobenzene. The root tips were then fixed, hydrolyzed, stained, and squashed by the technique of Huziwara (1957).

RESULTS AND DISCUSSION

Chromosome counts from 118 stands of *Xylorhiza* are recorded in Table 1. In addition, chromosome numbers for species previously thought to belong in *Xylorhiza* are included here or have been published elsewhere (Watson, 1973). Meiotic chromosome behavior was studied in the available taxa; chromosomes of most species were studied at mitotic metaphase.

Chromosome numbers of all taxa in *Xylorhiza* are now known; the base number for the genus is $x = 6$. Populations of most taxa are uniformly diploid with $2n = 12$. Tetraploids ($2n = 24$) were found only in *X. tortifolia, X. venusta,* and *X. glabriuscula* var. *linearifolia.*

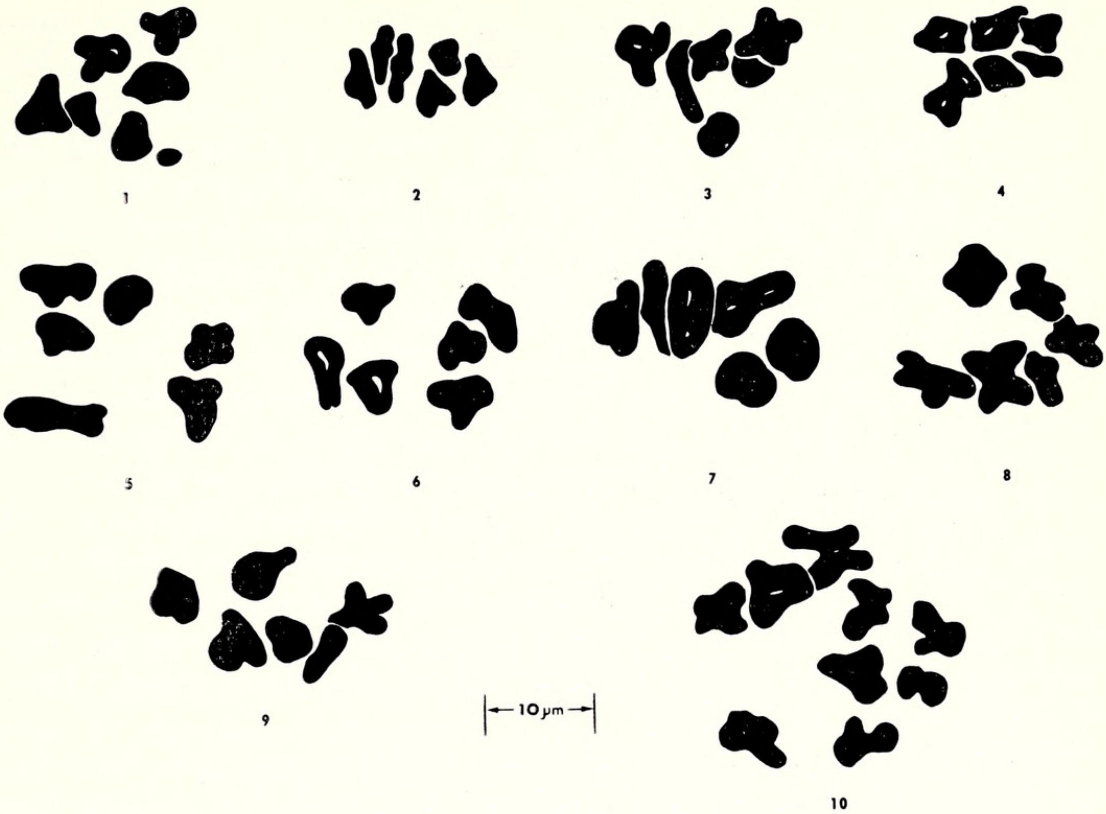
In most instances, meiosis in the diploids was regular with the forma-

TABLE 1. CHROMOSOME NUMBERS OF *Xylorhiza* SPP. AND *Aster kingii*. Chromosome counts determined from mitotic cells are denoted by an asterisk (*); other counts are from pollen mother cells. Populations with individuals having fragments are indicated by the superscript f. Collection numbers refer to *T. J. Watson;* vouchers are in TEX.

Xylorhiza cognata (H. M. Hall) T. J. Watson
$2n = 12$ CALIF.: Riverside Co., *365, 366, 606.*
Xylorhiza confertifolia (Cronquist) T. J. Watson
$2n = 12$ UTAH: Garfield Co., *312*, 313, 696, 697.*
Xylorhiza glabriuscula Nuttall var. *glabriuscula*
$2n = 12$ COLO.: Moffat Co., *891.* MONT.: Carbon Co., *470*^{f}*. UTAH: Daggett Co., *452.* WYO.: Albany Co., *488, 489;* Carbon Co., *479, 480, 481, 482, 484, 485, 487;* Natrona Co., *473, 478;* Sweetwater Co., *455, 458;* Uinta Co., *462;* Washakie Co., *463*, 464, 465.*
Xylorhiza glabriuscula var. *linearifolia* T. J. Watson
$2n = 12$ UTAH: Grand Co., *308*, 435, 436, 908.*
$2n = 24$ UTAH: Grand Co., *680, 905, 914, 916.*
Xylorhiza orcuttii (Vasey & Rose) Greene
$2n = 24$ CALIF.: San Diego Co., *364*, 603;* Imperial Co., *604.*
Xylorhiza tortifolia (Torrey & Gray) Greene var. *tortifolia*
$2n = 12$ ARIZ.: Mohave Co., *385, 386;* Yavapai Co., *387, 388;* Yuma Co., *610.* CALIF.: Inyo Co., *376, 377, 727;* Kern Co., *372, 373, 374, 375;* Riverside Co., *607;* San Bernardino Co., *384, 722, 723.* NEV.: Clark Co., *380, 712, 715, 716, 717, 718, 720, 721;* Nye Co., *378, 379, 728, 729, 730.* UTAH: Grand Co., *316*.*
$2n = 24$ NEV.: Clark Co., *381, 382, 383, 713.*
Xylorhiza tortifolia var. *imberbis* (Cronquist) T. J. Watson
$2n = 12$ UTAH: Grand Co., *309*, 310, 911, 912, 913, 915.*
Xylorhiza venusta (M. E. Jones) Heller
$2n = 12$ COLO.: Delta Co., *429*, 430*, 431*, 665, 666, 667;* Moffat Co., *655, 656, 894;* Montrose Co., *427*, 428*, 668, 669;* Rio Blanco Co., *449*, 654, 898.* UTAH: Carbon Co., *918;* Emery Co., *304*;* Grand Co., *305*, 306*;* Uinta Co., *451*, 652*^{f}*, 653, 895.*
$2n = 24$ COLO.: Mesa Co., *432*, 662*.* UTAH: Garfield Co., *900;* Grand Co., *433*, 682, 683, 687, 690, 901, 904.*
Xylorhiza wrightii (A. Gray) Greene
$2n = 12$ TEX.: Brewster Co., *401*, 403*, 626;* Jeff Davis Co., *411*;* Presidio Co., *408*, 409.*
Aster kingii D. C. Eaton
$2n = 18$ UTAH: Salt Lake Co., *766.*

tion of six bivalents (Figs. 1–10) followed by normal disjunctions. In a few individuals of *X. glabriuscula* from Wyoming, a bridge at anaphase I was observed, suggesting that the plants were heterozygous for segmental rearrangements on one pair of chromosomes. Also, in a few individuals of *X. glabriuscula* and *X. venusta,* a pair of centric fragments was observed in pollen mother cells (Fig. 1) and/or in root tip cells. The fragments synapse and disjoin during meiosis I. At mitotic metaphase, the fragments are approximately one micrometer long and appear to be telocentric. The normal chromosome complement consists of submetacentrics that are 2.5–5.0 μm long at mitotic metaphase.

The tetraploids characteristically form multivalents at meiosis and are morphologically indistinguishable from diploids of the respective



FIGS. 1–10. Camera lucida drawings of meiotic metaphase chromosomes of *Xylorhiza* spp. and *Aster kingii.* All collections are those of T. J. Watson. 1. *X. glabriuscula, 2n* = 6_{II} + synapsed fragments, *470.* 2. *X. glabriuscula* var. *linearifolia, 2n* = 6_{II}, *908.* 3. *X. confertifolia, 2n* = 6_{II}, *697.* 4. *X. venusta, 2n* = 6_{II}, *669.* 5. *X. tortifolia, 2n* = 6_{II}, *372.* 6. *X. tortifolia* var. *imberbis, 2n* = 6_{II}, *911.* 7. *X. wrightii, 2n* = 6_{II}, *626.* 8. *X. cognata, 2n* = 6_{II}, *365.* 9. *X. orcuttii, 2n* = 6_{II}, *603.* 10. *Aster kingii, 2n* = 9_{II}, *766.*

taxa, suggesting that the plants are autotetraploids. The tetraploids of *X. tortifolia* are located at the northern distribution limits in Nevada. Tetraploids of *X. venusta* are found at the southwestern margin of the range in Utah and Colorado. Diploids and tetraploids of *X. glabriuscula* var. *linearifolia* grow intermixed over the small range of the taxon in western Utah.

The taxonomic status and placement of *Xylorhiza* have varied (for a complete taxonomic history see Watson, 1977). Recent investigators (Cronquist and Keck, 1957; Turner and Horne, 1964) feel that *Xylorhiza* Nutt., *Machaeranthera* Nees (sensu stricto), and *Haplopappus* Cass. section *Blepharodon* DC. are closely allied. In their view, *Machaeranthera* series *Originales* Cronq. & Keck is a pivotal, infrasectional taxon through which the three groups are related. Cronquist and Keck (1957) consider *Xylorhiza* and the remainder of *Machaeranthera* to have been derived from an *Originales*-like ancestry and construe *M. blephariphylla* of this series to be the most primitive extant taxon in the *Xylorhiza–Machaeranthera* alliance. Chromosome numbers of the taxa involved seem instructive in these regards.

Most species of *Originales* and those species of *Blepharodon* related to *Originales* are reported to be on a base of $x = 4$. Although $2n = 10$ has been reported from *M. blephariphylla* (Jackson, 1959; as *M. gymnocephala*), Hartman (1976) feels that the count was erroneous. He has recorded $2n = 8$ from three populations of this species and has found plants from one of the populations to have 2 or 3 pairs of small, supernumerary chromosomes in addition to the normal complement of four pairs. Thus, Hartman regards *Originales* and related members of *Blepharodon* to be unibasic with $x = 4$. If *Xylorhiza* ($x = 6$) has evolved from an *M. blephariphylla*-like ancestor or from another extinct or extant member of *Originales*, the chromosome number of the former is a result of an aneuploid gain. However, it is noteworthy that plants serving to link *Xylorhiza* to *Originales* by morphology and phenology and having a documented base number of $x = 5$ are unknown. Species on a base of $x = 5$ are found in *Machaeranthera* but these taxa belong to other subgeneric groups (i.e., series *Variables* and series *Verae* of Cronquist and Keck, and section *Psilactis* Turner and Horne) that cannot be related directly to *Xylorhiza*.

Some investigators (Raven et al., 1960; Solbrig et al, 1969) hold that the primitive base number for the Astereae as a whole is $x = 9$ and that the lower chromosome numbers in the tribe were generally derived through aneuploid reduction (for a contrasting viewpoint see Turner et al., 1961). According to this hypothesis, the chromosome level at which *Xylorhiza* diverged would precede that of *Machaeranthera*. Also, Solbrig et al. (1969), Anderson et al. (1974), and Hartman (1976) have noted the frequent occurrence of $x = 6$ in taxa that have been included in or bear relationship to *Haplopappus* and *Machaeranthera* (e.g., *Grindelia, Prionopsis, Xanthocephalum, Isopappus, Pyrrocoma, Isocoma, Hazardia, Xylorhiza* and the "phyllocephalus group" sensu Hartman, 1976). This observation led Hartman (1976) to suggest that $x = 6$ is a more primitive number for this alliance and that the lower base numbers (i.e., $x = 4,5$) are derived. It is interesting to note that one of the few documented cases of descending aneuploidy in natural populations is known from *Haplopappus* sect. *Blepharodon* (i.e., *Haplopappus gracilis–H. ravenii;* Jackson, 1962; 1965).

The foregoing observations suggest that *Xylorhiza* diverged early from the line that gave rise to *Machaeranthera* and *Haplopappus* in North America. However, before any credible phylogenetic interpretations can be made, it appears to me that the relationships of the North American Astereae to the poorly known *Haplopappus* sect. *Haplopappus* (sect. *Euhaplopappus* of Hall, 1928) of South America need to be explored. The latter taxon seemingly connects various elements in the *Xylorhiza–Machaeranthera–Haplopappus* alliance of North America (see Watson, 1977). Chromosome numbers for only ten of the South American species are known: most have $2n = 10$ (Grau, 1976; L. C. Anderson, personal communication), but *H. cuneifolius* has $2n = 12$ (B. L. Turner and J. Bacon, personal communication).

The chromosome number of *Aster kingii* ($2n = 18$) is reported here for the first time. This taxon was included in *Machaeranthera* sect. *Xylorhiza* by Cronquist and Keck (1957). However, it is phenologically, ecologically, morphologically, and chromosomally anomalous there. The plants of *A. kingii* flower in mid-summer and are found in coniferous forests in cracks of granitic outcrops at subalpine elevations in the Wasatch Mountains of Utah. Members of *Xylorhiza* flower in early spring and are distributed in relatively deep soils of deserts and semi-arid grasslands. Although plants of *A. kingii* have taproots surmounted by a caudex, the roots are small and resemble those of the alpine *Asters*, e.g., *A. alpigenus* (T. & G.) Gray. Individuals of *A. kingii* are cespitose and have relatively small capitula with phyllaries that have anthocyanic margins and squarrose tips; the disc florets are anthocyanic. None of these features is found in species of *Xylorhiza*.

The presence of taproots and squarrose phyllaries in *A. kingii* suggests *Machaeranthera*. However, with the exception of *M. brevilingulata* ($2n = 18$; Turner and Horne, 1964; Powell and King, 1969), which is better placed in *Aster* or *Conyza* (Hartman, 1976), *Machaeranthera* consists of diploids with $2n = 8$ or 10 and tetraploids with $2n = 16$ (see Hartman, 1976).

Aster kingii is probably most closely allied with species of *Aster* in which $2n = 18$ is a common number (Raven et al., 1960; Solbrig et al., 1964; Solbrig et al., 1969; Anderson et al., 1974; and others). Some members of *Aster* have taproots (e.g., *A. alpigenus*) and others have squarrose phyllaries (e.g., *A. conspicuus* Lindl.). The florets and capitula of *A. kingii* resemble those of the more widespread *A. integrifolius* Nutt., although the latter lacks squarrose phyllaries and differs in habit. This similarity was noticed by Gray (1884), who treated the two species together within *Aster* proper.

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