CHROMOSOME NUMBERS OF CRUCIFERAE

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There has been a steady increase in our knowledge of chromosome numbers of the family *Cruciferae* following the comprehensive paper by Manton (1932). However, the point has scarcely been reached where these data can be put to their maximum usefulness. Many more counts, together with authentic determinations of the taxa involved, supported by voucher specimens, are needed before a new comprehensive evaluation of cytological data on the internal classification of the family is justified.

The problem of generic delineation is an unusually difficult one in the *Cruciferae* (cf. Rollins, 1960, 1962). In some instances, a consistency of chromosome number within genera coupled with differences between related genera are helpful in determining where generic lines of demarkation are rightfully placed. The reliability of any such patterns that emerge will be dependent upon the completeness and accuracy of the chromosome counts. Proper application of these data to solutions of particular problems demands broad considerations of diverse kinds of information which can be convincing only if they are evaluated and presented in considerable detail. Obviously, this is not our present purpose. The following listing of chromosome numbers and the accompanying comments are intended to help in rounding out the needed chromosome data and to highlight some cytologically interesting problems that have turned up in the *Cruciferae* during the past three decades of research on this interesting family.

ACKNOWLEDGEMENTS

The chromosome numbers given have been determined as the opportunity of examining the material has presented itself over a number of years, beginning in the early 1940's. Aside from counts I have made, a number of assistants and colleagues have contributed to the counts listed. Those made in a preliminary way by assistants were verified. The late Dr. L. O. Gaiser made a large number of counts, particularly on root-tip material. More recently, Dr. Otto T. Solbrig has examined and reported on fixations we have acquired. I am particularly indebted to Dr. Solbrig for his interest and help. Fixed material has been contributed by a number of collaborators, especially by Dr. Peter Raven. I wish to thank those who have contributed in any way to this study, particularly Dr. Kuldip R. Khanna, who actively collaborated with me in part of this research. Financial support for portions of this work has been given by the National Science Foundation.

Arabis

A. *crandallii* Robinson
  2n = 14: Gunnison Co., Colorado. Ripley and Barneby 10206, GH.
  2n = 14: Hinsdale Co., Colorado. Rollins 51165, GH.

A. *crandallii* x A. *Holboellii* Hornem., var. *retrofracta* (Grah.) Rydb.
  2n = 21: Gunnison Co., Colorado. Rollins 5194, GH.

A. *demissa* Greene, var. *russeola* Rollins
  2n = 21: Sweetwater Co., Wyoming. Rollins & Porter 5134, GH.

A. *divaricarpa* A. Nels
  2n = 14: Park Co., Colorado. Rollins & Weber 51290. GH.
  2n = 14: Conejos Co., Colorado. W. A. Weber 7845. GH.
  2n = 14: Park Co., Montana. Rollins & Porter 51244, GH.
  2n = 14: Park Co., Wyoming. Rollins & Porter 51252, GH.
  2n = 22: Siskiyou Co., California. J. T. Howell 15193, GH.

A. *drummondii* Gray
  2n = 14: Park Co., Colorado. Rollins & Weber 51289, GH.
  2n = 14: Park Co., Montana. Rollins & Porter 51246, GH.
  2n = 14: Park Co., Wyoming. Rollins & Porter 51250, GH.

A. *fendleri* (Wats.) Greene, var. *spatifolia* (Rydb.) Rollins
  2n = 14: Douglas Co., Colorado. Rollins 5147, GH.

A. *holboellii* Hornem., var. *pendulocarpa* (A. Nels.) Rollins
  2n = 14: Yellowstone National Park, Wyoming. Rollins & Porter 51281, GH.

A. *holboellii* var. *pinetorum* (Tidestr.) Rollins
  2n = 21: Sweetwater Co., Wyoming. Rollins & Porter 5135, GH.

A. *holboellii* var. *retrofracta* (Grah.) Rydberg
  2n = 14: Siskiyou Co., California. L. Constance *s.n.*, GH.
  2n = 14: Park Co., Montana. Rollins & Porter 51245, GH.

A. *lemmonii* Watson
  2n = 14: Park Co., Wyoming. C. L. Porter 5888, GH.

A. *lyrata* L., var. *kamchatica* Fischer
  2n = 16: Kurupa River Valley, Arctic Slope of Alaska. Hodgdon 8664, GH.

$2n = 32$: Nixon Mine, Kuskokwim Mts., Alaska. Drury 3380, GH.

A. *perstellata* Braun, var. *ampla* Rollins

$n = 7$: Davidson Co., Tennessee. Rollins, Solbrig, Hilferty & Lloyd 6012, GH.

Polyploidy was firmly established in certain species of *Arabis* by evidence presented earlier (Rollins, 1941). Also, the data showed that $x = 7$ was a common fundamental number in the genus. Mulligan (1964) suggests that all species of *Arabis* exclusively North American have a chromosome number based on $x = 7$, whereas the European and Asiatic species are based on $x = 8$. We have no data contrary to this division but I suspect the correlation is with phylogenetic relationship rather than with geography. It just happens that we do not have counts on any of the exclusively North American species that are obviously related to those of Eurasia. To test the point, counts are needed in such species as *Arabis blepharophylla* H. & A., *A. oregana* Roll., *A. modesta* Roll., *A. aculeolata* Greene, *A. furcata* Wats., *A. Nuttallii* Robins., and *A. crucisetosa* Const. & Roll.

The discovery of apomixis in *Arabis holboellii* Hornem. by Böcher (1951) opened the way to a more reasonable explanation of the inconsistent chromosome numbers in *Arabis* than was available earlier. Where apomixis is operative, triploids and various aneuploid numbers can persist in wild populations without difficulty and several different chromosome numbers within a given species are then not surprising.

There is very good evidence (Rollins, 1946) that interspecific hybridization occurs in *Arabis* and I am convinced that hybridization between taxa at specific and infraspecific levels is widespread in the genus. Hybridization, polyploidy and apomixis undoubtedly operate together to provide several polymorphic groups within the genus.

Taxonomically, the most difficult and puzzling complexes are the following, designated by the name of the species with which other less prominent taxa are associated: (1) the *Arabis holboellii* complex, (2) the *Arabis sparsiflora* complex, (3) the *Arabis divaricarpa* complex, (4) the *Arabis fendleri* complex, (5) the *Arabis lemmonii* complex. Although we do not have direct evidence as yet, it is very probable that all three phenomena (i.e., hybridization, polyploidy and apomixis), occur separately or together to provide the complex patterns of variation found in each complex.

Barbarea

B. orthoceras Ledeb.

$n = 8$: San Luis Obispo Co., California. Breedlove 2030, GH.

This count is in line with that of Mulligan (1964) for the species and of other authors for the genus as a whole. The fundamental number $x = 8$ is well established.

Cakile

C. fusiformis Greene

$n = 9$: Aransas Co., Texas. Rollins & Correll 5964, GH.

C. geniculata (Robins.) Millsp.

$n = 9$: Galveston Co., Texas. Rüdenberg. March, 1966, G.H. Count by L. Rüdenberg.

Previous counts on other species of *Cakile* are from more northerly stations in Europe, Asia and North America. However, all counts agree with a fundamental number of $x = 9$. There is still a major need for studies of variation patterns in populations of *Cakile*. Pobedimova's (1964) recognition of eight species in North America and the West Indies requires a careful evaluation.

Cardamine

C. breweri Watson

$n = 42$-48: Fresno Co., California. Breedlove 5242, GH.

C. parviflora L., var. *arenicola* (Britt.) Schulz

$n = 22$-24: Morgan Co., Alabama. Rollins *et al.* 6103, GH.

C. digitata Richardson

$2n = 32$: Umiat, near Colville River, Alaska. Thompson 1217, GH.

Only one of the three determinations given above was wholly satisfactory, that of *C. digitata*. Material of the other two taxa proved to be very difficult and a definitive number could not be settled upon. It is clear that $x = 8$ is a fundamental number in *Cardamine* and that polypoidy is widespread in the genus.

Caulanthus

C. coulteri Watson

$n = 14$: Santa Barbara Co., California. Breedlove 1929, GH.

C. flavescens (Hook.) Payson

$n = 14$: Alameda Co., California. Breedlove 4295. GH.

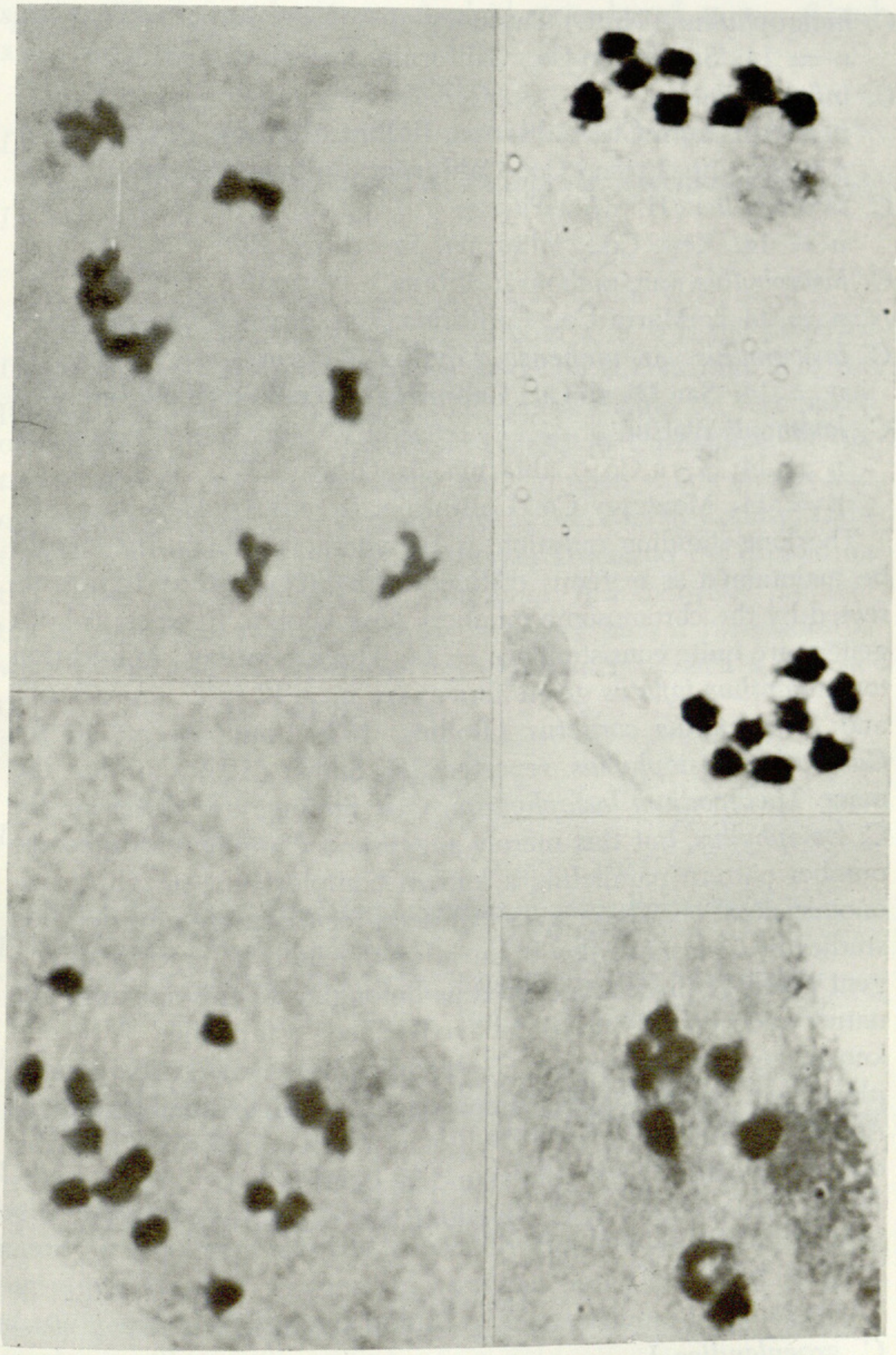

PLATE 1. Upper left, chromosomes of *Lesquerella lasiocarpa*, $n = 7$, Rollins and Correll 5950; upper right, chromosomes of *Lesquerella argyrea*, $n = 8$, Rollins and Correll 5944; lower left, chromosomes of *Caulanthus lemmonii*, $n = 14$, Breedlove 1954; lower right, chromosomes of *Tropidocarpum gracile*, $n = 8$, Breedlove 1822. All figures $\times$ 3900.

C. heterophyllus (Nutt.) Payson
$n = 14$: San Diego Co., California. Breedlove 1831, GH.

C. inflatus Watson
$n = 10$: Kern Co., California. Rollins 4160, DS.
$n =$ ca. 10: Fresno Co., California. Rollins 4159, DS.

C. lasiophyllus (H. & A.) Payson
$n = 14$: Kern Co., California. Breedlove 1951, GH.

C. lasiophyllus var. *inaliens* (Robins.) Payson.
$n = 14$?: Marin Co., California. Breedlove 4402, GH.

C. lasiophyllus var. *utahensis* (Rydb.) Payson
$n = 14$: San Diego Co., California. Breedlove 1859, GH.

C. lemmonii Watson
$n = 14$: Kern Co., California. Breedlove 1954, GH. Plate 1.
$n = 14$: Monterey Co., California. Breedlove 4312, GH.

The long-standing question as to whether *Caulanthus* should be maintained as a genus distinct from *Streptanthus* is not affected by the chromosome numbers now known. Species in both genera are quite consistently $n = 14$. The exceptions, in addition to *Caulanthus inflatus* given above, are $n = 12$ in *C. crassicaulis* and *Streptanthus cordatus* (Rollins, 1939) and $2n = 48$ for *Caulanthus lasiophyllus* reported by Snow (1959) under the name *Thelypodium lasiophyllum*. Our findings are different for *C. lasiophyllus*, but this merely suggests a complex chromosome number pattern paralleling a known complex and puzzling taxonomic situation. There is a great need for extensive and detailed studies of *C. lasiophyllus* because of the morphologically divergent plants at present accepted as belonging to this species. The nature and range of variation have not been established. A second known problem involving *C. lasiophyllus* involves its generic placement. Schulz (1924) associated it with a small group of Asiatic species comprising the genus *Microsysimbrium* but this does not seem to be a well founded solution.

The chromosomes of *C. lemmonii* are shown in Plate 1.

Cochlearia

C. groenlandica L.
$2n = 14$: Prince Charles Island, Canada. W. K. W. Baldwin 1894, GH.

The number $2n = 14$ is in accordance with numerous counts from Greenland, Canada and Iceland (Saunte, 1955) for this species. The genus has two polyploid series based on x = 6 and x = 7.

Dentaria

D. integrifolia Nuttall
n = 16: Santa Barbara Co., California. Breedlove 1773, GH.
D. integrifolia, var. *californica* (Nutt.) Jepson
n = 8: San Mateo Co., California. Rollins 2947, DS.
n = 16: San Mateo Co., California. Rollins 4196, DS.

The fundamental chromosome number x = 8 is the same for *Dentaria* and *Cardamine* and no evidence is contributed to the problem of whether both of these genera should be recognized or whether all species should be placed in *Cardamine*. *D. integrifolia* var. *californica* occurs both in open valley swales and on wooded slopes. In a limited area in San Mateo County, California, we found the polyploid in open areas and the diploid on the slopes of the Santa Cruz Mountains. A worthwhile problem for investigation would be to see whether such a correlation is widespread and to determine the significance of such a correlation if it does exist species-wide.

Dithyrea

D. californica Harvey
n = 10: Mohave Co., Arizona. Rollins 4164, DS.
n = 10: San Diego Co., California. Breedlove 1855, GH.
D. wislizenii Engelmann
n = 9, 2*n* = 18: Pinal Co., Arizona. Rollins 4168, GH.
n = 9: Presidio Co., Texas. Rollins & Correll 61100, GH.
D. wislizenii, var. *palmeri* Payson
n = 9: Howard Co., Texas. Rollins 53116, GH.

The number *n* = 10 for *D. californica* is the same as that of Lewis (1959) and of Raven *et al.* (1965), and *n* = 9 appears to be a common number in *D. wislizenii*. More counts need to be made on the latter species, especially the annual winter-blooming populations of Arizona. In addition, data from other species of the genus are required before a clear pattern of chromosome numbers will emerge.

Draba

D. glabella Pursh
2*n* = ca. 75: Point Jay, Alaska. J. H. Thomas 2297, GH.

D. lanceolata Royle

$n = 16$: Park-Summit Co. line, Colorado. Rollins, Weber & Livingston 5155, GH.

D. oligosperma Nutt.

$2n =$ ca. 60: Albany Co., Wyoming. Ripley & Barneby 10536, GH.

The taxonomy of *Draba* is very confused. This is particularly true of the Arctic and subarctic species and those of high altitudes in the mountains. Chromosome counts on many of the species are high, ranging upward from $n = 16$. A polyploid pattern based on $x = 8$ for *Draba* appears to be emerging but the chromosomes are so small in many instances that it is extremely difficult to obtain a certain count. We have no solid evidence that apomixis occurs in the genus. However, on the basis of the frequent and probably variable chromosome numbers found, it is a fairly safe prediction that apomixis together with interspecific hybridization and polyploidy are responsible for the confused taxonomic picture in the genus.

Erysimum

E. capitatum (Dougl.) Greene

$n = 18$: Contra Costa Co., California. Breedlove 4282, GH.

$n = 18$: Santa Clara Co., California. Breedlove 4673, GH.

E. concinnum Eastwood

$n =$ ca. 18: Marin Co., California. Breedlove 4449, GH.

E. pallasii (Pursh) Fernald

$2n = 36$: Lake Noluk, Brooks Range, Alaska. H. J. Thompson, DS.

Most of the definitive counts made on *Erysimum* indicate a fundamental number of $x = 9$. Our counts on *E. capitatum* are the same as that given by Raven *et al.* (1965) for *E. capitatum* and *E. capitatum* var. *bealianum*. The number $2n = 36$ for *E. pallasii* is in line with other counts in the genus but is somewhat different from an estimated count of $2n =$ ca. 28 by Holmen (1952) for this species. Our count also differs from the counts of $n = 12$ and $2n = 24$ given by Mulligan (1966) for *E. pallasii*.

Eutrema

E. edwardsii R. Brown

$2n = 18$: North slope, Brooks Range, Alaska. Thompson 1342, GH.

Eutrema edwardsii is a widespread species of arctic and subarctic regions occurring on all continents that extend into these high latitudes. It is morphologically variable and also appears to have several chromosome races. The counts of $2n = 28$ and $2n = 42$ by Mulligan (1964) substantiate the same counts by others. Our count of $2n = 18$ introduces a complication that is not at present open to resolution.

Halimolobos

H. perplexa (Hend.) Rollins
$2n = 14$: Adams Co., Idaho. M. Ownbey 3293, GH.

Previous counts (Jørgensen, Sørensen and Westergaard, 1958, Mulligan, 1964) on *H. mollis* agree on $2n = 16$, pointing to a base number of $x = 8$. However, our finding of $2n = 14$ for *H. perplexa* suggests $x = 7$ may be another fundamental number in the genus.

Lepidium

L. densiflorum Schrader
$n =$ ca. 16: Morgan Co., Alabama. Rollins *et al.* 6115, GH.

L. jaredii Brandegee
$n = 8$, $2n = 16$: San Benito Co., California. Wiggins & Rollins 18, GH.

L. perfoliatum L.
$n = 8$: White Pine Co., Nevada. Breedlove 5814, GH.

L. strictum (Wats.) Rattan
$n =$ ca. 16: Santa Cruz Co., California. Breedlove 4635, GH.

Lepidium continues to check out as "a very uniform polyploid genus," as suggested by Manton (1932) in her early paper on the cytology of the *Cruciferae*. *L. jaredii* is a very distinct localized species of California and it is interesting to find that its chromosome number conforms to the pattern otherwise known in the genus.

Leavenworthia

Reference is made to table 1, pages 9 & 10, Contributions from the Gray Herbarium No. 192, 1963, where a detailed listing of chromosome numbers is given. The numbers $n = 11$, $n = 15$ and $n = 24$ are found in the genus. No new counts have been made.

Lesquerella

L. alpina (Nutt.) Watson, var. *spathulata* (Rydb.) Payson
$2n = 12$: Custer Co., South Dakota. Ripley & Barneby *s.n.*, GH.

L. angustifolia Nuttall
$n = 5$: Choctaw Co., Oklahoma. Rollins 5971, GH.
$n = 5$: Choctaw Co., Oklahoma. Rollins 6151, GH.

L. arenosa (Richards.) Rydberg
$2n = 18$: Custer Co., South Dakota. Ripley & Barneby 10559, GH.

L. argyrea (Gray) Watson
$n = 6$: Victoria Co., Texas. Rollins 5361, GH.
$n = 7$: Victoria Co., Texas. Rollins 5566, GH.
$n = 7$: South of Saltillo, Coahuila, Mexico. Rollins & Tryon 58121, GH.
$n = 8$: Kennedy Co., Texas. Rollins & Correll 5961, GH.
$n = 8$: Webb Co., Texas. Rollins & Correll 5944, GH. PLATE 1.
$n = 9$: Uvalde Co., Texas. Rollins & Correll 5942, GH.
$n = 12$: Refugio Co., Texas. Rollins 5359, GH.
$n =$ ca. 15: Refugio Co., Texas. Rollins 5564, GH.
$n = 16$, $n = 17 \pm 1$: Webb Co., Texas. Rollins & Correll 5946, GH.
$n = 18$: Llano Co., Texas. Rollins 53104 and 53105, GH.

L. arizonica Watson
$n = 5$: Mohave Co., Arizona. Rollins 4167, GH.

L. auriculata (Engelm. & Gray) Watson
$n = 8$: Comanche Co., Oklahoma. Rollins 53123, GH.
$n = 8$: Grady Co., Oklahoma. Rollins 53126, GH.

L. densiflora (Gray) Watson
$n = 7$: Llano Co., Texas. Rollins 53103, GH.
$n = 7$: Llano Co., Texas. Rollins 5574, GH.
$n = 7$: Gillespie Co., Texas. Rollins 53106, GH.
$n = 7$: Dewitt Co., Texas. Rollins 5560, GH.

L. densipila Rollins
$n = 8$: Williamson Co., Tennessee. R. & D. Rollins 5215, GH.
$n = 8$: Williamson Co., Tennessee. Rollins 5315, GH.
$n = 8$: Williamson Co., Tennessee. Rollins 53137, GH.
$n = 8$: Marshall Co., Tennessee. Rollins 5321, GH.
$n = 8$: Marshall Co., Tennessee. Rollins 53140, GH.
$n = 8$: Rutherford Co., Tennessee. Rollins 55124, GH.

$n = 8$: Maury Co., Tennessee. Rollins 55146, GH.
$n = 8$: Morgan Co., Alabama. Rollins & Chambers 5710, GH.
$n = 8$: Morgan Co., Alabama. Rollins 5924, GH.
$n = 8$: Morgan Co., Alabama. Rollins *et al.* 6105, GH.
$n = 8$: Lawrence Co., Alabama. Rollins *et al.* 6127, GH.

L. *densipila* × L. *lescurii*
$n = 8$ Cheatham Co., Tennessee. Rollins 5326, GH.
$n = 8$ Cheatham Co., Tennessee. Rollins 53130, GH.
$n = 8$ Williamson Co., Tennessee. Rollins 5325, GH.
$n = 8$ Williamson Co., Tennessee. Rollins 53135, GH.

L. *engelmannii* (Gray) Watson
$n = 18$: Guadalupe Co., Texas. Rollins 5366, GH.

L. *fendleri* (Gray) Watson
$2n = 12$: Brewster Co., Texas. B. H. Warnock *s.n.*, GH.
$n = 6$: Howard Co., Texas. Rollins 53117, GH.
$n = 6$: Jeff Davis Co., Texas. Rollins 53114, GH.
$n = 6$: South of Saltillo, Coahuila, Mexico. Rollins & Tryon 58131, GH.
$n = 12$: Andrews Co., Texas. Rollins & Correll 61149, GH.

L. *filiformis* Rollins
$n = 7$: Dade Co., Missouri. Rollins 61158, GH.

L. *globosa* (Desv.) Watson
$n = 7$: Davidson Co., Tennessee. Rollins 5312, GH.
$n = 7$: Davidson Co., Tennessee. Rollins 53132, GH.
$n = 7$: Davidson Co., Tennessee. R. & D. Rollins 5213, GH.
$n = 7$: Maury Co., Tennessee. Rollins & Quarterman 55150, GH.

L. *gordonii* (Gray) Watson
$n = 6$: Baylor Co., Texas. Rollins 53120, GH. PLATE 3.
$2n = 12$: Brewster Co., Texas. B. H. Warnock *s.n.*, GH. PLATE 2.

L. *gracilis* (Hook.) Watson
$n = 6$: Lowndes Co., Mississippi. Rollins *et al.* 5644, GH.
$n = 6$: Bryan Co., Oklahoma. Rollins 5970, GH.
$n = 6$: Ellis Co., Texas. Rollins 5347, GH.
$n = 6$: Kaufman Co., Texas. Rollins 5343 and 5344, GH.
$n = 6$: Leon Co., Texas. Rollins & Correll 5968, GH.
$n = 6$: McLennan Co., Texas. Rollins 5349, GH.
$n = 6$: Williamson Co., Texas. Rollins 5554, GH.

L. *gracilis* var. *repanda* (Nutt.) Payson
$n = 6$: Cotton Co., Oklahoma. Rollins 53121, GH.

L. grandiflora (Hook.) Watson
n = 9: Austin Co., Texas. Rollins 5352, GH.
n = 9: Austin Co., Texas. Rollins & Correll 5965, GH.
n = 9: Dewitt Co., Texas. Rollins 5561, GH.
n = 9: Gonzales Co., Texas. Rollins 5363, GH.
n = 9: Wilson Co., Texas. Rollins 5364 and 5365, GH.
L. intermedia (Wats.) Heller
2*n* = 18: Garfield Co., Utah. Rollins 51200, GH.
L. lasiocarpa (Hook. ex Gray) Watson
n = 7: Cameron Co., Texas. Rollins & Correll 5950, GH. PLATE 1.
L. latifolia A. Nelson
n = 5; 2n = 10: Clark Co., Nevada. Clokey 8358, DS.
L. lescurii (Gray) Watson
n = 8: Cheatham Co., Tennessee. Rollins 53131, GH.
n = 8: Davidson Co., Tennessee. Rollins 53127, GH.
n = 8: Davidson Co., Tennessee. R. & D. Rollins 5209, GH.
n = 8: Rutherford Co., Tennessee. Rollins 55174, GH.
n = 8: Williamson Co., Tennessee. Rollins 53136, GH.
n = 8: Williamson Co., Tennessee. Rollins 55111, GH.
L. lindheimeri (Gray) Watson
n = 6: Refugio Co., Texas. Rollins 5562 and 5563, GH.
n = 6: Victoria Co., Texas. Rollins 5360, GH.
n = 6: Victoria Co., Texas. Rollins 5565, GH.
L. ludoviciana (Nutt.) Watson
2*n* = 10: Moffat Co., Colorado. Rollins & Porter 5115, GH.
L. lyrata Rollins
n = 8: Franklin Co., Alabama. Rollins 5547 and 5548, GH.
n = 8: Franklin Co., Alabama. Rollins *et al.* 5599, GH.
n = 8: Franklin Co., Alabama. Rollins 55188, GH.
L. × *maxima* Rollins *(L. densipila* × *stonensis)*
n = 8: Davidson Co., Tennessee. Rollins *et al.* 5222, GH.
n = 8: Davidson Co., Tennessee. Rollins 5313 and 53142, GH.
L. mcvaughiana Rollins
2*n* = 12: Brewster Co., Texas. Warnock & Turner 8646, GH.
2*n* = 12: Pecos Co., Texas. B. H. Warnock *s.n.*
L. ovalifolia Rydb., var. *alba* Goodman
n = 6: Caddo Co., Oklahoma. Rollins 53125, GH.
n = 6: Comanche Co., Oklahoma. Rollins 53124, GH.
L. palmeri Watson
n = 5: Pima Co., Arizona. J. Poindexter 1, DS.

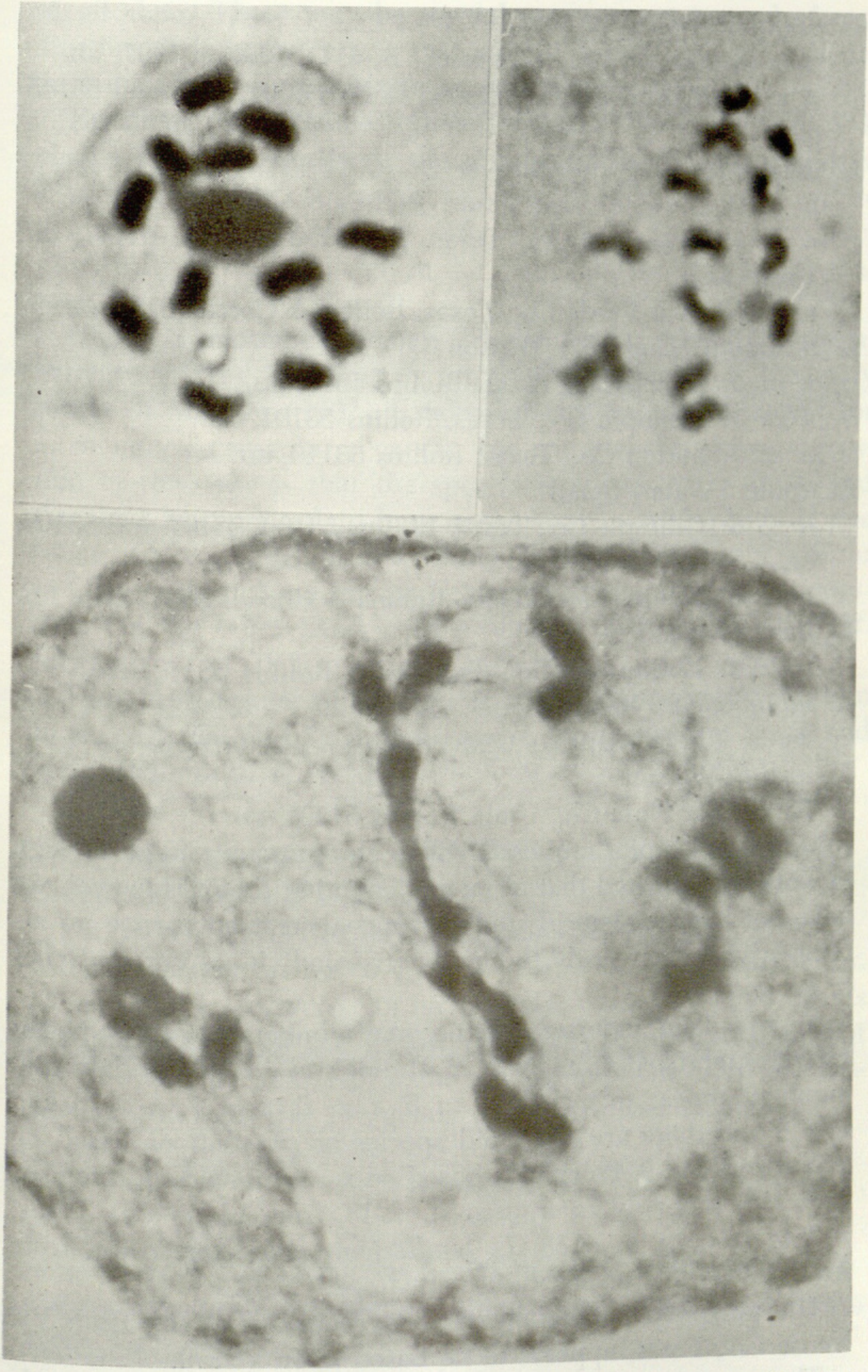

PLATE 2. Upper left, chromosomes in a tapetal cell of *Lesquerella gordonii*, $2n = 12$, Warnock *s.n.;* upper right, chromosomes of *Streptanthus cutleri*, $n = 14$, Rollins and Correll 61111; lower, chromosomes of *Lesquerella purpurea*, $n = 9$, Rollins and Correll 61117. All figures $\times$ 3900.

L. perforata Rollins

$n = 8$: Wilson Co., Tennessee. R. & D. Rollins 5207, GH.

$n = 8$: Wilson Co., Tennessee. Rollins 5304, 5306 and 53145, GH.

L. purpurea (Gray) Watson

$n = 9$: Brewster Co., Texas. Rollins & Correll 6181, GH.

$n = 9$: Hudspeth Co., Texas. Rollins & Correll 61117, GH. PLATE 2.

$n = 18$: Val Verde Co., Texas. Rollins & Correll 6160, GH.

L. recurvata (Engelm.) Watson

$n = 5$: Comal Co., Texas. Rollins 5387, GH.

$n = 5$: Gillespie Co., Texas. Rollins 53101, GH.

$n = 5$: Sutton Co., Texas. Rollins 53110, GH.

L. sessilis (Wats.) Small

$n = 6$: Gillespie Co., Texas. Rollins 53100; 53107 and 53109, GH.

$n = 6$: Kimble Co., Texas. Rollins & Correll 5937, GH.

L. stonensis Rollins

$n = 8$: Rutherford Co., Tennessee. Rollins 55177, GH.

L. subumbellata Rollins

$2n = 10$: Uintah Co., Utah. Rollins & Porter 5119, GH.

L. wardii Watson

$2n = 12$: Piute Co., Utah. Rollins 51221, GH.

Most species of *Lesquerella* have chromosomes large enough to work with beyond that of merely counting them. However, we have not had cytological study as a goal in itself, hence no attempts have been made to characterize individual chromosomes or genomes.

An aneuploid series of chromosome numbers between species extends unbroken from $n = 5$ through $n = 9$. Fundamental numbers appear to include $x = 5$, $x = 6$, $x = 7$, $x = 8$ and $x = 9$ and there are polyploid species or populations based on $x = 6$ and $x = 9$. Polyploids based on $x = 6$ include *L. arenosa*, $2n = 18$; probably *L. argyrea*, $n = 18$, from Llano Co., Texas; *L. engelmannii*, $n = 18$; *L. fendleri*, $n = 12$, one count from Andrews Co., Texas and *L. intermedia*, $2n = 18$.

The polyploid population of *L. purpurea*, $n = 18$, from Val Verde Co., Texas, appears to be based upon $x = 9$.

The most complex chromosome number situation so far encountered in *Lesquerella* occurs in *L. argyrea*. The taxonomy of what must at present be termed the "*L. argyrea* complex" is not at all clear. There may be several taxa present instead of one. Further, it is fairly certain that natural hybridization is a factor in producing the complex taxonomic pattern found.

Excellent chromosome number integrity based on $x = 8$ is shown by the majority of the group of related annual species bearing auriculate cauline leaves (Rollins, 1955). The one certain exception is *L. grandiflora* with $n = 9$. *L. lasiocarpa,* rather doubtfully to be associated in the same subgeneric grouping, has $n = 7$.

High chromosome numbers have been reported for taxa at extremes of the distribution range of *Lesquerella* if the early report of Manton (1932) is taken at face value. Her report for *L. mendocina* was $2n =$ ca. 50. The one fact that raises a question in this case is that the species is attributed to Chile and the seed is supposed to have come from a wild plant. If one relies only on undisputed evidence, *Lesquerella* does not occur in Chile, thus making this particular count slightly open to question. On the other hand, counts of $n = 30$ and $2n = 60$ (cf. Jørgensen *et al.* 1958) seem well established for *L. arctica.*

The chromosomes of *L. argyrea* and *L. lasiocarpa* are shown in PLATE 1, those of *L. gordonii* and *L. purpurea* in PLATE 2, and of *L. gordonii* in PLATE 3.

Lyrocarpa

L. coulteri Hooker & Harvey

$2n = 20$: Pinal Co., Arizona. Nichol 23, US.

Raven (1959) presented a count of $n = 20$ for *L. coulteri* var. *palmeri* (as *L. palmeri*). As far as I am aware, only two counts have been made in the genus. Polyploidy is obviously present but it would be unsafe to make any assumptions as to the fundamental number for the genus without further evidence.

Nerisyrenia

N. camporum (Gray) Greene

$n = 9$: Brewster Co., Texas. Rollins & Correll 6180, GH.

$n = 11$: Torreon-Saltillo, Coahuila, Mexico. Rollins & Tryon 58293, GH.

N. linearifolia (Wats.) Greene

$n = 9$: Culberson Co., Texas. Rollins & Correll 61144, GH.

We now have three separate chromosome numbers for *N.*

camporum, $n = 7$ (Rollins, 1939a) and the two given above. Plants identified as *N. camporum* form extensive populations at frequent intervals from trans-Pecos Texas and New Mexico far to the South and West in the Chihuahuan Desert of Mexico. The variation present is extensive and puzzling. The differing chromosome numbers is a clue that suggests sexual reproduction is not strictly adhered to throughout the species. The possibility that several taxa are being masked by the presently accepted taxonomy has to be considered also.

Physaria

P. acutifolia Rydberg

$2n = 8$: Gunnison Co., Colorado. Ripley & Barneby 10200, GH.

P. australis (Pays.) Rollins

$2n = 8$: Boulder Co., Colorado. Rollins 5145, GH.

$2n = 10$: Uintah Co., Utah. Rollins 3091, GH.

$2n = 14$: Albany Co., Wyoming. Ripley & Barneby 10543, GH.

P. chambersii Rollins

$2n = 10$: Emery Co., Utah. Rollins 51183, GH.

P. chambersii, var. *membranacea* Rollins

$2n =$ ca. 20. Garfield Co., Utah. Rollins 51207, GH.

P. oregona Watson

$2n = 8$: Idaho Co., Idaho. Ripley & Barneby 10729, GH.

Earlier (Rollins, 1939b) it appeared that the chromosome numbers in *Physaria* would be straightforward, based on $x = 4$. At least, this assumption could be made if the first three counts of three different species were indicative of the broader picture in the genus. The count of $n = 8$ for *P. vitulifera* (Weber and Brewbaker, 1950) did not disturb the assumption that $x = 4$ is the fundamental number even though polyploidy was then established in the genus. However, the presently reported counts show that a more complex situation exists in *P. australis* than was shown earlier, and it is clear from counts of *P. chambersii* that $x = 5$ must also be a fundamental number in the genus. This does not take into account the odd number of $2n = 14$ in *P. australis* from Albany Co., Wyoming, which shows no relationship to the other counts.

Rorippa

R. curvipes Greene
$n = 8$: Gunnison Co., Colorado, Rollins 51172, GH.
R. curvisiliqua (Hook.) Bessey
$n = 8$: Josephine Co., Oregon. Constance & Rollins 2943, GH.
R. sinuata (Nutt.) A. S. Hitchcock
$n = 8$: Thomas Co., Kansas. Rollins 5101, GH.
R. subumbellata Rollins
$n = 5$: Eldorado Co., California. Rollins 3027, GH.

The fundamental number $x = 8$ has become well established in *Rorippa* with most of the recent counts merely confirming and extending earlier records. A polyploid series exists but deviations from a multiple series were not recorded prior to the present count of $n = 5$ for *R. subumbellata*. This disturbance of an otherwise consistent chromosome number pattern in the genus is anomalous and the significance of it is not known.

Selenia

S. aurea Nuttall
$n = 23$: Garland Co., Arkansas. Rollins & Chambers 5756, GH.
S. grandis Martin
$n = 12$: Dimmit Co., Texas. Barclay 706, GH.

Selenia grandis grows very well under greenhouse conditions and we were able to sample the material repeatedly for reassurance of an accurate count. Material of *S. aurea* was fixed in the field. These first known counts for the genus suggest polyploidy. The disrupted ranges of most of the species provide a basis for an evolutionary pattern that could prove to be exceedingly interesting. This is a genus that deserves careful re-study even though it was the relatively recent subject of a paper by Martin (1940).

Sibara

S. pectinata Greene
$n = 14$: Desierto Viscaino Region, Baja California, Mexico. Gentry 7396, GH.
S. virginica (L.) Rollins
$2n = 16$: Marshall Co., Tennessee. Sharp *et al.* 11188, GH.

Of the two previous counts in *Sibara* (Rollins, 1947) $2n = 26$ for *S. desertii* and $2n = 28$ for *S. viereckii*, the latter fits with the count for *S. pectinata*. The other two counts show little relationship to each other or to the $n = 14$ number. All species of *Sibara*, except *S. virginica*, are limited in distribution and are infrequently collected. It will probably take many years to resolve what is at present a puzzling series of chromosome numbers in the genus.

Sisymbrium

S. *altissimum* L.

$n = 7$: Lake County, California. Breedlove 5134, GH.

S. *linearifolium* (Gray) Payson

$n = 11$: Las Animas Co., Colorado. Rollins 1818, GH.

$n = 11$: Brewster Co., Texas. Rollins & Correll 6168 and 6139, GH.

S. *linifolium* Nuttall

$n = 7$: Albany Co., Wyoming. Rollins & Porter 5113, GH.

$n = 8$: Uinta Co., Wyoming. Rollins 1773, GH.

S. *orientale* L.

$n = 7$: San Diego Co., California. Breedlove 1816, GH.

The two counts for the introduced species, *S. altissimum* and *S. orientale* are the same as those of most other European species of *Sisymbrium*. *S. linifolium* appears to fit the same pattern but the count discrepancy of $n = 7$ and $n = 8$ may have some significance. This species is morphologically very variable and the infraspecific taxonomy requires intensive study for a better understanding than is now available. The very different count of $n = 11$ for *S. linearifolium* lends support to taxonomic treatments that place this species outside of *Sisymbrium*.

Stanleya

S. *pinnata* (Pursh) Britton, var. *integrifolia* (James) Rollins

$n = 14$: Brewster Co., Texas. Rollins 6191, GH.

The count of $n = 14$ does not accord with my previous counts (Rollins, 1939c) which indicated $x = 12$ as the fundamental number for *Stanleya*. On the other hand, $n = 14$ fits an emerging $x = 14$ that is widespread in *Caulanthus*, *Thelypodium* and *Strepthanthus*, genera somewhat related to *Stanleya*.

Strepthanthella

S. *longirostris* (Wats.) Rydberg
$2n = 28$: Sweetwater Co., Wyoming. Rollins & Porter 5144, GH.
S. *longirostris*, var. *derelicta* J. T. Howell
$n = 14$: San Diego Co., California. Breedlove 1865, GH.

Although *Streptanthella* is usually given the status of a monotypic genus in current manuals and floras, it is by no means certain that this is the correct taxonomic interpretation. It is probable that the one species, S. *longirostris*, should be associated with such species as *Caulanthus cooperi* but perhaps not in the genus *Caulanthus*. The chromosome number does not contribute anything toward solving the problem.

Streptanthus

S. *barbiger* Greene
$n = 14$: Lake Co., California. Breedlove 5145, GH.
S. *breweri* Gray
$n = 14$: Colusa Co., California. Breedlove 5181, GH.
$n = 14$: Napa Co., California. Breedlove 5088, GH.
S. *carinatus* Wright
$n =$ ca. 14: Brewster Co., Texas. Rollins & Correll 6178, GH.
$n = 14$: Presidio Co., Texas. Rollins & Correll 61105, GH. PLATE 3.
S. *cordatus* Nuttall
$n = 12$: Mohave Co., Arizona. Rollins 4166, GH.
S. *cutleri* Cory
$n = 14$: Brewster Co., Texas. Rollins & Correll 61111, GH. PLATE 2.
S. *diversifolia* Watson
$n = 14$: Fresno Co., California. Breedlove 5270, GH.
S. *glandulosa* Hooker
$n = 14$: Lake Co., California. Breedlove 5158, GH.
$n =$ ca. 14: Santa Clara Co., California. Breedlove 4986, GH.
S. *insignis* Jepson
$n = 14$: Monterey Co., California. Breedlove 2375, GH.
$n = 14$: San Benito Co., California. Wiggins & Rollins 24 and 34, GH.

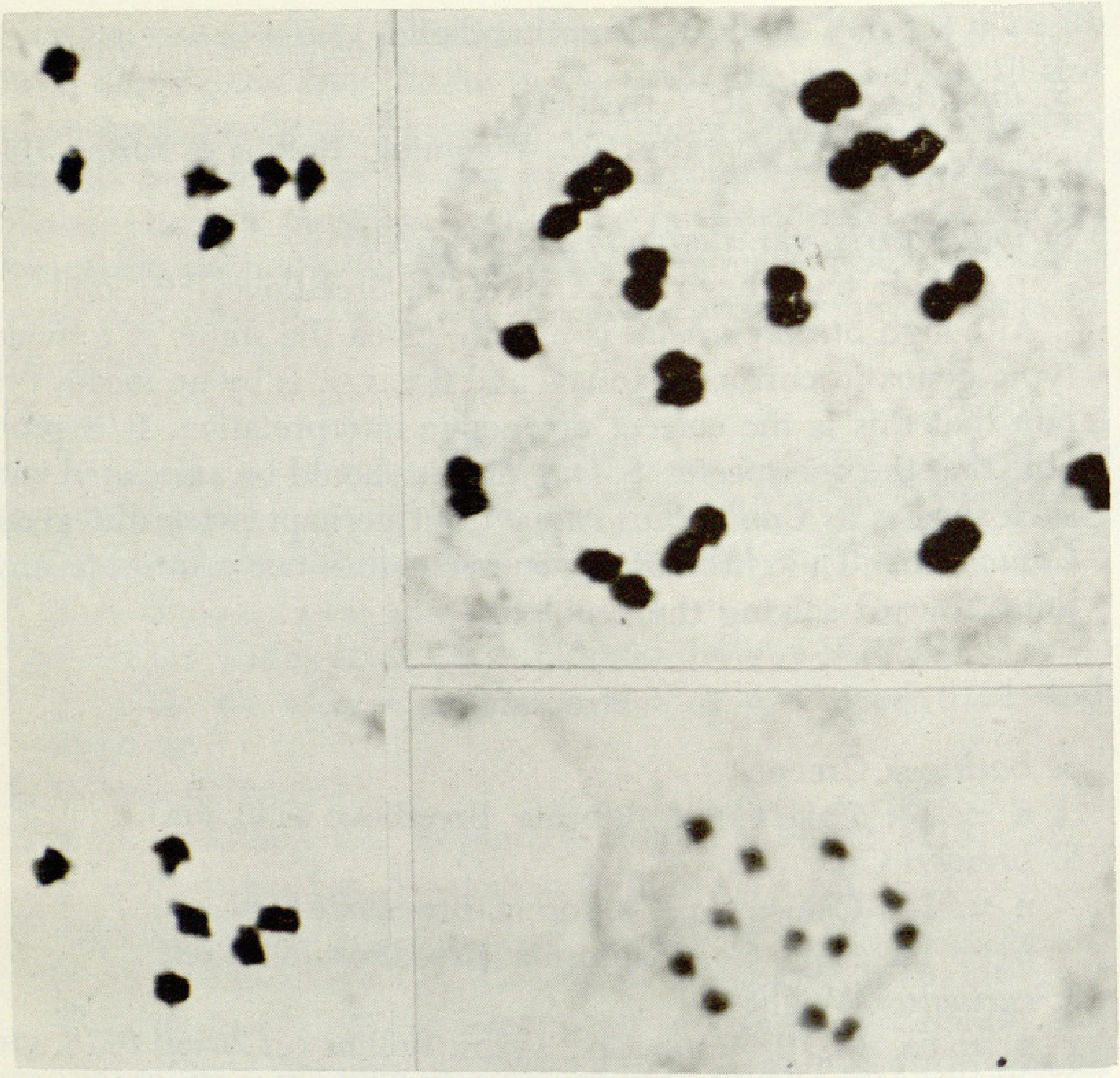

PLATE 3. Left, chromosomes of *Lesquerella gordonii*, $n = 6$, Rollins 53120; upper right, chromosomes of *Streptanthus carinatus*, $n = 14$, Rollins and Correll 61105; lower right, chromosomes of *Selenia grandis*, $n = 12$, Barclay 706. All figures × 3900.

S. *niger* Greene

$n = 14$: Marin Co., California. Breedlove 4962, GH.

S. *secundus* Greene

$n = 14$: Sonoma Co., California. Constance & Rollins 2863, GH.

S. *tortuosus* Kellogg

$n = 14$: Siskiyou Co., California. Constance & Rollins 2901, GH.

$n = 14$: Tuolumne Co., California. Breedlove 4830, GH.

There is near uniformity of the chromosome number $n = 14$ in *Streptanthus*. The known exception is S. *cordata* with $n = 12$. Further counts are needed in the group to which S. *cordatus* belongs. The species involved were segregated from *Streptanthus* and placed in the genus *Cartiera* by Greene (1906) and by Schulz (1936). The one count pointed to here suggests the possibility of chromosome number support for such a separation. However, the uniformity elsewhere in *Streptanthus* does not support a wholesale breaking up of the genus as attempted by Greene (l.c.) and followed by Schulz (l.c.).

Chromosomes of *S. cutleri* are shown in PLATE 2. Those of *S. carinatus* are shown in PLATE 3.

Synthlipsis

S. greggii Gray
$n = 10$: Northeast of Durango, Durango, Mexico. Rollins & Tryon 58280, GH.

This is the first count in *Synthlipsis*. The three known species (Rollins, 1959) are found mainly in Mexico.

Thelypodium

T. flavescens (Hook.) Watson
$n = 14$: Monterey Co., California. Breedlove 2180, GH.

T. flexuosum Robinson
$n = 13$: Harney Co., Oregon. Raven 18452, GH.

T. laciniatum (Hook.) Endlicher, var. *milleflorum* (A. Nels.) Payson
$n =$ ca. 14: Eureka Co., California. Raven 18533, GH.

T. laciniatum, var. *streptanthoides* (Leiberg) Payson
$n =$ ca. 12: Grant Co., Washington. Raven 18487, GH.

T. lemmonii Greene
$n = 14$: San Benito Co., California. Wiggins & Rollins 36, GH.

T. texanum (Cory) Rollins
$n = 13$: Brewster Co., Texas. Rollins & Correll 6188, GH.
$n = 13$: Brewster Co., Texas. Rollins & Correll 6176, GH.

A relatively high fundamental number (or numbers) is emerging for *Thelypodium*. This finding is in general accord with the presence of similar numbers in related genera such as *Stanleya* and *Caulanthus*. The counts given for *T. laciniatum* are tentative because good figures for counting could not be found in the material available for study.

Thlaspi

T. fendleri Gray

$2n = 14$: Mt. Ord, Brewster Co., Texas. B. H. Warnock *s.n.*, GH.

$2n = 28$: Hinsdale Co., Colorado. Rollins 51107, GH.

T. glaucum A. Nelson

$2n = 14$: Douglas Co., Colorado. Rollins & Livingston 5148, GH.

T. parviflorum A. Nelson

$n = 7$: Sheridan Co., Wyoming. Williams 3092, GH.

Thlaspi is widely distributed in the Northern Hemisphere but also occurs sparingly in temperate areas of the Southern Hemisphere. The genus is relatively well-marked and is readily distinguishable from others of the family. The chromosome number too is relatively uniform, based on $x = 7$. Our material shows polyploidy to be present in *T. fendleri.*

Tropidocarpum

T. gracile Hooker

$n = 8$: San Diego Co., California. Breedlove 1822, GH.

$n = 8$: Santa Barbara Co., California. Breedlove 1904, GH.

Thysanocarpus

T. curvipes Hooker

$n = 7$: Humboldt Co., California. Constance & Rollins 2884, GH.

T. elegans Fischer & Meyer

$2n = 28$: San Luis Obispo Co., California. M. P. & A. G. Vestal *s.n.*, GH.

Manton (1932) gave a count of $2n = 28$ for *T. curvipes.* If all identifications are correct, this means polyploidy is present within *T. curvipes.* The presence of $2n = 28$ in *T. elegans* proves that multiple chromosome numbers are present in the genus, at least. The taxonomy of *Thysanocarpus* is very much in need of a careful study and revision.

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