

THE GENUS *SILPHIUM* IN OHIO^{1, 2}

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ABSTRACT

The genus *Silphium* is represented in Ohio by four species, *S. perfoliatum* L., *S. trifoliatum* L., *S. laciniatum* L., and *S. terebinthinaceum* Jacqs. Two of these species, *S. laciniatum* and *S. terebinthinaceum*, have hybridized in a prairie habitat west of Marion, Ohio. This population has been analyzed using the Gay Method of population analysis. In contrast to a similar population of hybridizing individuals from Coles County, Illinois, where backcrossing is apparently in the direction of *S. laciniatum*, backcrossing in the Marion, Ohio, population appears to be in the direction of *S. terebinthinaceum*.

The genus *Silphium* is represented in Ohio by four species: *S. perfoliatum* L., *S. trifoliatum* L., *S. laciniatum* L., and *S. terebinthinaceum* Jacqs. The objective of this paper is to describe their taxonomy, morphology, ecology, and hybridization as it is known in Ohio. A natural hybridizing population is analyzed by the hybrid number method of Gay (1960), which is a modification of the hybrid index method of Anderson (1949).

KEY TO SPECIES IN OHIO

Stems leafy

Leaves connate—perfoliate; stems quadrangular.....1. *S. perfoliatum*
Leaves usually with short petioles, commonly verticillate in 3's or 4's, sometimes
alternate.....2. *S. trifoliatum*

Stems naked except a few reduced leaves

Leaves pinnatifid or bipinnatifid; flowering stems with hispid or hirsute spreading
hairs.....3. *S. laciniatum*
Leaves elliptic, sharply toothed, not pinnatifid; stems glabrous or essentially so.....
4. *S. terebinthinaceum*

1. *S. perfoliatum* L. ssp. *perfoliatum*. Cup-plant

Perennial, stem conspicuously angled, 1-3 m tall, glabrous or with a few scattered hairs near the base. Leaves with connate-perfoliate bases, blades broad at base, nearly deltoid to broadly ovate, irregularly toothed, scabrous above, hispid below. Upper stems branched bearing numerous heads. Bracts of inflorescence ovate in 2 or 3 series, glabrous except on ciliate margins. Ray flowers 20-25. Achenes obovate with well developed wings, sinus deep. Woodland margins, along streams and bottom land. Widely distributed in Ohio. This species can be hybridized artificially with *S. trifoliatum*, but no natural hybrids are known to occur in Ohio. *Silphium perfoliatum* ssp. *connatum* (L.) Cruden occurs in the mountainous regions of West Virginia, Virginia and North Carolina and is not known to occur in Ohio. A biosystematic treatment of this species will appear elsewhere.

2. *S. trifoliatum* L.

Perennial with thick, fibrous roots, creeping. Stem glabrous, often slightly glaucous, 1-2 m. tall. Leaves often verticillate in 3's or 4's, but just as often merely opposite or occasionally alternate; leaf blades lanceolate to ovate-lanceolate, toothed, usually scabrous above. Heads many, bracts imbricate, subequal, glabrous except for ciliate margins; rays light yellow, averaging 9. Achenes orbicular to ovate, wing pointed at apex. Woodlands and prairies.

This species has been treated by some authors as being composed of two taxa, variety *trifoliatum* and variety *latifolium* based on pubescence of leaves and frequency of trifoliate-ness of leaves, the latter variety most commonly glabrous and leaves merely opposite. These two varieties are represented in Ohio. The biosystematics of these varieties is under intensive study by Mr. Wallace Weber and results of this investigation will be reported elsewhere.

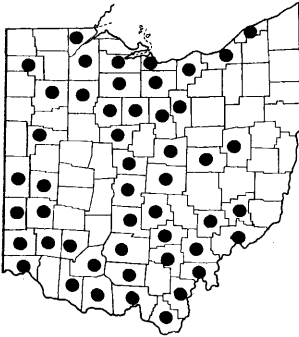
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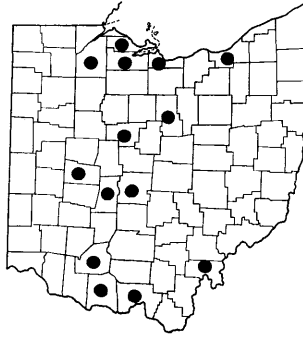
In Ohio, this species has been collected in 14 counties, in both glaciated and unglaciated regions. Some evidence based on studies by Mr. Weber indicates that plants from these two areas represent at least ecotypes.

3. *Silphium laciniatum* L. Compass-plant

Perennial, coarse and rough, taproot 3-5 inches thick at crown, extending 1-3 feet in ground. Stem 2-3 m. tall, hispid of spreading hairs. Leaves alternate, mostly basal, reduced upward, deeply pinnatifid or even bipinnatifid, hispid to hirsute. Heads 10-15 and usually short peduncled to nearly sessile; bracts acuminate, imbricate, hispid, often reflexed with age; rays 15-30, yellow. This species is extremely rare in Ohio; in fact, I have seen it growing from only one station near Wilgus in Lawrence County. Evidence from studying material in the herbarium of The Ohio State University indicates that this species was much more abundant in central and west central Ohio at about the time when these areas were beginning to be extensively cultivated. Hybridization with the next species, *S. terebinthinaceum*, is known to occur occasionally in localities in Indiana and Illinois where it grows in more dry prairie sites.



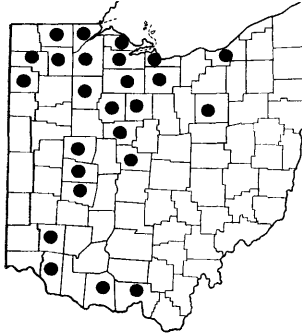
S. perfoliatum L. 1



S. trifoliatum L. 2



S. laciniatum L. 3



S. terebinthinaceum Jacq. 4

FIGURES 1-4. Distribution of the genus *Silphium* in Ohio as represented in the herbarium of The Ohio State University. Figure 1, *S. perfoliatum* L., figure 2, *S. trifoliatum* L., figure 3, *S. laciniatum* L., figure 4, *S. terebinthinaceum* Jacq.

4. *S. terebinthinaceum* Jacqs. Prairie dock

Perennial with very thick taproot similar to the preceding species. Stem 6-8 feet tall, essentially glabrous, leafless or essentially so. Leaves basal, large and long petiolate, the blade broadly ovate, cordate at base, sharply toothed, scabrous to glabrous. Upper stems branched, heads numerous, bracts imbricate, glabrous, elliptic, inner slightly oblong, rays 12-25. Achenes obovate with narrow wing. This species is abundant in the wet prairies of central, north central, and north western Ohio. One recognizable variety is variety *lucybraunii* Sterr. and is associated with smaller prairie outcrops in southern Ohio, particularly those of Adams County.

This species hybridizes with *S. laciniatum* L. and the hybrid is likely to be confused with *S. pinnatifidum* Ell., which does not occur in Ohio.

HYBRIDIZATION STUDY

Silphium laciniatum L. and *S. terebinthinaceum* Jacqs. are known to hybridize in several localities in Illinois and Indiana where their ranges overlap (Fisher, 1959).

However, the hybridizing population I have examined in Ohio is significantly different from hybridizing populations in Illinois and Indiana and deserves special mention.

Several reputed hybrids between those two species are in the herbarium of The Ohio State University. A number of specimens were collected several years ago in Franklin County by Prof. J. H. Schaffner. These locations have been visited and the hybrids are apparently not present; in fact, some of these locations are presently occupied by housing developments near Columbus. One population west of Marion, Ohio, in Marion County, was visited in the summer of 1959 and on numerous occasions since for the purpose of assembling population samples. In 1960, several clones were removed to the research garden at The Ohio State University for further study.

One of the obvious differences in the Marion County, Ohio, population is that, in addition to the occasional hybrid, there is rather extensive backcrossing in the direction of *S. terebinthinaceum*. In the Illinois and Indiana populations, the degree of backcrossing was difficult to determine but was in the direction of *S. laciniatum*. In the Marion County, Ohio, population, there is only one parent species represented, *S. terebinthinaceum*. The nearest station for *S. laciniatum* is nearly 200 miles to the southeast.

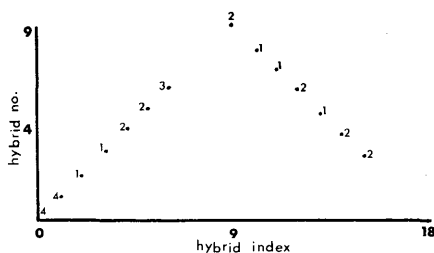


FIGURE 5. Graph of the hybrid number and hybrid index as applied to hybridizing population of *S. terebinthinaceum* and *S. laciniatum*. The numbers adjacent to the glyphs represent the numbers of plants graphed at that point.

Methods of analyzing population. The method used in this study is called the hybrid number method (Gay, 1960) and is a modification of the hybrid index method described by Anderson (1949). It is a modification in that it is used in combination with the hybrid index method. Its chief advantage is that it permits meaningful averages of introgressing populations. Comparison between various populations can be made visually, by graphing the mean hybrid number against the mean hybrid index.

The hybrid index was prepared by scoring the following characters: number of leaf lobes, angle of lateral vein (third from leaf base) and midrib, total of lateral veins, number of hairs per unit area (6 square mm), and width of blade at broadest point. These characters were selected because by these characters these two species are easily separated.

The range of raw scores for each plant is included in table 1. The raw scores were grouped and given values from 0-5, except pubescence which was scored on a 0-3 scale. Therefore, the total hybrid index for a plant representative of *S. terebinthinaceum* would be 0, while a plant representative of *S. laciniatum* would be at the highest or 18.

After the hybrid index for each plant was computed, its hybrid number was determined in the following manner. Since the hybrid index scale extends from 0-x, the hybrid number scale extends from 0 to x/2. From the hybrid index 0 to x/2, the hybrid number equals the hybrid index. From the hybrid index x/2 to x, the hybrid number equals x minus the hybrid index. In this population,

x equals 18, since this is the greatest possible score an individual could receive, and is representative of *S. laciniatum*. From these data, the mean hybrid index and mean hybrid number of the population is computed.

Results of population analysis. The apex of the triangle formed by the glyphs in figure 5 represented the most hybrid nature possible for any individuals, because their hybrid index is 9 and their hybrid number is 9. Two plants collected from this population are graphed at this point. These plants compare favorably

TABLE 1. Measurements of 28 plants of a hybrid population of *Silphium* near Marion, Ohio

Plant no.	No. of lobes	Angle of lateral veins	No. lateral veins	No. hairs per unit area (6 mm ²)	Width of blade at broadest point	Hybrid index	Hybrid number
1	26 (5)	70° (2)	31 (3)	48 (3)	21.4 (2)	15	3
2	21 (4)	55° (4)	28 (3)	13 (1)	18.5 (2)	14	4
3	29 (5)	70° (2)	40 (2)	3 (0)	22.5 (2)	11	7
4	27 (5)	75° (2)	33 (3)	1 (0)	20.8 (2)	12	6
5	17 (3)	70° (2)	39 (2)	0 (0)	18.4 (2)	9	9
6	26 (5)	58° (4)	24 (4)	0 (0)	19.5 (2)	15	3
7	20 (3)	65° (3)	29 (3)	44 (3)	23.1 (2)	14	4
8	17 (3)	85° (1)	36 (2)	16 (1)	19.0 (2)	9	9
9	22 (4)	60° (3)	37 (2)	18 (1)	22.2 (2)	12	6
10	10 (1)	55° (4)	34 (2)	10 (1)	23.0 (2)	10	8
11	12 (2)	55° (4)	40 (2)	41 (3)	22.0 (2)	13	5
12	8 (1)	75° (2)	45 (1)	9 (0)	27.1 (1)	5	5
13	0 (0)	100° (0)	34 (2)	37 (2)	22.8 (2)	6	6
14	0 (0)	90° (0)	52 (0)	13 (1)	27.5 (1)	2	2
15	3 (0)	60° (3)	38 (2)	6 (0)	24.5 (1)	6	6
16	1 (0)	90° (0)	32 (3)	27 (2)	28.5 (1)	6	6
17	0 (0)	85° (1)	38 (2)	20 (1)	19.8 (2)	6	6
18	0 (0)	90° (0)	28 (3)	13 (1)	25.5 (1)	5	5
19	0 (0)	85° (1)	39 (2)	21 (1)	32.2 (0)	4	4
20	0 (0)	85° (1)	50 (0)	17 (1)	29.1 (1)	3	3
21	0 (0)	93° (0)	50 (0)	0 (0)	32.2 (0)	0	0
22	0 (0)	96° (0)	51 (0)	6 (0)	30.0 (0)	1	1
23	0 (0)	94° (0)	55 (0)	4 (0)	33.6 (0)	0	0
24	0 (0)	96° (0)	56 (0)	0 (0)	34.3 (0)	0	0
25	0 (0)	98° (0)	53 (0)	10 (1)	33.2 (0)	1	1
26	0 (0)	100° (0)	45 (1)	8 (0)	34.5 (0)	1	1
27	0 (0)	96° (0)	48 (1)	8 (0)	36.0 (0)	1	1
28	0 (0)	95° (0)	50 (0)	6 (0)	32.6 (0)	0	0
Total						181	111
Mean						6.1	3.2

morphologically to the artificial hybrid from the research field at The Ohio State University. Nine plants are graphed as hybrids between the hybrid peak and *S. laciniatum*, although 5 are closer to the hybrid peak. Seventeen plants are graphed along a line from the hybrid peak and *S. terebinthinaceum*. There are no plants representative of *S. laciniatum* in the population. All totaled, more plants of the population have scores ranging between *S. terebinthinaceum* and the hybrid peak than between the hybrid peak and *S. laciniatum*. This would be expected if backcrossing in this natural population is in the direction of *S. terebinthinaceum*. With this modified hybrid index method, a single specimen can be represented in terms of hybridity, since the hybrid index measures the hybridity from *S. terebinthinaceum* and *S. laciniatum* while the hybrid number is a measure of hybridity from either "pure" species and the F₁ hybrid. Another advantage of this method is that one can compare more than one population visually by graphing the mean hybrid number against the mean hybrid index. This permits graphing an entire population at one point and several populations can be included on the same graph.

In figure 6, a population from Coles County, Illinois (Fisher 1959), is compared with the population from Marion County, Ohio. Backcrossing is occurring in the direction of *S. laciniatum* in the Illinois population (B), while backcrossing is occurring in the direction of *S. terebinthinaceum* in the Ohio population (A).

Artificial hybridizations. Although *S. terebinthinaceum* and *S. laciniatum* hybridize occasionally in nature, they can be caused to hybridize in the research garden only with difficulty. Since 1957, attempts to hybridize these two species have resulted in only 3 F₁ hybrids. Meiosis in the hybrids is normal and stainability of pollen averages 73%. Seed-set in the F₁ hybrid is high, averaging 98%. Morphologically, this hybrid is intermediate and is similar to two plants collected

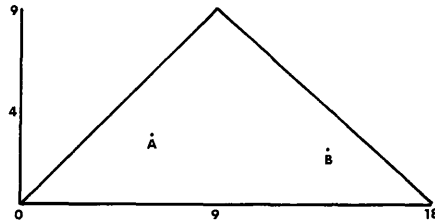


FIGURE 6. Graph of mean hybrid number (vertical axis) and mean hybrid index (horizontal axis) of two populations of *Silphium*: population A from Coles County, Illinois, and population B from Marion County, Ohio.

at the Marion, Ohio, station, to one plant at the Switz City, Indiana, station, but to no plants at the Coles County, Illinois, station, since the latter station represents plants as backcross segregates to *S. laciniatum*.

SUMMARY AND CONCLUSIONS

The genus *Silphium* in Ohio consists of 4 species, although *S. laciniatum* is quite rare and consists of only one known colony. Before cultivation of the land, particularly the prairies in Ohio, these species were probably widely distributed. Today, *S. terebinthinaceum* and *S. trifoliatum* may be found primarily as prairie relics along railroads and highways. *Silphium perfoliatum* is widespread in Ohio.

Silphium terebinthinaceum and *S. laciniatum* have hybridized in the past, as evidenced by a hybrid population west of Marion, Ohio. In this population, backcrossing and hybrid segregation appear to be in the direction of *S. terebinthinaceum*. Analysis of the population indicates that, statistically, 9 of the 28 plants sampled represent varying degrees of hybridity ranging from the F₁ to *S. laciniatum*, although no hybrid plants are especially near *S. laciniatum*.

Furthermore, 4 plants of the described population are statistically *S. terebinthinaceum* and 13 range in hybridity from typical *S. terebinthinaceum* to the statistical F₁ hybrid. In contrast, in a population from Coles County, Illinois, backcrossing is apparently in the direction of *S. laciniatum*.

LITERATURE CITED

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