CYTOGEOGRAPHY OF CLAYTONIA VIRGINICA AND ITS ALLIES

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ABSTRACT

On the basis of chromosome numbers from more than 1,000 individuals of *Claytonia virginica* L. (*Portulacaceae*) throughout its range, a complex evolution of major cytotypes is discussed in relation to distribution and morphology. Chromosomal diversity is thought to have evolved from a base of $n = 6$ by hyperaneuploidy to $n = 7$ and 8 with each race giving rise to widespread and dominant primary tetraploids ($n = 12, 14, 16$). These in turn, and largely by hypoaneuploidy, formed many secondary tetraploid races, the most significant of which are $n = 11$ and 15. Higher polyploids from $6x$ to $12x$ where $x = 6$, and $6x$ and $8x$ where $x = 7$ are also discussed. Infraspecific phylogeny is compared with data for two allied species, *C. caroliniana* Michx. and *C. lanceolata* Pursh, which show striking parallels with *C. virginica* in chromosomal evolution. By one morphological character, leaf width, the cytotypes separate into two groups, not along diploid vs. polypoid lines, but rather a narrow-leafed var. *acutiflora* DC. with $n = 6, 7, 12\pm$, and $14\pm$ and a broad-leafed var. *virginica* with $n = 8$ and $16\pm$.

From collections made throughout eastern North America over 1,000 plants of *Claytonia virginica* L. (*Portulacaceae*) have been examined chromosomally. With the exception of Rothwell (1959) earlier studies have been limited in scope although all have made a substantial contribution to a cytogeographic understanding of the species (Bell, 1965; Davis & Bowmer, 1966; Lewis, 1959, 1962, 1967; Lewis et al., 1962, 1967; Rothwell & Kump, 1965). While these studies illustrated a wide diversity of chromosome number for *C. virginica* ($2n = 12$ to ca 191) none was extensive enough to indicate total distribution of all major cytotypes; rather only for a few from very limited areas, viz. dominance of $x = 7$ in eastern Texas (Lewis, 1962), $x = 8$ in Indiana (Rothwell, 1959), and $n = 12$ and 15 in the St. Louis, Missouri area (Lewis et al., 1967). We shall attempt with our additional data to present the distribution of cytotypes occuring in the eastern half of the continent and to suggest their probable evolution. Cytogeography and evolution of *C. virginica* will be compared with several allied species as well as briefly with the primitive species of *Claytonia*. In addition gross morphological diversity will be correlated with the various cytotypes and discussed in relation to distribution.

Cytological procedures followed those of Lewis (1962) and voucher specimens for each population were collected and are housed in the Missouri Botanical Garden herbarium (MO).
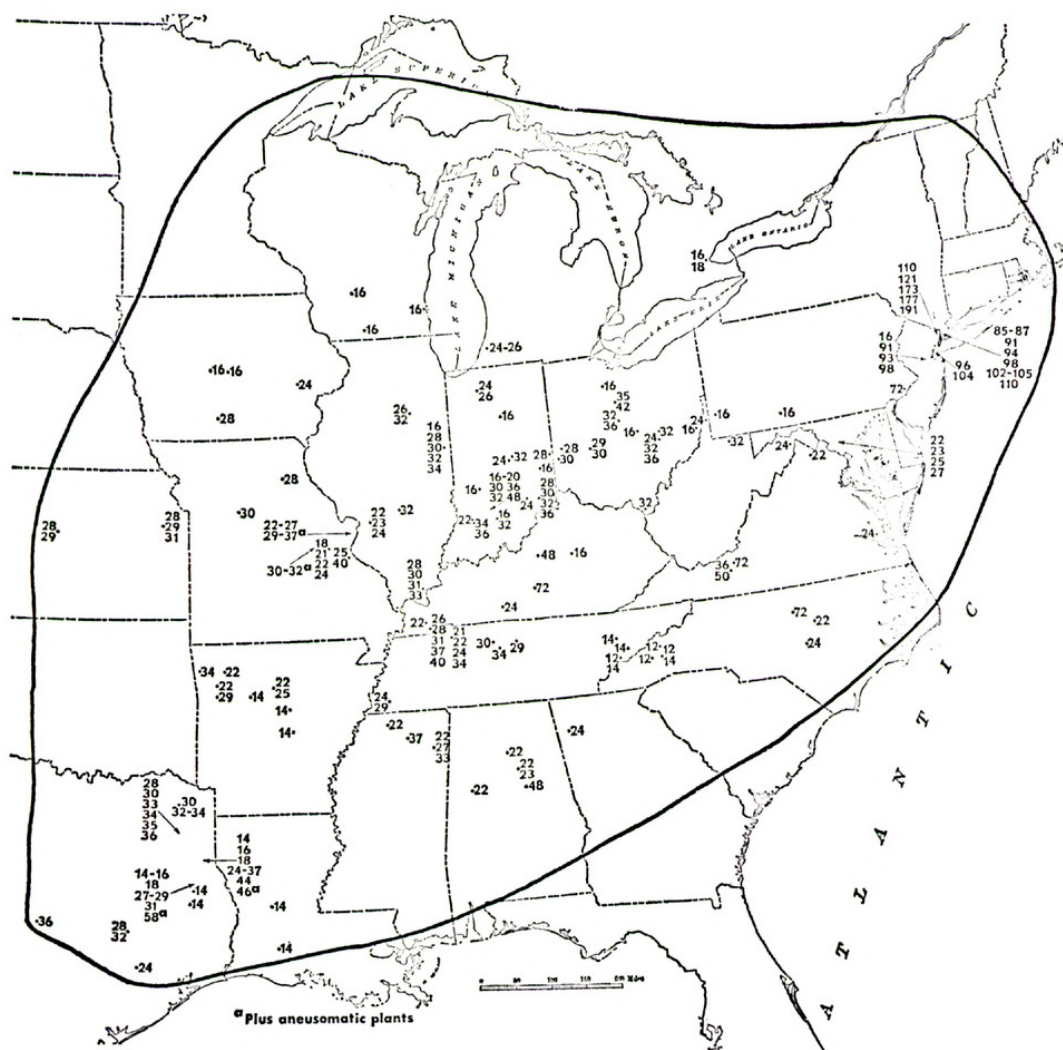
Fig. 1. Approximate distribution of *Claytonia virginica* in the eastern United States and adjacent Canada with known diploid (2n) chromosome numbers. Each dot or arrow-head represents the locality of a population or population area studied.

RESULTS AND DISCUSSION

Below are listed the chromosome numbers found for varying numbers of plants sampled at random from numerous populations. The exact locality of each population, arranged alphabetically by state and province, is noted together with the diploid number (frequency in parenthesis) and the meiotic configurations from PMC analysis generally at metaphase I or more rarely at anaphase I or metaphase II. Occasionally a count is based on somatic divisions either from root tips or floral buds. In addition earlier chromosomal reports for *C. virginica* are incorporated in the list and all are summarized by locality as diploid numbers in Fig. 1.

ALABAMA

Blount Co, 5.7 mi NW of Oneonta, *Lewis 6523:* **2n = 22**(4)—3 plants 11_{II}, 1 plant 11_{II} (+0−2 fragments).

St Clair Co, 1 mi NW of jct of Hwys 231 & 35, *Lewis 6524:* **2n = 22**(2), **23**(1)—2 plants 11_{II}, 1 plant $11_{II}+1_I$.

Talladega Co, Sycamore, *Lewis 6525:* **2n = 48**(5)—3 plants 24_{II}, 2 plants 24_{II}(+1 fragment).

Tuscaloosa Co, Tuscaloosa: **2n = 22**(2)—Rothwell (1959).

ARKANSAS

Faulkner Co, N Cadron Creek, 17.5 mi N of Conway, *Suda 8:* **2n = 14**(4)—4 plants 17_{II}.

Franklin Co, 13.6 mi S of Franklin-Madison Co line, *Oliver 466:* **2n = 29**(1) —1 plant $14_{II}+1_I$.

Madison Co, 9.3 mi SE of Madison-Washington Co line, *Oliver 468:* **2n = 22**(2)—2 plants 11_{II}.

Pope Co, 2.5 mi SE of Atkins, *Oliver 464:* **2n = 14**(4)—4 plants 7_{II}.

Pulaski Co, Burns Pk, Little Rock, *Suda 7:* **2n = 14**(11)—10 plants 7_{II}, 1 plant $6_{II}+2_I$ & 7_{II}.

Van Buren Co, 0.8 mi W of Bee Branch & jct of Hwys 92 and 65, *Oliver 463:* **2n = 22**(1), **25**(1)—1 plant 11_{II}, 1 plant $12_{II}+1_I$.

Washington Co, 0.1 mi NW of jct of Hwys 62 & 59, *Oliver 469:* **2n = 34**(1) —1 plant 17_{II}.

GEORGIA

Floyd Co, Rome, *Davis 6001* (as *C. bodinii* Holz.): **n = 12**(1)—Davis & Bowmer (1966).

ILLINOIS

Fayette Co: **2n = 32**(mc*)—Rothwell (1959).

Livingston Co, Rooks Creek, 4 mi W of Pontiac, *Lewis 6805:* **2n = 26**(1), **32**(1)—1 plant $11_{II}+4_I$.

Madison Co, 0.8 mi SW of Pocahontas, *Oliver 470:* **2n = 22**(2), **23**(1), **24**(1)—2 plants 11_{II}, 1 plant $11_{II}+1_I$, 1 plant 12_{II}.

Pope Co, 1.2 mi S of Renshaw, *Lewis 6596:* **2n = 28**(1), **30**(1), **31**(1) **33**(1) —1 plant 14+14, 1 plant 15_{II}, 1 plant $15_{II}+1_I$, 1 plant $16_{II}+1_I$.

Vermilion Co, *Bell 1441:* **n = 8, 14, 15, 16, 17**—Bell (1965).

INDIANA

Daviess Co, Westphalia: **2n = 22**(15)—Rothwell (1959); 1 mi S of Westphalia: **2n = 34, 36**(mc)—Rothwell (1959).

Fayette Co: **2n = 16**(mc)—Rothwell (1959).

Hancock Co.: 2 mi W. of Gem, *Lewis 6687:* **2n = ca 32**(1)—1 plant ca $14_{II}+4_I$.

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* Mass collection of buds, number of plants studied unknown.

Jennings Co, N Vernon: $2n = 24(4)$—Rothwell (1959).

Lawrence Co: $2n = 16, 32$(mc)—Rothwell (1959).

Marion Co, N city limits of Acton, *Oliver 474:* $2n = 24(1)$—1 plant 12_{II}.

Miami Co: $2n = 16$(mc)—Rothwell (1959).

Monroe Co, Beech Flats: $2n = 30(5), 32(5), 36(3), 48(1)$—Rothwell (1959); id., Indiana Univ Campus: $2n = 16(73), 17(5), 18(13), 19(1), 20(3), 30(1), 32(1)$—Rothwell (1959).

Owen Co: $2n = 16$(mc)—Rothwell (1959).

Ripley Co, Versailles: $2n = 28(1), 30(2), 32(2),$ ca $36(1)$—Rothwell (1959).

Starke Co, San Pierre: $2n = 24$ (1), $26(1)$—Rothwell (1959).

Wayne Co, 1 mi W of Centerville, *Oliver 475:* $2n = 28(2)$— 2 plants 14_{II}.

IOWA

Boone Co: $2n = 16$(mc)—Rothwell (1959).

Clarke Co, ca 2 mi S of Osceloa, *Lewis 6623:* $2n = $ ca $28(1)$—1 plant ca 14_{II}.

Johnson Co: $2n = 24$(mc)—Rothwell (1959).

Story Co: $2n = 16$(mc)—Rothwell (1959).

KANSAS

Douglas Co, Baldwin woods, SW of Vinland, *Lewis 6614:* $2n = 28(2), 29(2), 31(2)$—2 plants 14_{II}, 2 plants $14_{II}+1_I$, 2 plants $15_{II}+1_I$.

Ellsworth Co, ca 0.5 mi SW of Ellsworth-Salina Co line & Hwy 40, *Lewis 6615:* $2n = 28(1), 29(3)$—1 plant 14_{II}, 2 plants $14_{II}+1_I$ & $14+15$, 1 plant $14_{II}+1_I$ & $12_{II}+1_{III}+2_I$.

KENTUCKY

Calloway Co, 8.7 mi SE of Murray, *Lewis 6593:* $2n = 22(1)$—1 plant 11_{II}; id., 0.2 mi S of Hwys 641 and 464, *Lewis 6594:* $2n = 26(1), 28(1), 31(1), 37(1)$ (Lewis, 1967), $40(1)$—1 plant $12_{II}+2_I(+0-1$ fragment), 1 plant $12_{II}+4_I$ & $13_{II}+2_I$, 1 plant $15_{II}+1_I$ & two weeks later $13_{II}+5_I$, 1 plant $17_{II}+6_I(+2-3$ fragments).

Green Co, 1.4 mi NW of Greensburg, *Lewis 5603:* $n = 36(2)$—Lewis et al. (1962).

Jessamine Co: $2n = 16$(mc)—Rothwell (1959).

Nelson Co, Nazareth, *Lewis 6637:* $2n = 48(1)$—1 plant 24_{II}.

Warren Co, 0.7 mi NW of Petros, *Lewis 5606:* $n = 12(2)$—Lewis et al. (1962).

LOUISIANA

Acadia Par, 5.5 mi NNW of Iota, *Lewis 6600:* $2n = 14(3)$— 3 plants 7_{II}.

Rapides Par, 1 mi S of Hatwells, *Lewis 6602:* $2n = 14(3)$— 3 plants 7_{II}.

MARYLAND

Montgomery Co, 15 mi N of Washington, *Lewis 6633:* $2n = 22(2), 23(1)$ (Lewis, 1967), $25(1), 27(1)$—2 plants 11_{II}, 1 plant $11_{II}+1_I$, 1plant $12_{II}+1_I$, 1 plant $12_{II}+3_I$.

MICHIGAN

Berrien Co, 10.3 mi NE of Three Oaks, *Oliver 484:* $2n = 24(1), 25(1), 26(1)$—1 plant 12_{II}, 1 plant $12_{II}+1_I$, 1 plant $13+13$.

MISSISSIPPI

Itawamba Co, 6 mi W of Fulton, *Lewis 6501:* **2n = 22**(1), **27**(1), **33**(1)—
1 plant 11_{II}, 1 plant $13_{II}+1_I$, 1 plant $16_{II}+1_I$.

Marshall Co, ca 1 mi SE of Holly Springs, *Lewis 6499:* **2n = 22**(4)—4 plants
11_{II}.

Union Co, 4.7 mi NW of Tallachatchie River by Hwy 78, *Lewis 6500:* **2n =
37**(1)—1 plant $18_{II}+1_I$.

MISSOURI

Franklin Co, Gray Summit, *MacBryde 6:* **2n = 31**(1)—1 plant $15_{II}+1_I$; id.,
MacBryde 7: **2n = 30-31**(1)—1 plant 15_{II} & $15_{II}+1_I$ (aneusomatic); id.,
MacBryde 8: **2n = 30**(1)—1 plant 15_{II}; id., **2n = 30**(1), **32**(3)—Rothwell
(1959); St Clair, village of Parkway, *MacBryde 1:* **2n = 18**(1), **21**(1), **22**(2)—1
plant $8_{II}+2_I$, 1 plant $10_{II}+1_I$ (+0−1 fragment), 1 plant $9_{II}+4_I$ & 11+11, 1
plant $9_{II}+1_{III}+1_I$ (rare), $10_{II}+2_I$(few) & 11_{II} [1966]; id., *Suda 18:* **2n = 22**(3),
24(1), **26**(1)—1 plant $10_{II}+2_I$, 2 plants 11_{II}, 1 plant 12_{II}, 1 plant 13_{II} [1967];
St Clair High School, *MacBryde 2:* **2n = 22**(3)—3 plants 11_{II} [1966]; id.,
MacBryde 3: **2n = 24**(2)—2 plants 12_{II}.

Jefferson Co, vic of Rice Lodge, *Lewis 6603:* **2n = 25**(1), **40**(1)—1 plant
$12_{II}+1_I$, 1 plant $18_{II}+4_I$(+0−1 fragment).

St Louis & St Louis Co: **2n = 22**(9), **23**(6), **24**(49), **25**(8), **26**(9), **27**(1),
29(4), **30**(46), **31**(18), **32**(12), **33**(3), **34**(3), **35**(1), **36**(2), **37**(2)—Lewis,
Suda & MacBryde (1967); id., Barque Creek; **2n = 32**(1), **34**(1)—Rothwell
(1959); id., Clay City: **2n = 22**(mc)—Rothwell (1959).

Saline Co, Blackwater River, 1.3 mi S of Hwys 40 & YY, *Lewis 6611:* **2n = ca
30**(1)—1 plant ca 15_{II}.

Shelby Co, Salt River at Hwy 36, *Lewis 6627:* **2n = 28**(1)— 1 plant 14_{II}.

NEW YORK

Bronx, Bronx Pk: **2n = 91**(1), **98**(1), **103**(1), **105**(1); id., Pelham Bay Pk:
2n = 85(1), **86**(1), **87**(1); id., Van Cortlandt Pk: **2n = 94**(1), **102**(1), **104**(1),
110(1)—Rothwell & Kump (1965).

Staten I, Latourette Pk: **2n = ca 96**(1); Willowbrook Pk: **2n = 104**(1)—
Rothwell & Kump (1965).

NEW JERSEY

Bergen Co, Palisades Interstate Pk: **2n = 110**(1), **121**(1), **173**(1), **177**(1),
ca 191(1)—Rothwell & Kump (1965).

Somerset Co, East Millstone, **2n = 93**(1)—Rothwell & Kump (1965); id.,
Martinsville: **2n = 98**(1)—Rothwell & Kump (1965); id., Pluckemin: **2n =
16**(23), **91**(1), **93**(1)—Rothwell & Kump (1965).

NORTH CAROLINA

Buncombe Co: **2n = 12**(2), **14**(1)—Rothwell (1959); id., 0.2 mi W of Swan-
nanoa, *Lewis 6582:* **2n = 12**(2)—2 plants 6_{II}.

Harnett Co: **2n = 24**(mc)—Rothwell (1959).

Haywood Co, 2 mi E of Maggie Post Office, *Lewis 6581:* **2n = 12**(5)—5 plants 6_{II}; id., *Lewis 6662:* **2n = 12**(2)—2 plants 6_{II}.

Orange Co: **2n = 72**(2)—Rothwell (1959).

Wake Co, Raleigh: **2n = 22**(3)—Rothwell (1959).

OHIO

Belmont Co, 4.2 mi E of Hwy 149 by Hwy 70, *Lewis 6682:* **2n = 16**(4)—4 plants 8_{II}.

Clark Co, 1.2 mi E of Harmony, *Lewis 6685:* **2n = 29**(1), **30**(1)—1 plant $13_{II}+3_I$ & $14_{II}+1_I$, 1 plant 15_{II}.

Crawford Co, 1.7 mi S of Bucyrus, *Oliver 478:* **2n = 35**(3), **42**(1)—3 plants $17_{II}+1_I$, 1 plant $20_{II}+2_I$ & 21_{II}.

Delaware Co: Delaware-Franklin Co line & Hwy 23, *Oliver 477:* **2n = 32**(1), **36**(1)—1 plant 16_{II}, 1 plant 18_{II}.

Lawrence Co: **2n = 32**(mc)— Rothwell (1959).

Licking Co: 1.5 mi E of Hwy 79 by Hwy 70, *Lewis 6684:* **2n = 16**(4)—4 plants 8_{II}.

Montgomery Co, 1 mi E of Englewood, *Oliver 476:* **2n = 28**(1)—1 plant 14_{II}.

Muskingum Co, ca 2 mi W of Bridgeville, *Lewis 6683:* **2n = 32**(2)—2 plants 16_{II}; id., Zanesville, *Davis 6011:* **n = 12, 16, 18**—Davis & Bowmer (1966).

Preble Co, ca 2 mi W of Lewisberg, *Lewis 6686:* **2n = ca 30**(1)— 1 plant ca 15_{II}.

Seneca Co, 0.3 mi E of jct of Hwys 4 & 162, *Oliver 479:* **2n = 16**(1)—1 plant $8+8$.

ONTARIO

Wentworth Co, Royal Bot Gard, Hamilton, *Lewis 6630:* **2n = 16**(1), **18**(1)— 1 plant 8_{II}, 1 plant 9_{II}.

PENNSYLVANIA

Bedford Co, 1 mi W of Manns Choice, *Lewis 6680:* **2n = 16**(5)— 1 plant $7_{II}+2_I$, 4 plants 8_{II}.

Philadelphia Co, Philadelphia, *Davis 6007:* **n = 36**—Davis & Bowmer (1966).

Washington Co, 3.5 mi ENE of Claysville by Hwy 70, *Lewis 6681:* **2n = 16**(5)—5 plants 8_{II}.

TENNESSEE

Davidson Co, suburbs NE of Nashville by Hwy 41A, *Lewis 6591:* **2n = 30**(2)—2 plants $14_{II}+2_I$; id., 0.4 mi S of Hwy 40 on Old Hickory Rd, *Lewis 6645:* **2n = 34**(1)—1 plant 17_{II}, $16_{II}+2_I$ & $15_{II}+1_{III}$ & 1_I.

Knox Co, Tennessee River opposite Airport I, *Lewis 6646:* **2n = 14**(2)—2 plants 7_{II}.

Sevier Co, 0.4 mi E of Gatlinberg, *Lewis 6651:* **2n = 14**(2)—2 plants 7_{II}; id., N slope of Sugarbay Mt, *Lewis 6649:* **2n = 12**(2), **14**(3)—2 plants 6_{II}, 3 plants 7_{II}.

Shelby Co, 0.8 mi NW of Capleville, *Lewis 6496:* **2n = 24**(1), **29**(1)—1 plant 12_{II}, 1 plant $10_{II}+1_{III}+6_I$, $11_{II}+7_I$ & $12_{II}+5_I$.

Stewart Co, 2.8 mi E of Tennessee River by Hwy 79, *Lewis 6592:* **2n = 21**(1), **22**(3), **24**(2), **34**(1)—1 plant $10_{II}+1_I$, 3 plants 11_{II}, 2 plants 12_{II}, 1 plant $16_{II}+2_I$.

Wilson Co, Lebanon, *Lewis 6590:* **2n = 29**(1)—1 plant $12_{II}+5_I$ (+0−1 fragment).

TEXAS

Angelina Co, Lufkin: **2n = 14**(1)—Lewis (1959).

Burnet Co, 4-5 mi S of Bertram, *Lewis 6479:* **2n = 36**(6)—4 plants 18_{II} & 18+18, 2 plants 18_{II} & $17_{II}+2_I$.

Brazos Co, College Sta: **2n = 28**(1), **32**(1)—Rothwell (1959).

Nacogdoches Co, 12 mi S of Nacogdoches: **2n = 14**(1)—Lewis (1959); id., vic of Nacogdoches, *Lewis 5551A-C:* **2n = 14**(78), **15**(1), **16**(5), **18**(2), **27**(1), **28**(1), **29**(1), **31**(2), **58**(1)—Lewis (1959, 1962).

Panola Co, Carthage & vic, *Lewis 5560A-O:* **2n = 14**(37), **25**(1), **26**(1), **28**(18), **29**(18), **30**(5), **31**(3), **32**(3), **33**(1), **36**(2), & aneusomatics—L e w i s (1962); id., *Lewis 5560E, F, J:* **2n = 14**(1), **28**(5), **29**(1), **30**(2), **32**(1), **35**(1)—4 plants 14_{II}, 1 plant $14_{II}+1_I$, 2 plants 15_{II}, 1 plant $13_{II}+6_I$ & $14_{II}+4_I$, 1 plant $13_{II}+1_{IV}+5_I$ & $14_{II}+7_I$ [1963]; id.,*Suda 1, 2, 2E, F, H-L:* **2n = 14**(24), **16**(1), **18**(2), **24**(8), **25**(2), **26**(6), **27**(3), **28**(52), **29**(18), **30**(11), **31**(1), **32**(4), **34**(1), **35**(3), **36**(1), **37**(2), **44**(1), **46**(1)—24 plants 7_{II} or 7+7, 1 plant 8_{II}, 2 plants 9_{II}, 8 plants 12_{II} or 12+12, 2 plants $12_{II}+1_I$, 6 plants 13_{II} or 13+13, 3 plants $13_{II}+1_I$, 3 plants $13_{II}+2_I$, 48 plants 14_{II} or 14+14, 1 plant 28_I, 1 plant $12_{II}+5_I$ & $13_{II}+3_I$, 2 plants $13_{II}+3_I$, 15 p l a n t s $14_{II}+1_I$, 1 plant $5_{II}+20_I$ & $10_{II}+10_I$, 1 plant $14_{II}+2_I$, 1 plant $14_{II}+2_I$ & 15_{II}, 8 plants 15_{II} or 15+15, 1 plant $15_{II}+1_I$, 1 plant $14_{II}+4_I$, 2 plants $15_{II}+2_I$, 1 plant 16_{II}, 1 plant $14_{II}+6_I$, 3 plants $14_{II}+7_I$, 1 plant $14_{II}+8_I$, 1 plant $15_{II}+7_I$, 1 plant $18_{II}+1_I$, 1 plant $20_{II}+4_I$, 1 plant $22_{II}+2_I$ & 23_{II}. [1967]

Titus Co, Mt Pleasant, *Suda 5:* **2n = 30**(4), **32**(1), **33**(1), **34**(1)—3 plants 15_{II}, 1 plant $13_{II}+1_{IV}$&15_{II}, 1 plant $15_{II}+2_I$&16_{II}, 1 plant $12_{II}+1_{VIII}+1_I$, 1 plant $12_{II}+1_{VIII}+2_I$.

Upshur Co, Gilmer, *Suda 4:* **2n = 28**(1), **30**(3), **33**(2), **34**(3), **35**(1), **36**(1)—1 plant 14_{II}, 1 plant $14_{II}+2_I$, 2 plants 15_{II}, 1 plant $12_{II}+1_{VIII}+1_I$, 1 plant $16_{II}+2_I$, 1 plant $13_{II}+1_{VIII}$, 1 plant $12_{II}+1_{VIII}+2_I$ & $16_{II}+2_I$, 1 plant 17_{II}, 1 plant $13_{II}+1_{VIII}+1_I$, 1 plant $15_{II}+1_{IV}+2_I$, $15_{II}+1_{VI}$, $16_{II}+1_{IV}$ & $17_{II}+2_I$.

Waller Co, Hempstead, *Davis 6000* (as *C. bodinii* Holz.): **n = 12**—Davis & Bowmer (1966).

VIRGINIA

Clark Co: 1.3 mi E of Shenandoah River by Hwy 50, *Lewis 6672:* **2n = 22**(7)—7 plants 11_{II}.

Montgomery Co, 3 mi SE of Blacksburg, *Lewis 6670:* **2n = ca 72**(2)—2 plants ca 36_{II}; id., McCoy, *Lewis 6671:* **2n = 36**(1), **50**(1)—1 plant $16_{II}+4_I$, $17_{II}+2_I$&18_{II}, 1 plant $21_{II}+1_{III}+5_I$ (+1 fragment).

James City Co, Williamsburg, *Davis 6005:* **n = 12**—Davis & Bowmer (1966).

WEST VIRGINIA

Hampshire Co, Ice Mt, 13 mi SE of Slavesville, *Lewis 6673:* **2n = 24**(6)—6 plants 12_{II}.

Monongalia Co, Morgantown, *Lewis 6678:* **2n = 32**(5)—5 plants 16_{II}.

Ohio Co, 1 mi W of W Va & Pa state line, *Davis 6010:* **n = 12**—Davis & Bowmer (1966).

WISCONSIN

Green Co: **2n = 16**(mc)—Rothwell (1959).

Milwaukee Co: **2n = 16**(mc)—Rothwell (1959).

Sank Co: **2n = 16**(mc)—Rothwell (1959).

Cytology

Before proceeding with a discussion of major cytotypes two phenomena will be noted briefly. These include aneusomaty, i.e. variation of chromosome number intra-individually, which was found by Lewis et al. (1967) in the St. Louis area and earlier in eastern Texas (Lewis, 1962). No additional data can be added to this phenomenon. We wish also to mention the results of Rothwell & Kump (1965) from the New York area in which they reported highly polyploid individuals ($2n$ = 85 to ca 191) occasionally associated with meiotically regular diploids ($2n$ = 16). Such individuals have not been found elsewhere, but their diversity in New York (perhaps formed in response to some local environmental circumstance, e.g. viruses) does illustrate a propensity for mass chromosomal duplication without apparent harm to the individual.

Elsewhere the results are more orderly. Of the three major diploid cytotypes (Fig. 2), that having n = 6 is restricted to the geologically old and well-known relict and refugial area in the southern Appalachian Mountains. Here, found in mixed and separate populations, are plants with n = 7. This race is also found in the geologically similar Ozarks and to the south of these mountains as a common weed almost to the Gulf of Mexico. The n = 7 race is now disjunct, but very probably had a common origin and was continuous much earlier. The third major diploid race is based on 8; it dominates the northern distribution of *C. virginica* and has by far the greatest continuous range of any diploid. To the south, its limits parallel somewhat the southern expansion of the last glaciation (Fig. 2). Rarely individuals with n = 8 occur outside this area, e.g. in eastern Texas, but they probably represent spontaneous, local aneuploids quite apart from the major trends of evolution.

Other diploid cytotypes are known, but these are rare and none has a distinct distribution. The n = 9 race, for example, is found very rarely in eastern Texas in populations dominated by plants with n = 7 and where n = 8 is rare in a declining frequency from n = 7-8-9 with only one plant having $2n$ = 15. Paralleling this Rothwell (1959) reported in a single population 73 plants with n = 8, 13 with n = 9, and 3 with n = 10 as well as aneuploids with $8_{II}+1_I$ and $9_{II}+1_I$. From only two plants of an Ontario population (*Lewis 6630*) we found one plant with n = 8 and one with n = 9. Although it cannot be excluded that a race dominated by plants having n = 9 may yet be found in the northern range of *C.*
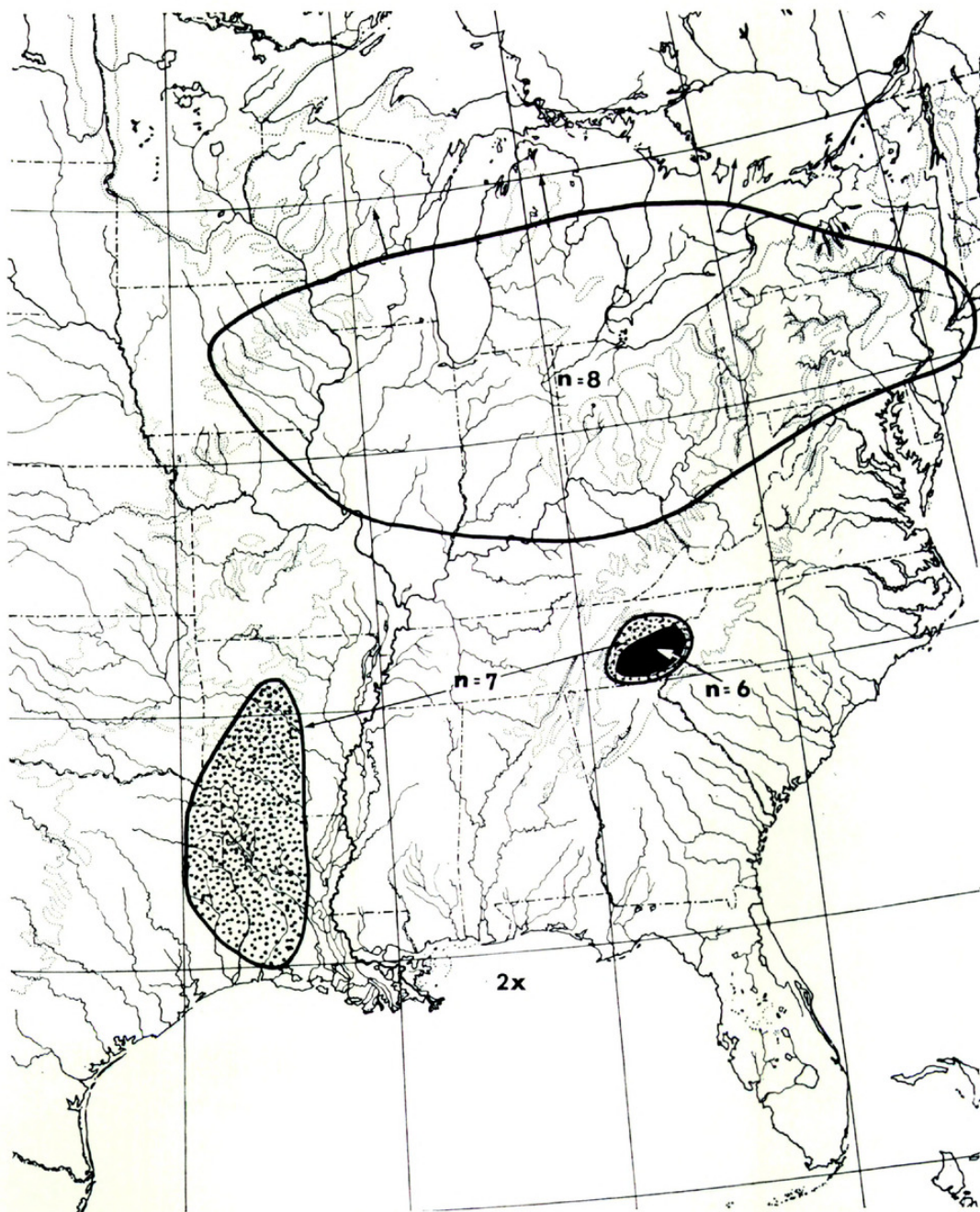
Fig. 2. Distribution of the major diploid cytotypes ($n = 6, 7, 8$) of *Claytonia virginica* in eastern North America.

virginica, where counts are as yet meagre, autodiploids other than $n = 6, 7$, and 8 are infrequent and sporadic and probably arose by chromosomal gain through meiotic nondisjunction over and over again locally from plants representing the dominant diploid for the area.

The primary tetraploid cytotypes of each of the major diploid races ($n = 12$, 14, 16) are very common and have widespread overlapping distributions (Fig. 3).
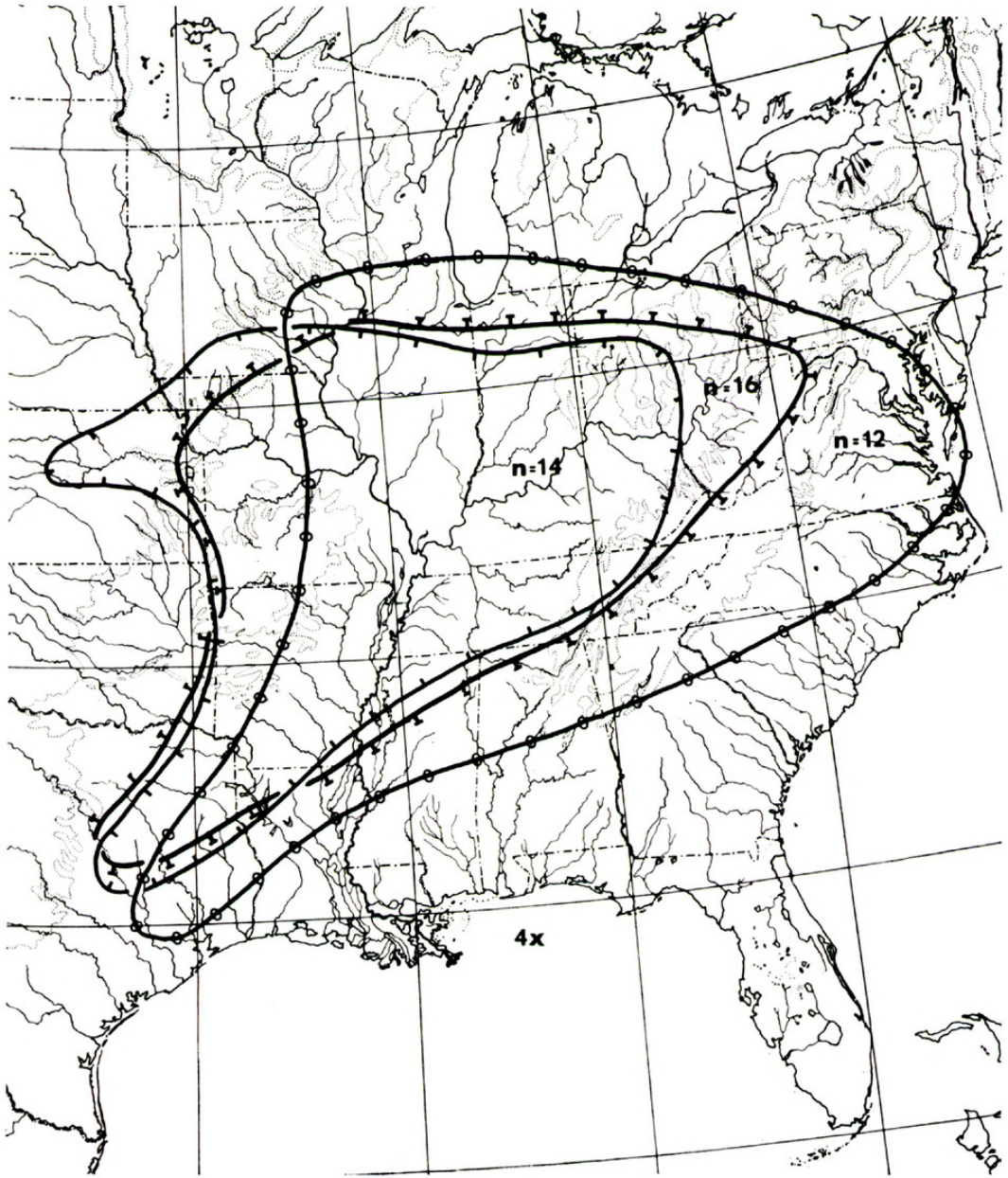
Fig. 3. Distribution of the major tetraploid cytotypes ($n = 12, 14, 16$) of *Claytonia virginica* in eastern North America.

All major tetraploids may be found together, but invariably one or two races dominate at any one locality. For example in the St. Louis area, where diploids are unknown, two tetraploid races are dominant and more or less of equal frequency; they usually are found at distinct localities even in this small area although both races are occasionally found together.

Secondary tetraploid races are also frequent, but usually in association with primary tetraploid cytotypes from which they probably arose. In the St. Louis area $n = 15$ is much more common than $n = 16$, but at several localities both occur
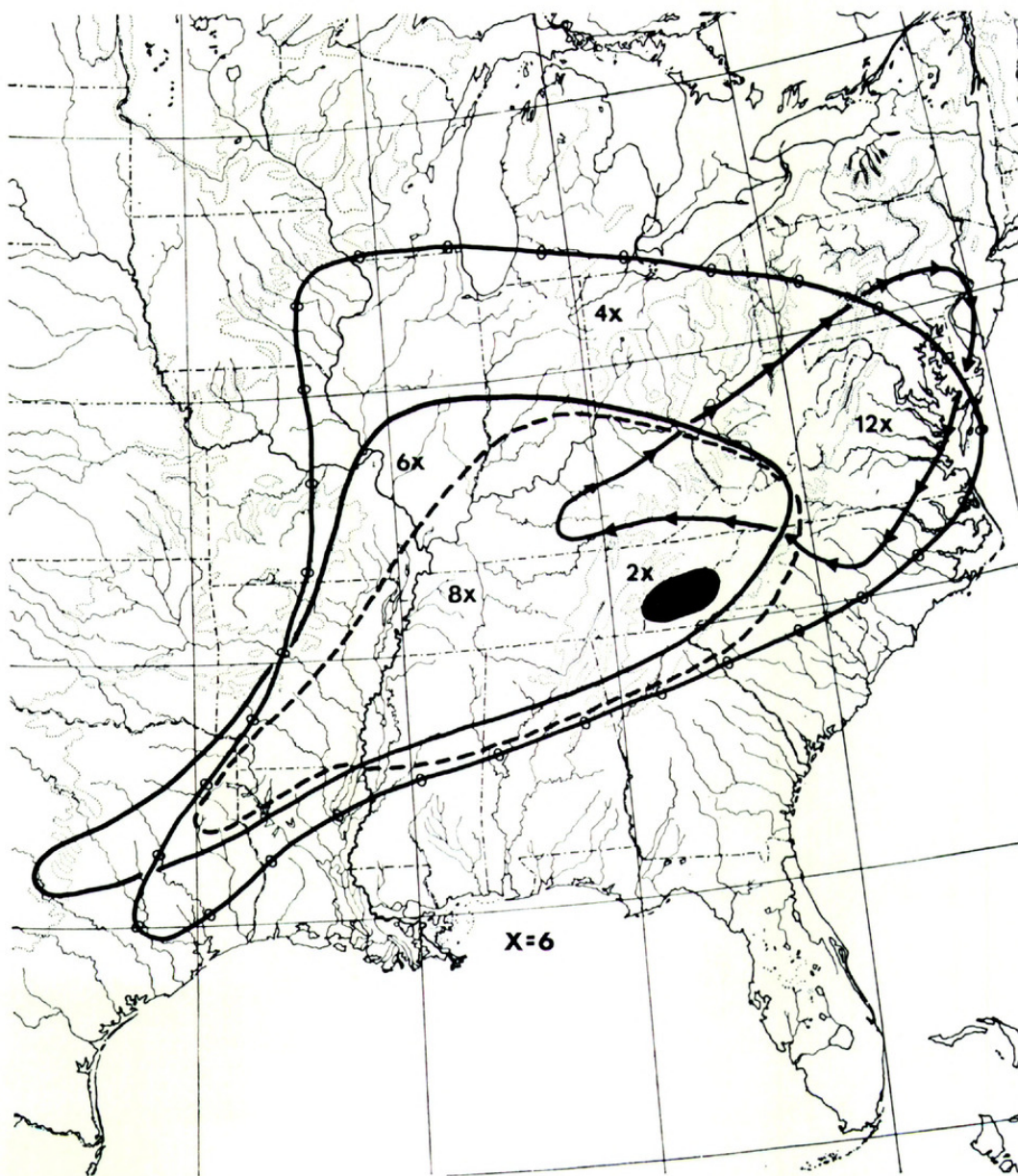
Fig. 4. Distribution of the $x = 6$ cytotypes of *Claytonia virginica* in eastern North America.

in addition to $15_{II} + 1_I$. Elsewhere particularly in the Midwest this pattern is repeated or reversed, i.e. dominance of $n = 16$ with fewer secondary tetraploids (cf. Fig. 1). Widespread also are plants with $n = 11$; these are secondary tetraploids probably formed by hypoaneuploidy from those with $n = 12$ with which they are usually associated. Sporadically throughout the range of *C. virginica* other secondary tetraploids are found, but none is frequent.

Of the higher polyploid races only those with $n = 18$, presumably hexaploids in the $x = 6$ line, are frequent and widespread; less common are those with $n =$

24 ($8x$) and 36 ($12x$) based on 6. More infrequent still are those with $n = 21$ ($6x$) and 28 ($8x$) where $x = 7$.

To facilitate their study according to base number the major cytotypes with distributions are illustrated in Fig. 4-6. The $x = 6$ line has the greatest range and is the most highly polyploid (Fig. 4); as already noted the $2x$ is restricted to the southern Appalachians and the $4x$ is widely distributed; the $6x$ is less frequent but found within the range of the tetraploid; the $8x$ is rare though similar to the hexaploid in distribution; and the $12x$ is also rare but more restricted (mid-Atlantic states and mid-Appalachians).

For the $x = 7$ race (Fig. 5) we have noted the disjunct distribution of the southern $2x$ as well as the wide range of the $4x$ race. The occurrence of the $6x$ and $8x$ races are shown in Fig. 5; both are very rare and local.

Only two races are clearly based on 8. The diploid is northern, the tetraploid extends more to the south and both are of wide range (Fig. 6). No octoploid, $n = 32$, is known.

Comparative frequency for all significant cytotypes is presented in Fig. 7, a rough index at best because sampling has been better in some areas than in others. Yet the diagram does accurately reflect, we believe, an increase in frequency among the diploid races from $n = 6$ to 8 with an abrupt decrease to $n = 9$ and 10 (representatives of the latter race may have evolved by chromosomal loss from tetraploids or by hyperaneuploidy from diploids). This sequence suggests hyperaneuploidy from $n = 6$, a very old and apparently relict race for *C. virginica* and one which may be basic for the genus if not the family (see below). Perhaps also the antiquity of this basic number is reflected by the extensive polyploid series from $n = 6$, far greater than for any other basic line.

Judging from Fig. 7, however, *C. virginica* is dominated by plants at the tetraploid level. They presumably evolved along at least three distinct lines from $n = 6$ to 12, $n = 7$ to 14, and $n = 8$ to 16, perhaps through unreduced gametes. The first successful mutation was probably from $n = 6$ to 12, the former now very restricted, the latter now forming one of the largest and most frequent cytotypes in the species. They are not known to be sympatric although our data are meagre from the mid-Appalachian region where they might occur together. Cytotypes of the other lines, however, are often found at the same locality, e.g. $n = 7$ and 14 in eastern Texas, $n = 8$ and 16 in Indiana.

A significant feature of tetraploids is the frequency of their secondary races, particularly $n = 11$ and 15 (Fig. 7). Their origins from $n = 12$ and 16, respectively, have already been noted. Other such tetraploids are known and these in total account for a large fraction of individuals examined. Clearly chromosomal change at the tetraploid level has been much greater than at the diploid level; presumably this redundancy of chromosomes has allowed a greater shift in complements without deleterious effects. Moreover change among tetraploids appears strongly downward (hypoaneutetraploidy) in contrast to the diploid level where chromosomal gain has apparently been more important (hyperaneudiploidy).

Probably through unreduced gametes or less likely by doubling of $2x$-$4x$ crosses (no definite triploid has yet been found) or by both, the higher polyploids
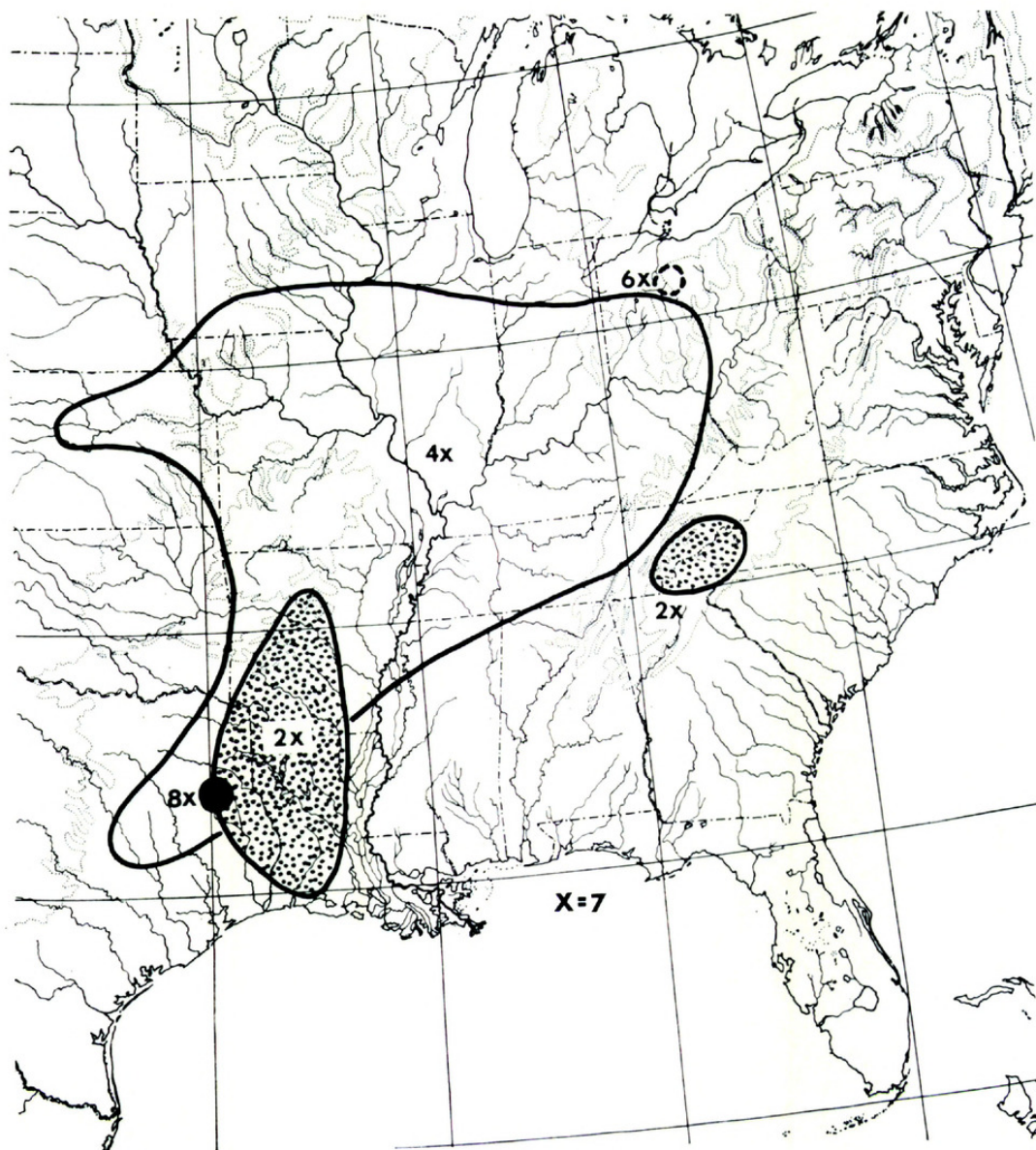
Fig. 5. Distribution of the $x = 7$ cytotypes of *Claytonia virginica* in eastern North America.

evolved. Their frequency and direction of evolution are suggested in Fig. 7.

After this scheme of infraspecific phylogeny for *C. virginica* had been organized, we decided to compare it with the chromosomal data available for several closely related species; fortunately, the best known cytologically in the genus were two allied corm-bearing species. These are *C. caroliniana* Michx. of the Appalachians and northern parts of eastern North America and *C. lanceolata* Pursh from the Rocky Mountains (cf. Lewis, 1967, Table 2).

Claytonia caroliniana consists of two dominant cytotypes, $n = 8$ and 12, with very few plants representing other races (Fig. 8). The $n = 12$ race is found in the southern Appalachians while the $n = 8$ race is known from northern West Virginia
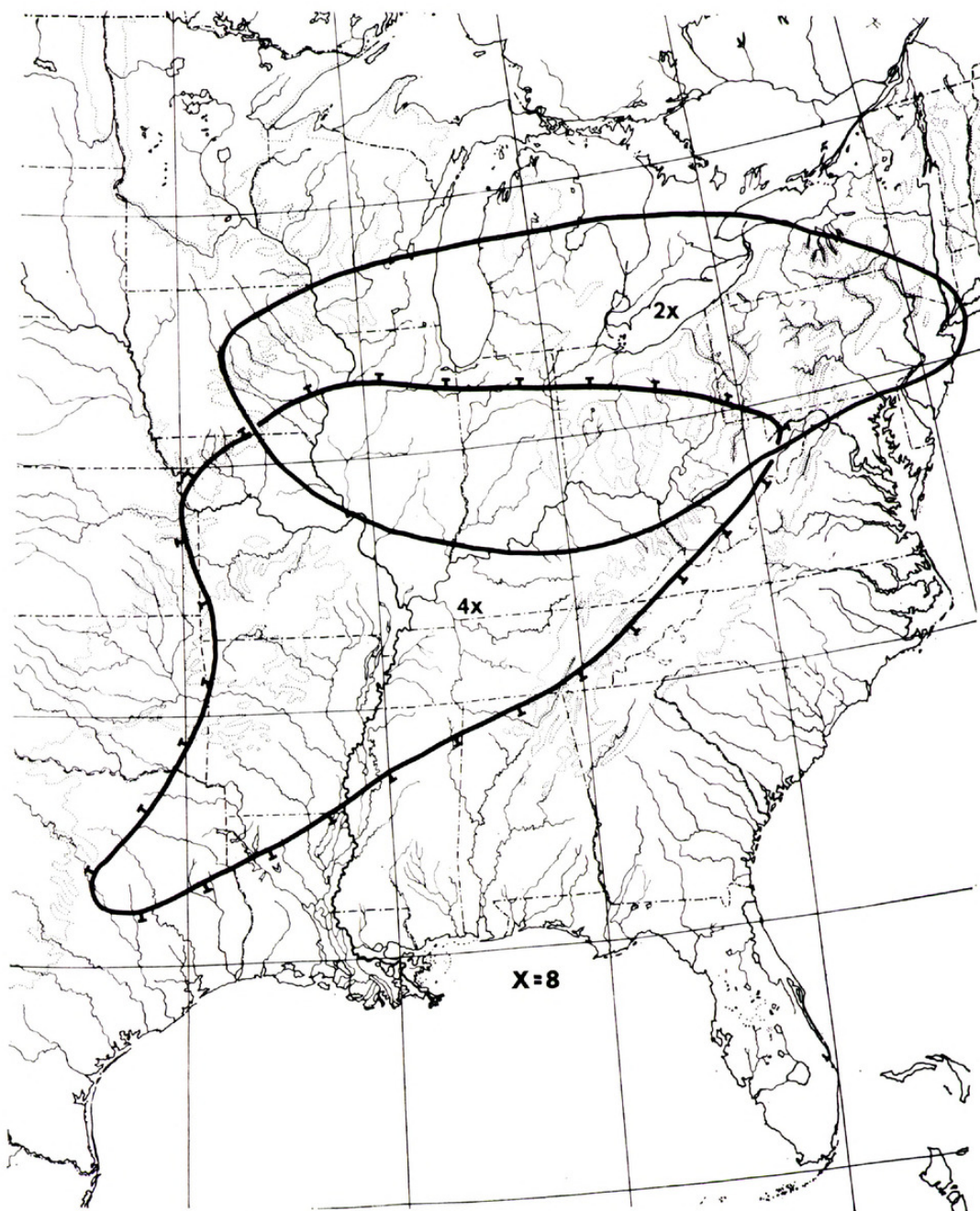
Fig. 6. Distribution of the $x = 8$ cytotypes of *Claytonia virginica* in eastern North America.

to Quebec. Heretofore these cytotypes with their distinct if not nearly disjunct distributions failed to have "meaning"—how could such races different by four pairs of chromosome evolve? However, superimposed on the scheme for *C. virginica* we find: (a) hyperaneudiploidy from $n = 6$ to 8; (b) loss of two diploid races ($n = 6$ and 7) both of which are of restricted frequency in *C. virginica;* (c) proliferation of the $n = 8$ race to the north, a characteristic feature of *C. virginica;* (d) before extinction of $n = 6$ the evolution of the tetraploid $n = 12$, a race well-
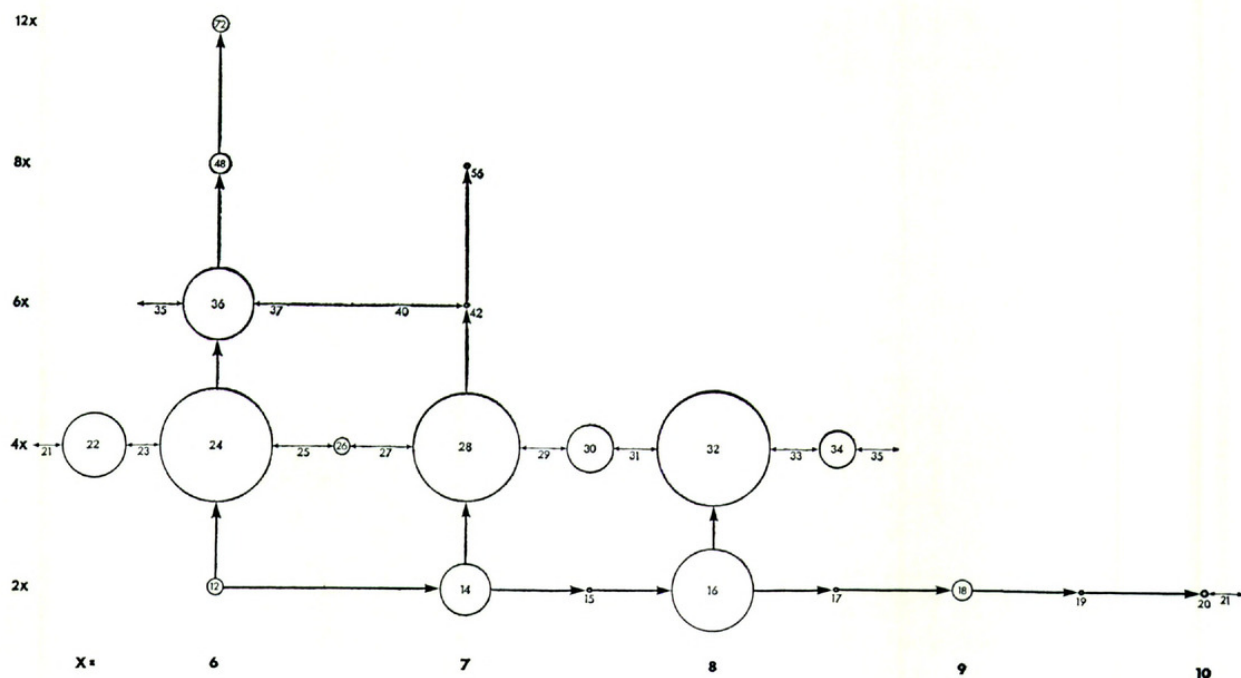
Fig. 7. Comparative frequency of cytotypes (as 2n) in *Claytonia virginica* and suggested evolutionary direction. The smallest circle represents the occurrence of a race in one population, others to scale.

established also in *C. virginica;* and (e) evolution to a higher polyploid level based on 6, again a development typical of *C. virginica*. Such parallels are striking and they serve to strengthen the infraspecific scheme proposed for *C. virginica* where greater diversity tends to shroud conclusions.

Claytonia lanceolata also possesses a dominant race with $n = 8$ now known from Washington, Oregon, Idaho, Colorado, and Utah (cf. Lewis, 1967) as well as a widespread $n = 12$ race (Fig. 8). Particularly at the diploid level infraspecific evolution has been similar to *C. caroliniana;* at the polyploid level close to *C. virginica* where $x = 6$ ($4x, 6x, 8x, 12x$).

Thus the only closely allied, widespread, corm-bearing species of *Claytonia* share a similar phylogeny, but how does this proposal for an advanced perennial group (Swanson, 1966) compare with the most primitive species in the genus? Swanson considers those perennials having taproots in the sect. *Caudicosa* (Gray) Von Poellnitz primitive; of these, two species are known chromosomally (definite counts only). *Claytonia sibirica* L. has three races, $n = 6, 12, 18$, based on numerous counts from many areas (Lewis, 1967). Three races are also reported for *C. megarhiza* (Gray) Parry ex S. Wats. from only three populations (or plants ?): var. *megarhiza* with $n = 16$ from Colorado (Davis & Bowmer, 1966) and $2n = 36$ from Alberta (Taylor & Brockman, 1966), and var. *bellidifolia* (Rydb.) C. L. Hitchc. from Oregon as $n = 12$ (Davis & Bowmer, 1966). It appears that *C. megarhiza* is yet another multibasic species, but having in common with *C. sibirica* both $n = 12$ and 18 which are $4x$ and $6x$ races based on 6. Therefore, the primitive

sect. *Caudicosa* has at least one predominant base number, $x = 6$, a number very probably basic for the genus, including the corm-bearing species.

The only other well-studied portulacaceous genus is *Talinum* where $x = 12$. In all probability this base is derived from $x = 6$ which may prove to be the prototypic number of the family.
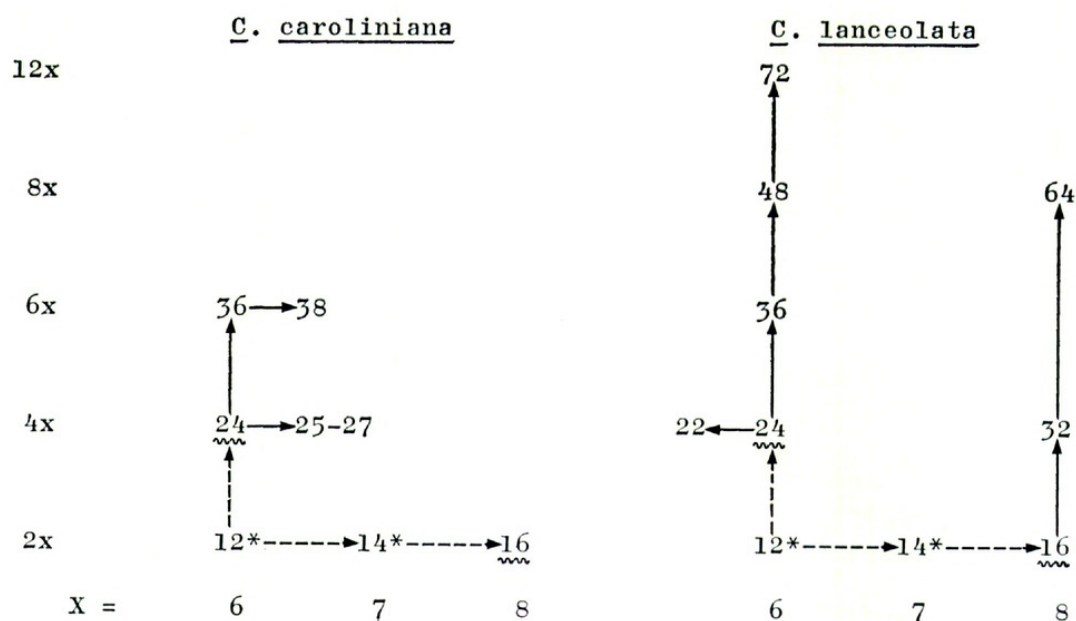
Morphology

Variation in gross morphology of *C. virginica* is aptly summarized by Davis (1966) who noted that the narrow-leafed variety which he called *simsii*[2] "cannot be distinguished from var. *virginica* by shape, length, or texture of sepals, bracts, or petals, because there are all gradations and combinations of characters between the extremes. However, in the southern part of the range many of the plants tend to be smaller and have very narrow leaves." Even though the narrow-leafed variety is frequent in the southern range of the species the broad-leafed form is also known in the south (Alabama and Mississippi) while the narrow-leafed variety is abundant as far north as eastern Missouri (Lewis et al., 1967) and northern West Virginia (*Lewis 6673*) and Maryland (*Lewis 6633*). In what way, if at all, do these varieties correlate with the many cytotypes and their distributions?

From among the largely $2x$ and $4x$ cytotypes with $x = 7$ examined in eastern Texas, Lewis (1962) found only the narrow-leafed variety. There was no difference between diploids and tetraploids in leaf width or in any other character studied. However, from the St. Louis area, Lewis et al. (1967) reported the dominance of two polyploid races in nearly equal frequency with the narrow-leafed variety having $n = 12 \pm 1$ and the broad-leafed having $n = 15 + 3.5, -1$. Thus the diploid race $n = 7$ in Texas and the tetraploid race $n = 12$ in Missouri were typical of var. *acutiflora* whereas the tetraploid race $n = 15$ in Missouri typified the var.

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[2] Gleason & Cronquist (1963) suggested that the typical variety is probably the more southern, narrow-leafed form. Davis (1966) assumed the broad-leafed one typical, but in his revision he neither designates a lectotype nor mentions this problem.

Among three specimens mounted on one sheet collected by *Kalm s.n.* (LINN, not seen; from IDC micro-edition 285.1), the widest leaf of *C. virginica* measures 4 mm—the collection probably represents the more northern, broad-leafed variety (i.e. from Pennsylvania to the north or west, and with $n = 8$ or $16 \pm$). Since Kalm returned to Sweden from eastern North America in 1751 we assume that Linnaeus saw his material before publishing the species two years later. We find no reason to ignore Kalm's collection in favor of pre-Linnaean sources, even though, for example, Linnaeus referred to the plate (*t. 102, fig. 3*) from Plukenet's Almagestum Botanicum. Plukenet clearly had the narrow-leafed *C. virginica* (width measures only 1.5 mm) and this was probably obtained from the mid or south Atlantic states (Virginia ?) with $n = 12 \pm$. Thus Linnaeus included the two major elements in his *C. virginica* of which we designate *Kalm s.n.* (LINN) lectotype of the var. *virginica* with broad leaves.

For the narrow-leafed form of *C. virginica* we cannot follow Davis (1966) who named it var. *simsii* (Sweet) R. J. Davis; at least two earlier names are available at that rank. The earliest is *C. virginica* [as *virginiana*] var. *acutiflora* DC. (Prodr. 3: 361, 1828) which includes citation of Sim's plate in Curtis's Botanical Magazine 14: *pl. 941*, 1806 (lectotype chosen by Davis for var. *simsii*) as well as that by Plukenet. The illustration by Sim's is questionably of the narrow-leafed variety though clearly that by Plukenet is and we select his plate in the Almagestum Botanicum, *t. 102, fig. 3*, 1696, lectotype of the narrow-leafed var. *acutiflora* DC.

Fig. 8. Suggested evolution of the cytotypes (as 2n) known for *Claytonia caroliniana* and *C. lanceolata*. Underscored numbers are dominant.

virginica. This suggests no correlation between leaf width and ploidy (cf. Lewis, 1967), yet a morphological-cytogeographic analysis over the range of *C. virginica* gave a different interpretation.

As summarized in Table 1 plants with $n = 6$ (2x) have leaf widths of $\overline{X} = 2.0(\pm 0.1)$ mm which are similar to those with $n = 7$ (2x), $\overline{X} = 2.3(\pm 0.4)$ mm. In addition plants with $n = 12\pm 1$ (4x) are narrow-leafed, $\overline{X} = 2.4 \ (\pm 0.3)$ mm, as reported by Lewis et al. (1967) from the St. Louis area only. In the south, where $n = 14$ is common, 4x plants also have narrow leaves, $\overline{X} = 2.3 \ (\pm 0.9)$ mm. Therefore, plants having cytotypes of $n = 6, 7, 12\pm 1$, as well as 14+ in the south have very similar leaf widths from $\overline{X} = 2.0\text{-}2.4$ mm. On the other hand significantly wider leaves are characteristic of plants with $n = 8$ (2x), $\overline{X} = 5.0(\pm 0.6)$ mm, and commonly $n = 16$ (4x) from the north, $\overline{X} = 5.4(\pm 0.4)$ mm, i.e. both 2x and 4x races where $x = 8$ are similar in leaf width.

Data for polyploids above the 4x level are scanty and the few studied form no distinct dichotomy—some with the same cytotype may have broad and narrow leaves, suggesting, as noted below, parallel evolution along narrow- and broad-leafed lines. Our sample is too small to unravel a complexity involving numerous 6x to 12x races, but consisting of only a small fraction of plants examined.

Sufficient numbers of specimens at the tetraploid level have been studied, however, to emphasize that morphology must be considered in relation to distribution and chromosome number. In the north, broad-leafed plants with $2n = 32$ are dominant in many populations; those with $2n = 30(31)$ and less commonly $2n = 28(29)$ also occur either together or at different localities, yet they

Table 1. Leaf width of plants of *Claytonia virginica* throughout its range and grouped by populational chromosome number.

Chromosome no. (2n)	Leaf width (mm)*			No. of plants	No. of populations
	$\overline{\times}$	$\overline{\times}s$	$\overline{\times}s_{\overline{x}}$		
12	2.0	0.2	0.1	14	3
12, 14	3.3	0.7	0.3	3	1
14	2.3	0.9	0.4	33	6
16	5.0	1.4	0.6	15	5
24(±2)	2.4	1.0	0.3	50	10
28-48[a]	4.2	1.9	1.1	153	30

[a]By distribution

north (largely 2n = 32±2)	5.4	1.5	0.4	57	14
central** (2n=28-48)	4.2	2.5	0.9	50	7
south (largely 2n = 28±2)	2.3	0.9	0.3	47	9

* Calculated by populational mean of maximum leaf width per plant and reported as grand mean with standard deviation and standard error.

** ± east-west region from the southern Appalachians, central Tennessee, western Kentucky, southern Illinois, southern Missouri, to Kansas; "north" is north of this region, "south" is south of this region.

all are broad-leafed. In the south (e.g. Texas, which is the only well-sampled area) the dominant tetraploid is $2n = 28$. This race is often found near to or at the same locality with fewer plants having $2n = 29, 30, 31, 32$ etc., but in contrast to chromosomally similar plants in the north all are narrow-leafed in Texas. Using a specific example we find $2n = 30$ plants from Missouri with broad leaves, but plants with the same chromosome number from Texas have narrow leaves. Apparently their evolutionary pathways were quite distinct: the first as secondary tetraploids from the broad-leafed $x = 8$ line common in the Midwest (perhaps $n = 8+8-1$), the second also as secondary tetraploids but from the narrow-leafed $x = 7$ line dominant in Texas (perhaps $n = 7+7+1$). Both gave rise to plants having $2n = 30$, but one subrace arose via a broad-leafed northern $x = 8$ complex and the other in a parallel way from the narrow-leafed southern $x = 7$ complex.

In summary *C. virginica* has evolved from an ancestral narrow-leafed race having $n = 6$ from which the widespread $n = 12±$ and southern $n = 7$ races arose. From the latter was derived a $n = 14$ race also common in the south. These races and at least some of their higher polyploid derivates make up the narrow-leafed var. *acutiflora*. From continuing autoaneuploidy at the diploid level evolved the $n = 8$ race where, we believe, particular chromosomal redundancies with cer-