PROTOGYNY IN THE CRUCIFERAE AND NOTES ON ARABIS AND CAULANTHUS

REED C. ROLLINS

Since my early works on *Arabis* (Rollins 1936, 1941), I have grown many species of the genus and studied more than a score of North American species in flower in the greenhouse or experimental garden. However, none of these showed any evidence of functional protogyny and none had excerted anthers. Now, flowering material of the taxon I have previously called *Arabis suffrutescens* var. *perstylosa* shows both protogyny and excerted anthers to be present. When buds are fully grown and just before anthesis, the elongating style projects through the apex of the slightly opened bud exposing the stigma. This is clearly shown in the left hand photograph of Plate 1. After pollination, the style tends to bend to one side of the flower and the filaments elongate until the anthers of the paired stamens are well excerted above the corolla. Even the anthers of the shorter single stamens are above the ends of the petals when the flower is at full anthesis. The anther position is shown in the right hand photograph of Plate 1. Tests on three plants show them to be self-incompatible. This is taken as reasonably good evidence that the taxon as a whole is essentially self-incompatible.

Protogyny is not supposed to be present in the *Cruciferae* (Bateman 1955a) and even now we assume it is not common in this family or its occurrence would have been noted in the literature. Such a modification of the usual maturation sequence within the flower promotes outcrossing and is of significance for the survival of a population if there is a reduced gene pool and if other outcrossing mechanisms are not present or are ineffective by themselves.

The *Arabis* population from which our seeds were obtained apparently is a small localized one and there is some circumstantial evidence that this taxon itself is very restricted in numbers of populations, possibly consisting of a single population of a limited number of individuals. Only two collections of it have been made, both by Professor Lincoln Constance of the University of California at Berkeley. He made the first collection, in 1938, which was used as the basis for describing the new taxon, *A. suffrutescens* var. *perstylosa*. In 1969, Dr. Constance, accompanied by T. I. Chuang, made a second collection at the same site as the first, including mature seeds from which our plants were grown. At that time a considerable search of the area was made without the discovery of any new sites.

The one known population is on an open serpentine outcrop near rocks. Other crucifers, particularly taxa of the genus *Streptanthus*, occupy similar serpentine habitats (Kruckeberg 1951, 1954, 1957) and are often equally limited in their distributions. In the case of the *Arabis* here being con-

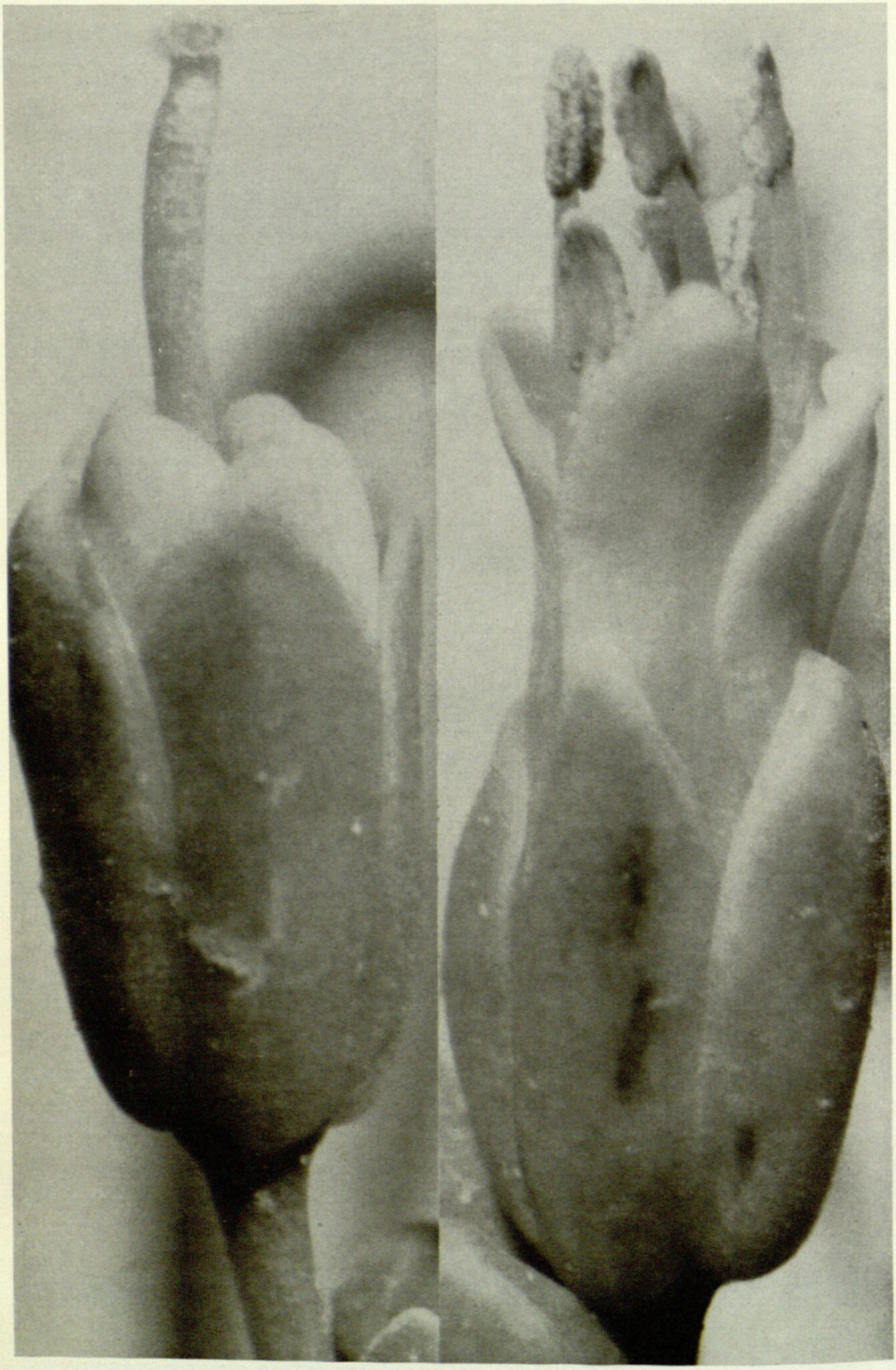

PLATE 1. *Arabis constancei.* Left, bud with projecting style. Right, flower at full anthesis. Both figures × 20. Photo by Frank White.

sidered, it is possible that the population has become too reduced in incompatibility allele number for self-incompatibility to function efficiently as an outcrossing mechanism. Selective pressure to promote outcrossing in some other way could be intense under such circumstances. The development of protogyny is one way the need for increased outcrossing could be insured by the population, if the incompatibility system became inefficient. It is interesting that new information has now completely negated the statement Bateman (*op. cit.*, p. 63) could make only a few years ago that, "there is no protandry, no protogyny and no dioecy in Crucifers." We have shown that protandry is present in two species of *Streptanthus* (Rollins 1963), dioecy was acknowledged to be characteristic of *Lepidium sisymbrioides* by Bateman (1955b), and now, protogyny is shown to be present in the family. There is evidence produced by one of my students, Mr. Ihsan Al-Shehbaz, that protogyny occurs in the genus *Thelypodium* and we now think it may be more widespread in the *Cruciferae* than we would have supposed at the time of our initial discovery of it.[1]

In the course of our study of the *Arabis* material referred to above, it has become clear that the taxon involved should be recognized on the specific level and not associated with *A. suffrutescens* as in my former treatment. Because of his involvement in obtaining the original, and subsequent collections, and his continued interest and help, I propose to name this species for my former mentor and long time friend, Dr. Lincoln Constance. Actually Dr. Constance and I published a new species of *Arabis* together [*A. crucisetosa*] many years ago (Constance & Rollins 1936).

Arabis constancei Rollins, sp. nov.

Herba perennis, caudicibus ramosis, caulibus simplicibus erectis glabris 1.5–3 dm. altis, foliis basilaribus integris glabris vel ciliolatis lineari-oblanceolatis 1.5–3 cm. longis, 2–3.5 mm. latis, foliis caulinis sessilibus non auriculatis glabris, sepalis glabris oblongis 3.5–4.5 mm. longis, ca. 2 mm. latis, petalis erectis anguste spathulatis albidis 5.5–7 mm. longis, staminibus erectis excertis filamentis elongatis, pedicellis recurvatis glabris 6–10 mm. longis, siliquis compressis glabris pendulis acutis vel accuminatis 4–5.5 cm. longis, 3–4 mm. latis, stylis 2.5–4.5 mm. longis, seminibus orbicularibus vel late ellipticis compressis alatis, cotyledonibus accumbentibus.

Holotype in the Gray Herbarium, collected near rocks on open serpentine, 7.6 miles southeast of Quincy on road to Blairsden, Plumas Co., California, July 11, 1969, *L. Constance & T. I. Chuang 3875*. Additional collection studied: open bare serpentine slope, above Middle Fork of the Feather River, 7.3 miles southeast of Quincy, Plumas Co., California, June 9, 1938, *L. Constance 2309* (GH).

Perennial; stems one to several from a branching subligneous caudex, erect, simple, wholly glabrous, 1.5–3 dm. high; basal leaves in dense rosettes, entire, linear-oblanceolate, acute, stiff, thickish, with a prominent mid-rib, bluish-green, ciliolate

[1]While the present paper was in process, an unpublished thesis entitled, "Investigations in the Floral Biology of the Arabis Holboellii Complex," by Thomas Frank Johnson was sent to me by Professor Arthur R. Kruckeberg. Johnson observed emergent pistils in *Arabis holboellii* and in *A. sparsiflora* which surely means that they are protogynous. Thus, we are certain of the prediction that protogyny is more common than we could have reasonably believed a few months ago.

on the margins with simple or forked trichomes to glabrous, 1.5–3 cm. long, 2–3.5 mm. wide; cauline leaves entire, oblong to lanceolate, sessile, non-auriculate, glabrous, reduced upward, overlapping below, remote above, 1–1.5 cm. long, 2–4 mm. wide; inflorescences 5–10–flowered, loose; flowers erect to divaricately ascending, nodding to reflexed after anthesis, sepals green, scarious-margined, glabrous, oblong, non-saccate or the outer pair slightly saccate, 3.5–4.5 mm. long, ca. 2 mm. wide; petals erect, narrowly spatulate, tapering gradually from blade to claw, 5.5–7 mm. long, white to off-white; stamens excerted, erect, introrse, filaments of paired stamens 7–8 mm. long, filaments of single stamens 6–7 mm. long, anthers ca. 1 mm. long; siliques pendulous to strictly reflexed, glabrous, strongly flattened, nearly straight but with uneven margins, nerved from base to middle or slightly above, acute to accuminate at apex, 4–5.5 cm. long, 3–4 mm. wide; styles 2.5–4.5 mm. long; fruiting pedicels strongly reflexed but not geniculate, glabrous, 6–10 mm. long; seeds flattened, nearly orbicular to slightly oblong, winged except for area of funicular attachment, ca. 3 mm. in diameter including wings; wing ca. 0.5 mm. wide; cotyledons accumbent; radicle separated from cotyledons by a deep groove. $2n = 14$.

There is no doubt that *Arabis constancei* is a close relative of *A. suffrutescens*. However, the exposed differences betwen these taxa have been increased in number as we have had more material to work with, particularly growing plants, from which we could make comparisons of characters. The sharpest differences are in the flowers which we did not have available for study at the time of our former treatment of this taxon.

Previously, we had indicated the plants of *Arabis constancei* to be wholly glabrous. But the new specimens of this species show the basal leaves frequently to be ciliolate-margined. If the leaves become glabrate, then there often is one or a few trichomes at the apex of the leaf. For some reason, the specimens of the earlier collection, *Constance 2309*, were wholly glabrous. This is also true of the plants we grew in the greenhouse even though the seeds were from wild plants which had at least some trichomes on their basal leaves.

Arabis constancei differs from *A. suffrutescens* in having non-auriculate instead of auriculate cauline leaves, greatly elongated styles instead of sessile stigmas or at most very short styles, excerted stamens rather than included stamens and seeds with wings about 0.5 mm. wide rather than 1 mm. wide. In general, there is less of a woody foot present in *A. constancei* than in *A. suffrutescens*. Also, there is a much better developed basal rosette with a denser cluster of leaves in the former than in the latter. In any given plant of *A. constancei* usually there are both fertile branches and sterile branches present. But in *A. suffrutescens*, sterile branches are not present or are exceedingly rare.

Caulanthus

At various times over the past thirty years, I have considered the generic problem posed by a strong similarity of several species, some of which are usually treated in the genus *Streptanthus* and others that are ordinarily placed in *Caulanthus*. Might not all these species be better put under *Streptanthus*, the older of the two names, as was done by Jepson (1936)? In setting up the genus *Caulanthus*, Watson (1871) was impressed by the

need to separate from *Streptanthus* a group of species having seeds with incumbent cotyledons, mostly terete to slightly obcompressed siliques and petals with reduced blades. He left to *Streptanthus* those species with siliques strongly flattened parallel to the septum, seeds with accumbent cotyledons and petals with developed blades. Greene (1904) strongly dissented from the treatment of Watson and a later one of Robinson (1895), but by proposing nine new genera to include the species mostly to be associated together in *Streptanthus* and *Caulanthus,* he was hardly of any help in developing a reasonable classification for the group. Payson (1923) provided an important presentation of the problem and of a classification that was more or less in accord with the treatment of the earliest authors. His monograph has helped to establish *Caulanthus* in the manuals and floras and I believe this is nearer the mark than would be a return to a more inclusive *Streptanthus.* However, we are quite aware that *Streptanthus* and *Caulanthus* illustrate once again one of the most frequently encountered problems in the taxonomy of the family *Cruciferae,* that of indistinct boundaries separating the genera. In my judgment, it is in the interest of a reasonable and workable classification to accept both *Caulanthus* and *Streptanthus.*

It was necessary to review this matter and arrive at a decision in order to be able to handle the identities of certain specimens received from several areas in the intermountain basin. For the present, I shall deal with one new taxon that falls clearly into the genus *Caulanthus.* However, since Jones (1893) referred to specimens of it in the protologue of the original description of *Thelypodium elegans,* it is first necessary to point out that although the species described below resembles *T. elegans* [*Sisymbrium elegans* (Jones) Payson] in a general way, the two taxa are very distinct. I have examined the holotype and three isotypes of *T. elegans.* These are consistent with the description insofar as the characters of the plants are concerned and differ only with respect to the minor fact that the labels all read May 6, 1891 instead of May 7, 1891 as given in the protologue. Attached to the holotype is a card giving the description in Jones' handwriting, largely as he published it. However, two collections with the same data as the type series, "Westwater, Colo., May 6, 1891, collected by Marcus E. Jones, A.M.," one at California Academy of Sciences and one at the Gray Herbarium, are similar to specimens from Green River, Utah, referred to below and do not belong to the type series. It is assumed that there was some mixing of two collections before they were distributed, perhaps by Jones himself. In the protologue, Jones states "A form from Green River, Utah, that I refer to this species is simple stemmed and with appressed pods." Two collections from the Jones herbarium in the Pomona College herbarium dated May 7, 1891 and May 9, 1890 from Green River, Utah, undoubtedly represent the material mentioned. These and several more recent collections from the Green River area belong to *Caulanthus divaricatus* rather than to *Sisymbrium elegans.*

Caulanthus divaricatus Rollins, sp. nov.

Herba annua, caulibus erectis simplicibus vel superne ramosis 2–9 dm. altis inferne pubescentibus vel glabratis superne glabris ramis divaricatis, foliis inferne integris vel dentatis sessilibus non-auriculatis oblongis obtusis glabris vel sparse pubescentibus 4–10 cm. longis, 1–3 cm. latis, foliis superne auriculatis ovatis imbricatis glabris 2–8 cm. longis, 1–2 cm. latis, sepalis erectis non-saccatis ochroleucis 3.5–4 mm. longis, petalis ochroleucis vel inferne albidis 7–9 mm. longis, antheris sagittatis ca. 1.5 mm. longis, pedicellis divaricatis tenuibus glabris vel sparse pubescentibus 7–12 mm. longis, siliquis teretibus divaricatis glabris vel sparse pubescentibus 6–9 cm. longis, stylis clavatis 1.5–2 mm. longis, seminibus oblongis immarginatis 1.5–2 mm. longis, cotyledonibus incumbentibus.

Holotype in the Gray Herbarium collected about 75 miles west of Blanding and 10 miles east of Hite, Twp. 34 S. R. 14 E., San Juan Co., Utah, May 16, 1961, *Arthur Cronquist 9033*. Isotype NY.

Plants annual, single stemmed and without a true basal rosette of leaves; stems erect, virgately branched above, rarely simple, densely pubescent below with contorted and twisted whitish flat trichomes to nearly glabrous, usually glabrous above, 2–9 dm. high; lowest cauline leaves densely overlapping, sessile but scarcely auriculate, entire to irregularly dentate, oblong, obtuse, strongly 1-nerved, sparsely pubescent to glabrous 4–10 cm. long, 1–3 cm. wide; cauline leaves becoming strongly auriculate upward from the lowest members, upper leaves less closely overlapped, more ovate in shape and more acute than the lower; all branches terminated by dense inflorescences; flower pedicels divaricately ascending, slender, sparsely pubescent to glabrous; sepals erect scarcely saccate to non-saccate ochroleucous 3.5–4 mm. long; petals erect, strongly nerved, 7–9 mm. long; claw whitish, obovate, abrupty narrowed at blade junction, 4–5 mm. long, ca. 2 mm. wide; blade vertically folded and crisped, yellowish, 3–4 mm. long, ca. 1 mm. wide; filaments erect, 4–4.5 mm. long; anthers slightly excerted, sagittate, introrse, not coiled, ca. 1.5 mm. long; paired stamens only slightly longer than single stamens; mold of glandular tissue subtending base of paired filaments, nearly encircling single filaments except for an area below filament insertion; ovary terete, usually very sparsely pubescent; stigma slightly larger in diameter than style, slightly bilobed, the lobes over the replum margin; fruiting pedicels divaricately ascending to more widely spreading, straight, slender, sparsely pubescent to glabrous, 7–12 mm. long; siliques terete, straight, nearly erect to divaricately ascending or more widely spreading as the plants mature, sparsely pubescent to glabrous, 6–9 cm. long, nearly sessile to gynophorate, gynophore, if present, up to 1 mm. long; valves strongly 1-nerved and with 2 weaker secondary nerves; styles subclavate, 1.5–2 mm. long, ca. 1 mm. wide, wingless or with a minor distal wing-like projection; cotyledons incumbent. Plate 2.

There is some variation represented by the specimens cited below but most of this appears to be uncorrelated. The differences such as glabrous vs. pubescent individuals are present in the same populations as are differences in the length of the gynophore. The position of the pedicels and of the siliques appears to be related to maturity. Both pedicels and siliques are nearly erect in the earlier stages becoming more widely spreading as the infructescences mature.

Caulanthus divaricatus has flowers that are yellowish in overall appearance because the sepals, short petal blades and anthers are yellow to straw colored. However, the claw of the petal which is included within the calyx is much lighter and in living material we have in the greenhouse this part of the petal is nearly white. In dried specimens, the same appears to be true. The broad claw which abruptly narrows to a constriction at the junction of the crisped blade is a feature of most species of *Caulanthus* and

PLATE 2. *Caulanthus divaricatus*. Photo of the holotype, × 2/3. Photo by Frank White.

serves to distinguish this species from others in *Sisymbrium* with which it might otherwise be confused.

OTHER COLLECTIONS STUDIED. **Utah Carbon Co.:** 2 miles n. of Price, *D. E. Bright 10* (BYU); Price, S. *Flowers 1438, 1438a* (UT). **Emery Co.:** 1 mile n. of Castle Dale, *Bassett Maguire 18334* (NY); about 10 miles east of Huntington, *Higgins & Reveal 1256* (GH, NY); Clawson, *Ripley & Barneby 4735* (CAS, GH); 3 miles n. of Woodside, *S. L. Welsh 6887* (BYU, NY); Gunnison Butte, *O. S. Walsh 31* (UT); 1 mi. s. of jct. 24 & Notom Rd., R. 7 E., T. 30 S., *Atwood 1255* (GH). **Grand Co.:** Westwater,[2] May 6, 1891, *M. E. Jones s. n.* (CAS, GH); Grand River near Moab, June 3, 1915, *M. E. Jones s. n.* (GH); Cisco, May 6, 1891, *M. E. Jones s.n.* (UC); Green River, May 7, 1891, *M. E. Jones s.n.* (POM); same, May 9, 1890 (POM, UC); same, May 23, 1914 (CAS, MICH, POM); 10 Mile Creek, near Green River, May 26, 1915, *M. E. Jones s.n.* (CAS, F, NY, UC). **Wayne Co.:** about 29 miles southwest of Hanksville, *Arthur Cronquist 8934* (GH, NY). **Garfield Co.:** about 25 miles s. of Hanksville, *Welsh, Atwood & Higgins 8953* (BYU). **San Juan Co.:** Whirlwind Draw, R. 15 E., T. 39 S., *H. Rooney 245* (BYU).

[2]Not "Colo" meaning the state of Colorado as would be assumed from the way the label is written and as was given by Jones in his citation of the type of *Thelypodium elegans*. A clue to this mistake is found in Jones' handwritten note on one of the sheets in which he says, "Westwater on the Colo.," meaning the Colorado River. Westwater is in Utah, although it is near the Colorado border.

LITERATURE CITED

BATEMAN, A. J. 1955a. Self-incompatibility Systems in Angiosperms III. *Cruciferae*. Heredity **9**: 53–68.

————. 1955b. Note on Dioecy in the *Cruciferae*. Heredity **9**: 415.

CONSTANCE, L. AND R. C. ROLLINS. 1936. New or otherwise Noteworthy Northwestern Plants II. Two New Species from the Grand Canyon of the Snake River. Proc. Biol. Soc. Wash. **49**: 147–150.

GREENE, E. L. 1904. Certain West American *Cruciferae*. Leaflets Bot. Obs. and Crit. **1**: 81–90; cf., 224–229.

JEPSON, W. L. 1936. A Flora of California **I**: 20–35.

JONES, M. E. 1893. Contributions to Western Botany. No. 5. Zoe **IV**: 254–282.

KRUCKEBERG, A. R. 1951. Intraspecific Variability in the Response of Certain Native Plant Species to Serpentine Soil. Amer. Journ. Bot. **38**: 408–419.

————. 1954. The Ecology of Serpentine Soils. III. Plant Species in Relation to Serpentine Soils. Ecology **35**: 267–274.

————. 1957. Variation in Fertility of Hybrids between Isolated Populations of the Serpentine Species, *Streptanthus glandulosus* Hook. Evolution **XI**: 185–211.

PAYSON, E. B. 1923. A Monographic Study of *Thelypodium* and Its Immediate Allies. Ann. Mo. Bot. Gard. **9**: 233–324.

ROBINSON, B. L. 1895. *Cruciferae*. Gray and Watson, Synoptical Flora of North America **1**: pt. 1. 98–180.

ROLLINS, R. C. 1936. The Genus *Arabis* L. in the Pacific Northwest. Res. Studies State Coll. Wash. **IV**: 1–52.

————. 1941. A Monographic Study of *Arabis* in Western North America. Rhodora **43**: 289–325, 348–411, 425–485.

————. 1963. Protandry in Two Species of *Streptanthus* (*Cruciferae*). Rhodora **65**: 45–49.

WATSON, S. 1871. Botany. U.S. Geol. Expl. Fortieth Parallel **V**: 14–31.