III. SMELOWSKIA AND POLYCTENIUM

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(Plate 496)

To students of the *Cruciferae* the accurate definition of genera is an acute problem. This is understandable when the uniformity of flower- and fruit-morphology is considered together with the apparent youth of the family. While this "naturalness" has become an enigma to those chiefly interested in developing a suitable classification, the same characteristic presents a fertile field of investigation for the phylogenist, since the differences between genera are sometimes relatively small and it is often possible to trace evolutionary trends within the family with considerable facility. However, an adequate and accurate system of nomenclature based upon all the available evidence must be built up before finality in a phylogenetic scheme for the family can be developed. Accordingly a program of research is under way which is designed to clarify the generic relationships of certain groups in the *Cruciferae* which occur in North America.

In addition to the usual methods in systematic botany a certain amount of micro-technique has been employed in the present study. Serial sections of flowers and fruits of *Smelowskia* and *Polyctenium* have been prepared for detailed examination. Since fresh material was not available, flowers and fruits from herbarium material were swelled to normal by leaving them over-night in a 5% solution of KOH. The tissues of the material were then softened by a 12-hour treatment with a ten percent solution of hydrofluoric acid. From this point the ordinary paraffin method of embedding and sectioning was employed. The sections were stained with safranin and fast green.

Probably the most useful and significant microscopical observations in a study of this nature are those which accurately establish the relative position of parts and organs. Thus it has been possible to show (PLATE 496, FIG. 14) that the long stamens in the flower of *Smelowskia* are proximal to the transverse long axis of the ovary, whereas the lateral short stamens are proximal to a line running across the short axis. In *Polyctenium* (PLATE 496, FIG. 2) the compression of the normal mature silique is the opposite. The long stamens are proximal to a median transverse line through the short axis of the silique and the short stamens are near a transverse line passed through

¹ The Society of Fellows of Harvard University.

the long axis. Thus the compression of the silique is contrary to the septum in Polyctenium and parallel to it in Smelowskia. Serial sections of young and old flowers show these differences to be constant for the two genera, and, although it might be argued that a change from one type of orientation to the other is relatively simple, yet such an accomplished change is highly important when considered together with correlated changes which accompany it. Smelowskia and Polyctenium are clearly related genera, though there is little evidence to indicate that their entire history has been similar. Smelowskia is essentially an arctic-alpine genus with two areas of concentration, the Cascade and Rocky Mountains of western North America and the Altai and adjacent ranges of Siberia and the Turkestans. The genus extends as far south as Mt. Lassen in the Sierra Nevada of California and to southern Colorado in the Rocky Mountains. Polyctenium, on the other hand, inhabits a unified semiarid area at relatively low elevations in northeastern California, southern and eastern Oregon and western Idaho. Further evidence of the distinctness of these two genera may be found in the number of ovules, length of funiculus, size of seed, petal-shape, type of foliage and general habit of growth. The leaves of Smelowskia are petiolate, pliable and usually covered with a dense whitish tomentum; the plants are caespitose, with the caudices covered by leaf bases; the petals differentiated into claw and rounded blade; the funiculus short (less than 1 mm.) and stubby; the ovules 2-10, maturing to relatively large seeds (2 mm. long). Polyctenium, on the other hand, has non-petiolate, highly dissected, wiry leaves with linear segments; sparse, never whitish, pubescence; caudices free of leaf-bases; and truncate petals which taper from apex to base. A weak funiculus 1 mm. long attaches the small (1 mm. long) seed to the replum and 12-28 ovules are present in the silique.

In 1875 Watson¹ described a plant from southern Oregon as Smelowskia ? Fremontii. Appended to the description he says "it much resembles S. calycina in habit, but the characters of the fruit do not fully accord with those of the genus." It is significant, in light of subsequent treatments and as confirmatory evidence for the present study, that he considered the plants to be somewhat anomolous in Smelowskia. Though Robinson (Syn. Fl.) admitted this species to Smelowskia without qualification, Greene,² upon encountering the

¹ Watson, Proc. Am. Acad. Arts & Sci. ii. 123 (1875).

² Greene, Erythea iii. 69 (1895).

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same biological unit, described it as a new species of Braya to which genus it is not particularly related. He later recognized his own plants to be conspecific with those of Watson, but refused even then to admit them to the genus Smelowskia. In describing Polyctenium as a new genus, Greene¹ said in part, "to the eye of experience there is not a suggestion here of the genus Smelowskia, which are not only soft-wooly herbs, but their herbage is soft as to texture, that is, it is yielding or pliable, whereas in *Polyctenium* it is in every partrigid, wiry as to the stems and as to the leaves stiffly accrose." Thus with a strong emphasis on habital and vegetative characteristics but without a thorough examination of the morphology of flower and fruit, the genus Polyctenium was created; at the same time two new species were described and attributed to it. The superficiality of Greene's observations does not alter the fact that he was correct in separating these two genera. Subsequent treatments of Smelowskia have included Polyctenium as a synonym, though O.E. Schulz² gave it the rank of a section. In view of this lack of uniformity of treatment and clear elucidation of the facts involved, the objects of the present study were: (1) to determine the facts of floral morphology, (2) to use these criteria to establish the two units as a single genus or as two genera, as the facts dictated, and (3) to present a systematic treatment of this group for North America.

It is a pleasure to acknowledge my indebtedness to Professor M. L. Fernald, Director, and other members of the staff of the Gray Herbarium, where facilities for study have been made readily available and constantly at my disposal. That portion of the work which involved micro-technique was done in the laboratory of Professor R. H. Wetmore. An expression of appreciation is made to the curators of the following herbaria, who have generously loaned specimens or allowed me the privilege of examining material in their care: University of California (C); Missouri Botanical Garden (M); University of Notre Dame (ND); New York Botanical Garden (NY); Rocky Mountain Herbarium (RM); United States National Herbarium (US); University of Washington (UW). Specimens cited (G) or not otherwise designated are in the Gray Herbarium of Harvard University. Collections from my own herbarium are designated (R).

¹ Greene, Leafl. ii. 219 (1912).

² O. E. Schulz in Engler, Pflanzenr. iv¹⁰⁵. 358 (1924).

SYNOPSIS OF SMELOWSKIA IN NORTH AMERICA

a. Mature fruits oblong, tapering at both ends, 5–12 mm. long;
seeds 4-10; basal leaf-bases strongly ciliate with long
acicular hairs; lobes of basal leaves oblong or cuneate,
rarely dissected to mid-rib; stems simpleS. calycina & vars.
b. Cauline leaves entire or trilobate at apex; basal leaves en-
tire or remotely toothed, less than 2.5 cm. long; inflores-
cence lax-corymbose; plants of Alaska and Siberia adja-
cent to the Bering Straitvar. integrifolia.
b. Cauline leaves pinnatifid; basal leaves pinnately dissected
or tending to become entire, more than 2.5 cm. long;
inflorescence congested-corymbosevar. typica.
a. Mature fruits ovate to slightly oblong, truncate at base, 3-6
mm. long; seeds 2–6; basal leaf-bases lacking pronounced
ciliation; lobes of basal leaves ovate and dissected to mid-
rib, stems often branchedS. ovalis & vars.
c. Plants densely caespitose, clothed in long simple hairs;
fruits 4–6 mm. long; plants of northern Californiavar. congesta.
c. Plants less dense; leaf-blades with a short, often branched
pubescence; fruits 2-4 mm. longvar. typica.

S. CALYCINA (Stephan) C. A. Meyer. Perennial, caespitose, the multiple caudex clothed with old leaf-bases; stems several to numerous, simple, pubescent with short branched and long simple hairs, 5-15 cm. long; basal leaves numerous, petiolate, pinnately divided or very rarely almost entire, segments oblong to cuneate, densely clothed with a whitish, chiefly branched, pubescence, bases strongly ciliate with long white acicular hairs; cauline leaves similar but nearly sessile, few, the lobes more linear, tending to be reduced upwards on the stem, 1-3 cm. long; pedicels ascending, pubescent with long simple hairs, 5-10 mm. long; sepals pubescent, oblong, 2.5-3.5 mm. long, 1-1.5 mm. wide; petals white, rounded at apex, differentiated into claw and blade, 5-7 mm. long, 3-4 mm. wide; pods linear to oblong, tapering at both ends, glabrous or rarely pubsecent with simple hairs, slightly flattened parallel to septum or nearly terete, 5–12 mm. long, 1.5-2.5 mm. wide, style 1.5 mm. or less, valves nerved from base to apex, stigma expanded; seeds few (4-10), marginless, 2 mm. long, funiculus short and stout, cotyledons incumbent.

Var. typica. S. calycina C. A. Meyer in Ledeb. Fl. Alt. iii. 170 (1831); Gray, Proc. Acad. Nat. Sci. Phila. no. 43: 58 (1863); Watson, U. S. Geol. Expl. (fortieth parallel) v. 24 (1871); Parry in Hayden, U. S. Geol. Surv. Wyo. 484. (1871); Porter & Coulter, Syn. Fl. Colo. 8 (1874); Macoun, Catal. Canad. Pl. i. pt. 1: 56. 490 (1883); Coulter, Man. Bot. Rky. Mt. Reg. 24 (1885); Tweedy, Fl. Yellowst. Nat. Park 28 (1886); Macoun, Check-List Canad. Pl. 10. (1889); Nelson, Bull. Wyo. Exp. Sta. 28: 83 (1896); Howell, Fl. Northw. Am. i. 57 (1897) in part; Rydb. Mem. N. Y. Bot. Gard. i. 183 (1900); Piper, Contrib. U. S. Nat. Herb. xi. 300 (1906); Brown, Alp. Fl. Canad. Rky. Mts. 121 (1907) t. xxxi; Frye & Rigg, Northw. Fl. 189 (1912); Clements & Clements, Rky. Mt. Flowers, 27 (1914); G. N. Jones, Univ. Wash. Publ. Biol. v. 161 (1936), including S. ovalis. S. calycina prol.

americana O. E. Schulz in Engler, Pflanzenr. iv¹⁰⁵. 356. (1924) & Pflanzenf. xviib. 656 (1936). Lepidium calycinum Stephan in Willd. Spec. Pl. iii¹. 433 (1801). Hutchinsia calycina Desv. Journ. Bot. iii. 4. 168 (1814); DC. Syst. ii. 388 (1821) & Prodr. i. 178 (1824); Hook. Fl. Bor.-Am. i. 58 (1830) t. xvii. fig. B; T. & G. Fl. North Am. i¹. 114 (1838); Ledeb. Fl. Ross. i. 200 (1842). H. calycina & americana Regel & Herder, Bull. Soc. Nat. Mosc. xxxix². 101 (1866) excl. pl. Alaska & Oreg. S. americana Rvdb. Bull. Torr. Bot. Club xxix. 239 (1902); Blankinship, Mont. Agric. Col. Sci. Studies i. 2. 60 (1905); Rydb. Fl. Colo. 153 (1906); Coulter & Nelson, New Man. Bot. Centr. Rky. Mts. 224 (1909); Rydb. Fl. Rky. Mts. 329 (1917); Henry, Fl. So. Br. Columb. 142 (1918); Standley, Contrib. U. S. Nat. Herb. xxii⁵. 346 (1921); Tidestrom, Contrib. U. S. Nat. Herb. xxv. 239 (1925); Standley, Pl. Glac. Nat. Park, 45 (1927), fig. 58. S. lineariloba Rydb. Bull. Torr. Bot. Club, xxxi. 555 (1904) and Fl. Colo. 153 (1906); Cockerell, Am. Nat. xl. n. 480: 865 (1906); Rydb. Fl. Rky. Mts. 329 (1917); Holm, Mem. Nat. Acad. Sci. Wash. xix. 9 (1923); Schulz, l. c. 357 and Das Pflanzenf. xviib. 656 (1936); Graham, Ann. Carneg. Mus. xxvi. 222 (1937). S. lineariloba f. virescens Schulz l. c. S. lobata Rydb. Bull. Torr. Bot. Club xxxix. 327 (1912); Rydb. Fl. Rky. Mts. 329 (1917).-Southern Colorado and Utah to Washington, British Columbia and Alberta and in the Altai region of south-central Siberia. CANADA: locality uncertain, Palliser's Brit. N. Am. Exp., Rocky Mts. 1858, E. Bourgeau (NY, G, type & isotype of S. lobata Rydb.). ALBERTA: Sheep Mt., July 1895, *Macoun 10315*; Elbow River, June–Jul. 1897, *Macoun 18172*; Crow Nest, lat. 49° 30′, Aug. 1897, *Macoun* (ND); north of Kootenai Pass, July 1883, Dawson. BRITISH COLUMBIA: Skagit Valley, July 1905, Macoun 70847; 40-50 miles sw. of Banff, Jul.-Aug. 1905, B. P. Clark. UNITED STATES: exact locality unknown; Rky. Mts. lat. 49° n. 1861, Lyall; sw. Calif. to so. Utah, May-Oct. 1898, C. A. Purpus (C). MONTANA: Upper Marias Pass, Aug. 1883, Canby 32; Bald Mt. July 1880, S. Watson 36; McDonald's Peak, July 1883, Canby 32; Spanish Peaks, July 1901, J. Vogel; Glacier Park, Gunsight Mt., Aug. 1919, Somes 31 (NY); Glacier Park, Baring Basin, July 25, 1933, McLaughlin 2904 (UW). WYOMING: Saltlick Mt., ne. of Kendall, Aug. 1922, E. B. & L. B. Payson 2952 (G, RM); the Thunderer, Yellowstone Nat. Park, July 1899, A. & E. Nelson 5821 (G, RM); Teton Pass Mts., July 1920, E. B. & L. B. Payson 2095 (G, RM); Wind River Mts., July 1922, E. B. & L. B. Payson 2890 (G, RM); Red Mt. ne. of Smoot, July 1923, Payson & Armstrong 3629 (G, RM); nw. Wyo. 1873, Parry 17; Laramie, July 1891, Nelson 5; Frozen Lake, Park Co., July 1937, L. O. & R. P. Williams 3584 (R). COLORADO: Rky. Mts. lat. 39°-41°, 1862, Hall & Harbour; near Trout Lake, San Miguel Co., Aug. 1924, E. B. & L. B. Payson 4181 (G, RM); Ethel Peak, Larimer Co., Aug. 1903, Goodding 1888 (G, RM); Mt. nw. of Como, July 1895, Crandall & Cowan 66; La Plata Mts., July 1898, Baker, Earle & Tracy 580 (G, isotype of S. lineariloba f. virescens O. E.

Schulz); Douglass Mt., 1878, M. E. Jones 447 (NY, type of S. lineariloba Rydb.); Hamilton Pass, Aug. 1875, E. L. Greene 671. IDAHO: Smoky Mts., Blaine Co., Aug. 1916, Macbride & Payson 2733 (G, RM); south end Soldier Mts., June 1916, Macbride & Payson 2889 (G, NY, RM); Mt. Hyndman, July 30, 1936, Thompson 13,631; Henry Lake, Fremont Co., July 1920, E. B. & L. B. Payson 1958 (G, RM); Stevens Peak, Aug. 1895, Leiberg 1480. UTAH: Ridge nw. Paradise Park, Uinta Basin, July 1933, Graham 8433; Big Cottonwood Canyon, Salt Lake Co., June 1905, Garett 1301; July 1905, Rydberg 6821; American Fork Canyon, July 1885, Leonard; Uinta Mts., Aug. 1869, S. Watson 100; July 1926, E. B. & L. B. Payson 4916 (G, RM); La Sal Mts., July 1924, E. B. & L. B. Payson 3982 (G, RM). NEVADA: East Humboldt Mts., Aug. 1868, S. Watson 100; Sept. 1868, S. Watson 100. OREGON: Wallowa Mts., Aug. 1886, Cusick 1347 (C, G). WASHING-TON: Mt. Stuart, Aug. 1883, T. S. Brandegee 641; July 1931, Thompson 7679; Olympic Mts. Jefferson Co., Aug. 1931, Thompson 8002; Mt. Angeles, Clallam Co., July and Aug. 1931, G. N. Jones 3171 and 3799 (UW); June 1932, Thompson 8389; July 1931, Thompson 7386 and 7394; Hurricane Ridge, June 1934, Thompson 10591 (G, UW); Sept. 6, 1937, Thompson 14,214 (R); Olympic Mts., 1889, J. M. Grant.

Ever since Rydberg¹ published S. americana after having made the following observation, "while in Europe last summer, I looked up the Asiatic type of S. calycina and this differs considerably from ours in the long villous pubescence," many botanists have hesitated to associate the plants of North America specifically with those of Siberia. The fact that the author neither amplified nor elucidated his statement, leaves much to be desired, since anyone familiar with our plants knows that the pubescence of the upper stem, pedicels and sepals is of a "long villous" type. This point, insignificant at the outset, is of no value in separating the plants from the two areas. My studies on this problem have revealed two very minor quantitative differences, both of which are covered by the natural variation in American plants and would likely lose even the slight conspicuousness here recorded, if a larger series of Asiatic specimens were considered. The average length of the style is a fraction of a millimeter longer and the pod averages 1-2 mm. shorter in the Siberian plants than in those from this country. However, on the whole, plants from the two continents are so similar in all important morphological features that they cannot be satisfactorily maintained as even varietally distinct.

Several variations of minor importance, as illustrated by a large series of specimens, may well be noted with profit. Plants from the

¹Rydberg, Bull. Torr. Bot. Club xxxix. 239 (1902).

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Olympic Mountains of Washington and from northern Montana extending northward tend to be whitish from a very dense pubescence. That this is probably a climatological response is indicated by the fact that a gradual reduction in the amount of indument may be observed on specimens from localities proceeding from north to south along the Rocky Mountain axis. Rydberg gave weight to the abundance of vestiture in describing S. lobata, while O. E. Schulz described S. lineariloba f. virescens largely on the basis of a reduced amount of pubescence. Neither of these forms seem to merit nomenclatorial rank, however, since the distinguishing characters attributed to them are either unstable or of very minor significance. The fruits vary in length as does the length of the style. For example, the short pods (5-6 mm.) and styles (less than 1 mm.) found on the type-specimen of S. lobata from British North America, are also found on specimens from Wyoming (Payson & Payson 2952) and much farther south in Utah (Payson & Payson 3982) neither of which exhibit the supposedly distinctive correlated characters. Leaf-shape and degree of lobation are highly variable, lacking correlation with stable features and occurring at various geographical points throughout the range of the species. Thus it seems clear that S. lineariloba, founded chiefly on length of pod and leaf-lobation, S. lineariloba forma virescens, founded on scantiness of pubescence, and S. lobata, founded largely on abundance of vestiture, leaf-lobation and length of silique and style, should be included under the variable but understandable S. calycina.

Var. integrifolia (Seemann), comb. nov. Leaves entire or divided toward apex only, spatulate to somewhat cuneate, petiolate, 1-2.5 cm. long, 2-7 mm. wide; stems 5-12 cm. long; inflorescence laxcorymbose; pedicels 5-10 mm. long, spreading; siliques ellipsoidal, narrowed toward base, glabrous, valves nerved; style less than 1 mm. long; seeds oblong, 2 mm. long, 1 mm. broad, 2-4 in each silique. Hutchinsia calycina var. integrifolia Seemann, Bot. Voy. Herald 25 (1852). H. calycina var. B, Hook. Fl. Bor.-Am. i. 59 (1830); Hook. & Arnott, Bot. Beechey's Voy. 122 (1832); T. & G. Fl. No. Am. i. 114 (1838). H. calycina var. Y, Ledeb. Fl. Ross. i. 201 (1842). Smelowskia calycina Robinson in Gray, Syn. Fl. No. Am. i. 136 (1895) in part. S. calycina prol. americana f. integrifolia O. E. Schulz in Engler, Pflanzenr. iv¹⁰⁵. 356 (1924).-Western coast of Alaska and eastern coast of Siberia (?) adjacent to Bering Strait. ALASKA: Port Clarence, July 1899, Trelease & Saunders 3986 (M); Anvil Peak near Nome, July 1936, G. N. Jones 9094; July 8 and Aug. 16, 1900, Flett 1631 (UW). SIBERIA: Plover Bay, 1881, John Muir 228 (G, this fragmentary specimen not certainly determinable as var. integrifolia but presumably belonging here).

First described as var. β under *Hutchinsia calycina* by Hooker, this entity, originally collected on Cape Mulgrave by Lay & Collie, has received a variety of unsatisfactory treatments. Torrey & Gray and Ledebour followed Hooker in separating the unit as a variety with entire leaves but failed to give it a name. Seemann, in enumerating his collections from Alaska, designated a plant from Cape Kruzenstern as var. *integrifolia*, citing Hooker's description of var. β and erroneously ascribing the name to him. O. E. Schulz correctly cited Seemann as the author of the name when relegating this unit to the status of a form; but, not having seen specimens, he apparently regarded the characters repeatedly emphasized by earlier workers as of only minor importance. Mature fruiting specimens show characters which well merit the rank of variety for this entity.

S. OVALIS M. E. Jones. Perennial, multiple caudex clothed with dead leaf-bases; stems simple or often branched, densely pubescent with a long simple and short branched pubescence, 5–15 cm. long; basal leaves petiolate, pinnately divided, segments obovate, densely clothed with a whitish chiefly branched pubescence, 2–6 cm. long; cauline similar, few, 1–3 cm. long; inflorescence corymbose, elongating but dense in fruit; pedicels ascending, densely pubescent with long simple hairs, 4–8 mm. long; sepals oblong, scarious-margined, hairy, 3–3.5 mm. long, 1–1.5 mm. wide; petals white, rounded at apex, differentiated into claw and blade, 4–5 mm. long, 2 mm. wide; pod glabrous, ovoid to ovate, 4–6 mm. long, 4 mm. broad, valves faintly nerved at base; style less than 1 mm. long; stigma expanded; seeds few (2–6), oblong but pointed on distal end, marginless, cotyledons incumbent.

Var. typica. S. ovalis M. E. Jones, Proc. Calif. Acad. Sci. v². 624 (1895); Piper, Mazama ii². 109 (1900); Piper, Contrib. U. S. Nat. Herb. xi. 301 (1906); Frye & Rigg, Northwest Fl. 189 (1912); Piper & Beattie, Fl. Nw. Coast, 174 (1915); Rydb. Fl. Rky. Mts. 329 (1917); Flett, Fl. Mt. Rainier, 47 (1922); O. E. Schulz in Engler, Pflanzenr. iv¹⁰⁵. 357 (1924) and Pflanzenf. xviib. 656 (1936); St. John & Warren, Am. Midl. Nat. xviii. 969 (1937).—Cascade Mountains of Oregon and Washington.¹ OREGON: Three Sisters, 1881, L. F. Henderson. WASHINGTON: Mt. Adams, Aug. 12, 1882, Howell 3846 (US, type; M, NY, isotypes)²; Sept. 1877, Suksdorf; July 1899, Flett (US); Aug. 1892, L. F. Henderson (UW); Aug. 1894, Lloyd (NY); Mt. Rainier,

¹S. ovalis is cited from the Olympic Mts. by G. N. Jones, Univ. Wash. Publ. Biol. V. 161 (1936). However, I have recently consulted with Dr. Jones and we have concluded that the specimens on which the report was based are immature S. calycina. ²The only specimen from Mt. Adams collected on Aug. 12, in the U. S. Nat. Herb., is that of Howell. M. E. Jones I. c. gave the year of the type-collection as 1892; however, even though Howell's specimen bears the date 1882, it is selected as the type since there seems to be no other alternative.

Aug. 1897, Merriam (US); Aug. 1895, Piper 2063 (US); Aug. 1934, Thompson 11,087 (G, M, UW); Aug. 1933, Thompson 10,000 (G, NY, US, UW); Aug. 1901, Flett 1999 (NY); Aug. 1892, Allen 61; July 1937, G. N. Jones 10,325; Indian Head Peak, Chelan Co., July 1921, St. John 4839 (G, M, NY); Mt. Maude, Chelan Co., Aug. 1933, Morrill 335 (UW); Mt. Stuart, July 1931, Thompson 7679 (NY, US); July 1898, Elmer 1095 (US); 1883, Brandegee 641 (US); head of Ingals Cr., Aug. 1898, Whited 838 (US); Wenatche region, Aug. 1883, Tweedy 865 (US); above Hidden Lakes, Okanogan Co., Aug. 1916, McDaniels 13,469 (US); Burch Mt., Okanogan Co., June 1934, Thompson 10,837 (G, NY, UW); Fremont Mt., Pierce Co., July 1934, Thompson 11,087 (M).

Var. congesta var. nov., caespitosa incana pubescenti-tomentosa; siliculis ovatis 4-6 mm. longis; stylo ± 1 mm. longo. Caespitose, pubescent throughout with long simple hairs; inflorescence corymbose, elongating only slightly in fruit; petals white or pinkish; pods ovate, truncate at base, tapering at apex; style ± 1 mm. long.—S. calycina Brewer & Watson, Bot. Calif. i. 42 (1876); Greene, Fl. Francis. 252 (1891) as to Calif. Pl. cited; Jepson, Man. Fl. Pl. Calif. 427 (1925) as to Calif. pl. cited; Jepson, Flora Calif. ii. 59 (1936) as to pl. cited. S. ovalis Rydb. Fl. Rky. Mts. 329 (1917) as to Calif. range; O. E. Schulz, l. c. as to Calif. pl. cited. CALIFORNIA: Lassen Peak, Shasta Co., 1875, Lemmon 21 (G, type; C, M, NY, isotypes); Aug. 1882, Mrs. R. M. Austin (C); undated, Chestnut & Drew 189 (ND).

Isolated nearly two hundred and fifty miles south of the nearest known collection of var. *typica*, this natural entity seems to have stabilized itself sufficiently to receive nomenclatorial designation. The outstanding characteristics are those of the pubescence which is of a long-villous type, covering the above-ground parts of the plants except the petals and fruits, and the siliques which are larger, longer, tapering at apex and tipped with a longer style than in var. *typica*.

Smelowskia ovalis is perfectly distinct from S. calycina with which it has been confused by some botanists. It is true that there is a marked superficial resemblance between specimens of the two species at anthesis or even when the fruits are young, but a closer scrutiny has consistently revealed differences which have been emphasized in the key and which are of a constant nature. The pronounced acicular hairs along the margins of the leaf-bases of S. calycina are exceedingly useful in determining vegetative or young specimens. In fruiting specimens a useful character for easy differentiation is found at the apex of the replum after the valves have been removed. In S. ovalis the replum forms an obtuse angle beneath the style, while in S. calycina the angle is invariably acute.

Var. typica of S. ovalis shows a perplexing variation in length and shape of pod and length of style, but a complete transition between the extremes has been repeatedly observed. Thompson 10,837 and G. N. Jones 10,325 from Mount Rainier, Thompson 10,837 from Burch Mt. and Suksdorf's specimen from Mount Adams all have pods which tend to be lanceolate, often approaching 4 mm. in length, and styles which usually approximate 1 mm. in length. However, the two Thompson collections show an almost complete transition from the ovoid short-styled pod more characteristic of the typical form of the species to the condition described above. Since these deviations from typical S. ovalis are neither stable nor geographically localized, they may be regarded as illustrating the natural variation of the species. This tendency of S. ovalis to vary toward S. calycina in pod-length and -shape as well as length of style points to its probable recent origin from the latter species. Assuming Smelowskia to have originated in south-central Siberia, where the largest number of species exist at the present time, the migration-route through Alaska to the Cordillera of North America is marked by the relict C. calycina var. integrifolia. This variety, now isolated from the parent species from both west and south, has been differentiated to its present biological status under environmental conditions strikingly different from those of the Altai and the Cordillera of our west, which have tended to preserve the specific nature of S. calycina var. typica in the two areas. It seems highly probable from the present geographic distribution of S. calycina that it formerly extended without disruption from the Altai to the Cordillera. From the restricted area in which S. ovalis is found, one might conclude that differentiation from the parent species took place after the genus had migrated well down onto the Cordilleran mountains.

Smelowskia ovalis reputedly grows at the highest elevation at which phanerogamic plants are found on Mount Rainier and other peaks of the Cascade Range.

SYNOPSIS OF THE GENUS POLYCTENIUM

mm. long, 1-1.5 mm. wide; plants sparsely pubescent

P. Fremontii var. typicum.

P. FREMONTII (Watson) Greene. Perennial, more or less caespitose; stems few to several from a branching naked caudex, simple or rarely

Rhodora

branched, sparsely to abundantly pubescent with simple or branched hairs, 5–15 cm. long; basal leaves sessile, 1–2 cm. long, pinnately divided into linear divisions, pubescent with stiff simple or forked or dendritic hairs, segments pungent; cauline similar, sessile, several to many, 5–12 mm. long; pedicels ascending, pubescent or glabrous, 4–6 mm. long; inflorescence corymbose, becoming racemose in fruit; sepals oblong, glabrous or slightly pubescent, 2–3 mm. long, 1–1.5 mm. broad; petals white, cuneate, truncate at apex, 5–6 mm. long, 3–4 mm. broad; pods glabrous, flattened contrary to septum or nearly terete, 6–13 mm. long, 1–1.5 mm. wide; style less than 1 mm. long, stigma unexpanded; seeds numerous (12–28), marginless, 1 mm. long, attached by a weak funiculus 1 mm. long, cotyledons incumbent.

Var. typicum. P. Fremontii Greene, Leafl. ii. 219 (1912). Smelowskia ? Fremontii Watson, Proc. Am. Acad. Arts & Sci. xi. 123 (1875). S. Fremontii Brewer & Watson, Bot. Calif. i. 42 (1876); Robinson in Gray, Syn. Fl. No. Am. i¹. 136 (1895); Howell, Fl. Northw. Am. i. 57 (1897); Frye & Rigg, Northw. Fl. 189 (1912); Schulz in Engler, Pflanzenr. iv¹⁰⁵. 358 (1924); Jepson, Man. Fl. Pl. Calif. 427 (1925); Tidestrom, Contrib. U. S. Nat. Herb. xxv. 239 (1925); Jepson, Fl. Calif. ii. 59 (1936). S. Fremontii var. glabella Schulz I. c. 359. Braya pectinata Greene, Erythea iii. 69 (1895). P. glabellum Greene, l. c.-Northern California and southern and eastern Oregon to central Idaho. IDAHO: Sawtooth Nat. Forest, 1910, C. N. Woods 28 (RM). CALIFORNIA: without locality, 1873, J. G. Lemmon; Ewing Creek, Modoc Co., May 1894, Mrs. R. M. Austin (C, type of Braya pectinata Greene); Modoc Co., May 1879, Miss S. A. Plummer; Portola, Plumas Co., July 1911, K. Brandegee (C); Plumas Co., June 1878, Mrs. R. M. Austin; Eagle Lake and Madeline Plains, Lassen Co., J. G. Lemmon (C); Bray, Siskiyou Co., May 1913, L. E. Smith 227. OREGON: head of Dry Creek, Malheur Co., May 1896, Leiberg 2147 (US, NY, type and isotype of P. glabellum Greene); camp at Dry Creek, Crook Co., June 1894, Leiberg 336 (C, G); base of Steens Mts., May 1885, Howell 351; June 1885, Cusick 1246; hills about Lake Klamath, Klamath Co., May 1846, Fremont 384 (G, TYPE); Swan Lake Valley, Klamath Co., May 1896, Applegate 41; stony dry swales of desert, Harney Co., June 1901, Cusick 2612 (C, G); 7 mi. west of Riley, Harney Co., May 1914, Mrs. R. D. Cooper; north end of Summer Lake, Lake Co., June 1911, Eggleston 6856a; Bear Valley, Blue Mts., May 1885, Howell 769 (C); Prineville to Button Springs, June 1894, Leiberg 336 (US).

Var. bisulcatum (Greene), comb. nov. Caespitose, rather densely pubescent with branched hairs; sepals pubescent; pods decidedly flattened contrary to replum, pubescent at least when young, somewhat bisulcate, 5–8 mm. long, 1.5–2 mm. wide.—*P. bisulcatum* Greene, Leafl. ii. 220 (1912). *Smelowskia Fremontii* var. *bisulcata* O. E. Schulz op. cit.—Known only from the type-collection, OREGON: Silvies Valley, Blue Mts., May 1885, *Howell 346* (US, TYPE; G, NY isotypes).

Polyctenium Fremontii is reasonably homogeneous and occupies a geographical area which is unbroken by any major barrier. As the species is here interpreted, the natural variation easily includes Greene's P. glabellum which appears to be only a lax form developed as a result of shading or perhaps the receipt of a larger amount of water than the species normally obtains. Indeed Leiberg's notation "along streams" on the type-specimen is significant in this connection, since the species is usually found in a dry habitat. The laxity of habit, inflorescence and foliage, the branching stems and scanty pubescence of Greene's type are approached by a specimen collected in June 1894, between Prineville and Button Springs, Oregon, by Leiberg. These characters, though not quite typical, are possessed to a lesser extent by other plants throughout the natural range of the species. Thus it is evident that P. glabellum should be considered synonymous with the older P. Fremontii, even though Schulz, op. cit., who saw no specimens, retained it as a variety.

Possessing many features in common with *P. Fremontii* but with short, flattened, pubescent and somewhat bisulcate pods, *P. bisul*catum Greene appears sufficiently distinct to require nomenclatorial recognition, but in varietal rank. A specimen, loaned for study by the Herbarium of the University of California and possessing short obtuse pods, a prominent style and other minor characters, was collected by Mrs. R. M. Austin in California. This specimen, probably representing a new and undescribed variety, is related to var. bisulcatum by virtue of its short pods but is otherwise distinctive. It is left undescribed because the material is fragmentary and accurate data are lacking.

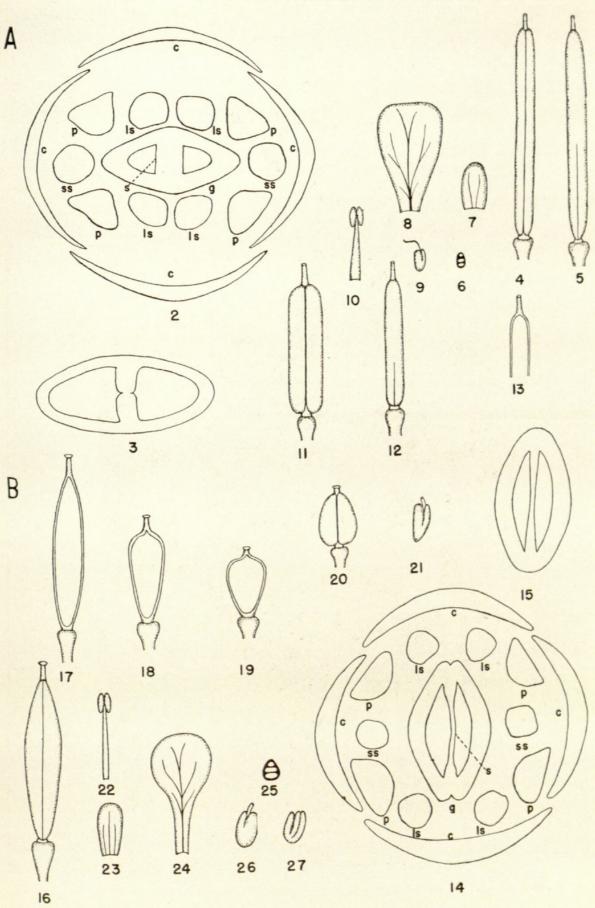
EXPLANATION OF PLATE 4961

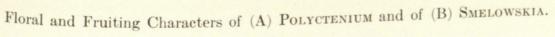
A, POLYCTENIUM. FIGS. 2-10: POLYCTENIUM FREMONTII VAR. TYPICUM-FIGS. 11-13: P. FREMONTII VAR. BISULCATUM. FIG. 2: diagram of a transverse section, at lower filament-level, of a young flower, c sepal, p petal, ls long stamen, ss short stamen, s septum, g gynoecium. FIG. 3: diagram of transverse section through mature silique. FIGS. 4 and 5: two lateral views (at right angles to each other) of a mature silique. FIG. 6: transverse section of a seed. FIG. 7: sepal. FIG. 8: petal. FIG. 9: lateral view of seed. FIG. 10: stamen.

B, SMELOWSKIA. FIGS. 14-17 and 22-27: SMELOWSKIA CALYCINA var. TYPICA. FIG. 18: S. OVALIS VAR. CONGESTA. FIGS. 19-21: S. OVALIS VAR. TYPICA. FIG. 14: diagram of a transverse section, at lower filament-level, of a young flower, symbols as in FIG. 2. FIG. 15: diagram of a transverse section through mature silique. FIG. 16: lateral view of a mature silique. FIGS. 17, 18 and 19: lateral view of replum of three entities. FIG. 20: lateral view of silique. FIG. 21: lateral view of seed.

¹All figures $\times 3\frac{1}{2}$, except 2, 3, 14, and 15 which were drawn free-hand from a microscopic enlargement.









Rollins, Reed C. 1938. "Smelowskia and Polyctenium." *Contributions from the Gray Herbarium of Harvard University* (122), 294–305. https://doi.org/10.5962/p.336203.

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