THE CHROMOSOME MORPHOLOGY IN THE GENUS *SILPHIUM* (COMPOSITAE)[1, 2, 3]

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ABSTRACT

A detailed morphologic study of the mitotic chromosomes of root tips in each of the currently recognized species of *Silphium* reveals a diploid complement of 14 chromosomes. The karyotypes of the species are similar and cannot be separated into distinct groups. Although there is variation among the species in both arms of the chromosomes, the short arm varies in length more than the long arm. Although the short arms of Chromosomes VI and VII are extremely short, there are no satellites. The chromosomes possess a distinct and recognizable morphology.

The genus *Silphium* (Compositae) is a taxonomically complex group of plants that can be separated conveniently into eight morphologically distinct groups of species (T. R. Fisher, personal communication); Small (1933) recognized five morphological groups. The natural distribution of the genus extends from the Dakotas to west-central Texas, east to central Florida, and north to Virginia.

The first report of chromosomes in *Siliphium* is that of Merrell (1900), who reported $n=8$, which is probably the reduction number. He also reported that the dividing nuclei in the larger tapetal cells appear to have more than 8 chromosomes, probably 16. Taylor (1926) reported $2n=14$ chromosomes in root tips of *S. perfoliatum*. Fisher and Cruden (1962) confirmed Taylor's count of $2n=14$ for *S. perfoliatum*. Taylor also lists six morphologically distinguishable pairs of chromosomes. That the mitotic chromosomes had such distinct morphology was confirmed by Fisher and Cruden (1962). Subsequent detailed hybridization and cytological experiments indicated that the species of *Silphium* have had a history of reciprocal translocations, and that three groups of species differ in chromosomal end arrangement. These findings are being reported by T. R. Fisher elsewhere.

This investigation considers in detail the morphology of the mitotic chromosomes of root tips in each of the currently recognized species of the genus *Silphium*.

MATERIALS AND METHODS

The species used in this study were originally collected over a period of eight years from a number of different sites in eastern United States. The collection sites and the collectors are listed in Table 1. Seeds from these plants were brought back, planted, and grown under greenhouse conditions, and were later transplanted to the research garden. The specific plants used in this study were then transplanted from the research garden to the greenhouses of the Department of Botany and Plant Pathology of The Ohio State University. A few of the slide preparations were made from root tips of plants growing in soil. However, most root tips were obtained from plants growing hydroponically in Modified Bristol's Solution (Bold, 1949).

All root tips investigated were removed from young, rapidly growing roots. They were collected at various times during the day, and at different times of the year. No periodicity of mitosis was recognized. The root tips were collected

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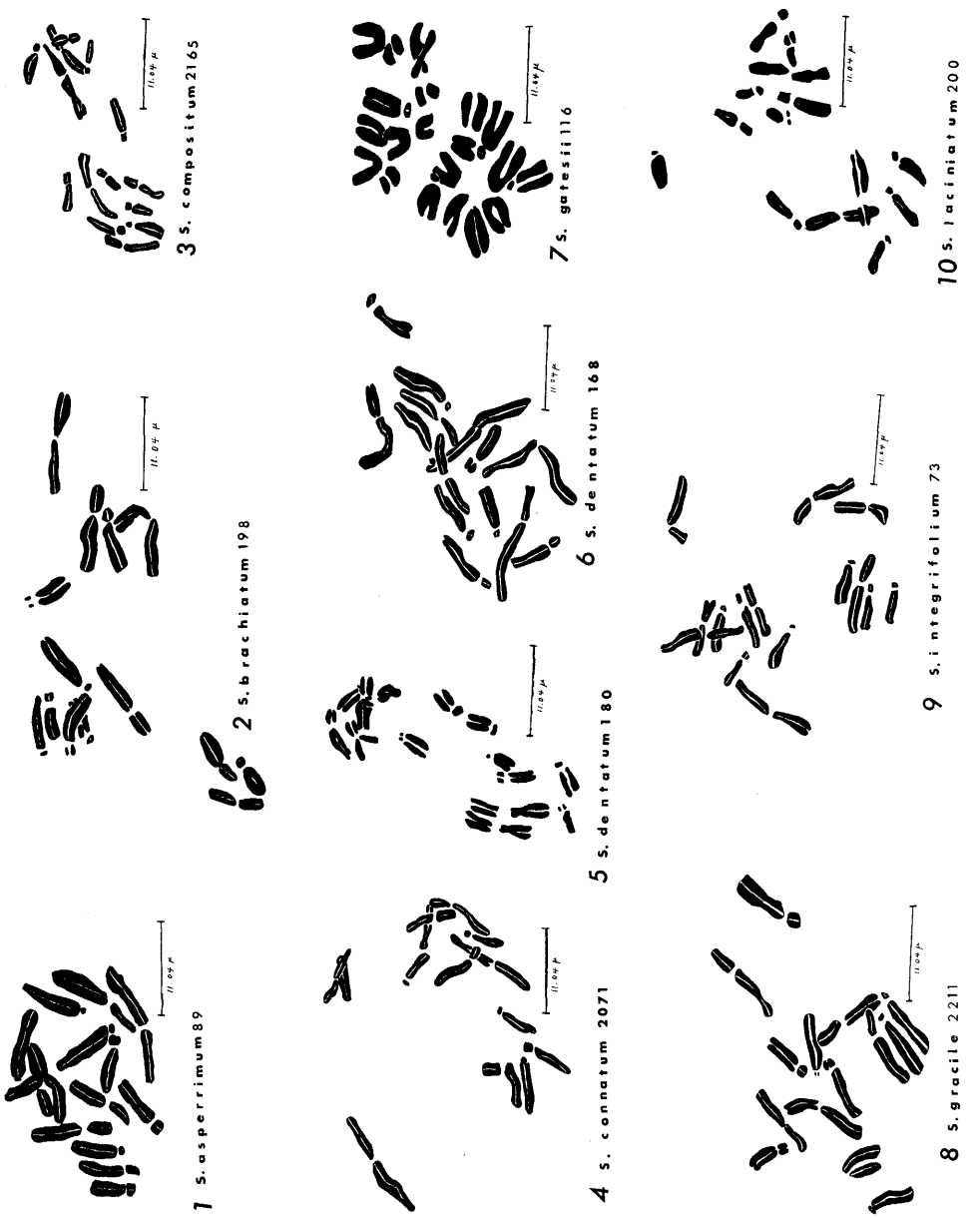
and pretreated in 0.1% colchicine solution for one hour and fixed in 1:3 acetic acid, ethanol. They were stained with aceto-carmine (saturated solution of carmine in 45% acetic acid) and squashed under a cover glass. If the slide contained a sufficient number of reproducing cells, the material was frozen with dry ice, and the cover slip removed. Dehydration was accomplished by placing the

TABLE 1. Collectors and collection sites for species of plants used in this study

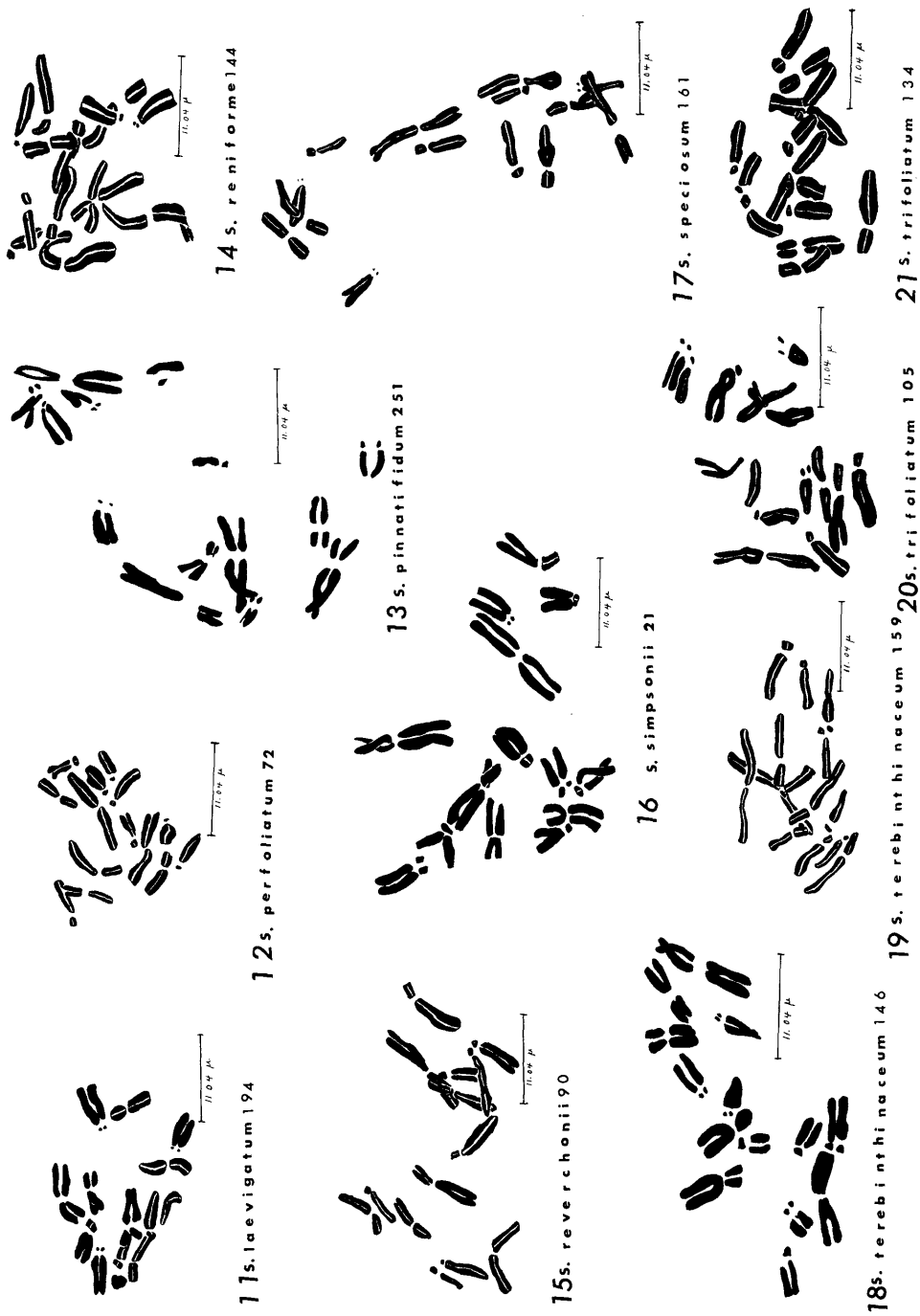
Species	Research field no.	Source of material
S. asperrimum Hook.	89	Dallas County, Texas. Shinners s.n.
S. brachiatum Gatt.	198	Along roadside on Route 35, 6 miles east of junction of Route 72, Jackson Co., Ala. Fisher 1775
S. compositum Michx.	2165	One mile on Route 10 south of Banoah School. Clay banks along roadside of County Road 2043. Catawba Co., N.C. Fisher and Speer 2165
S. connatum L.	2071	Fayette Co., W. Va. Hicks and Bartley s.n.
S. dentatum Ell.	180	Six miles north of Covington, Newton Co., Ga. Fisher 1755
S. dentatum Ell.	168	Athens, Clark Co., Ga. Fisher 168
S. gatesii Mohr	116	Dolly Ridge Road near Birmingham, Jefferson Co., Ala. E. Garnett s.n.
S. gracile Gray	2211	On U. S. Routes 69 and 287, 8.65 miles northwest of junction with Texas 327: 3.1 miles southeast of Village Mills southern limits. Hardin Co., Texas. Pinkava 696
S. integrifolium Michx.	73	Near Chalmers, White Co., Ind. Fisher 624
S. laciniatum L.	200	Along Route 231, 2 miles north of Switz City, Green Co., Ind. Fisher 200
S. laevigatum Pursh.	194	Little Mountain State Park near fishing camp, along road, Marshall Co., Ala. Fisher 1771
S. perfoliatum L.	72	Along Clear Creek and Route 46, Brown Co., Ind. Fisher s.n.
S. pinnatifidum Ell.	251	1½ miles west of Lietchfield, Grayson Co., Ky. Fisher 2026
S. reniforme Raf.	144	On Route 321, 5 miles south of Blowing Rock, Caldwell Co., N.C. Fisher s.n.
S. reverchonii Bush.	90	3.6 miles west of Hallsville, Harrison Co., Texas. Shinners 24159
S. simpsonii Greene	21	Edge of pine forest along U. S. 167 about 5 miles north of Turkey Creek, Evangeline Parish, La. Heiser 4010
S. speciosum Nutt.	161	Prairie Ravine, Flint Hill area, 6 miles west, 6 miles south of Emporia, Lyon Co., Kan. R. L. McGregor 14170
S. terebinthinaceum Jacq.	146	One mile east of Ashmore, Coles Co., Ill. Fisher 146
S. terebinthinaceum Jacq.	159	One mile east of Ashmore, Coles Co., Ill. Fisher 159
S. trifoliatum L.	134	Rutherford Co., N.C. A. E. Radford s.n.
S. trifoliatum L.	105	Chuckery Cemetery, Madison Co., Ohio. Fisher s.n.

slides in 95% and 100% ethanol for approximately three minutes each. The material was then permanently mounted in Euparal.

Chromosomes of metaphase complements were drawn with the aid of a camera lucida at a magnification of approximately 1,125 x and are reproduced as figures 1–21. The chromosome complement of five cells of each species was measured, using an ocular micrometer. The two arms were measured exclusive of the centromere. The chromosomes of each cell were designated on the basis of the



FIGURES 1–10. Camera lucida drawings of chromosomes of metaphase complements.



FIGURES 11–21. Camera lucide drawings of chromosomes of metaphase complements.

TABLE 2. The mean length of the two arms, the average total length, and the average ratio of the length of the long arm to that of the short arm for each chromosome of the species studied

Chromosome number	Length of long arm in microns	Length of short arm in microns	Total in microns	Ratio
I	6.41	5.19	11.61	1.23
II	5.85	2.76	8.62	2.46
III	4.83	2.39	7.22	2.04
IV	4.87	1.68	6.55	3.57
V	4.65	1.39	6.05	4.46
VI	4.57	0.73	5.31	6.57
VII	3.71	0.96	4.68	4.03

total length, the longest being Chromosome I and the shortest being Chromosome VII.

A ratio was computed by dividing the length of the long arm by that of the short arm. Although several factors may affect the absolute length of a chromosome, the ratio is more likely to remain constant and serve as a more significant indicator. Table 2 lists for each chromosome the mean length of the two arms, the average total length, and the average ratio of the length of the long arm to that of the short arm. Figures 22a and 22b are graphs of these measurements.

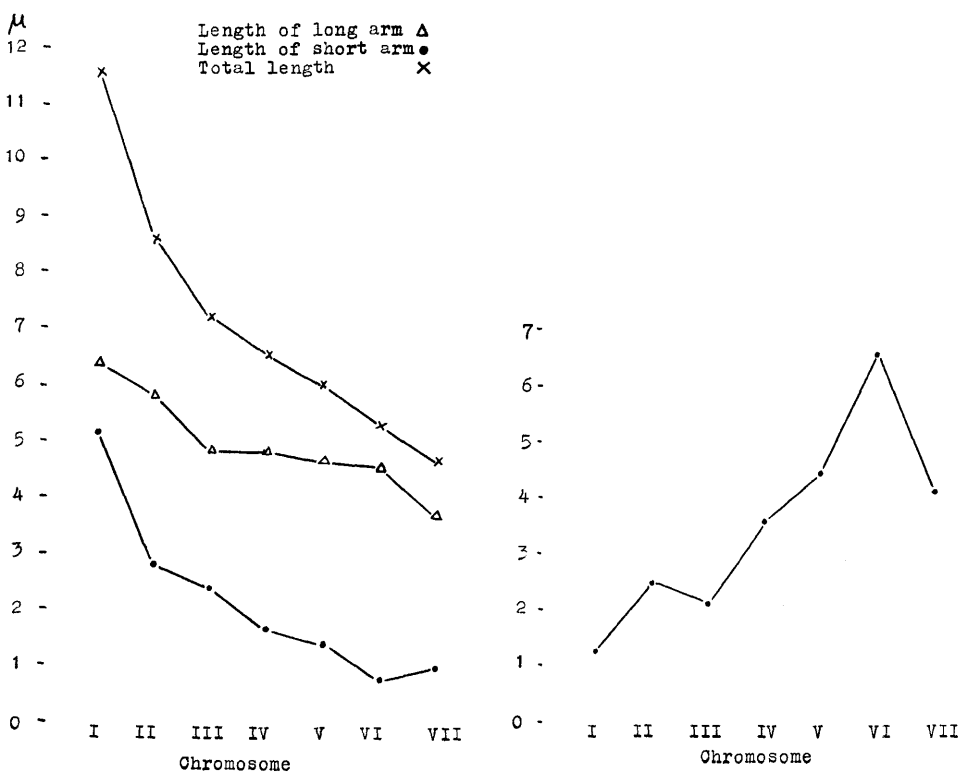


FIGURE 22a. Graph of the mean lengths of the two arms and of the average total length for each chromosome of the species studied.

FIGURE 22b. The average ratio of the length of the long arm to that of the short arm for each chromsome of the species studied.

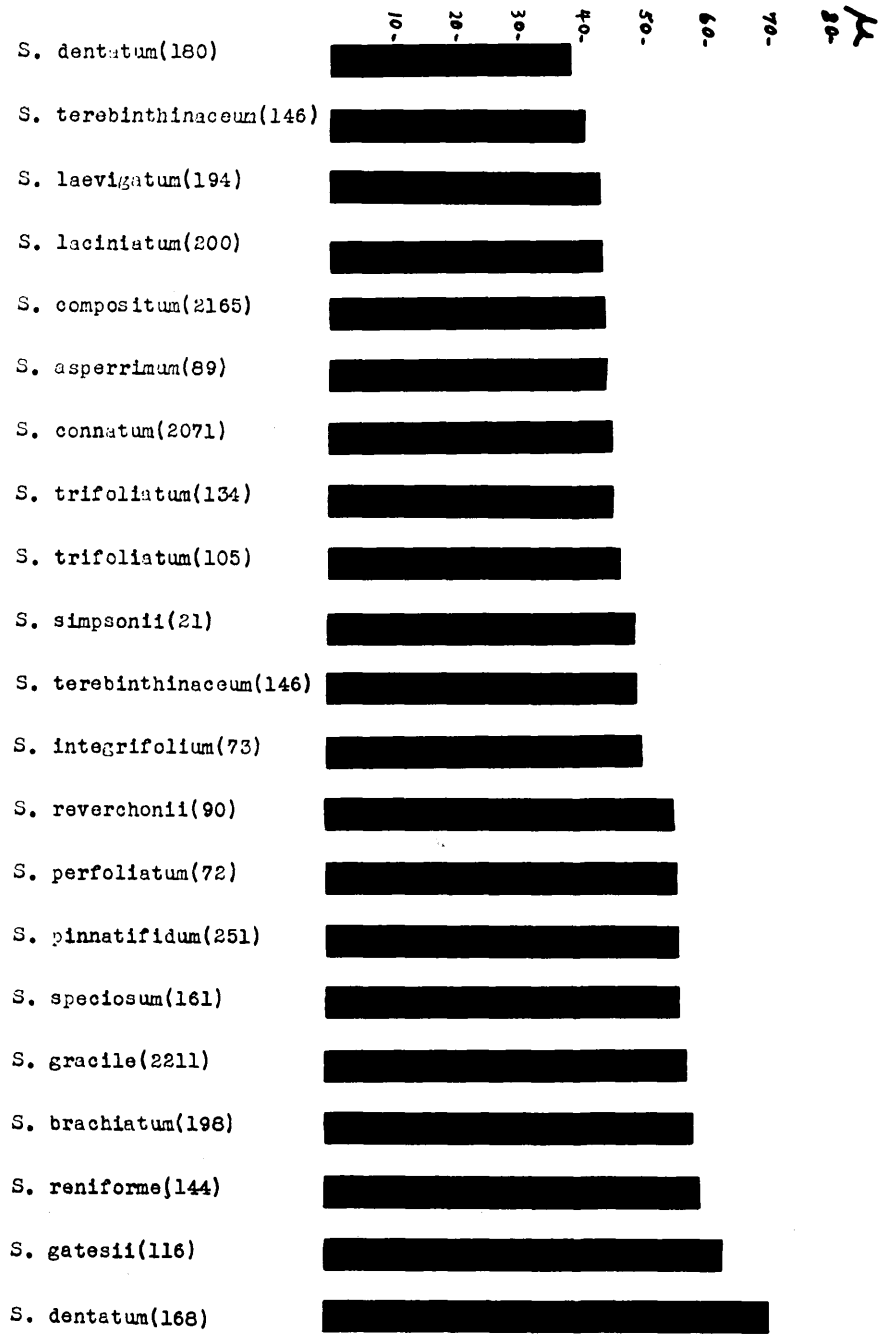
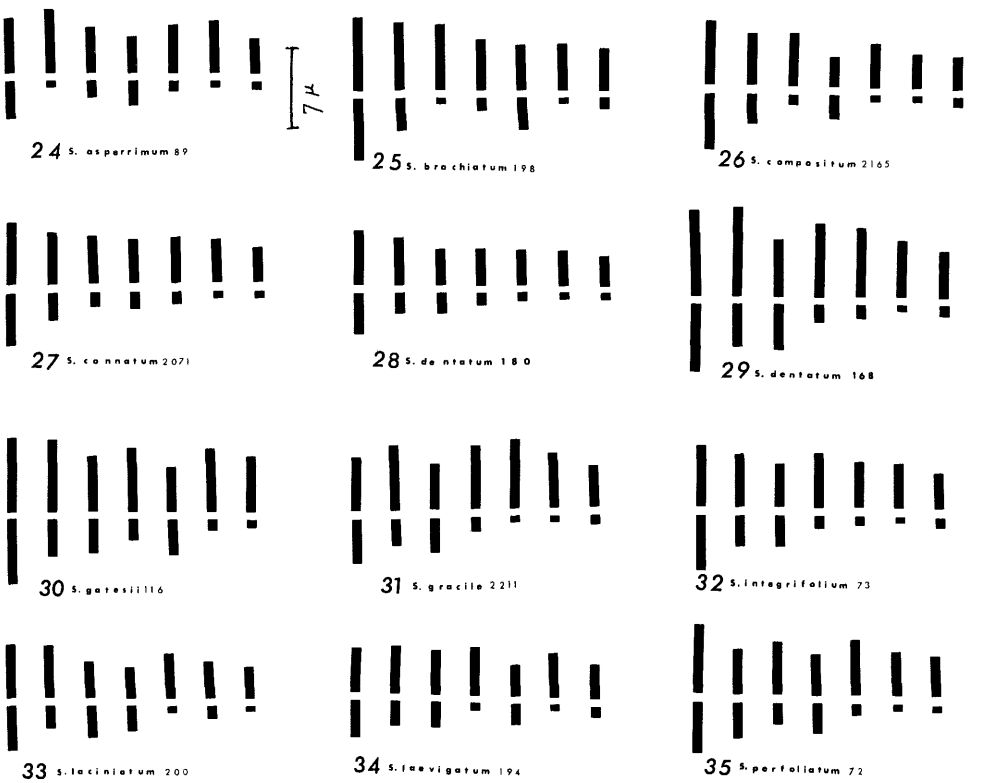


FIGURE 23. Bar graph of the mean sum of the length of both arms of all seven chromosomes of the species studied.

Figure 23 is a bar graph of the mean sum of the length of both arms of all seven chromosomes of the species studied. The average length of the two arms of all seven chromosomes of each species is represented in figures 24–44. These measurements represent the average of the chromosomes of five cells and are arranged according to increasing length from right to left.



FIGURES 24–35. Average length of the two arms of all seven chromosomes for each species studied.

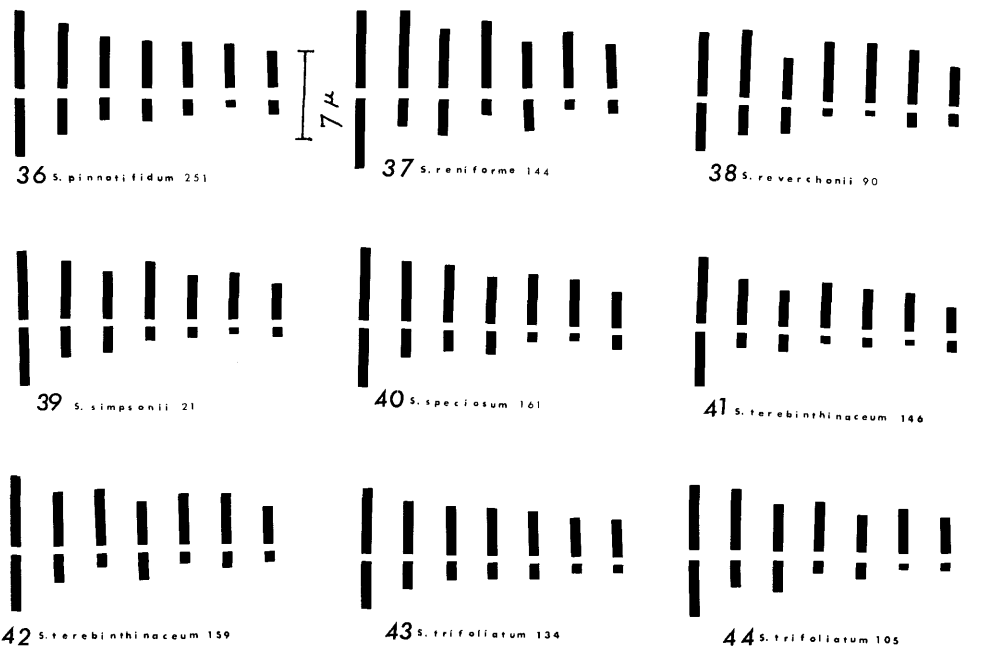
RESULTS

Chromosome I. The longest chromosome is designated Chromosome I. Because it is longer than all the rest, it is readily identified. The centromere is nearly median in all species. The total length of the two arms ranges from 8.34 μ to 14.96μ. The length of the long arm ranges from 4.54 μ to 8.22 μ, and the length of the short arm ranges from 3.80 μ to 6.78 μ. In general, the total length of the short and long arms are comparatively similar among the different species. However, there is considerable difference between the total lengths, and the lengths of the two arms of the species with the shorter chromosomes and those with the longer ones. The ratios of the lengths of the long arm to those of the short arm vary little among the species. These data suggest that this chromosome is the least variable of the seven.

Chromosome II. The length of the long arm ranges from 4.40 μ to 8.74 μ, and the length of the short arm ranges from 5.89 μ to 12.86 μ. With the exception of *S. asperrimum* (89), the length of the arms varies only slightly more than those

of Chromosome I. *S. asperrimum* (89) is the only species which deviates markedly from the others by having an extremely short arm. The ratio of the length of the long arm to that of the short arm varies much more than in Chromosome I. The ratios range from 1.25 to 10.26. However, with the exception of *S. asperrimum* (89), the ratios do not fluctuate nearly so much as in Chromosomes III, IV, V, VI, and VII. (Numbers in parentheses following names of species are research field numbers.)

Chromosome III. The total length of both arms, the length of the short arm, and the ratio of the length of the long arm to that of the short arm vary much more in Chromosome III than in Chromosomes I and II. However, there is no more variation with respect to the length of the long arm than there is in Chro-



FIGURES 36–44. Average length of the two arms of all seven chromosomes for each species studied.

mosomes I and II. The length of the long arm ranges from 3.52 μ to 6.55 μ, the length of the short arm ranges from 0.53 μ to 4.52 μ, and the total length ranges from 5.54 μ to 10.14 μ. The ratio of the lengths of the long arm to those of the short arm ranges from 1.24 to 11.29. The ratios fluctuate much more than in Chromosomes I and II, but not so much as in Chromosomes IV, V, and VI. The most pronounced deviations from the common lengths are found in *S. connatum* (2071), *S. asperrimum* (89), *S. pinnatifidum* (251), *S. compositum* (2165), *S. terebinthinaceum* (159), and especially in *S. brachiatum* (198), which has extremely short arms.

Chromosome IV. The length of the long arm ranges from 2.95 μ to 7.10 μ, and the length of the short arm ranges from 0.70 μ to 3.08 μ. The total length ranges from 4.89 μ to 8.92 μ. The length of the short arm and the total length vary more than in Chromosomes I and II. The ratios range from 1.28 to 8.25, and are quite erratic. *S. terebinthinaceum* (146), *S. laevigatum* (194), and *S. reverchonii* (90) have especially irregular ratios.

Chromosome V. The total length ranges from 4.35 μ to 8.07 μ, the length of the long arm ranges from 3.16 μ to 7.06 μ, and the length of the short arm ranges from 0.55 μ to 3.50 μ. With the exception of *S. reniforme* (144), *S. gatesii* (116), and *S. brachiatum* (198), the length of the short arm is shorter than that of Chromosomes I, II, III, and IV of most species. The ratios range from 1.25 to 11.57, and are so irregular that, in this respect, there is no apparent pattern among these species of *Silphium*. Those which have especially high ratios are *S. compositum* (2165), *S. laciniatum* (200), *S. reverchonii* (90), and *S. gracile* (2211).

Chromosome VI. The length of the long arm ranges from 3.40 μ to 6.30 μ. The length of the short arm ranges from 0.50 μ to 1.30 μ, and the total length ranges from 4.07 μ to 7.38 μ. There is little variation among the species in the total length and the length of the long and short arms of these chromosomes. These measurements are more consistent than those for any other chromosome except Chromosome VII. However, there is much variation in the ratios, which range from 3.49 to 9.00. The short arm is extremely short, being less than 1 μ except in *S. laciniatum* (200), *S. reverchonii* (90), and *S. gatesii* (116). Because of the extreme shortness of the short arm, a small change in the length of the short arm produces a large change in the ratio. Therefore the ratios are very irregular, and so are probably not so significant in this chromosome.

Chromosome VII. The length of the long arm ranges from 2.63 μ to 5.60 μ, and the length of the short arm ranges from 0.55 μ to 1.42 μ. There is little variation among the species in the length of the long and short arms, and in the total length. These measurements are less variable than those for any other chromosome except Chromosome VI. The short arm is approximately the same length as in Chromosome VI, generally about 1 μ long. Because the short arm is so extremely short that a slight change produces a great change in the ratio, the ratios are somewhat irregular, ranging from 2.39 to 6.66. Therefore as in Chromosome VI, the ratio probably is not so important as in the other five chromosomes.

DISCUSSION

All species studied have a diploid complement of 14 chromosomes. Compared with many other genera, such as *Crepis* (Babcock and Jenkins, 1947), the karyotypes of the different species are strikingly similar.

The results do not seem to identify any distinct groups of species. Although in general there is much similarity in the length of the arms and the total length of the chromosomes, there are many obvious differences.

There is variation among the species in the lengths of both arms of the chromosome; the short arm, however, varies more than the long one.

There are no satellites, but the short arms of Chromosomes VI and VII are extremely short and at times may be mistaken for satellites. These extremely short arms are probably the "rod-like appendages to the proximal end" observed by Taylor (1926). With few exceptions, the short arms of these two chromosomes are less than 1 μ long.

Three of the species in this study are represented twice: *S. dentatum* by number 180 and number 168, *S. terebinthinaceum* by numbers 146 and 159, and *S. trifoliatum* by numbers 134 and 105. It is interesting to note that, by almost all criteria used in this study except the ratio of the length of the long arm to that of the short arm, the two representatives of *S. dentatum* are greatly different. In fact, with respect to the average total length of Chromosomes I through VI, number 180 has the least total length and number 168 has the greatest total length. Except for Chromosome V, the ratios of the various chromosomes are very similar. The two representatives of *S. terebinthinaceum* are somewhat divergent in their characteristics, too, although not so much so as the representatives of *S. dentatum*. The representatives of *S. trifoliatum* seem to be extremely similar with respect to the characteristics used in this study.

With a few notable exceptions, the chromosomes of the species of *Silphium* which were studied in this project do seem to have a distinct morphology. The lengths of the two arms of the Chromosomes II, III, IV, and V are more variable than those of Chromosomes I, VI, and VII. Stebbins (1950) has recognized phylogenetic trends in the changes of the absolute chromosome size. It is not yet possible to ascertain any evolutionary relationships in the genus *Silphium* based on chromosome morphology.

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