RETZER, J. L. 1956. Alpine soils of the Rocky Mountains. Jour. Soil Science 7:22–32.
ROOF, J. B. 1961. The manzanitas of California's Point Sur region. Leafl. West. Bot. 9:188–196.
RYDBERG, P. A. 1922. Flora of the Rocky Mountains and adjacent plains. New York.
SCHRÖTER, C. 1926. Das Pflanzenleben der Alpen. Raustein, Zurich.
SHAW, R. J. 1958. Vascular plants of Grand Teton National Park. Am. Midl. Nat. 59:146–166.
SPRAGUE, E. F. 1962. Pollination and evolution in Pedicularis. Aliso 5:181–209.
TIDESTROM, I. 1925. Flora of Utah and Nevada. Cont. U. S. Nat. Herb. 25.
WEBER, W. A. 1961 Handbook of plants of the Colorado Front Range. 2nd ed. Univ. Colorado Press, Boulder.
————. 1961a. Additions to the flora of Colorado. III. Univ. Colo. Stud. D. 7:1–26.
WOOTON, E. O. and P. C. STANDLEY. 1915. Flora of New Mexico. Cont. U. S. Nat. Herb. 19.

NATURAL AND ARTIFICIAL HYBRIDS OF BESSEYA AND SYNTHYRIS (SCROPHULARIACEAE)

A. R. KRUCKEBERG AND F. L. HEDGLIN[1]

Within the Scrophulariaceae is a group of five genera well set apart from others in the family (Pennell, 1933). All are characterized by basal, petiolate leaves, scapose inflorescences, and weakly zygomorphic (veronica-like) flowers. Two of the genera, *Synthyris* and *Besseya* occur in western North America, from sea-level to timberline. Species of *Synthyris* are either woodland inhabitants or occur as elements of the snow-flush flora of high montane slopes. *Besseya* species are less mesic in habitat; the most common species, *B. rubra,* occurs in open yellow-pine forests or the bunch grass-forb-shrub vegetation type.

The intriguing distribution of species in *Besseya* and *Synthyris* as well as in their Eurasian relatives has prompted a long-range study of the clan. Morphological, cytological, and breeding criteria will be sought to determine the relationships of the highly disjunctively distributed species.

NATURAL HYBRIDS

Early in the study it was called to our attention that *B. rubra* (Dougl.) Rydb. and *S. missurica* (Raf.) Penn. underwent sporadic hybridization in the Clearwater River drainage of west central Idaho. The first collections of the hybrid were made by Fred Warren, a student of Harold St. John at Washington State College. Living plants of this initial collection are still growing in Carl English's garden in Seattle and have been examined by the authors.

[1] The authors acknowledge with gratitude the aid given by Carl S. English, Jr., who provided us with living plants, C. Leo Hitchcock, for counsel during the study, and to the several collectors who furnished buds and living plants. Photographs by Audio-Visual Services, University of Washington. A portion of the research was supported by funds granted the senior author from the State of Washington Initiative No. 171 Fund.

In March of 1958, following directions given by English, the authors located an area near Kamiah, Idaho, where the hybrids occurred. The site had been disturbed by logging about ten years earlier and signs of spring cattle-grazing were noticed. Second-growth ponderosa pine and douglas fir were the dominant trees, and *Ribes, Symphoricarpos, Rosa,* and *Holodiscus* constituted the major shrub vegetation. The terrain was dominated by a broad, gently rounded ridge running northeast to southwest. *Besseya rubra* grew on the open, grassy crown of the exposed ridge, while *S. missurica* occurred on the cool, shaded northwest-facing slope, among shrub thickets. The few hybrid plants were found here and there in a zone between the areas of the two species, closest to the lower edge of the area occupied by *B. rubra,* and following the contour on the northwest-facing slope a few feet below the edge of the ridge. Both species as well as the hybrids were in bud and full bloom.

No insects were noticed visiting the plants while the authors reconnoitered the area, though hymenopterons have been observed on other species of *Synthyris* elsewhere. The pollination necessary for hybridization was probably performed by insect vectors.

Inflorescences and buds were taken for later study prior to digging hybrid plants for transplanting to the greenhouse at the University of Washington. Several inflorescences of the parental species were also collected.

Comparison of the hybrid and parental plants revealed the hybrids to be intermediate in several characters (table 1, and fig. 1a). Most striking of all was the corolla of the hybrids—perhaps half the size of showy-flowered *S. missurica. Besseya rubra* is apetalous (Hedglin, 1959).

Fertility and Cytological Behavior of Natural Hybrids

Pollen Stainability: 19.5 %—Hybrid; 88.6%—*S. missurica;* 89.2%—*B. rubra.*
Hybrid seed: None from selfing the hybrids.
Backcross seed: A very few; 2–3 backcross progeny recovered.
Meiosis: n = 12 pairs in both species and commonly 12 pairs in hybrid. Of 426 meiotic figures examined, 186 (42.7%) were abnormal (one or more lagging chromosomes). Metaphase II figures with laggards: 70/102 (70%) (fig. 2a,b).

Artificial Hybrids

Attempts to synthesize the hybrid from its putative parents met with easy and rapid success. Greenhouse hybrids, made in both directions, flowered the second year after crossing. Though somewhat more variable, the synthetic hybrids were a good match for the Kamiah natural hybrids. Some of the F_1 plants approached *Synthyris* in morphology, especially in having showier corollas than the natural hybrid; others were good intermediates (fig. 1b).

Pollen stainability: 7.5 to 40.0% stainable pollen.
Meiosis: 2, rarely numerous laggards at metaphase I & II; *S. missurica* × *B. rubra* 156/231 (67.5%) irregular figures at metaphase I; *B. rubra* × *S. missurica* 134/278 (46.5%) irregular figures at metaphase I (fig. 2c,d).

FIG. 1. Inflorescences and single basal leaves of parents, natural hybrid, and artificial hybrid, *B. rubra* and *S. missurica:* 1a, *B. rubra* (left), natural hybrid (center), and *S. missurica* (right); 1b, *B. rubra* (left), artificial hybrid (center), and *S. missurica* (right).

TABLE 1. COMPARISON OF THE NATURAL HYBRID WITH ITS PARENTS

FEATURE	*S. missurica*	HYBRID	*B. rubra*
leaf shape	reniform, cordate	ovate, cordate	elliptic-ovate, truncate
leaf pubescence	glabrous	glabrate with age	villous-pubescent
scape pubescence	nearly glabrous	white-villous, glabrate below	villous-puberulent
number of bracts	3 to 7	5 to 12	12 to 15
bract shape	widely obovate, slightly toothed	rhombic to obovate, lower slightly petioled, toothed	obovate to elliptic, crenate-dentate, lower petioled
sepal shape	lanceolate, entire	lance-ovate, irreg. margins	ovate, irreg. toothed
sepal size	3 mm long	4 mm long	6 mm long
corolla size	6–7 mm long	4 (6)[1] mm long	absent
corolla color	blue	purple	
stamen color	blue	purple	red

[1] One plant had flowers with the corolla 6 mm long and light blue.

OTHER HYBRIDS

At the same time that the artificial intergeneric hybrid was made, crosses between other species of *Synthyris* were tried. To date only the larger-leaved woodland species have been used as parents: the high-montane, laciniate-leaved species rarely flower in cultivation. *Synthyris platycarpa, S. missurica, S. reniformis, S. schizantha,* and *S. stellata* have been intercrossed; all are n = 12. To date, only the crosses, *S. missurica* × *S. reniformis* and *S. missurica* × *S. platycarpa* have given F_1 hybrids. Flowering plants of *S. missurica* × *S. reniformis* are shown (fig. 3); the hybrids approach *reniformis* in stature and inflorescence pattern, but definitely reflect the influence of *missurica*. Of the nine hybrid plants, seven had no stainable pollen. Meiotic figures, though not severely abnormal, had a fairly high frequency (*ca.* 50%) of aberrant figures (one or more laggards and/or univalents, fig. 2d,e).

Other interspecific hybrids will be attempted as the opportunity permits.

CHROMOSOME NUMBERS IN BESSEYA AND SYNTHYRIS

Chromosome counts have been made on a number of taxa in *Besseya* and *Synthyris* (table 2). All taxa but one thus far sampled are diploids, with the gametic number of 12 chromosomes. The one exception, *Besseya plantaginea,* is a tetraploid. We eventually plan to obtain counts on all North American taxa as well as on members of the European and Asian genera, *Wulfenia, Lagotis,* and *Picrorhiza*. Cytological material of any of these will be much appreciated.

CONCLUSIONS

The occurrence of the natural hybrid, *S. missurica* × *B. rubra,* in a habitat of disturbed conditions, offers opportunity for introgression, either

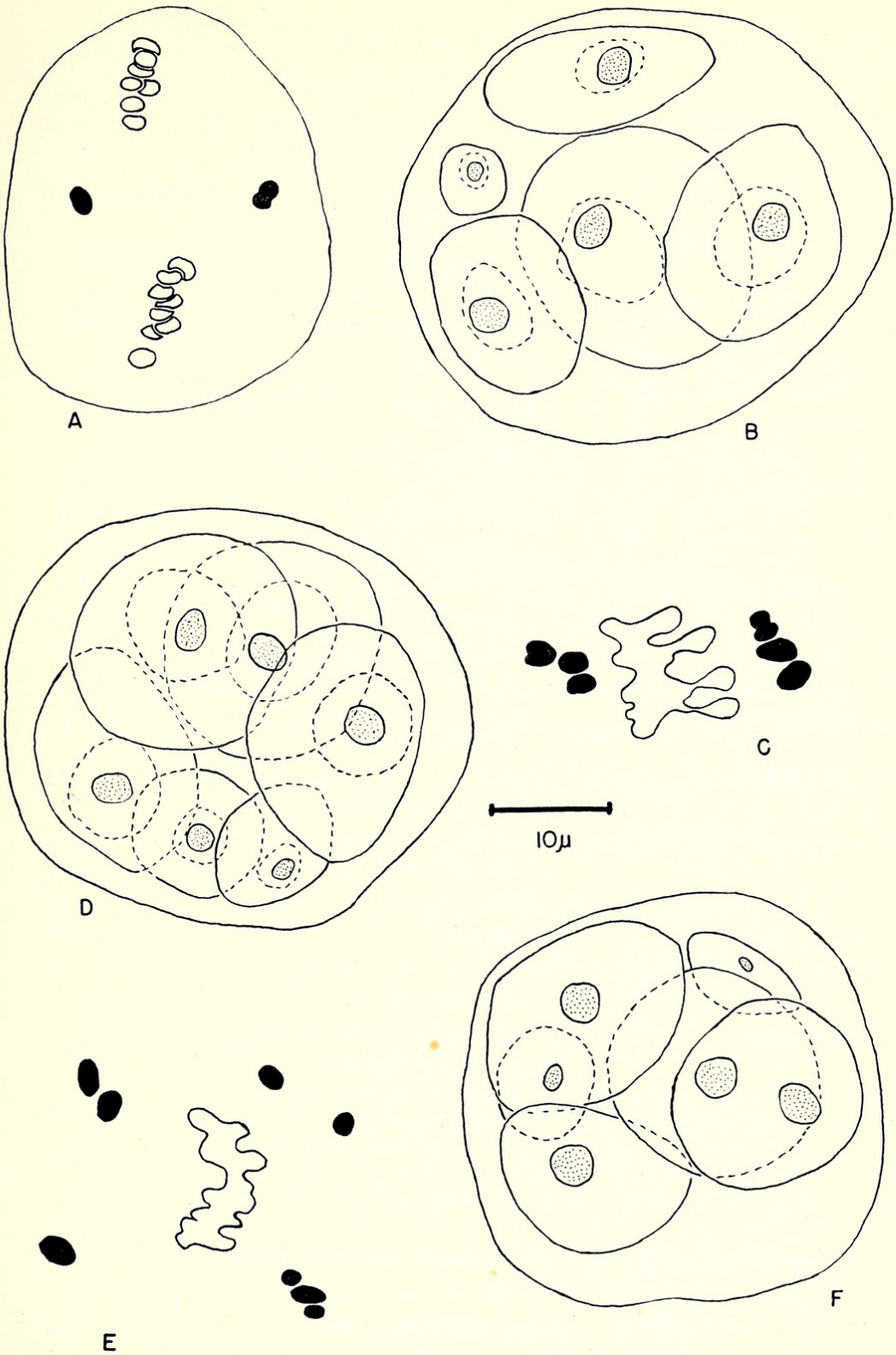

FIG. 2. Abnormal meiotic behavior of hybrids of *Synthyris* and *Besseya*: 2a, metaphase II with two lagging univalents, *B. rubra* × *S. missurica* (natural hybrid); 2b, pollen tetrad with four spores and one microcyte (natural hybrid); 2c, metaphase I with 5 univalents off metaphase plate, *B. rubra* × *S. missurica* (artificial hybrid); 2d, pollen tetrad with four spores and two microcytes (artificial hybrid); 2e, metaphase I with eight univalents off metaphase plate, *S. reniformis* × *S. missurica;* 2f, pollen tetrad with four spores and two microcytes, *S. reniformis* × *S. missurica.*

TABLE 2. CHROMOSOME NUMBERS IN BESSEYA AND SYNTHYRIS

SPECIES	LOCALITY AND VOUCHER	n NUMBER
Besseya bullii (Eat.) Rydb.	Wolf Lake, Jackson Co., Michigan. *Gillett 1148**	12
B. plantaginea (James) Rydb.	White Mountains, Apache Co., Arizona *Kruckeberg 4583**	24
B. rubra (Dougl.) Rydb.	E of Kooskia, Idaho Co., Idaho. *Hedglin 17**	12
	Pattee Canyon, Missoula Co., Montana. *Preece 2265*	12
Synthyris missurica (Raf.) Penn.	Clearwater River, Idaho Co., Idaho. *Hedglin 16**	12
S. pinnatifida Wats. var. *pinnatifida*	Tony Grove Lake, Cache Co., Utah. *Hedglin 31*	12
	Bloomington Lake, Bear Lake Co., Idaho. *Hedglin 35**	12
S. pinnatifida var. *canescens* (Penn.) Cronq.	White Cloud Mountains, Custer Co., Idaho. *Kruckeberg 4536**	12
	W of Challis, Custer Co., Idaho. *Hedglin 39*	12
S. platycarpa Gail & Penn.	Indian Hill, Idaho Co., Idaho. *Kruckeberg 4109**	12
S. reniformis (Dougl.) Benth.	Marin Co., California. *McMillan 1931* (McMillan, 1949)	12
	New Era, Clackamas Co., Oregon. *Hedglin 5**	12
	Drain, Douglas Co., Oregon. *Hedglin 1*	12
	Pierce Co., Washington. *Kruckeberg s. n.*	12
S. stellata Penn.	Columbia River Gorge, Multnomah Co., Oregon. *Hedglin 7**	12
S. missurica × *B. rubra*	Kamiah, Lewis Co., Idaho. *Hedglin 18**	12

* Prepared slides available (WTU).

locally or extensively. Fertility, though low, is sufficient for slow infiltration of genetic material into one or the other parental species. As yet there is no field evidence for introgression and it appears that as yet the intergeneric hybrid is of rare occurrence and is not in the process of contaminating either of the parents. The fact that this natural intergeneric hybrid and its artificial counterpart is more fertile than the wholly sterile hybrid between *S. reniformis* and *S. missurica* suggests that species in *Synthyris* and *Besseya* are genetically congeneric. Should the natural hybrid lead to introgressant populations, it would seem even

FIG. 3. Inflorescences and single basal leaves of *S. reniformis* (left), hybrid (center), and *S. missurica* (right).

more natural to retain species of *Besseya* in *Synthyris*—as was done up to the time of Rydberg (1903).

Department of Botany
University of Washington, Seattle
Federal Emergency Science School
Lagos, Nigeria

LITERATURE CITED

HEDGLIN, F. L. 1959. A survey of the genus Synthyris. Master's degree thesis (unpublished). Univ. of Washington, Seattle.

MCMILLAN, C. 1949. *In* Documented chromosome numbers of plants. Madroño 10:95.

PENNELL, F. W. 1933. A revision of Synthyris and Besseya. Proc. Acad. Phila. 85:77–106.

RYDBERG, P. A. 1903. Some generic segregations. Bull. Torrey Club 30:271–281.

NOTES AND NEWS

HOWARD E. MCMINN.—Professor McMinn passed away at his home in Oakland, California, on August 25, 1963, after a lengthy illness. From 1918 to 1957 Mr. McMinn was professor of botany at Mills College. During his long career he published several books, the best known being "An Illustrated Manual of Pacific Coast Trees" and "An Illustrated Manual of California Shrubs," and comprehensive monographs of the genera *Ceanothus* and *Diplacus*. A detailed biographical account will be published in a forthcoming number of Madroño.