A monograph of *Boykinia, Peltoboykinia, Bolandra* and *Suksdorfia* (Saxifragaceae)

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GORNALL, R. J. & BOHM, B. A., 1984. **A monograph of *Boykinia, Peltoboykinia, Bolandra* and *Suksdorfia* (Saxifragaceae).** An evaluation of the limits and infra-generic taxonomy of the genus *Boykinia* and its allies is presented. In the past, *Boykinia* has been split into the following segregate genera: *Boykinia* and *Telesonix* (from North America) and *Neoboykinia* and *Peltoboykinia* (from Japan). The situation is complicated by other closely related genera, the limits of which also need clarification. Narrowly defined, they comprise *Suksdorfia, Hemieva, Bolandra, Sullivantia* and *Jepsonia* (all from North America) and *Hieronymusia* (from South America). This monograph draws on a variety of sources for information, including a morphological comparison of all taxa, using a wide range of both living and herbarium material, and observations on leaf anatomy, trichomes, pollen grains and seeds; reference is also made to our previously published work on flavonoids, chromosome numbers and breeding relationships. General ecological observations were made during field work in western North America. The results of these investigations confirm that the genera form a closely related group. Much of the evidence combines to suggest the following conclusions. *Boykinia* includes nine species in three sections: section *Boykinia* (*B. aconitifolia, B. intermedia, B. lycoctonifolia, B. major, B. occidentalis* and *B. rotundifolia*), section *Renifolium* (*B. richardsonii*) and section *Telesonix* (*B. jamesii* and *B. heucheriformis*). *Peltoboykinia* (*P. tellimoides* and *P. watanabei*) is recognized as a distinct genus allied to both *Saxifraga* and *Boykinia*. *Suksdorfia*, expanded to include *Hemieva* and *Hieronymusia*, has three species: *S. violacea, S. alchemilloides* and *S. ranunculifolia*. *Bolandra* is very closely related to *Suksdorfia* but is retained as a separate genus containing two species, *B. californica* and *B. oregana*. *Sullivantia* and *Jepsonia* are accepted as genera related to, but distinct from, *Boykinia*.

KEY WORDS: *Bolandra* – *Boykinia* – *Peltoboykinia* – Saxifragaceae – *Suksdorfia* – taxonomy.

CONTENTS

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INTRODUCTION

The last reasonably detailed taxonomic treatment of the Saxifragaceae *sensu lato* on a world-wide basis was by Engler (1930). He divided it into 15 subfamilies. The genera monographed in the present study belong to subfamily Saxifragoideae, tribe Saxifrageae, subtribe Saxifraginae. This subtribe contains about 24 genera, of which *Saxifraga* is the largest, with over 300 species. On the basis of floral morphology, Klopfer (1973) recognized two groups within the subtribe:

a collection of genera centred around *Heuchera*, with parietal placentation and (usually) polytelic inflorescences;

a collection of genera centred around *Saxifraga*, with axile placentation and monotelic inflorescences.

It is to this latter group that the genera discussed in this study belong (Table 1). Within this group, *Boykinia* and its closest allies form a smaller unit which is primarily North American and, if the generic concepts of Dandy (1927) and Engler (1930) are adopted, comprises: *Bolandra, Boykinia, Hieronymusia, Jepsonia, Suksdorfia, Sullivantia.* The main problem in this group is one of generic limits. Ornduff (1969a) observed that many of them were separated by "somewhat weak and arbitrary morphological criteria", although Savile (1961) justified this on the grounds that the subtribe was in the process of active evolution. Nevertheless, *Jepsonia* may be distinguished by its characteristic caudex, distylous breeding system and by its habit of flowering before producing leaves (Ornduff, 1969b). Of the remaining five genera, four are treated in this

Table 1. Genera with axile placentation and monotelic inflorescences, belonging to subtribe Saxifraginae (Engler, 1930)

Boykinia and its closest allies	Other related genera
Bolandra	*Bergenia*
Boykinia	*Darmera* (= *Peltiphyllum*)
Hieronymusia	*Mukdenia* (= *Aceriphyllum*)
*Jepsonia**	*Oresitrophe*
Suksdorfia	*Saxifraga*
Sullivantia†	*Saxifragella*
	Saxifragopsis
	Zahlbrucknera

*Revised by Ornduff (1969b).
†Revised by Soltis (1980, 1981a).

study. The omitted genus, *Sullivantia*, has been dealt with by Soltis (1980; 1981a,b), however, it will be discussed at relevant points in this study. The problem of generic limits arises not only from the closeness of the relationship between the five genera recognized by Engler, but also from the existence of several small segregate genera (*Neoboykinia, Peltoboykinia, Telesonix* and *Hemieva*) which have been split off at one time or another.

Many of the species treated here were originally assigned to *Saxifraga*. However, as more and more members of the group were discovered, a greater appreciation of the patterns of variability required that the broadly conceived *Saxifraga* be broken up into more coherent groups. There was no immediate agreement on the limits of the resultant segregate genera, and many species have been assigned to different ones at various times. A history of these diverse alignments is given in Table 2, which is laid out using the classification adopted in this monograph.

It is against this background, and in the absence of any detailed study of the genera on a world-wide basis (Spongberg, 1972), that we decided to embark on a monographic treatment. By using evidence from anatomy, morphology,

Table 2. Classification and list of taxa recognized in this study. A brief history of the various generic alignments is given but only the original authors are cited— the references can be found in the synonymy of each species

Taxon	Alternative genus
Peltoboykinia (Engl.) Hara	
P. tellimoides (Maxim.) Hara (1937)	*Saxifraga* (Maximowicz, 1871)
	Boykinia (Engler, 1919)
P. watanabei (Yatabe) Hara 1937	*Saxifraga* (Yatabe, 1892)
	Boykinia (Engler, 1919)
Boykinia Nutt. (*Nom. cons.*)	
section *Telesonix* (Raf.) Gornall & Bohm	
B. jamesii (Torrey) Engler (1891)	*Saxifraga* (Torrey, 1827)
	Telesonix (Rafinesque, 1838)
B. heucheriformis (Rydb.) Rosendahl (1905)	*Telesonix* (Rafinesque, 1838)
	Saxifraga (Jones, 1910)
section *Renifolium* Rosendahl ex Engler	
B. richardsonii (Hook.) Rothrock (1868)	*Saxifraga* (Hooker, 1832)
	Hemieva (Rafinesque, 1838)
section *Boykinia*	
B. aconitifolia Nuttall (1834)	*Saxifraga* (Fielding & Gardner, 1844)
B. intermedia (Piper) G. N. Jones (1936)	
B. lycoctonifolia (Maxim.) Engler (1891)	*Saxifraga* (Maximowicz, 1886)
	Neoboykinia (Hara, 1937)
B. major A. Gray 1876)	
B. occidentalis Torrey & Gray (1840)	*Saxifraga* (Nuttall in Torrey & Gray, 1840)
B. rotundifolia Parry in Gray (1878)	
Bolandra A. Gray	
B. californica A. Gray (1867)	
B. oregana S. Watson (1879)	*Hemieva* (Nelson & Macbride, exsiccata 1896)
Susdorfia A. Gray (*nom. cons.*)	
S. violacea A. Gray (1879)	*Hemieva* (Wheelock 1896)
S. alchemilloides (Griseb.) Engler (1891)	*Saxifraga* (Grisebach, 1879)
	Hieronymusia (Engler, 1918)
S. ranunculifolia (Hook.) Engler (1891)	*Saxifraga* (Hooker, 1832)
	Hemieva (Rafinesque, 1838)
	Boykinia (Greene, 1891)

palynology, cytology, breeding behaviour, chemistry, ecology and geography, we have tried to produce a defensible classification of this group of genera.

The study is based on living material, and on pressed specimens from the following herbaria [abbreviations as in Holmgren *et al.* (1981)]: ALA, ALTA, AUA, BM, CAL, CAN, CM, COLO, DAO, DS, F, GA, GH, GOET, ID, JEPS, K, LE, LIL, MAK, MIN, MO, MONTU, NCU, ND, NDG, NY, OSC, OXF, P, PENN, PH, POM, RM, RSA, SD, TENN, TI, UBC, UC, UNA, UNC, UTC, US, UVIC, V, WILLU, WS, WTU.

Representative specimens are listed on a microfiche obtainable on application from the Executive Secretary, The Linnean Society of London, Burlington House, Piccadilly, London W1V 0LQ, at a cost of £2.00.

SOURCES OF INFORMATION

Plant morphology

Rhizomes: Boykinia and *Peltoboykinia* have thick, scaly rhizomes ranging from 5 to 20 mm in diameter. In *Boykinia* the rhizomes are branched and in two species (*B. intermedia* and *B. lycoctonifolia*) large parts of the rhizome system can be found creeping over the surface of the ground. These above-ground segments are pigmented with anthocyanins, smooth and not at all scaly. Roots and leaves emerge from each node. It seems reasonable to interpret these organs as stolons, although the internodes are quite short (Fig. 1).

Both *Suksdorfia* and *Bolandra* have bulbiliferous rhizomes. Each bulbil is a simple reduced shoot axis and can vary from white, pale yellow, pink to brown or black. Similar bulbils are found in *Lithophragma* (Taylor, 1965). Engler (1891, 1918:266) reported that *S. alchemilloides* lacked a bulbiliferous rhizome, although all herbarium specimens examined by us definitely have one (Fig. 2). Grisebach (1879), in his protologue, described the rhizome of *S. alchemilloides* as "tuberiforme".

Orobanche uniflora L. parasitizes the roots of the North American species of *Suksdorfia*. The association of *O. uniflora* with other members of the herbaceous Saxifragaceae has been commented on recently by Taylor (1965).

Leaves: The leaves of all genera are produced in a 3/8 phyllotactic spiral. Two categories of leaf may be identified: basal and cauline. Basal leaves are produced in a tight spiral at the base of a plant, and cauline leaves form an acropetal series showing progressive morphological reduction, becoming minute bracts in the upper branches of the inflorescence. Those on the stem itself are associated

Figures 1 & 2. Fig. 1. Stolon production in *Boykinia intermedia*. Scale bar = 20 mm. Fig. 2. Bulbiliferous rhizome in *Suksdorfia alchemilloides*. Scale bar = 5 mm.

with various kinds of stipules. Characters of the leaves and stipules are taxonomically useful in separating species and, sometimes, genera.

Basal leaf shape and outline: Leaves vary from reniform to orbicular, and display varying degrees of lobing and toothing of the margins. Leaf shapes and outlines are also variable within individual species, and a representative array is shown
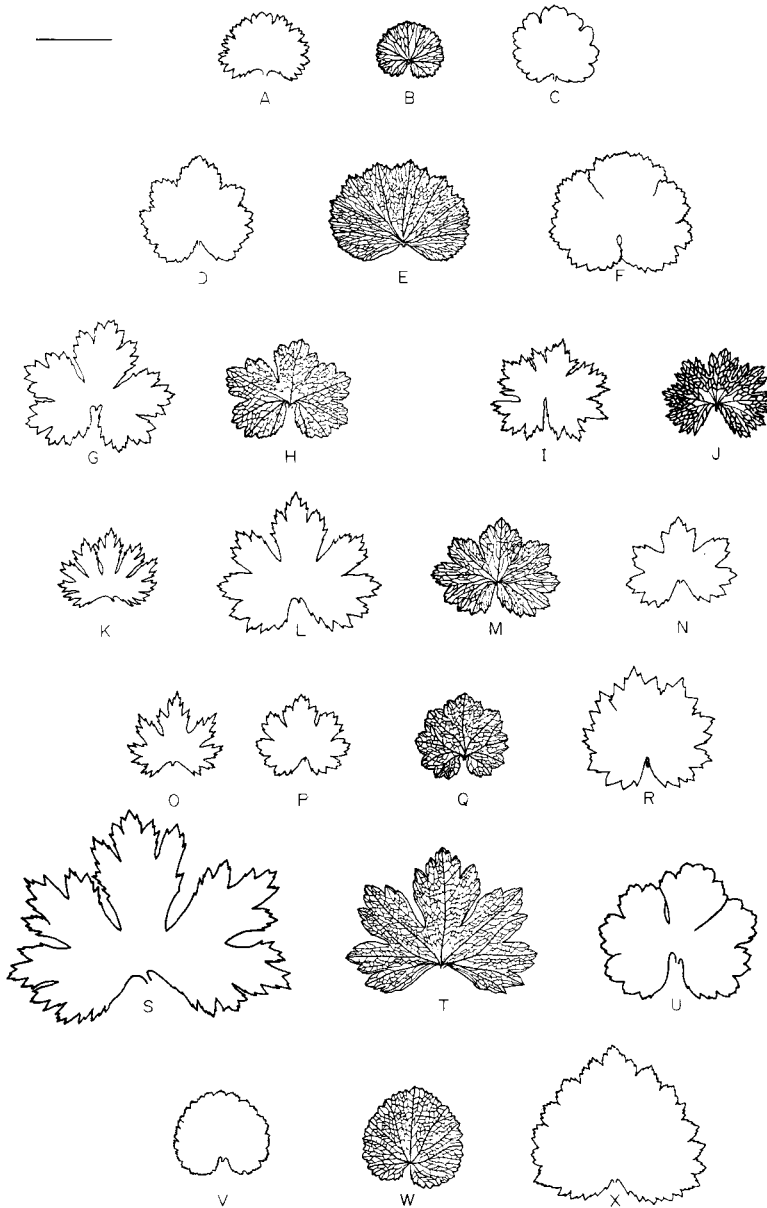

Figure 3. Variation in leaf shape and venation pattern in *Boykinia*. A–C. *B. jamesii* and *B. heucheriformis* (both species show similar variation). Scale bar = 25 mm. D–F. *B. richardsonii*. G, H. *B. intermedia*. I, J. *B. lycoctonifolia*. K–N. *B. aconitifolia*. O–R. *B. occidentalis*. S–U. *B. major*. V–X. *B. rotundifolia*. Scale bar = 50 mm (D–X).
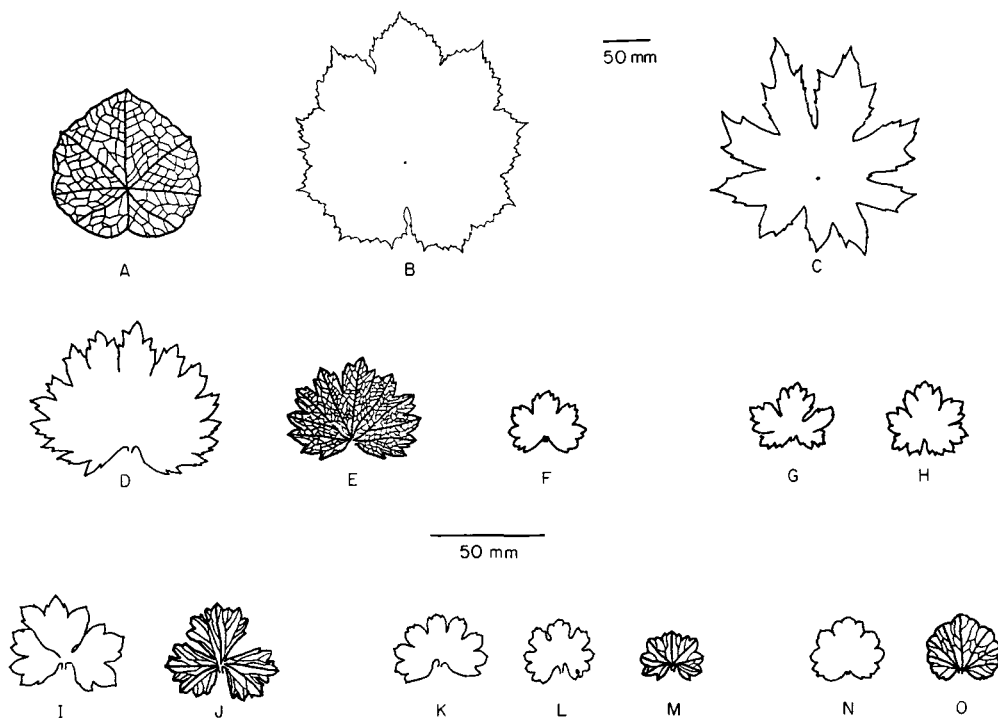
Figure 4. Variation in leaf shape and venation pattern in *Peltoboykinia*, *Bolandra* and *Suksdorfia*. A, B. *Peltoboykinia tellimoides*. C. *P. watanabei*. D–F. *Bolandra oregana*. G, H. *B. californica*. I, J. *Suksdorfia ranunculifolia*. K, M. *S. violacea*. N, O. *S. alchemilloides*.

in Figs 3 & 4. At least part of the variation within many of the species results from heteroblasty. The phenomenon is most noticeable in *Boykinia* section *Boykinia* where the early leaves in the basal rosette tend to be more reniform than later leaves, and their teeth tend to be rounded-ovate, rather than acute or lanceolate, as in later leaves. Despite this, leaf-tooth shape has been used as a taxonomic character in splitting off a segregate species from *Boykinia aconitifolia* (Rydberg, 1905) and in helping to distinguish between *Bolandra* species (Bacigalupi, 1944).

Peltoboykinia is unique among the genera studied in having peltate leaves. In terms of leaf shape the initial metaphylls of both *Peltoboykinia* species are quite prominently lobed and dentate during the early part of their development, but as they age and enlarge the lobes broaden laterally to reach the mature orbiculate, very shallowly lobed condition. In *P. tellimoides* there is little or no heteroblasty. However, in *P. watanabei*, although the earliest basal leaves are orbicular and shallowly lobed when mature, the later basal leaves do not undergo the lateral growth in the lobes to such an extent as seen in the early leaves. Rather, the later leaves adopt a prominently 5–9 lobed condition, each lobe elongating and becoming longer than wide. This heteroblasty in *P. watanabei* is not apparent from herbarium specimens, since usually only one or two of the youngest basal leaves are present at flowering.

The selective forces determining leaf shape and outline are complex and relate to competition for light, nutrients and water (Givnish, 1978).

Texture: Leaves of *Peltoboykinia* and *Boykinia* sections *Boykinia* and *Renifolium* are canaliculate on their upper surfaces and costate on their lower surfaces. In *Boykinia* section *Telesonix* and *Suksdorfia* the upper leaf surface is canaliculate-smooth and the lower surface is slightly ribbed. *Bolandra* is transitional between these two conditions. Leaves of all four genera bear trichomes and these structures are described later.

Leaves of *Peltoboykinia* are strikingly lustrous on their lower surfaces (cf. Ohwi (1965) who stated that the upper surface is lustrous) a condition not found in the other genera, although *Boykinia occidentalis* does approach it sometimes. Leaves in *Boykinia* section *Telesonix* and in *Suksdorfia* are somewhat fleshy, a condition probably related to their xeric habitats.

Venation: Study of leaf venation in all taxa was based on cleared basal leaves, following the method of Payne (1969). The terminology is that of Hickey (1973). Illustrations of the various venation patterns are shown in Figs 3 & 4.

All species examined are very similar, having actinodromous venation with the primary veins arising from the basal position. The primary veins are branched, and fairly straight or somewhat sinuous, in all species. Secondaries arise with an acute angle of divergence (45–80°), and branch from a straight or somewhat sinuous course. Tertiary venation in *Boykinia*, *Suksdorfia* and *Bolandra* is random-reticulate but tends to be orthogonal-reticulate in *Peltoboykinia*. Quaternary venation in all genera is orthogonal-reticulate. Higher order venation forms a reticulum in which the individual levels cannot be distinguished. Striking differences among taxa occur in the prominence of the venation patterns visible to the naked eye. This is a reflection of leaf texture and size of the veins present. In *Bolandra* and *Boykinia* the reticulum appears more complicated than in the other genera. Marginal ultimate venation is incomplete in all taxa, veinlets ending freely adjacent to the leaf margin. Larger veins (primary and secondary) converge at the tip of each large leaf lobe to produce a hydathode, structures common in the Saxifraginae (Metcalfe & Chalk, 1950).

Table 3. Frequencies of veinlet terminations and areolae in *Boykinia*, *Peltoboykinia*, *Suksdorfia* and *Bolandra*

Taxon	Mean no. areolae mm^{-2}($\pm$s.d.)	Mean no. veinlet endings areola^{-1} ($\pm$s.d.)	Mean no. veinlet endings mm^{-2}($\pm$s.d.)
Boykinia aconitifolia	3.0 ± 0.2	1.0 ± 0.2	3.0 ± 0.6
B. intermedia	3.3 ± 0.3	0.9 ± 0.1	2.8 ± 0.5
B. lycoctonifolia	2.9 ± 0.6	1.3 ± 0.1	3.6 ± 0.5
B. major	4.6 ± 0.3	1.3 ± 0.1	5.9 ± 0.6
B. occidentalis	2.4 ± 0.5	0.8 ± 0.2	1.9 ± 0.6
B. rotundifolia	2.5 ± 0.5	1.5 ± 0.4	3.5 ± 0.4
B. richardsonii	3.0 ± 0.4	1.2 ± 0.1	3.3 ± 0.6
B. heucheriformis	6.1 ± 0.1	1.0 ± 0.1	5.9 ± 0.4
B. jamesii	6.3 ± 1.7	1.2 ± 0.2	6.1 ± 0.7
Peltoboykinia tellimoides	0.5 ± 0.3	1.3 ± 0.5	0.5 ± 0.2
P. watanabei	2.5 ± 0.8	1.0 ± 0.5	2.2 ± 0.8
Suksdorfia alchemilloides	1.4 ± 0.3	0.9 ± 0.2	1.2 ± 0.3
S. ranunculifolia	3.5 ± 0.4	2.8 ± 0.4	9.9 ± 1.0
S. violacea	5.8 ± 0.3	1.3 ± 0.1	7.7 ± 0.6
Bolandra californica	3.5 ± 1.0	1.8 ± 0.4	4.3 ± 0.7
B. oregana	1.3 ± 0.1	1.6 ± 0.1	2.0 ± 0.2

The higher order venation forms a network of imperfect areolae which are variable in size, irregularly polygonal and randomly oriented. Details of the density of areolae and veinlet terminations are given in Table 3. Although differences between species exist, most notable being the large areolae in *Peltoboykinia*, no defensible taxonomic groupings are suggested.

Watari (1939) investigated the leaf anatomy of various species of Saxifragaceae, including *Peltoboykinia* (one species) and *Boykinia* (three species, one of which was *B. lycoctonifolia*. Details of nodal anatomy and petiole vascular system support the recognition of *Peltoboykinia* but not of *Neoboykinia*.

Cauline leaves and stipules: Cauline leaves form a reduction series, beginning from the larger basal leaves, and becoming small bracts in the higher levels of the inflorescence. Lower leaves are petiolate and the upper ones become increasingly sessile.

In all species, stipules subtend the leaves. The lower stipules, subtending the basal and lower cauline leaves, are composed of wing-like extensions of the base of the petiole. Genera and species vary in the morphology of the upper stipules and it can be a useful taxonomic character. In *Suksdorfia*, *Bolandra*, *Boykinia major*, *B. lycoctonifolia* and *B. intermedia* the upper stipules are usually foliaceous (Fig. 5) and often become adnate to the cauline leaves. In all other species of *Boykinia* and *Peltoboykinia* the upper stipules are similar to the lower structures, or are represented by small flaps (Fig. 5). In *Boykinia* section *Boykinia* the stipules, especially the lower ones, are fringed with brown bristles.

Stomata: The stomata of the Saxifraginae were the subject of a recent review by Moreau (1976). Stomatal characteristics were claimed to be of taxonomic significance although it is not clear exactly quite what this constituted. Moreau (1976) reported that *Boykinia occidentalis* had both anomocytic and anisocytic, mesoperigenous stomata as well as cyclocytic perigenous kinds. *Peltoboykinia tellimoides* was reported to possess both mesoperigenous and perigenous anomocytic stomata. In both species, stomatal development occurs non-synchronously over the whole leaf.

In the present study only the distribution of mature structures in epidermal peels of both upper and lower surfaces of the basal leaves was examined. All species have anomocytic stomata scattered in a dense array over the lower surface of their basal leaves. Occasionally one or two adjacent epidermal cells were somewhat smaller and in these cases the stomata could be described as anisocytic. No cyclocytic stomata were observed.

Taxonomically important variation between species occurs in the frequency of stomata on the upper surfaces of the leaves (Table 4). In *Suksdorfia*, and *Boykinia* sections *Renifolium* and *Telesonix*, stomata can be found commonly on the upper leaf surface. In *Peltoboykinia* and some species of section *Boykinia* such stomata are very infrequent and usually absent. In the remaining species of section *Boykinia* (*occidentalis*, *rotundifolia* and *aconitifolia*) and in *Bolandra* they are present in low numbers.

There seems to be a rough correlation between open, xeric habitats and species with high frequencies of stomata on their upper leaf surface, e.g. *Suksdorfia* and *Boykinia* section *Telesonix*. Stomatal sizes are also given in Table 4. There is no clear correlation with chromosome number.
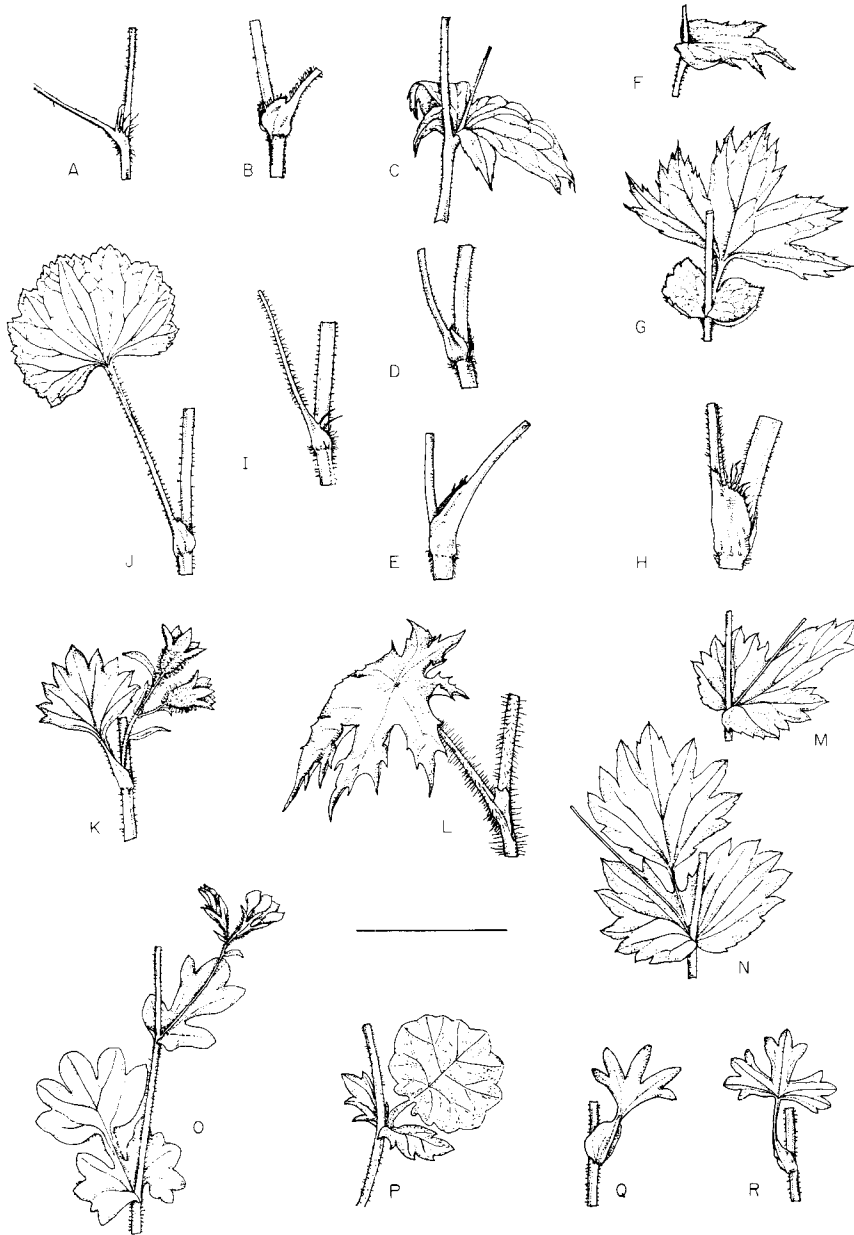
Figure 5. Stipule morphology in *Boykinia*, *Peltoboykinia*, *Bolandra* and *Suksdorfia*. A. *Boykinia occidentalis*. B. *B. lycoctonifolia*. C–E. *B. intermedia* (basipetal sequence). F–H. *B. major* (basipetal sequence). I. *B. aconitifolia*. J. *B. richardsonii*. K. *B. heucheriformis*. L. *Peltoboykinia watanabei*. M, N. *Bolandra oregana* (basipetal sequence). O. *Suksdorfia violacea*. P. *S. alchemilloides*. Q, R. *S. ranunculifolia*. Scale bar = 50 mm for A–L: 25 mm for M–R.

Trichomes: Rosendahl (1905), in a study of North American Saxifraginae, observed a similarity in trichome structure between *Bolandra* and *Suksdorfia*, and between *Boykinia* and *Sullivantia*. Moreau (1976) also examined the trichomes in a number of Saxifraginae, including *Peltoboykinia tellimoides* and *Boykinia*

Table 4. Stomatal lengths, and frequencies on upper surfaces of leaves

Taxon	Relative stomatal frequency on upper surface of leaf	Mean stomatal length ±s.d. μm ($N=10$)
Boykinia aconitifolia	Occasional	21.9±2.8
B. intermedia	Absent/very rare	24.0±2.9
B. lycoctonifolia	Absent/very rare	30.9±5.6
B. major	Absent/very rare	28.8±5.3
B. occidentalis	Moderately common	26.9±1.7
B. rotundifolia	Moderately common	27.7±2.2
B. richardsonii	Common	38.8±3.8
B. heucheriformis	Common	30.6±1.9
B. jamesii	Common	34.4±4.7
Peltoboykinia tellimoides	Absent/very rare	36.4±3.9
P. watanabei	Absent/very rare	31.2±4.8
Suksdorfia alchemilloides	Common	30.1±3.3
S. ranunculifolia	Common	34.1±4.4
S. violacea	Common	28.0±3.1
Bolandra californica	Occasional	27.7±3.2
B. oregana	Occasional	33.8±3.3

occidentalis, but his study did not encompass all organs of the plant and the results were clearly incomplete. In the present study trichome structures from all organs were observed. Six categories of trichome were identified (Fig. 6):

  multicellular, multiseriate glandular;
  multicellular, multiseriate eglandular with many brown, dead cells (brown chaff);
  multicellular, uniseriate glandular;
  multicellular, uniseriate eglandular with many brown, dead cells (brown chaff);
  multicellular, uniseriate eglandular;
  unicellular, eglandular.

Observations of young plants of *Boykinia occidentalis* and *Peltoboykinia watanabei* indicate that the brown, chaffy trichomes are derived developmentally from glandular forms. There is a loss of the glandular head followed by progressive, basipetally directed cell death. The dead cells turn brown, curl and twist. This process is less marked in *B. rotundifolia,* where only a few multiseriate glands normally degenerate, leaving the stem viscid-hirsute. However, some herbarium specimens possess quite a number of brown chaffy hairs.

The variation in trichome size among the species is continuous, and has a considerable intra-individual component, so little taxonomic significance can be attached to it. Rather, it is trichome anatomy which is taxonomically important, and is especially helpful in defining generic limits. A summary of the results is given in Table 5.

Boykinia section *Boykinia* is characterized by a trichome complement of multiseriate glands, brown chaff, and unicellular eglandular hairs. *Boykinia* sections *Renifolium* and *Telesonix* are similar except that they normally lack the brown chaff. The brown chaff is most common at the base of the stem, basal leaf petioles, and around the lower stem nodes. This trichome form is especially common in *B. occidentalis* and some specimens can look quite villous. On the upper part of the stem toward the inflorescence, the multicellular, multiseriate
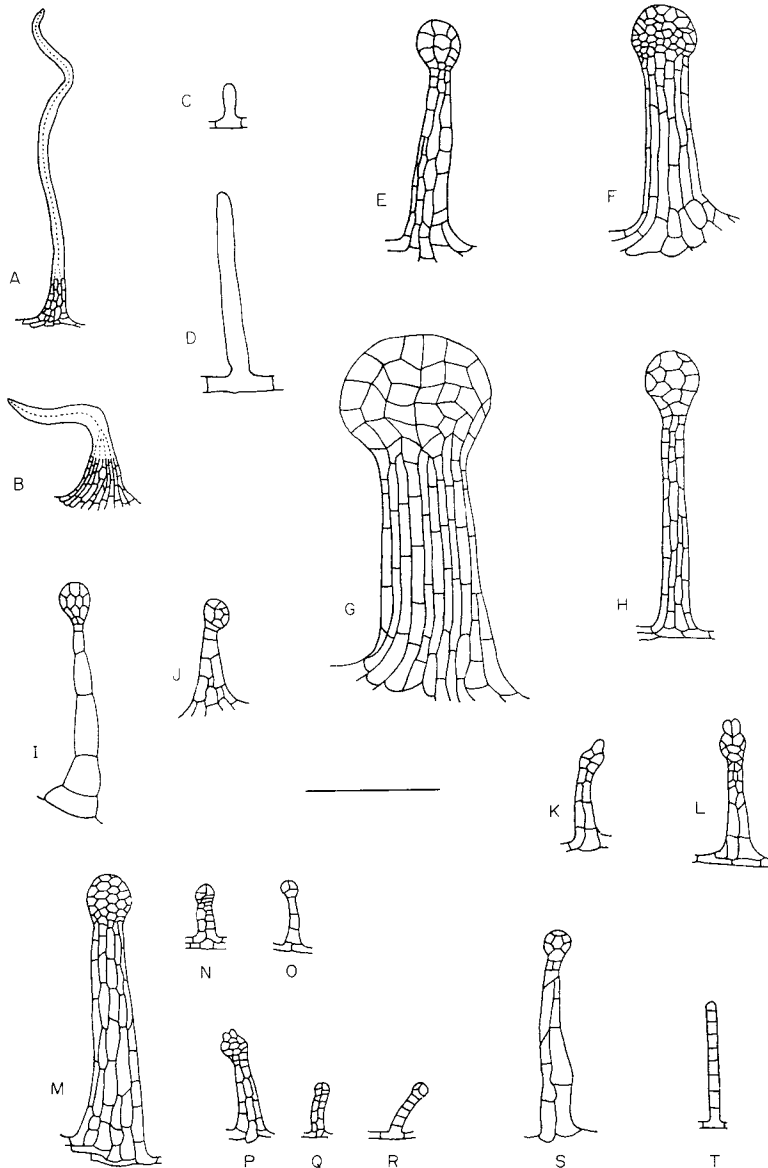
Figure 6. Variation in trichome anatomy, illustrating the different types. A, B. Brown, chaffy, multiseriate, eglandular trichomes. Scale bar = 750 μm. C, D. Unicellular, eglandular trichomes. Scale bar = 250 μm. E–S. Multicellular, glandular trichomes. Scale bar = 250 μm. E. *Boykinia lycoctonifolia*. F. *B. major*. G. *B. richardsonii*. H. *B. heucheriformis*. I, J. *Peltoboykinia watanabei*. K, L. *Bolandra oregana*. M–O. *Suksdorfia ranunculifolia*. P–R. *S. violacea*. S. *S. alchemilloides*. T. Uniseriate, eglandular tichome occurring on the anthers and stigmata of *Suksdorfia aalchemilloides*. Scale bar = 60 μm.

glands become increasingly frequent. They reach their maximum density on the pedicels and hypanthium. The multicellular gland head is usually spherical or ellipsoid, but occasionally has protruding papillae as in *Bolandra* and *Suksdorfia*. The unicellular eglandular trichomes occur densely on the inflorescence

Table 5. Distribution of predominant kinds of trichome among *Boykinia*, *Peltoboykinia*, *Suksdorfia* and *Bolandra*

| | Unicellular | Multicellular | | | | | |
| | | Uniseriate | | | Multiseriate | | |
	Eglandular	Glandular	Chaff	Eglandular	Glandular	Chaff
Boykinia occidentalis	+	−	−	−	+	+
B. intermedia	+	−	−	−	+	+
B. major	+	−	−	−	+	+
B. aconitifolia	+	−	−	−	+	+
B. lycoctonifolia	+	−	−	−	+	+
B. rotundifolia	+	−	−	−	+	(+)
B. richardsonii	+	−	−	−	+	−(+)
B. jamesii	+	−	−	−	+	−(+)
B. heucheriformis	+	−	−	−	+	−(+)
Peltoboykinia tellimoides	−	+*	(+)	−	−	−
P. watanabei	−	+*	(+)	−	−	−
Suksdorfia ranunculifolia	−(+)	−	−	−	+*	−
S. violacea	+	−	−	−	+*	−
S. alchemilloides	+	−	−	+	+	−
Bolandra californica	−	−	−	−	+*	−
B. oregana	−	−	−	−	+*	−

*Trichomes occur which are transitional between multi- and uniseriate.
Only entry in parentheses = always occurring but in very low numbers.
Alternative entry in parentheses = a rare condition, not always encountered.

branches, pedicels and upper bracts where they form an understory to the multiseriate glandular hairs. On the leaves, trichomes often are associated with the veins and also occur along the leaf margins, being especially prominent here in section *Telesonix*. The laminae are generally less densely pubescent than are the stem or petioles, but all three hair forms are present, with the multiseriate glands and chaff being the commonest. Unicellular hairs become more frequent on those leaves nearer the stem apex.

The genus *Peltoboykinia* has multicellular, uniseriate glandular trichomes. Occasional glands are multiseriate below and uniseriate above, and thus may be regarded as transitional. The trichomes occur most prominently on the stem, petioles, inflorescence branches, pedicels, calyces and, most notably, the petals, but are also present on the leaves, associated with the veins. In older plants, the lower nodes bear brown, chaffy, uniseriate, eglandular trichomes.

In *Bolandra*, the trichomes are multicellular, multiseriate and glandular, although transitions to a uniseriate condition often occur where the trichome is multiseriate below but uniseriate above; much variation occurs and almost all stages between the multi- and uniseriate states can be found. The multicellular gland heads usually have from one to three prominent papillae. The glands occur on the leaves, often associated with the veins, and on the petioles, stem, inflorescence branches and pedicels. The hypanthium is usually glabrous.

Suksdorfia possesses multicellular, multiseriate glands, together with forms transitional to the uniseriate condition. The multicellular gland heads sometimes have from one to three papillae, although these are less marked in *S. alchemilloides*. Unicellular hairs are densely arrayed on the peduncles and
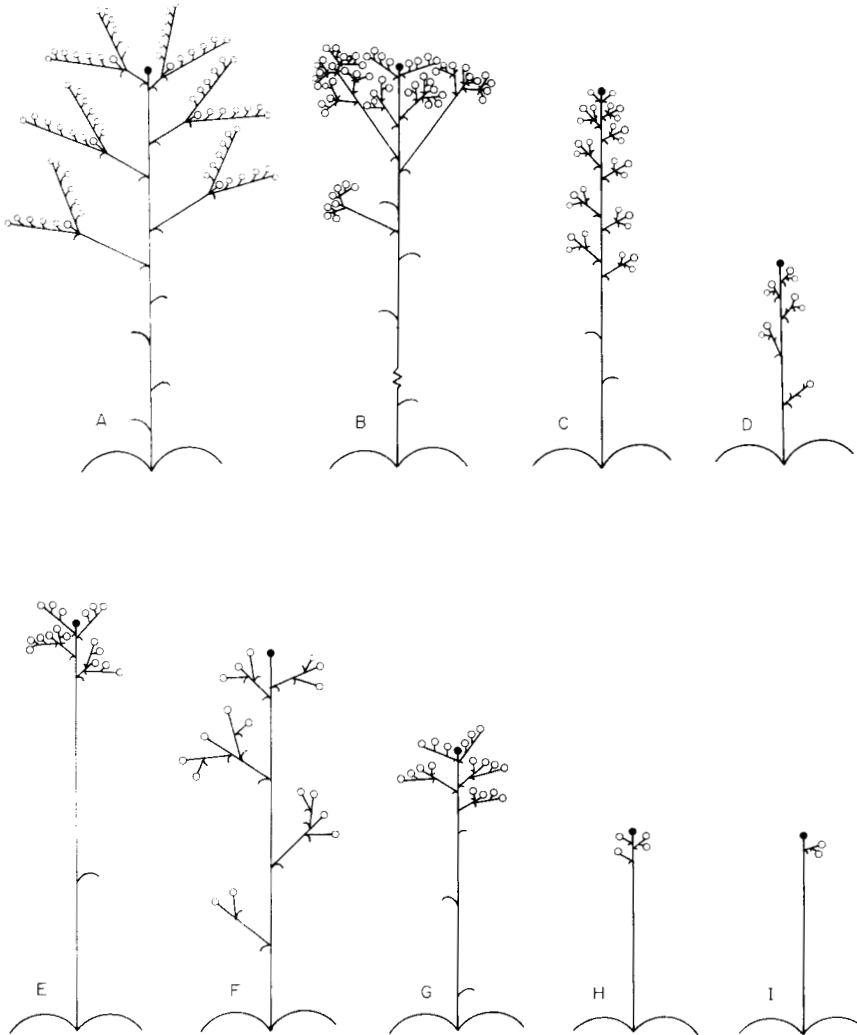
Figure 7. Diagrammatic representation of inflorescence structures. A, B. *Boykinia* section *Boykinia*. C. *Boykinia* section *Renifolium*. D. *Boykinia* section *Telesonix*. E. *Peltoboykinia*. F. *Bolandra*. G. *Suksdorfia ranunculifolia*. H. *S. alchemilloides*. I. *S. violacea*.

pedicels of *S. violacea* and *S. alchemilloides*. They are usually absent (or very rare) in *S. ranunculifolia*. The distribution of all these hair forms over the plant follows the pattern found in *Boykinia*. *Suksdorfia alchemilloides* is distinct in having characteristic, red, slender, multicellular, uniseriate, eglandular hairs located on the anthers and sometimes among the stigmatic papillae.

Function: The glandular portion of the hairs consists of a multicellular globular head which often contains anthocyanins and, at least in *Boykinia*, the spicy, aromatic principles (smelling somewhat like coriander) which help characterize the genus. The spicy smell may serve to attract pollinators. We could detect no odour in *Peltoboykinia*, *Suksdorfia*, *Bolandra* or *Sullivantia*.

The sticky glands and, in some species, their associated unicellular trichomes are especially densely arrayed on the flower pedicels, and probably have a protective role against feeding and/or egg laying by insects (Levin, 1973). Indeed, they certainly trap a number of insects, particularly small Diptera.

Inflorescences: The genera *Boykinia, Peltoboykinia, Suksdorfia* and *Bolandra* all have monotelic (cymose) inflorescences, with a terminal flower and basipetal development of successive paracladia. Each paracladium is subtended by a bract or cauline leaf. In all taxa the inflorescence is initially highly congested and it is only after anthesis and especially during fruiting, following peduncle growth, that its structure becomes readily apparent. The following descriptions apply to this stage. Inflorescence structure is particularly valuable in helping divide *Boykinia* into sections. Diagrammatic representations of typical branching patterns are shown in Fig. 7.

The inflorescence branching pattern in all species of *Boykinia* section *Boykinia* is an open structure composed of first order paracladia, although in well-developed individuals second-order paracladia may be present, again subtended by bracts. Each paracladium consists of a terminal flower borne at the junction of a dichotomous branch pair, each branch of which bears several flowers in a typically helicoid arrangement. The terminal flower is often displaced to one side of the branch junction, and occasionally it is absent. *Boykinia major* is distinct in the section in having a corymbiform inflorescence, although *B. intermedia* can approach this sometimes. *Boykinia richardsonii* (section *Renifolium*) has a similar basic structure to that in section *Boykinia*; however, instead of forming an open structure, the paracladia are tightly organized into a contracted thrysoid inflorescence, each paracladium composed of a three-flowered dichasium. Species of section *Telesonix* have a similar inflorescence shape to that of *B. richardsonii* but their paracladia are represented by a terminal flower with typically only one lateral flower.

A structural series similar to that in *Boykinia* is found in *Suksdorfia*. Thus the inflorescence of *S. ranunculifolia* is similar to that of *Boykinia* section *Boykinia*. *Suksdorfia alchemilloides* and *S. violacea* have a simpler structure consisting of fewer paracladia, each of which comprises a terminal flower with one or two lateral blooms only. This resembles the condition found in *Boykinia* section *Telesonix*. Some plants have but a single terminal flower.

In *Bolandra* and *Peltoboykinia,* the inflorescence structure is as in *Boykinia* section *Boykinia,* although the number of flowers per paracladium is fewer. This is especially true of *Bolandra* where the very lax, open inflorescence typically has paracladia with a terminal and two lateral flowers only, although second-order paracladia may occur.

Flowers: The flowers of *Boykinia, Peltoboykinia, Suksdorfia,* and *Bolandra* are perfect and are composed of four or five whorls of parts: calyx, corolla, a one or two-whorled androecium, and a bicarpellate gynoecium. The flowers are typically actinomorphic, although some asymmetry is occasionally seen. Floral characters do little to help define generic limits but are taxonomically valuable at the sectional level and below. Illustrations of various species are shown in Figs 8 & 9.
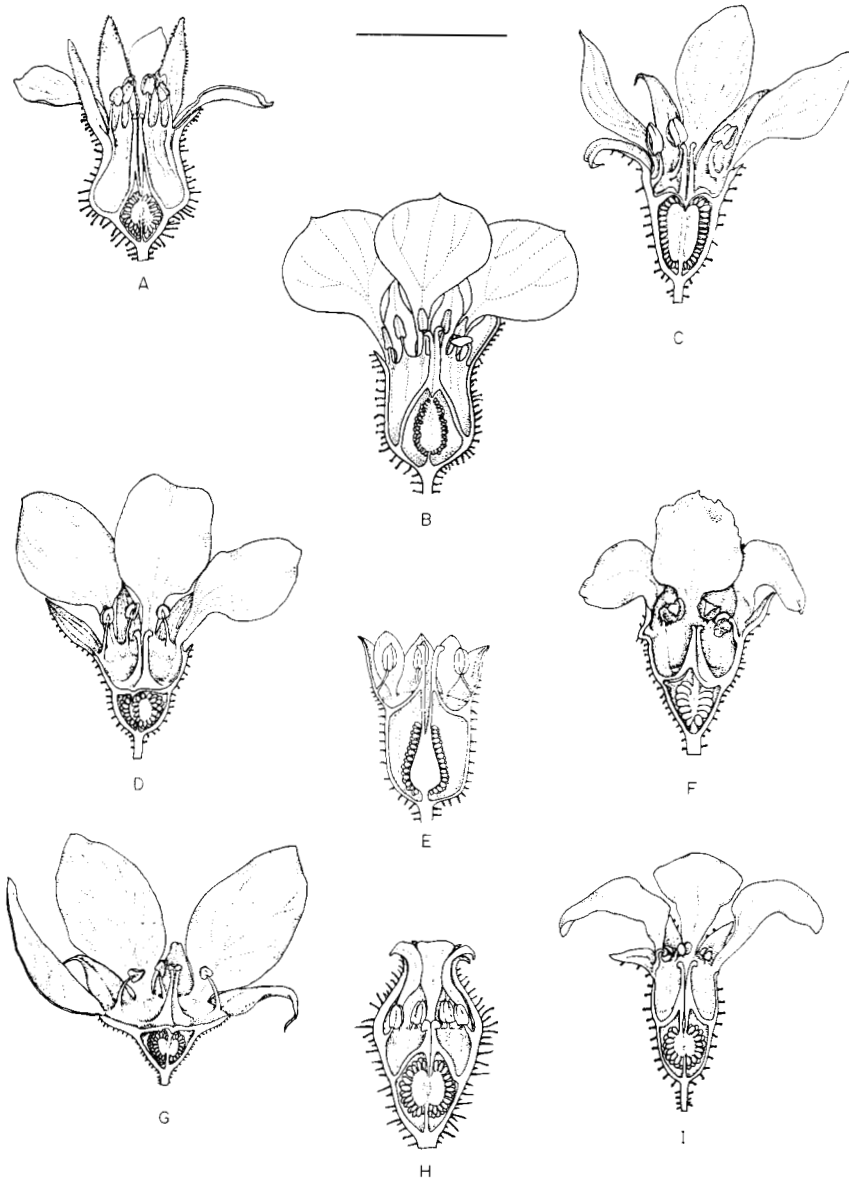
Figure 8. Floral morphology in *Boykinia*. A. *B. heucheriformis*. B. *B. jamesii*. C. *B. richardsonii*. D. *B. intermedia*. E. *B. lycoctonifolia*. F. *B. aconitifolia*. G. *B. major*. H. *B. rotundifolia*. I. *B. occidentalis*. Scale bar = 5 mm.

Calyx: In all species the calyx is composed of five sepals which are fused with the basal portions of the petals, stamens and carpels to form the hypanthium. The apices of the sepals are triangular to lanceolate, and free. The hypanthium is clothed in glandular hairs and, sometimes, smaller unicellular trichomes as well in all genera except *Bolandra*, where it is glabrous. In *Boykinia lycoctonifolia* the sepals are imbricate only at the base (Hara, 1937).
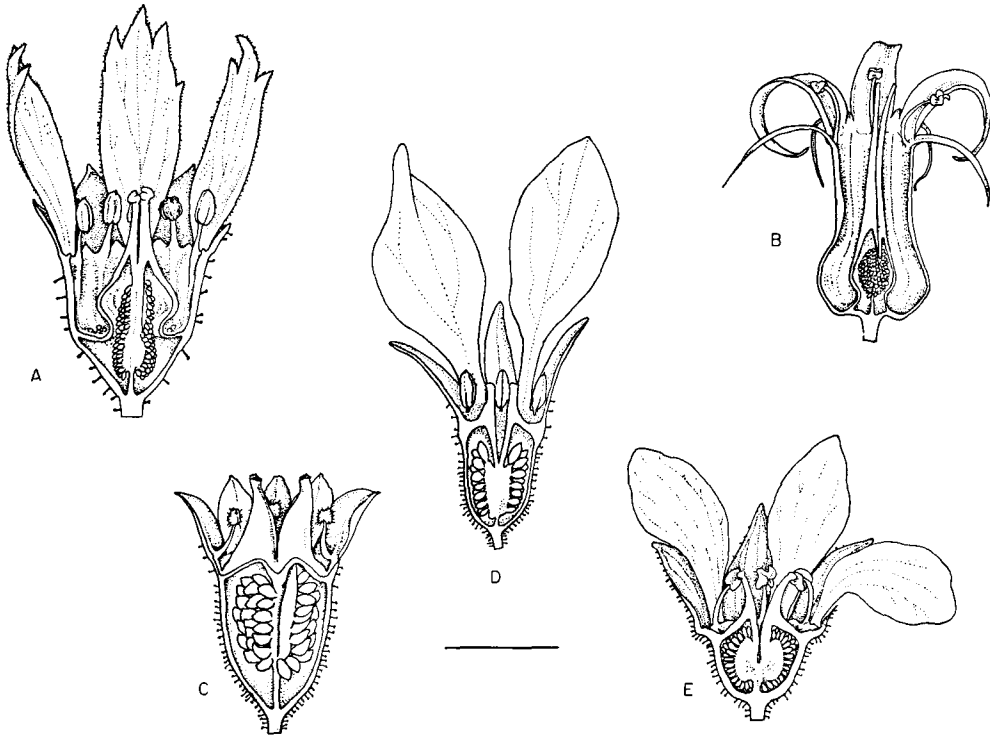
Figure 9. Floral morphology in *Peltoboykinia, Bolandra* and *Suksdorfia*. A. *Peltoboykinia tellimoides*. B. *Bolandra oregana*. Scale bar = 5 mm. C. *Suksdorfia alchemilloides*. D. *S. violacea*. E. *S. ranunculifolia*. Scale bar = 2 mm.

Corolla: Most species have white petals, but some have other colours: yellow-green in *Boykinia lycoctonifolia*; white with rose veins in *B. richardsonii*; crimson in *B. jamesii*; crimson-purple in *B. heucheriformis*; violet or almost white in *Suksdorfia violacea*; rose or white in *S. alchemilloides*. In *Peltoboykinia* petal colour in both species is identical (cf. Ohwi, 1965): newly emergent petals are a cream colour which darkens to a pale yellow at anthesis, and subsequently fades back to a cream colour. *Bolandra* is also somewhat variable in petal colour: most populations have red petals, but in some they can be yellow-green with red margins and occasionally just yellow-green. Some populations of *B. major* and *S. ranunculifolia* have flowers with purple blotches at the base of the petals. Petals of all species reflect UV light. The ring of yellow anthers and, in some species, the yellow nectariferous disc, seem to be the only honey guides, although these too reflect UV light.

Petal shape varies among the species studied (Fig. 10). Some species show a pronounced claw on the petal, in others it is reduced and in still others it is absent. *Bolandra* is distinct in having subulate petals. Petal margins are entire, except in *Peltoboykinia* which produces characteristic, toothed petals. However, in some populations of *B. major* some individuals also have toothed or serrated petals. The basis for this polymorphism is unknown. It occurs in both the Bitterroot Mountains and the Oregon Cascades. A similar polymorphism may

exist in *Suksdorfia violacea* (Suksdorf, in letter with holotype; Rydberg, 1905), although we have never observed it.

Anatomically, each petal possesses a single vascular bundle in the free part of its basal portion. Various numbers of traces diverge from this principal bundle in different species (Fig. 10). Only *Peltoboykinia* possesses petals with glandular hairs.
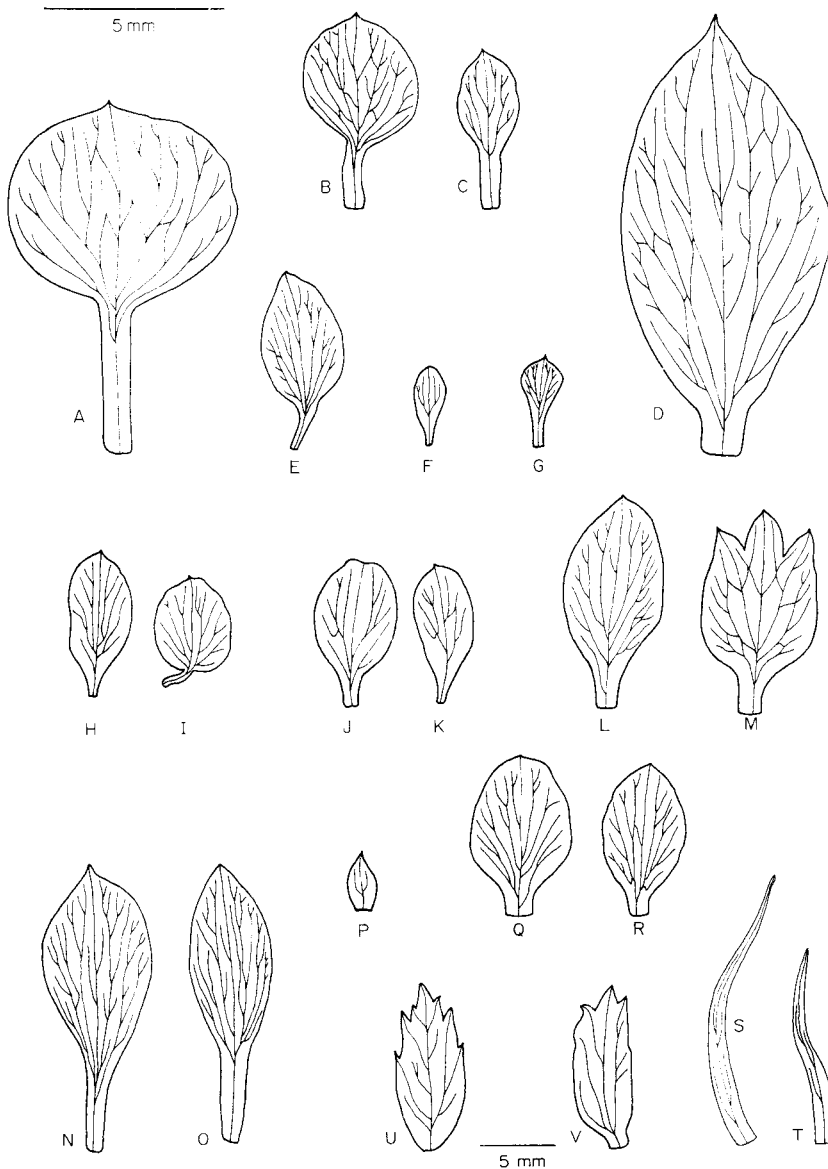
Figure 10. Variation in petal shape and venation. A. *Boykinia jamesii*. B, C. *B. heucheriformis*. D. *B. richardsonii*. E. *B. intermedia*. F. *B. lycoctonifolia*. G. *B. rotundifolia*. H, I. *B. aconitifolia*. J, K. *B. occidentalis*. L, M. *B. major*. N, O. *Suksdorfia violacea*. P. *S. alchemilloides*. Q, R. *S. ranunculifolia*. S. *Bolandra oregana*. T. *B. californica*. U. *Peltoboykinia tellimoides* (note smaller scale). V. *P. watanabei* (note smaller scale).

2

In nature, marcescent petals occur in *Boykinia lycoctonifolia*. They also occur in growth-room-maintained populations of *Boykinia occidentalis*, *B. intermedia* and *B. major*. In this protected environment, the abscission layer at the base of the petals fails to develop fully, and the petals persist on the flowers, resisting even vigorous disturbance. This is important because the character has been considered taxonomically valuable in the past (Hara, 1937). Petals are deciduous in growth-room material of *Peltoboykinia*.

Petal movements: In *Boykinia major* and *B. intermedia*, the petals close around the styles as the flower ages, forming a tube; these petal movements in old, possibly unreceptive or already fertilized flowers, may signal pollinators to keep away. In other species with petals longer than the sepals, e.g. *Boykinia occidentalis*, *B. richardonsii*, *B. jamesii*, *B. aconitifolia*, *Bolandra*, N American *Suksdorfia* species and *Peltoboykinia*, the petals become increasingly reflexed as the flower opens and ages. Species with short, or included petals (*Boykinia rotundifolia*, *B. heucheriformis*) show little or no movement of these organs. We have no data on petal movements in the S American *Suksdorfia alchemilloides* and the Japanese *Boykinia lycoctonifolia*.

Androecium: All stamens are free and are in two whorls of five each in *Peltoboykinia* and *Boykinia* section *Telesonix*, and in a single whorl of five in all the other species. In the diplostemonous species the outer whorl is anti-sepalous and dehisces earlier than the anti-petalous inner whorl. In the haplostemonous species the stamens are anti-sepalous. The stamen whorls are adnate to and arise from the hypanthium. A single veined, conical filament bears the anther which is cordate at the base and in *Boykinia* section *Boykinia*, *Suksdorfia alchemilloides*, *S. violacea* and *Peltoboykinia*, possesses a small apical mucro which is usually most marked in young undehisced anthers. It becomes less distinct and may disappear as the anther ages. Each anther has two thecae, each of which contains two microsporangia. Dehiscence is by longitudinal slits, the lateral portions of each theca becoming completely reflexed so as to present the pollen both introrsely and extrorsely, almost in a 360° arc. In many cases, pollen presentation is very close to the stigmata (*Boykinia occidentalis*, *B. rotundifolia*, *B. lycoctonifolia*, *Suksdorfia violacea* and *S. alchemilloides*). All species examined are protandrous, although the extent varies from species to species (Gornall & Bohm, 1984). The anthers of *Peltoboykinia* change from pale cream to black just before dehiscence. In all other species the anthers remain yellow.

Stamen movements: Initially the anthers form a close ring around the young styles. As the flower ages and the ovary and styles elongate, the petals and sepals spread out, pulling the stamens away from the styles. Anther dehiscence usually occurs before the flower reaches its maximum spread. There are no independent stamen movements as are found in *Saxifraga* (Spongberg, 1972), all positional changes being dependent on hypanthium shape alterations mediated by ovary growth.

Gynoecium: All genera studied have axile placentation, usually with two carpels forming a bilocular ovary. Carpel fusion varies among the species from partial to complete (Figs 8 & 9). In those species with the upper parts of their ovaries free, the placentation in this region is correctly termed marginal. In species with almost complete carpel fusion, the styles are joined by a delicate tissue which

often ruptures along some of its length allowing the styles to separate. As a taxonomic character it is thus potentially variable and should be used with care, especially in herbarium specimens. Ovary position varies between the species from nearly inferior to nearly superior. The variation has a developmental component because as a flower ages the ovary elongates, becoming less inferior. The length of the free hypanthium on the other hand is more or less constant throughout the life of a flower and is thus of value taxonomically, especially in species delimitation. Ovary position to a large extent dictates hypanthium shape: turbinate to campanulate in *Boykinia* and *Suksdorfia*; tubular-campanulate in *Peltoboykinia* and *Bolandra*. As seeds ripen the ovary swells and the capsule becomes urceolate in all taxa except in some populations of *Boykinia aconitifolia* whose capsules remain turbinate.

A nectary occurs in a band around the style base where the free hypanthium and the ovary wall meet. The nectary is composed of yellow, green or yellow-green glandular tissue and secretes a sugary solution just before the stigmata become receptive. It is disc-like in *Suksdorfia ranunculifolia*. Following pollination, as the flower ages, the styles, stigmata and petals become flushed with anthocyanins. The amount is variable and usually not apparent in the genus *Peltoboykinia*. If the pollination is successful, the carpels elongate and expand, an event noticeable after about 2 weeks. Developing ovules remain enclosed in the ovary in all genera. As the seeds ripen, the styles in species with little carpel fusion become increasingly divergent (*Boykinia, Peltoboykinia* and *Suksdorfia*). In other species the styles remain close together until dehiscence when they reflex (*Bolandra*). In all species the capsules dehisce by a longitudinal slit between the styles.

The stigmata are capitate with unicellular papillae in *Boykinia, Peltoboykinia, Bolandra* and in *Suksdorfia ranunculifolia,* but truncate in *Suksdorfia violacea* and *S. alchemilloides*. Recent cytochemical and physiological investigations of the angiosperm stigma have resulted in its classification into two main types: wet and dry (Heslop-Harrison, 1975). Wet types show a distinct surface secretion during their receptive period, whereas dry types do not. Within each type further subdivisions have been made based on the morphology of the receptive surface. In the present study, wet (group III) stigmata were observed throughout all the genera. The styles in all species studied have a canal which is lined with transmitting tissue. In the two *Peltoboykinia* species, the stylar canals are completely filled with this tissue.

Floral anatomy: Bensel & Palser (1975) have made a detailed study of floral anatomy in 26 species of Engler's Saxifragoideae, including *Boykinia occidentalis* and *Peltoboykinia tellimoides.* They concluded that the subfamily was remarkably homogeneous. The differences observed between the species of *Boykinia* and *Peltoboykinia* mainly involved the vascularization of the carpels. Investigation of other species in these genera and in *Suksdorfia* and *Bolandra* may reveal consistent differences of taxonomic value.

Embryology: Peltoboykinia, Boykinia, Bolandra and *Suksdorfia* have anatropous, bitegmic, crassinucellate ovules (Krach, 1976), which, together with a monosporic, *Polygonum*-type embryo sac, is the usual condition in the Saxifrageae (Davis, 1966). Embryogeny has not been studied properly in the genera considered here, but relatives are reported to exhibit either the Solanad-
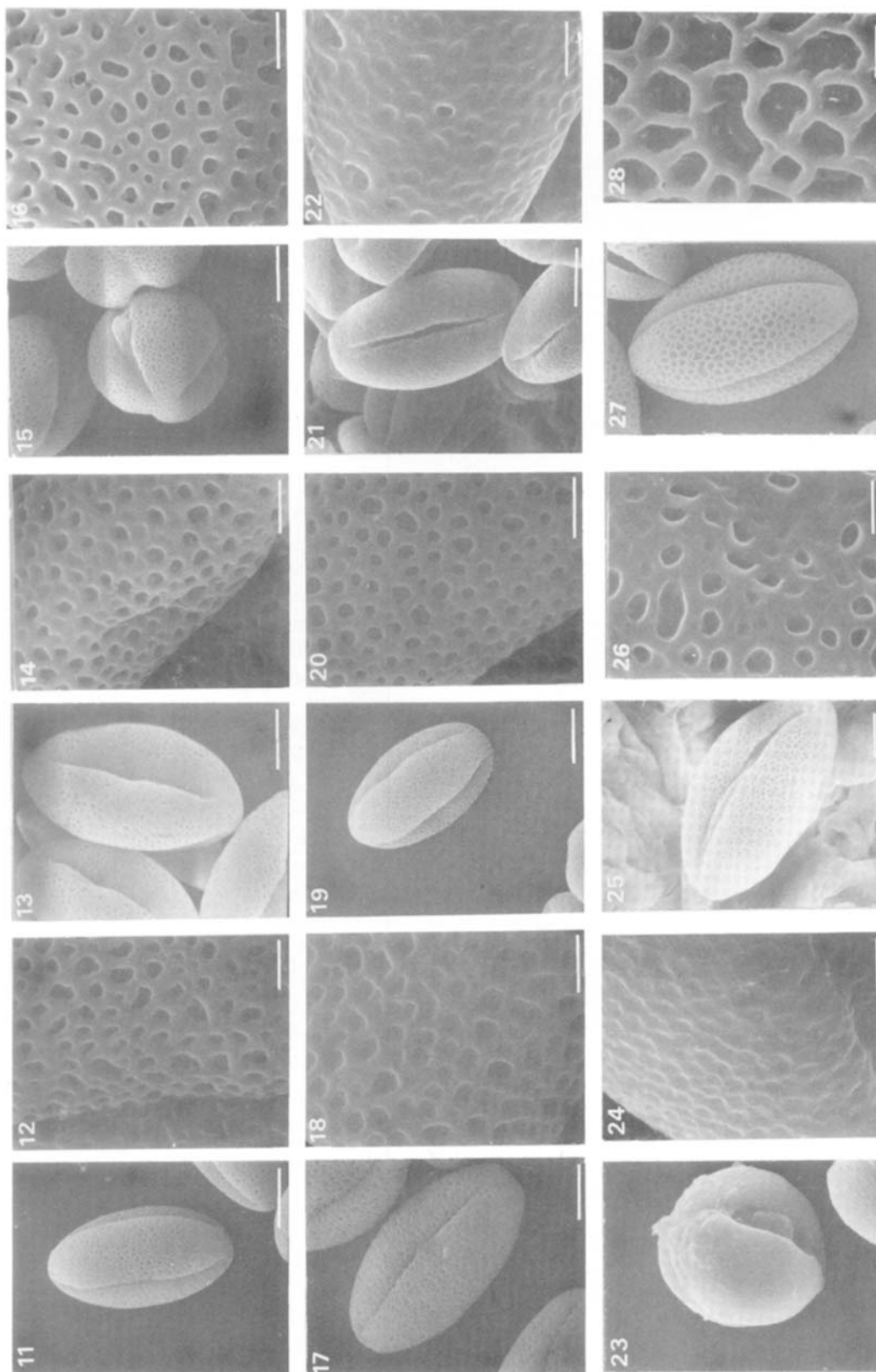
Figures 11–28. Pollen grains of *Boykinia*. Figs 11, 12. *B. aconitifolia*. Figs 13, 14. *B. intermedia*. Figs 15, 16. *B. lycoctonifolia*. Figs 17, 18. *B. major*. Figs 19, 20. *B. occidentalis*. Figs 21, 22. *B. rotundifolia*. Figs 23, 24. *B. jamesii*. Figs 25, 26. *B. heucheriformis*. Figs 27, 28. *B. richardsonii*. Scale bars = 5 μm (Figs 11, 13, 15, 17, 19, 21, 23, 25, 27) or 1 μm (Figs 12, 14, 16, 18, 20, 22, 24, 26, 28).
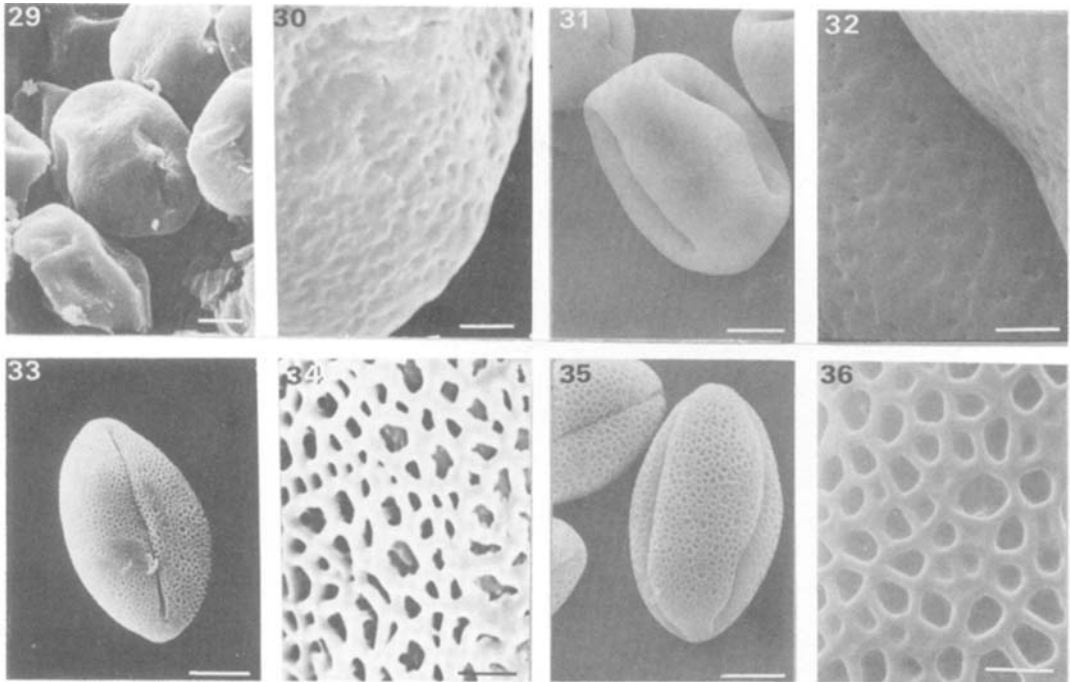
Figures 29–36. Pollen grains of *Peltoboykinia* and *Bolandra*. Figs 29, 30. *Peltoboykinia tellimoides*. Figs 31, 32. *P. watanabei*. Figs 33, 34. *Bolandra californica*. Figs 35, 36. *B. oregana*. Scale bars = 5 μm (Figs 29, 31, 33, 35) or 1 μm (Figs 30, 32, 34, 36).

type of development (Davis, 1966) or the Caryophyllad-type (Johansen, 1950; Lebegue, 1952; Kaplan, 1976). Endosperm formation is also variable. It is *ab initio* cellular in *Boykinia occidentalis*, but helobial in *Peltoboykinia tellimoides* (Dahlgren, 1930). The tribe is thus rather variable and embryological investigation of the genera at hand may prove useful in supporting their delimitation.

Teratological phenomena: Abortion of part or all of the androecium was observed in some flowers of growth-room populations of *Boykinia occidentalis* and *B. major*. Aberrant variation in petal, stamen and carpel number, usually an increase of one but sometimes more, was observed occasionally in *Boykinia* (a tendency also noted by Nuttall (1834)) and much more commonly in *Suksdorfia*. On one occasion, a cultivated individual of *Boykinia occidentalis* from Oregon (*Gornall 256*) developed one or two small, yellow-orange spots on the petals of some of its flowers, not unlike those found in some *Saxifraga* species. Subsequent flowers on this plant lacked these spots.

Pollen: The present study of *Peltoboykinia*, *Boykinia*, *Bolandra* and *Suksdorfia* was undertaken to complement the broader survey and review conducted by Hideux & Ferguson (1976) who examined *Boykinia aconitifolia*, *B. occidentalis*, *B. major*, *B. lycoctonifolia*, *B. richardsonii*, *Peltoboykinia tellimoides*, *Suksdorfia ranunculifolia*, *S. alchemilloides* and *Bolandra oregana*, as well as representatives of many other genera in the Saxifragaceae. These workers reported variation in tectum and aperture structures which has potential taxonomic significance at both generic and sectional levels.

Materials and methods: Pollen was examined by both light and SEM. For light microscopy, the pollen was acetolysed following Erdtman (1960) and mounted in Hoyer's medium. For SEM, anthers were critical-point-dried with CO_2. They were then mounted on stubs and the pollen grains dissected out and gold-coated. All size measurements were made with a light microscope on air-dried grains mounted in Hoyer's Medium. Microsporogenesis was studied by squashing young anthers in 1% acetocarmine.

Microsporogenesis: In species of all genera studied, cytokinesis of the pollen mother cells is simultaneous, the pollen grains are binucleate and are disseminated as monads.

Shape and size: Pollen grains are isopolar with a radial order three symmetry. Generally, in polar view, the apertural angle is obtuse and the inter-apertural zone convex, although infraspecific variation exists such that some populations of *Suksdorfia ranunculifolia*, *Suksdarfia violacea*, *Bolandra oregana* and *Boykinia richardsonii* may have an inter-apertural zone that is more lobate than convex. In equatorial view, pollen shape varies depending on the treatment given. Thus, when untreated grains are mounted in Hoyer's medium they appear oblate-spheroidal in all species. However, acetolysed grains mounted in Hoyer's medium vary from spheroidal to subprolate, the shapes reported by Ikuse (1956) and Hideux & Ferguson (1976). In material prepared for SEM, *Peltoboykinia*, *Bolandra* and all *Boykinia* species (except *B. lycoctonifolia*) have prolate grains in equatorial view. *Boykinia lycoctonifolia*, like *Suksdorfia*, has spheroidal grains. Pollen sizes are shown in Table 6. There is no clear

Table 6. Sizes of air-dried pollen grains mounted in Hoyer's Medium. Ten representative grains per collection were measured, results being expressed as the mean ± s.d.

Taxon	N	$P(\mu m)$*	$E(\mu m)$*
Boykinia aconitifolia	50	14.8 ± 1.3	16.2 ± 1.3
B. intermedia	30	17.2 ± 1.0	18.4 ± 1.2
B. lycoctonifolia	30	18.0 ± 0.7	19.2 ± 1.2
B. major	50	17.9 ± 1.5	20.2 ± 1.5
B. occidentalis	50	14.9 ± 0.8	16.5 ± 0.9
B. rotundifolia	50	16.1 ± 1.0	18.1 ± 0.9
B. richardsonii†			
Alaska Range	50	27.0 ± 1.3	29.0 ± 2.0
Brooks Range	50	27.4 ± 1.2	30.9 ± 1.5
B. heucheriformis	50	21.0 ± 1.0	24.2 ± 1.0
B. jamesii	20	20.3 ± 1.6	22.8 ± 1.4
Peltoboykinia tellimoides	30	22.7 ± 1.2	23.9 ± 1.3
P. watanabei	30	22.0 ± 1.0	24.4 ± 1.1
Suksdorfia alchemilloides	20	17.1 ± 1.2	14.5 ± 1.1
S. ranunculifolia	100	16.9 ± 1.2	17.1 ± 1.5
S. violacea	100	16.6 ± 1.2	18.0 ± 1.3
Bolandra californica	10	23.4 ± 1.6	26.8 ± 1.5
B. oregana	30	23.0 ± 1.8	25.4 ± 2.1

*P = polar diameter; E = equatorial diameter.

†There is no significant difference in mean polar diameter between collections from the Alaska Range ($2n = 36$?) and those from the Brooks Range ($2n = 84$): $F_{1,98} = 2.56$, $P > 5\%$. Mean equatorial diameter is significantly larger in plants from the Brooks Range: $F_{1,98} = 28.88$, $P < 1\%$.
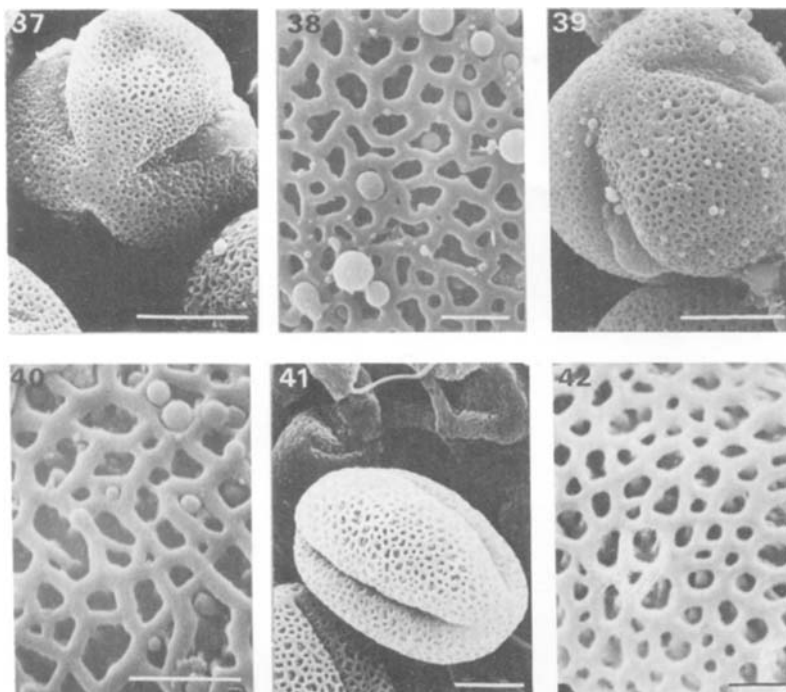
Figures 37–42. Pollen grains of *Suksdorfia*. Figs 37, 38. *Suksdorfia voilacea*. Figs 39, 40. *S. ranunculifolia*. Figs 41, 42. *S. alchemilloides*. Scale bars = 5 μm (Figs 37, 39, 41) or 1 μm (Figs 38, 40, 42).

correlation with chromosome number. Although pollen of the Brooks Range cytodeme ($2n = 84$) of *Boykinia richardsonii* has a significantly larger mean equatorial diameter than that of the Alaska Range cytodeme [where Knaben (1968) reported $2n = 36$], the standard deviations are too great for convenient taxonomic use.

Apertures: The pollen grains of all species in *Suksdorfia*, *Bolandra* and *Boykinia* section *Boykinia* are 3-colporate. The report by Ikuse (1956) of colporoidate pollen in *Boykinia lycoctonifolia* is not supported here. Species of *Peltoboykinia* and *Boykinia* sections *Telesonix* and *Renifolium* have 3-colpororoidate pollen. Hideux & Ferguson (1976) reported that the endexine is thickened in the area around each colpus in all the genera that we consider here.

Tectum: All genera have a homogeneous tectum but its structure varies between the species (Figs 11–42). In *Boykinia* section *Boykinia* (Figs 11–22), *B. aconitifolia*, *B. intermedia*, *B. lycoctonifolia* and *B. occidentalis* are all very similar, with a densely reticulate tectum. The ratio of muri to luminae widths is about one but this ratio increases towards the poles. *Boykinia rotundifolia* is different from the preceding species in that, although its tectum is densely reticulate to perforate, most of the luminae are occluded. *Boykinia major* is intermediate in this respect between *B. rotundifolia* and the other species in section *Boykinia*.

In *Boykinia* section *Telesonix* (Figs 23–26), *B. heucheriformis* has pollen very similar to those species of *Boykinia* section *Boykinia* with a reticulate tectum. There is some infraspecific variation in that the sample from Alberta (Fig. 25)
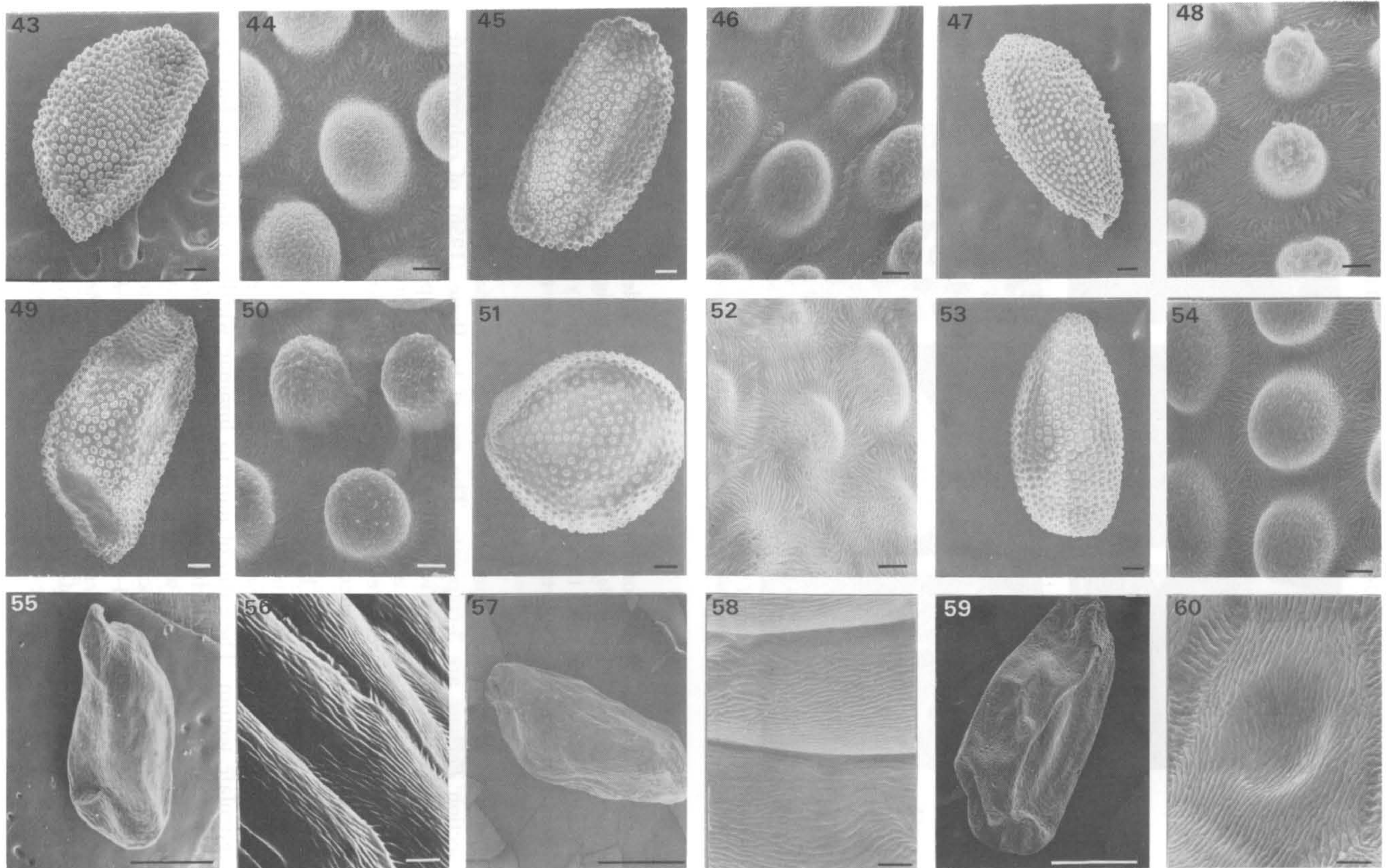
Figures 43-60. Seeds of *Boykinia*. Figs 43, 44. *B. aconitifolia*. Figs 45, 46. *B. intermedia*. Figs 47, 48. *B. lycoctonifolia*. Figs 49, 50. *B. major*. Figs 51, 52. *B. occidentalis*. Figs 53, 54. *B. rotundifolia*. Figs 55, 56. *B. jamesii*. Figs 57, 58. *B. heucheriformis*. Figs 59, 60. *B. richardsonii*. Scale bars = 500 μm (Figs 55, 57, 59) or 50 μm (Figs 43, 45, 47, 49, 51, 53) or 5 μm (Figs 44, 46, 48, 50, 52, 54, 56, 58, 60).

had a typical equatorial muri/luminae width ratio of less than one, whereas in the sample from Montana (Fig. 26) this ratio was more than one. *Boykinia jamesii* has pollen similar to that of *B. rotundifolia*, in that the luminae of its densely reticulate tectum are occluded.

In both species of *Peltoboykinia* (Figs 29–32) the tectum is perforate, sparingly so in *P. watanabei*. The muri/luminae width ratio is very large (i.e. the perforations are minute).

In all three *Suksdorfia* species (Figs 37–42), *Bolandra* (Figs 33–36) and *Boykinia richardsonii* (Figs 27, 28), the tectum is coarsely reticulate. The ratio of muri to luminae widths is usually less than one (i.e. large luminae) at the equator but increases at the poles where the tectum becomes perforate rather than reticulate. Within the luminae sculptural elements may be seen. The columellae in *Suksdorfia alchemilloides* are longer, relative to tectum thickness, than they are in the other species (Hideux & Ferguson, 1976).

Regarding exine thickness, Hideux & Ferguson (1976) reported values of about 1 μm in all the genera studied here, except in *Suksdorfia alchemilloides* where it can be as much as 2 μm.

Seeds: Studies of the seeds in the Saxifraginae have revealed considerable diversity in shape and testa ornamentation (Conolly, 1976; Engler, 1891, 1930; Kaplan, 1976, 1981; Krach, 1976; Miller & Thompson, 1979; Rosendahl, 1905). Differences between genera and species lie mainly in the distribution patterns of tubercles, or orientation and shape of the testa epidermal cells. In the present study, seed morphology was found to have taxonomic value at both generic and sectional levels.

Seed shape: Seeds of the species studied vary in shape and size, features which apparently can be influenced somewhat by the degree of crowding in the ovary. In *Boykinia, Peltoboykinia* and *Suksdorfia* the seeds range in shape from nearly spherical to ellipsoid; in *Bolandra* they are narrowly ellipsoid. A raphe is prominent in *Peltoboykinia* and *Suksdorfia* but less so in the other genera.

Testa ornamentation: An important feature in separating species and species groups is the testa surface (SEM, Figs 43–74). In all cases, very little infra-specific variation was seen.

In *Boykinia* section *Boykinia* the seeds are strikingly uniform in their testa ornamentation (Figs 43–54) and colour. The testa, which is nearly always black, has no creases or folds, and has very prominent, evenly spaced tubercles arranged longitudinally, more or less in rows. There is very little variation in the height and spatial arrangement of these tubercles. The epidermal cells are polygonal and the outer wall of each cell forms one tubercle. Much of the outer cell was is involved in this way, so that only the small area around its edge is 'flat'.

Boykinia richardsonii (Figs 59, 60) differs in that its dark brown testa is often creased or folded, but it is also covered in tubercles. These tubercles are relatively smaller than in *Boykinia* section *Boykinia,* and protrude only a little above the surrounding surface. Moreover, less surface area of the outer cell wall is devoted to tubercle formation, and hence the polygonal cell perimeter is clearly visible.
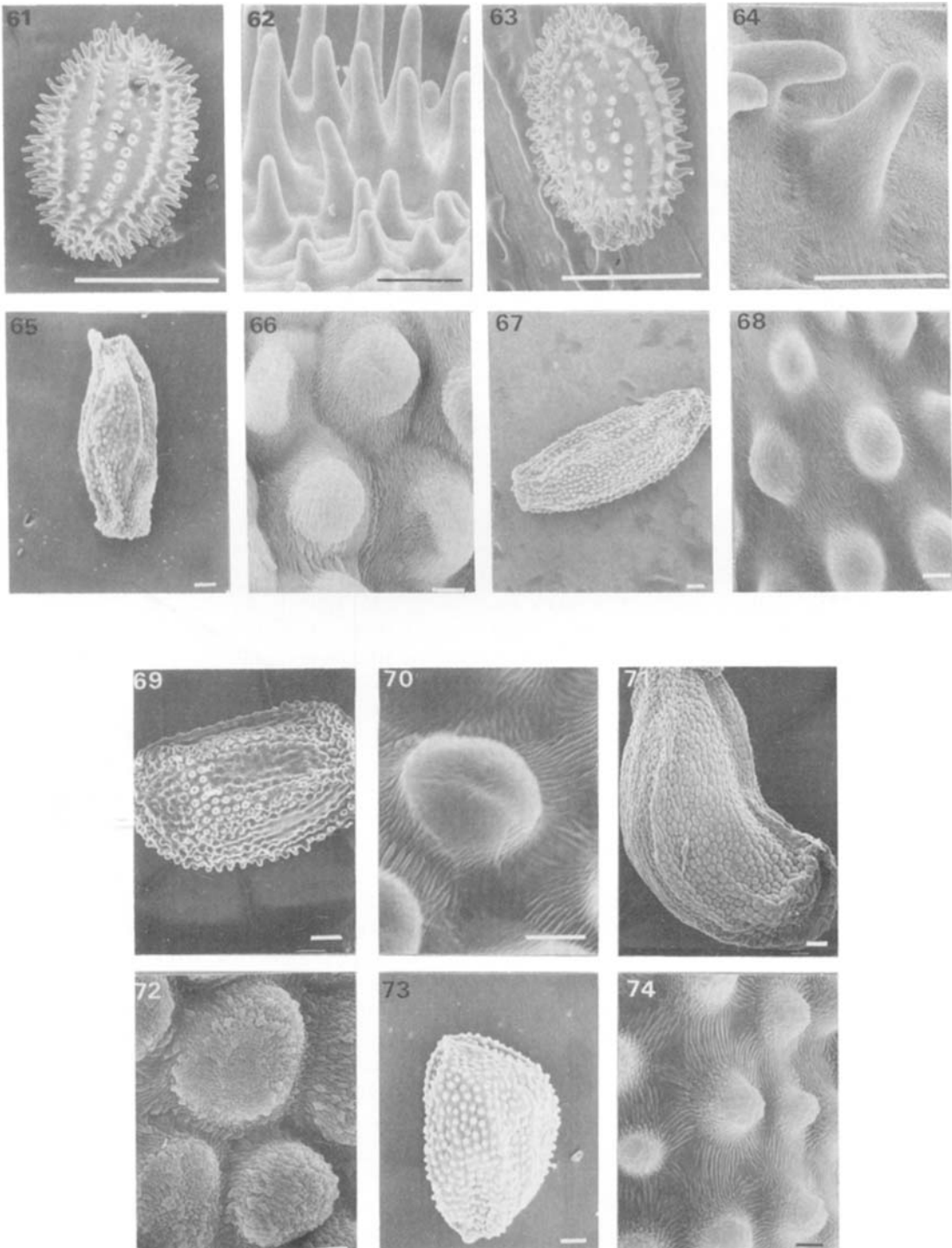
Figures 61–74. Seeds of *Peltoboykinia*, *Bolandra* and *Suksdorfia*. Figs 61, 62. *Peltoboykinia tellimoides*. Figs 63, 64. *P. watanabei*. Figs 65, 66. *Bolandra californica*. Figs 67, 68. *B. oregana*. Figs 69, 70. *Suksdorfia violacea*. Figs 71, 72. *S. ranunculifolia*. Figs 73, 74. *S. alchemilloides*. Scale bars = 500 μm (Figs 61, 63) or 50 μm (Figs 62, 64, 65, 67, 69, 71, 73) or 5 μm (Figs 66, 68, 70, 72, 74).

The seeds of *Boykinia* section *Telesonix* (Figs 55–58) lack tubercles of any kind but instead the outer walls of the dark brown seed coat cells bulge slightly. These epidermal cells are oblong rather than polygonal and the testa surface thus appears finely striate. It can also be rather creased or folded.

Peltoboykinia (Figs 61–64) shows another kind of testa ornamentation. The two species are similar. The dark brown testa is uncreased and most of its tubercles are very long, spine-like structures. They are generally arranged in 14–20, highly distinct, longitudinal rows, with a distinct gap between each row. The tubercles are formed in the same way as before except that the component epidermal cells are narrowly transversely oblong. There can be some variation in tubercle length and arrangement within individual seeds.

In *Bolandra* (Figs 65–68) the tubercles are arranged as in *Boykinia* section *Boykinia,* although they are somewhat smaller and the epidermal cells more elongated.

In *Suksdorfia* (Figs 69–74) the dark brown testa is often creased or folded. Tubercles are arranged longitudinally in rows and arise from irregularly polygonal epidermal cells. In *S. ranunculifolia* the tubercles are low domes, similar to those in *B. richardsonii* but differing in that each is composed of an entire outer cell wall, making the tubercles appear more closely packed. In *S. violacea* the tubercles are variable in form, even on a single seed, from low domes to much taller, papilla-like structures. The taller tubercles are often associated with the sides of ridges, whereas the domes tend to occur between ridges, but the occurrence of intermediates sometimes obscures this pattern. As in *Boykinia* section *Boykinia,* much of the outer surface of each epidermal cell is used in the formation of the tubercles. The arrangement and size of the tubercles in *S. alchemilloides* are similar to the pattern in *Boykinia* section *Boykinia.*

Although *Boykinia* is heterogeneous in its seed characters, the variation can be understood in terms of an evolutionary trend. Many other genera in the Saxifraginae show the transition from smooth to tuberculate seeds, e.g. *Chrysosplenium* (Hara, 1957), *Lithophragma* (Taylor, 1965), *Heuchera* (Rosendahl, Butters & Lakela, 1936) and *Saxifraga* (Miller & Thompson, 1979). Hara (1957) suggested that smoothness was primitive and tuberculateness was advanced; indeed the smooth-seeded *Boykinia* section *Telesonix* retains other primitive features such as ten stamens and colporoidate pollen.

Although there are also some distinct differences in testa-surface pattern between the three species of *Suksdorfia,* they are mostly related to tubercle size and it may be that the conditions in *Suksdorfia* represent early stages of differentiation according to the evolutionary trend just discussed.

Seed dispersal: Savile (1975) suggested a link between prominently tuberculate seeds and dispersal by birds or mammals (the seeds presumably catching in feathers or fur). However, the type of testa surface may be related to other things apart from mode of dispersal, including for example, moisture retention and surface area/volume ratio, factors which could be important in germination (New & Herriott, 1981).

It was observed that on being shed from the capsules, the seeds (tuberculate or not) frequently stick to the dense array of glandular trichomes found on the inflorescences in all species studied. This obviously inhibits dispersal and presumably affects the genetical structure of populations.

Savile (1975), reviewing the seed dispersal syndromes in some members of the Saxifraginae, noted that the N American *Suksdorfia* species and *Boykinia* section *Telesonix* have a censer mechanism whereby the flexible stems wave in the wind and throw out their seeds. In fact, all *Boykinia, Peltoboykinia, Sudsdorfia* and *Bolandra* species have this mechanism, which is the commonest in the family. In some very dwarf specimens of *Boykinia jamesii* and *B. heucheriformis* the stems are rather more rigid and dispersal is better described as of the vibrator type where the wind induces a resonant vibration, bouncing the seeds out. This mechanism is especially well-developed in some *Saxifraga* species (Savile, 1975).

Seedlings and early development

Seeds were germinated in pots of soil, or on beds of agar enriched with Hoagland's solution, at 17°C under a 16 h photoperiod. Germination occurred typically after about 3 weeks in both conditions, if fresh seed were used. The germination success rate was 70–90%. Germination is epigeal with the radicle emerging first followed by the hypocotyl and the two rarely three, cotyledons. The radicle tip is pigmented red with anthocyanins, a condition found in all actively growing roots, whether in the light or dark. Favarger (1957) reported that in some species of *Boykinia* (*B. aconitifolia, B. occidentalis*) the albumen of the germinating seed produces unicellular hairs; in other species (*B. rotundifolia, Peltoboykinia tellimoides*) the albumen does not.

In *Boykinia* sections *Boykinia* and *Telesonix* and in *Peltoboykinia, Bolandra* and *Suksdorfia*, the cotyledons are ovate, whereas in *B. richardsonii* (section *Renifolium*) they are narrowly ovate. They may be up to 3 mm long at maturity, the entire seedling being about 3 mm tall. In *Boykinia, Bolandra* and *Suksdorfia*, the shoot apex produces the first eophyll which is entire in the basal region but serrate to varying degrees toward its apex. This is quickly followed by a second eophyll, alternate to the first, and also serrate in the apical region. Subsequent foliage leaves form a rosette from which the floral axis later arises. In species whose metaphylls are lobed or otherwise divided, successive leaves show a sequence from the initially entire or partially serrate condition to the typical divided condition (Fig. 75).

In *Peltoboykinia* the first eophylls are not peltate (Fig. 75G), although in later ones the peltate nature becomes increasingly apparent. It is interesting that eophylls, and often young, spring leaves, of *Darmera* also lack the peltate syndrome (Jepson, 1936). In *Peltoboykinia* the first metaphylls have lobes which are almost laciniate in their young stage. These lobes subsequently undergo extensive lateral growth to reach the typical, broadly triangular condition.

Fungal parasites

Savile (1975, 1976) has recorded a lineage of microcyclic, heteroecious rusts (species of *Puccinia*), on 11 genera and 87 species of the Saxifraginae, which has helped to elucidate host relationships. Although there is no published data for *Boykinia* and its allies dealt with here, there is a herbarium specimen of *Boykinia occidentalis* (*Parks & Parks 670*, UC) which is infected with *Puccinia heucherae*. This rust also attacks N American species of *Heuchera, Mitella, Tiarella, Tolmiea* and *Saxifraga* section *Micranthes* (Savile, 1975).
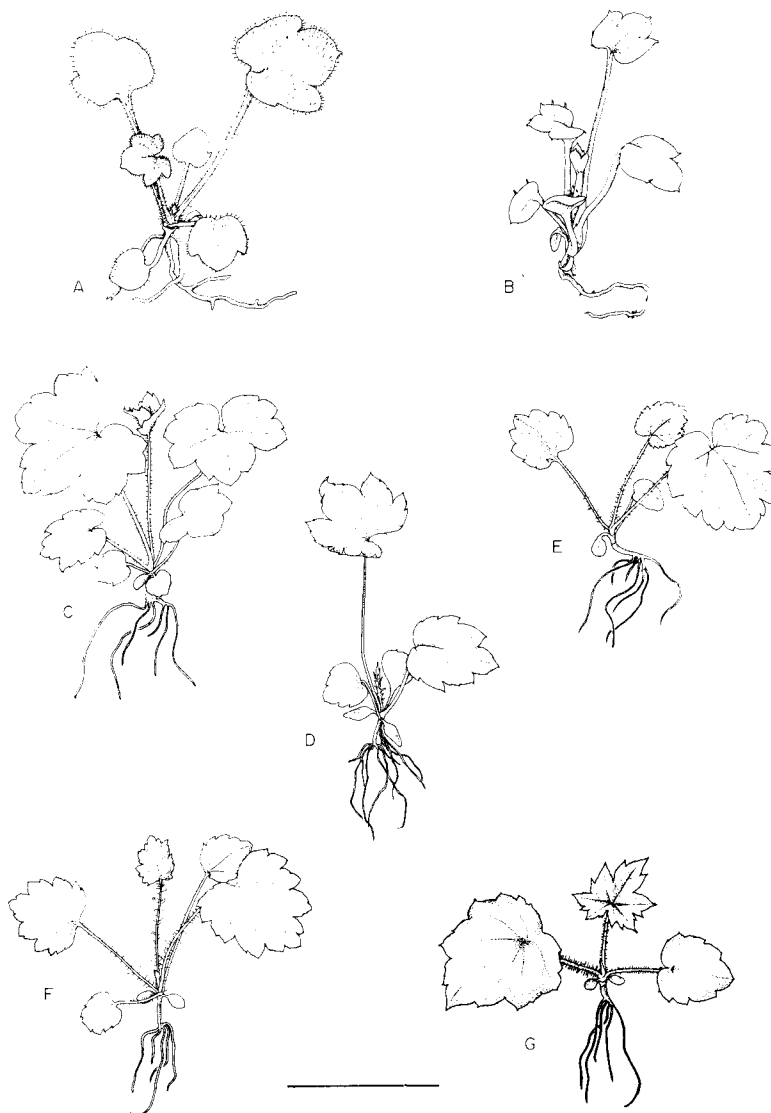
Figure 75. Six week old seedlings of representative species of *Boykinia* and *Peltoboykinia*. A. *Boykinia heucheriformis*. B. *B. richardsonii*. C. *B. major*. D. *B. intermedia*. E. *B. rotundifolia*. F. *B. occidentalis*. G. *Peltoboykinia tellimoides*. Scale bar = 25 mm.

Flavonoid chemistry

The flavonoid chemistry of *Peltoboykinia, Boykinia, Bolandra* and *Suksdorfia* has been described in detail by Gornall & Bohm (1980); *Sullivantia* has been investigated by Soltis (1980). A diverse array of flavone and flavonol mono-, di- and triglycosides occurs. 3-O-methylation and 6-oxygenation are common, as is 3,7-O-triglycosylation. Groups of flavonol monoglycosides with charged functions are also produced. The similarities indicate that all taxa are closely related. The data provide only limited help in defining generic limits, although

they do support the inclusion of the segregates *Telesonix* and *Neoboykinia* within *Boykinia*, and they also go some way towards distinguishing *Peltoboykinia* and *Suksdorfia* from *Boykinia*.

Cytology

The chromosome numbers of nearly all the species recognized in the present study have been reported or reviewed by Gornall, Bohm & Taylor (1983). *Boykinia*, *Bolandra* and *Suksdorfia* all have a base number of $x = 7$, the commonest in the subtribe; *Peltoboykinia* has $x = 11$. Therefore, with the exception of supporting the recognition of Peltoboykinia, chromosome numbers do little to resolve the problem of generic limits. Indeed, there is even evidence that *Boykinia* and the related genus *Sullivantia* share the same karyotype (Soltis, 1981b).

Breeding systems and relationships

The results of a series of experimental self- and inter- and intra-generic cross pollinations among *Peltoboykinia*, *Boykinia*, *Bolandra*, *Suksdorfia*, *Sullivantia* and *Jepsonia* have been reported by Gornall & Bohm (1984). *Boykinia major* and *B. intermedia* were found to be strongly self-incompatible (SI) and the evidence reviewed suggested that SI might be under multi-locus, gametophytic control. All other species are self-compatible to varying degrees, except for those of *Jepsonia* which are distylous and SI (Ornduff, 1969b).

Breeding relationships among the genera were found to be very important in helping to define generic limits. Gornall & Bohm (1984) reported that crosses between the genera consistently failed. In contrast, crosses within *Boykinia*, as circumscribed here, succeeded. Similarly, crosses between the two *Peltoboykinia* species also succeeded, as do those within *Sullivantia* (Soltis, 1981a) and *Jepsonia* (Ornduff, 1969b). These results strongly support the inclusion within *Boykinia* of the formerly segregated *Telesonix*, since hybrids between *B. heucheriformis* and *B. occidentalis* could be made.

Although crosses between *Suksdorfia* species failed this was not taken as support for recognizing segregate monotypic genera, for the following reasons. First, species of *Suksdorfia* have an insubstantial rhizome and a very short growing season, and are probably therefore short-lived perennials. Secondly, the two American species tested in the crossing programme have largely sympatric distributions, quite often with mixed populations. Strong breeding barriers between such species are common (Grant, 1971) and do not necessarily upset the circumscription of the genus as defined here. Generally, therefore, breeding relationships both reflect the coherence of the genera recognized here and emphasize the differences between them.

TAXONOMY

The focus of the modern genus concept is naturalness, a genus being defined by the mutual relationships of its constituent species. It also acknowledges that taxonomy deals with diversity: we have therefore found it unnecessary to maximize the homogeneity of every taxon. Indeed, an appreciation of the

pattern of variability in a genus is the key to its understanding (Burtt, 1964). When making taxonomic decisions, we have given due regard to tradition and the undesirability of unnecessary nomenclatural changes.

Regarding infra-generic classification, two categories are used: species and section. Species are separated by discontinuous correlated variation in at least two characters (one of which must be morphological) and often by biometric differences in others (Davis, 1978). Although the genus *Boykinia* is small, sections have been recognized partly because of historical precedent and partly to emphasize groups of closely related species.

The relative usefulness of the various taxonomic characters has been commented on in the appropriate section. Generally speaking, the size of a plant and its vegetative organs are greatly affected by environment and are therefore less reliable; but the utility of a particular feature may vary depending on context, and each case is judged individually. A summary of the distribution of the most important distinguishing features of the genera that we recognize is given in Table 7.

Peltoboykinia (Engler) H. Hara

Peltoboykinia (Engler) H. Hara, *Botanical Magazine, Tokyo, 51:* 251, 252 (1937).

SYNONYM: *Boykinia* section *Peltoboykinia* Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien, edition 2, 18a:* 120 (1930).

TYPE SPECIES: *Peltoboykinia tellimoides* (Maxim.) H. Hara

PERENNIAL HERBS, leafy stemmed and glandular-pubescent. RHIZOMES short, thick, scaly. LEAVES alternate in a 3/8 phyllotactic spiral, peltate, orbicular in outline, basal leaves long petiolate, shallowly lobed or deeply cleft, margins incised with mucronate or acute teeth, each tooth terminating in a rosid-type hydathode, venation actinodromous; cauline leaves becoming reduced, short-petiolate or sessile upwards. LEAF TEXTURE canaliculate on upper surface, costate and lustrous on lower surface. STOMATA anomocytic, mesoperigenous and perigenous, with non-synchronous development; rare on upper leaf surface, common on lower; STIPULES foliaceous or represented by basal dilations of petioles. TRICHOMES multicellular, uniseriate with multicellular, glandular, ellipsoid heads, present throughout the plant but especially prominent on the inflorescence branches. INFLORESCENCE monotelic, of first order paracladia, highly congested initially but spreading following anthesis and especially during fruiting; each paracladium subtended by a bract and consisting of a terminal flower (rarely absent) borne at or near the junction of a dichotomous branch pair, each branch bearing few to several flowers in a typically helicoid arrangement. FLOWERS perfect, actinomorphic. CALYX of 5 sepals connate below and forming a tubular-campanulate floral cup, ovary portion densely glandular-pubescent, free sepal lobes erect, lanceolate to triangular, sparingly pubescent, imbricate in bud. COROLLA of 5 cream to pale yellow petals inserted on rim of floral cup, cuneate or short clawed, clothed with glandular hairs, early deciduous, with a single vascular trace entering each petal base and margins dentate distally. NECTARY of green glandular tissue, in a band around base of styles where free hypanthium and ovary wall meet. STAMENS 10 in two whorls of

Table 7. Summary of the distribution of some important taxonomic characters distinguishing *Boykinia* and its allies

Character	*Peltoboykinia*	*Jepsonia*	*Boykinia*	*Sullivantia*	*Bolandra*	*Suksdorfia*
Rhizomes	Thick, scaly	Starchy caudex	Thick, scaly	Slender, not scaly	Bulbiliferous	Bulbiliferous
Leaves	Peltate	Not peltate	Not peltate	Not peltate	Not peltate	Not peltate
Lower surface	Costate, glossy	Costate, matt	Costate or slightly ribbed, matt	Smooth, matt	Ribbed, matt	Slightly ribbed, matt
Trichomes						
Glandular	Uniseriate; ellipsoid heads	Uni- and multiseriate; ellipsoid heads	Multiseriate; ellipsoid heads	Multiseriate; ellipsoid heads	Multiseriate; papillate heads	Multiseriate; sometimes papillate heads
Unicellular	–	–	+	–/(+)	–	+/–
Chaffy	+	–	+	–	–	–
Hypanthium shape	Tubular-campanulate	Campanulate	Campanulate	Campanulate	Tubular-campanulate	Campanulate
Petals	Spatulate; dentate; glandular	Spatulate; entire; glabrous	Spatulate or orbicular-clawed; entire; glabrous	Spatulate; entire; glabrous	Subulate; entire; glabrous	Oval or spatulate or orbicular-clawed; entire; glabrous
Stamens						
Number	10	10	5/10	5	5	5
Arrangement	Homostylous	Heterostylous	Homostylous	Homostylous	Homostylous	Homostylous
Pollen						
Apertures	Colporoidate	Colporoidate	Colporoidate or colporate	Colporate (2 or 3 orac/colpus)	Colporate	Colporate
Tectum	Perforate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate
Seeds						
Shape	Ellipsoid	Ellipsoid	Ellipsoid	Ellipsoid-winged	Narrowly ellipsoid;	Ellipsoid
Colour	Brown	Brown	Brown or black	Brown	Brown	Brown
Testa	Echinate	Smooth	Tuberculate or smooth	Smooth	Tuberculate	Tuberculate
Chromosome base no.	11	7	7	7	7	7
Flavonoids						
6-oxygenation	–	–	7/9 spp.	+	+	–
Diglycosides with arabinose or xylose	–	+	8/9 spp.	–	+	–
Habitat	Forest floor	Winter-wet, summer-dry, maritime climate; on rocky bluffs or exposed or shaded hillsides	Riparian woodland or alpine crags/talus	Dripping wet cliffs, usually shaded	Shaded, humid, summer-dry, rocky bluffs in woodland	Usually open, spring-wet, summer-dry, rocky bluffs

5, inserted on rim of floral cup, not exceeding calyx, outer whorl antisepalous, inner whorl anti-petalous; filaments single-veined, subulate; anthers 2-locular, pale cream turning black at anthesis, cordate at base and with a mucronate apex, dehiscing longitudinally, marcescent. MICROSPOROGENESIS with simultaneous cytokinesis. POLLEN binucleate, isopolar, 3-colporoidate, tectum minutely perforate. GYNOECIUM of 2 follicle-like carpels, connate below. OVARY one-third inferior or less, 2-loculate with numerous (hundreds) of bitegmic, crassinucellate, anatropous ovules on axile placentae, placentation restricted to connate portion of carpels. STYLES almost free, erect but becoming divergent in fruit, stylar canals completely filled with transmitting tissue; stigmata capitate, of 'wet Group III'-type. FRUIT a septicidal capsule formed by the tubular-campanulate floral cup, each carpel dehiscing ventrally in stylar region, styles spreading widely. SEEDS numerous (hundreds), small, ellipsoid, brown, often with a prominent raphe, testa echinate. ENDOSPERM helobial. EMBRYO small, straight. EMBRYOGENY unknown. EMBRYO SAC of *Polygonum*-type. GERMINATION epigeal, eophylls not peltate. ROOT TIPS pigmented red with anthocyanins. CHROMOSOME base number $x = 11$. FLAVONOID profile simple, comprising a few common flavonol glycosides (no myricetin) and a set of charged compounds.

GENERIC LIMITS: The genus *Peltoboykinia* can be recognized in its own right because it differs from *Saxifraga* in possessing a free hypanthium and has colporoidate pollen with a perforate tectum. It can also be well-separated from *Boykinia* and the other related genera treated here by the characters summarized in Table 7. Experimental hybridizations between *Peltoboykinia* and *Boykinia* also fail (Gornall & Bohm, 1984).

Maximowicz (1871) and Engler (1891:61) both suggested a possible affinity of *Peltoboykinia* with *Darmera* (= *Peltiphyllum*), presumably on the basis of peltate leaves and 10 stamens in both taxa. Although the genera also share glandular, uniseriate trichomes they are probably not very closely related because *Darmera* has a base chromosome number of $x = 17$ and lacks a free hypanthium. *Peltoboykinia* instead shows some affinities with *Boykinia* (pollen and flower morphology and flavonoid chemistry) and some with *Saxifraga* (trichome complement and chromosome number), and an intermediate position between the two genera therefore best reflects its relationships.

Key to the species of Peltoboykinia

1. Leaf lobes ovate-deltoid, broader than long; petals with a
    cuneate base; free hypanthium 3.5–5.0 mm long . . .*P. tellimoides*
1ʹ Leaf lobes narrowly cuneate-ovate, longer than broad; petals
    short-clawed; free hypanthium 2.0–3.0 mm long . . .*P. watanabei*

Peltoboykinia tellimoides (Maxim.) H. Hara, *Botanical Magazine, Tokyo, 51:* 252 (1937).

SYNONYMS: *Saxifraga tellimoides* Maximowicz, *Bulletin de l'Académie Impériale des Sciences de Saint-Pétersbourg, 16:* 215, 216 (1871).
Boykinia tellimoides Engler, in Engler & Irmscher, *Das Pflanzenreich, 69:* 675 (1919).

TYPE: Japan, Prov. Owari, *Siebold s.n.,* 1864 (HOLOTYPE LE!).

3

STEMS 350–850 mm tall. PETIOLES of basal leaves 200–420 mm long. BASAL LEAVES orbicular, cordate, (100–)150–300 mm long, 100–300 mm wide, divided up to about one-third their length into 7–13 lobes, margins incised with mucronate teeth. STIPULES a dilation of petiole base up to 3 mm long, occasionally foliaceous. INFLORESCENCE with from 1 to 7 flowers per paracladium. CALYX glandular, 8–15 mm long, divided about half its length into free sepal lobes 3–6 mm long. FREE HYPANTHIUM 3.5–5.0 mm long. PETALS (5–)9–17 mm long about 2–3 times longer than the sepal lobes, cuneate at the base. STAMENS shorter than sepal lobes, the filaments about as long as the undehisced anthers. SEEDS 625–875 μm long. $2n = 22$.

FLOWERING: May to July.

DISTRIBUTION AND ECOLOGY: *Peltoboykinia tellimoides* grows in the mountains of central and northern Honshu, Japan (Fig. 76); it is a component of the herb layer of the broad-leaved, deciduous *Fagus crenata* forests at elevations below 1500 m. The 10°C isotherm correlates with its distribution (Hara, 1958, 1959).

Peltoboykinia watanabei (Yatabe) H. Hara, *Botanical Magazine, Tokyo, 51:* 252 (1937).

SYNONYMS: *Saxifraga Watanabei* Yatabe, *Botanical Magazine, Tokyo, 6:* 7, 43, 44; t.2 (1892).

 Saxifraga tellimoides Maxim. var. *Watanabei* Makino, *Botanical Magazine, Tokyo, 15:* 12 (1901).

 Boykinia tellimoides (Maxim.) Engler var. *Watanabei* Engler, in Engler & Irmscher, *Das Pflanzenreich, 69:* 675 (1919).

 Boykinia Watanabei Makino, *Journal of Japanese Botany, 3:* 13, 14 (1926).

 Peltoboykinia tellimoides (Maxim.) H. Hara var. *watanabei* H. Hara, *Distribution Maps of Flowering Plants in Japan, 1:* map 17. Inoue Book Company, Tokyo (1958). Name invalid (Art. 33.2).

TYPE: Japan, Prov. Tosa, Nanokawa, *Kano Watanabe s.n.*, 12 vii 1889. (HOLOTYPE not seen).

NOMENCLATURAL NOTES: The protologue gives the year of collection as 1889, but we could find no specimen with this date. However, there is a specimen (*Watanabe* 1888 MAK!) which agrees in all other respects with the protologue (including the locality details) and it may be found to be the type.

STEMS 400–850 mm tall. PETIOLES of basal leaves (130–)200–450 mm long. BASAL LEAVES orbicular, cordate, (90–)150–400 mm long, 100–400 mm wide, divided one-half to two-thirds their length into 7–10 triangular lobes, margins incised with acute teeth. STIPULES a dilation of the petiole base up to 4 mm long, occasionally foliaceous. INFLORESCENCE with from 1 to 7 flowers per paracladium. CALYX 8–15 mm long, divided one-third to one-half its length into free sepal lobes 2–5 mm long. FREE HYPANTHIUM 2–3 mm long. PETALS 7–15 mm long, about 2–3 times longer than the sepal lobes, somewhat attenuated at the base. STAMENS shorter than sepal lobes, the filaments about as long as the undehisced anthers. SEEDS 615–740 μm long. $2n = 22$.

FLOWERING: June to July.

DISTRIBUTION AND ECOLOGY: *Peltoboykinia watanabei* inhabits the mountains of the southern Japanese islands of Shikoku and Kyushu (Fig. 76). Like *P. tellimoides*, it
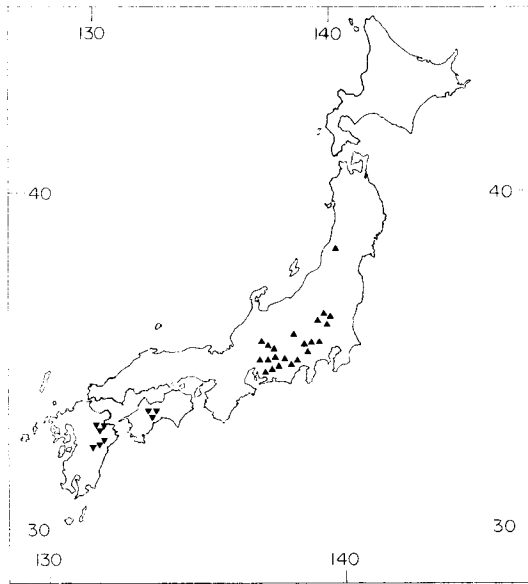
Figure 76. Distribution of *Peltoboykinia tellimoides* (▲) and *P. watanabei* (▼). Only representative collections are shown.

forms part of the herb layer of the *Fagus crenata* forests at elevations below 1500 m. The 15°C isotherm correlates with its distribution (Hara, 1958, 1959).

Boykinia Nuttall

Boykinia Nuttall (*nom. cons.*), *Journal of the Academy of Natural Sciences of Philadelphia*, 7: 113, 114 (1834).

SYNONYMS: *Telesonix* Rafinesque, *Flora Telluriana*, 2: 69 ("1836", 1837).
  Therofon Rafinesque, *New Flora and Botany of North America IV. Neobotanon:* 66 ("1836", 1838).
  Boyxinia Endlicher, *Genera Plantarum Supplementum*, 5: 21 (1850), (orth. var.).
  Therophon Rydberg, *North American Flora*, 22: 123 (1905), (orth. var.).
  Neoboykinia H. Hara, *Botanical Magazine, Tokyo*, 51: 252, 253 (1937).
  Non Boykiana Rafinesque, *Neogenyton*, 2 (1825), (orth. var.).
  Non Boykinia Nuttall ex Arnott, *Hooker's Journal of Botany*, 3: 276 (1841), *nomen nudum*.

TYPE SPECIES: *Boykinia aconitifolia* Nuttall.

NOMENCLATURAL NOTES: the genus was named after Dr Samuel Boykin (1786–1848), a planter, physician and naturalist from Milledgeville, Georgia, U.S.A. He must have been very popular because his name has been given to genera in the Lythraceae and Cucurbitaceae as well as the Saxifragaceae, thereby causing some confusion.

Rafinesque (1840) claimed to have erected the genus *Boykinia* in 1817 for a species of Lythraceae, although the name actually dates from 1825. Nuttall's

Boykinia was published in 1834 to accommodate a new saxifrage species, *B. aconitifolia*.The species had in fact been known for several years and Rafinesque (1838) claimed that he had created a new genus for the plant in 1828, naming it *Therofon napelloides*. The work he referred to was probably his *Neophyton Botanikon* (Kuntze, 1891), but this reached manuscript stage only and was never published (C. Boewe personnal communication, 1982; F.A. Stafleu personal communication, 1982). *Therofon napelloides* was not in fact published until 1838 (Rafinesque, 1838). Nuttall's *Boykinia* was eventually conserved against Rafinesque's earlier homonym (Dandy, 1935; Green, 1940). A still later homonym, attributed to Nuttall, was published by Arnott as a *nomen nudum* for a species of Cucurbitaceae (see list of rejected names).

PERENNIAL HERBS, leafy-stemmed and glandular-pubescent. RHIZOMES thick, scaly, creeping, branched, some species stoloniferous. LEAVES alternate in a 3/8 phyllotactic spiral, basal leaves orbicular to reniform in outline, long petiolate, palmately shallowly crenately-lobed or deeply cleft, margins incised with mucronate or acute teeth, each tooth terminating in a rosid-type hydathode, venation actinodromous; cauline leaves becoming reduced, short petiolate to sessile upwards. LEAF TEXTURE sometimes succulent, canaliculate to smooth on upper surface, costate to somewhat ribbed on lower surface. STOMATA anomocytic, mesoperigenous and perigenous, with non-synchronous development; rare to common on upper leaf surface, common on lower surface. STIPULES foliaceous or represented by basal dilations of petioles, often fringed with subulate bristles. TRICHOMES multiseriate with multicellular, glandular, ellipsoid heads, present throughout the plant; brown chaffy eglandular trichomes often present at least on lower stem nodes and especially around base; unicellular eglandular trichomes common on pedicels and hypanthia, less so elsewhere. INFLORESCENCE monotelic with usually one, but occasionally up to two orders of paracladia, highly congested initially but spreading following anthesis and especially during fruiting, densely glandular-pubescent; each paracladium subtended by a bract and consisting of a terminal flower (rarely absent) with one lateral flower or of a terminal flower borne at or near the junction of a dichotomous branch pair, each branch bearing from one to many flowers in a typically helicoid arrangement. FLOWERS perfect, actinomorphic or occasionally slightly irregular. CALYX of 5 sepals, connate below and forming a campanulate to turbinate floral cup, the ovary portion densely glandular-pubescent, free lobes variously pubescent to glabrate, erect or spreading, their apices acute. COROLLA of 5 white, yellowish-green or purplish petals inserted on rim of floral cup, cuneate to long clawed, glabrous, marcescent, with a single vascular trace entering each petal base, margins usually entire. NECTARY of glandular tissue, prominent and yellow or inconspicuous and green, in a band around base of styles where free hypanthium and ovary wall meet. STAMENS 5 or 10 in one or two whorls of 5 respectively, inserted on rim of floral cup; in diplostemonous species, outer whorl is antisepalous, inner whorl antipetalous; in haplostemonous species stamens are antisepalous; filaments single veined, subulate; anthers 2 locular, yellow, cordate at base, often which a mucronate apex, dehiscing longitudinally, marcescent. MICROSPOROGENESIS with simultaneous cytokinesis. POLLEN binucleate, isopolar 3-colporate or 3-colporoidate, tectum reticulate with luminae occluded in some species.

GYNOECIUM of 2 follicle-like carpels, connate below. OVARY one-half to completely inferior, 2-loculate with numerous bitegmic, crassinucellate, anatropous ovules on axile placentae, placentation restricted to connate portion of carpels. STYLES almost free to nearly united, erect but becoming divergent in fruit, stylar canals lined but not filled with transmitting tissue; stigmata capitate, of 'wet Group III'-type. FRUIT a septicidal capsule formed by the urceolate floral cup, each carpel dehiscing ventrally in stylar region, styles spreading widely. SEEDS numerous, ellipsoid, black or brown, with an inconspicuous raphe, testa smooth to minutely tuberculate. ENDOSPERM of the *ab initio* cellular-type. EMBRYO small, straight. EMBRYOGENY unknown. EMBRYO SAC *Polygonum*-type. GERMINATION epigeal. ROOT TIPS pigmented red with anthocyanins. CHROMOSOME base number $x = 7$. FLAVONOID profile comprising a complex array of flavonol, and sometimes flavone, glycosides, including a charged set, the aglycones frequently poly-O-methylated and with 6-oxygenation, myricetin rare.

GENERIC LIMITS: Many of the species were first described in *Saxifraga*, but because of their five stamens, a free hypanthium and a different appearance they have since been removed. The presence on all taxa of the unicellular eglandular trichomes (absent from *Saxifraga*), and colporate or colporoidate pollen (colpate in *Saxifraga*) provides further strong support for their separation as a distinct group. Only with *Boykinia jamesii* and *B. heucheriformis* has there been any lingering doubt, because of the presence of ten stamens, purple flowers, and chasmophilic habit (as in some species of *Saxifraga*). Originally put in *Saxifraga*, occasional floras still prefer to keep the species there (e.g. Harrington, 1954). Most either follow Rosendahl (1905) or Engler (1919, 1930) in placing them in *Boykinia*, or as seems more popular recently, in following Rafinesque (1837) by assigning them to their own genus, *Telesonix* (e.g. Hitchcock *et al.*, 1961; Scoggan, 1978). Since the species have all the characters of *Boykinia* including a very typical flavonoid profile (Gornall & Bohm, 1980) and trichome complement, they must certainly be placed here. The fact that synthetic hybrids with *B. occidentalis* have been made (Gornall & Bohm, 1984) adds powerful support to this conclusion.

Boykinia jamesii and *B. heucheriformis*, differ from the core members of the genus in section *Boykinia* by having, in addition to the characters noted above, a simpler inflorescence structure, smooth seeds and colporoidate pollen. The last three characters are somewhat reminiscent of the conditions found in *B. richardsonii*, and Hooker (1832) suggested that there was a close relationship between the three species. Rosendahl (1905) even erected a special section, *Boykinia* section *Renifolium*, to accommodate them, an arrangement which Engler (1930) validated. *Boykinia richardsonii* is characterized by high polyploidy ($2n = 84$), five stamens, an inflorescence structure based on 3-flowered paracladia (dichasia), narrowly ovate cotyledons, shallowly tuberculate seeds and a flavonoid profile emphasizing flavones. In contrast, *B. jamesii* and *B. heucheriformis* have complex flavonols, a chromosome number of $2n = 14$, ten stamens, an inflorescence structure based on 1- or 2-flowered paracladia, ovate cotyledons and smooth seeds. It seems preferable therefore to assign the species to separate sections. *Boykinia richardsonii* should remain in *Boykinia* section *Renifolium* and *B. jamesii* and *B. heucheriformis* are put in the new *Boykinia* section, *Telesonix*, based on the genus described by Rafinesque (1837).

The other species of *Boykinia* whose generic position has been in doubt is *B. lycoctonifolia*. Originally described in *Saxifraga*, it was soon recognized as a *Boykinia* (Engler, 1891). However, because of the customary separation of *Sullivantia* and *Suksdorfia* from *Boykinia*, Hara (1937) elevated *B. lycoctonifolia* to generic rank, *Neoboykinia*, on grounds of consistency, because of its small, greenish, persistent petals, and its very short free hypanthium. However, *Boykinia* is quite variable in its floral morpology, certainly enough to accommodate *B. lycoctonifolia*. In fact the species belongs to the core of the genus, in *Boykinia* section *Boykinia*, based on its inflorescence structure, pollen, anther and seed morphology, its trichome complement, leaf shape, flavonoid profile and its general appearance. No one has followed Hara (1937), not even himself (e.g. Hara, 1959: 11, 23, 25, 49).

Boykinia can be distinguished from *Sullivantia* by the characters summarized in Table 7. Rosendahl (1927) also contrasted the campanulate capsules in *Sullivantia* with the turbinate ones in *Boykinia*. He also noted a tendency for the lower paracladia of the inflorescence in *Sullivantia* to develop as trichasial cymes. *Boykinia* has this tendency much less well developed. In addition, interspecific hybrids can be made within *Sullivantia* and *Boykinia*, but not between them (Soltis, 1981a; Gornall & Bohm, 1984). Leaf texture in the two genera is also different, with the lower surfaces of *Boykinia* leaves having prominent vein ridges; *Sullivantia* leaves are smooth. *Sullivantia* also lacks stylar transmitting tissue whereas *Boykinia* does not (Bensel & Palser, 1975). Therefore, it seems justifiable to keep the two genera separate.

Probably the greatest difficulty in the delimitation of *Boykinia* lies in its relationship with *Suksdorfia*. In view of the similarities apparent from Table 7 it is not surprising that *S. ranunculifolia* was once considered as a possible *Boykinia* (Torrey & Gray, 1840; Gray, 1842). Gray (1876) listed it as a probable synonym of *B. occidentalis*. Greene (1891) later made the combination *Boykinia ranunculifolia*, but only a few authors have followed him (Engler, 1919; Jepson, 1936; Jones, 1938). Floral morphology also led Rafinesque (1837) to include *Boykinia richardsonii* with *Suksdorfia ranunculifolia* in his genus *Hemieva* (here regarded as synonymous with *Suksdorfia*), but this treatment has not been adopted since, and trichome complement, rhizome morphology, pollen morphology and flavonoid profile argue for its position in *Boykinia*.

Despite some morphologial similarities, none of the three *Suksdorfia* species would fit comfortably in *Boykinia*. Thus *Suksdorfia ranunculifolia* would have to be put in section *Boykinia* on grounds of inflorescence structure and pollen morphology. However, it lacks the chaffy trichomes and mucronate anthers typical of that section. It also usually lacks the unicellular trichomes found in all *Boykinia* species. *Suksdorfia alchemilloides* and *S. violacea* could be put in *Boykinia* sections *Renifolium* or *Telesonix* on the basis of inflorescence structure although they do not have the same pollen and seed morphologies as those sections. They would be equally out of place in section *Boykinia* because they lack chaffy trichomes and have simple inflorescences. If *Suksdorfia* were forced into *Boykinia* the variation pattern in the latter would be distorted, especially as *Bolandra* would probably have to be included as well, and it would be difficult to know where to stop lumping. The intergeneric breeding relationships also provide no support for the inclusion of *Suksdorfia* in *Boykinia*. In *Boykinia*, intra-generic hybrids can be made, whereas crosses with *Suksdorfia* fail (Gornall & Bohm,

1984). Furthermore, *Boykinia* and *Suksdorfia* have a distinct appearance such that both are clearly recognizable in the field as separate groups. *Suksdorfia* has a general slenderness, basal leaves with relatively uncomplicated venation, and, most importantly, a bulbiliferous rhizome. *Boykinia* is much more robust, its leaves have a more complex venation pattern, and its rhizome is thick and scaly.

How much weight should be given to these characters? In both *Boykinia* and *Suksdorfia,* species are separated from each other largely on grounds of floral morphology. Burtt (1964) suggested that in this kind of situation, evolutionary, or 'biological', genera might be recognized on the basis of characters different from those which are used in separating the species of the respective genera. In the present case, therefore, vegetative characters, principally the rhizome difference, may reflect a genuine evolutionary schism between *Boykinia* and *Suksdorfia.* Thus, many of the similarities in floral morphology and inflorescence structure can be attributed to parallelism. Both genera show the same ranges of variation in floral morphology, some species having large, showy flowers with prominent nectaries (e.g. *Boykinia major* and *Suksdorfia ranunculifolia*), and some having inconspicuous flowers with included petals (e.g. *B. rotundifolia* and *S. alchemilloides*). Variation in inflorescence structure is also similar: *S. ranunculifolia* has the same kind of branching pattern as in section *Boykinia,* and the simpler structures in *S. alchemilloides* and *S. violacea* are mirrored by a similar pattern in *Boykinia* section *Telesonix.*

Regarding the distinction between *Bolandra* and *Boykinia,* much of what has been said with reference to *Suksdorfia,* also applies. In addition to the distinguishing characters listed in Table 7, must be added the cross-incompatibility of *Bolandra* with *Boykinia* species (Gornall & Bohm, 1984).

Key to the sections and species of Boykinia

1. Inflorescence composed of paracladia in the form of many-flowered, usually helicoid, dichasial cymes; brown, chaffy trichomes present at least on the lower stem nodes; seeds finely tuberculate, anthers mucronate . . . . . *Boykinia* section *Boykinia* 3

1ʹ Inflorescence composed of paracladia in the form of simple dichasia, or reduced to one or two flowers; brown chaffy trichomes usually absent; seeds more or less smooth; anthers not mucronate 2

   2. Flowers predominently white (rose veins may be present); stamens 5 . . . . *Boykinia* section *Renifolium: B. richardsonii*
   2ʹ Flowers purple-crimson; stamens 10. . . *Boykinia* section *Telesonix* 8

3. Leaves reniform, divided to at least half their length; upper stipules often foliaceous 4

3ʹ Leaves orbicular, divided to less than half their length; upper stipules reduced to small, flap-like dilations of the petiole base, fringed with brown bristles 5

   4. Petals ovate to orbicular, narrowed abruptly to short claws; inflorescence somewhat corymbiform . . . . *B. major*
   4ʹ Petals obovate to spatulate, attenuate to the claws; inflorescence more pyramidal than corymbiform 6

5.   Petals longer than sepal lobes; free hypanthium *c.* 1 mm long;
     leaves crenate to usually cleft . . . . *B. occidentalis*

5'. Petals shorter or equalling sepal lobes; free hypanthium 1–2 mm
     long; leaves crenate-dentate . . . . *B. rotundifolia*

    6.   Petals white, longer than sepal lobes; free hypanthium
          > 0.8 mm long 7

    6'. Petals greenish, shorter or equalling sepal lobes; free
          hypanthium < 0.8 mm long . . . . *B. lycoctonifolia*

7.   Plant stoloniferous; upper stipules foliaceous; nectary prominent,
     yellow . . . . *B. intermedia*

7'. Plant not stoloniferous; upper stipules usually represented by flap-like
     dilations of the petiole bases; nectary obscure, green . . . *B. aconitifolia*

    8.   Petals violet-purple, only just exceeding sepal lobes (if at
          all); styles connate for about half their length . . *B. heucheriformis*

    8'. Petals crimson-purple, about twice as long as sepals; styles
          connate for at least three quarters of their length . . . *B. jamesii*

Boykinia section *Telesonix* (Raf.) **Gornall & Bohm, comb. et stat. nova**

BASIONYM: *Telesonix* Rafinesque, *Flora Telluriana, 2:* 69 ("1836", 1837).

TYPE SPECIES: *Boykinia jamesii* (Torrey) Engler.

LEAVES canaliculate-smooth on the upper surface and somewhat ribbed below; leaf texture somewhat succulent. INFLORESCENCE loose, composed of 1–3 flowered first-order paracladia. CALYX often purplish. COROLLA purplish. STAMENS 10, anthers not mucronate. POLLEN 3-colporoidate. SEEDS brown, smooth.

Originally, the two species of section *Telesonix* were confused with each other and treated as a single, variable species (Hooker, 1832). Rydberg (1897) was the first to describe some of their differences and recognized both variants at specific level. Following examination of a wide range of herbarium material, further differences have been noted (see species descriptions); in addition, the two taxa differ in flavonoid profile (Gornall & Bohm, 1980) and in pollen morphology (Figs 23–26). We think these differences warrant specific status rather than the varietal status advocated by Engler (1919) and Bacigalupi (1947).

Boykinia jamesii (Torrey) Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien III, 2a:* 51 (1891).

SYNONYMS: *Saxifraga Jamesii* Torrey, *Annals of the Lyceum of Natural History of New York, 2:* 204 (1827).
   Telesonix jamesii Rafinesque, *Flora Telluriana, 2:* 69 ("1836", 1837).
   Saxifraga jamesiana Walpers, *Repertorium botanices systematicae, 2:* 367 (1842), orth. var.
   Therofon Jamesii Wheelock, *Bulletin of the Torrey Botanical Club, 23:* 70 (1896).
TYPE: Rocky Mountains, *Dr James 8* (HOLOTYPE NY!; ISOTYPES K! COLO!) James' collection was made on 14 v 1820 at Pike's Peak, Colorado (Osterhout, 1920).

STEMS 60–180 mm tall, densely glandular. PETIOLES of basal leaves 10–45 mm long, glandular. BASAL LEAVES glandular-pubescent on both sides, reniform (width about 1.3 times the length) varying occasionally to orbicular and cordate; 10–30 mm long by 14–40 mm wide, margins 1–2 times crenate. STOMATA common on upper leaf surface. STIPULES a dilation of petiole base, 1–1.5 mm long sometimes fringed with whitish subulate bristles. INFLORESCENCE composed of 1–3 flowered paracladia. CALYX campanulate 7–12 mm long divided about half its length into lanceolate, erect, glandular sepals, 2–6 mm long. FREE HYPANTHIUM 1–2(–2.5) mm long. NECTARY green, inconspicuous. PETALS crimson-purple, (5–)7–11 mm long, 2–3 times longer than the sepals, and (2–)4–7 mm wide at their widest point, the lamina orbicular with a long claw 1–3 mm long, the angle between claw and lamina about 120°. STAMENS shorter than or equalling the sepals, the filaments about 0.6–1.5 times as long as the undehisced anthers. OVARY about half inferior, styles connate for at least three-quarters of their length. SEEDS 880–1380 μm long, $2n = 14$.

FLOWERING: July–August.

DISTRIBUTION AND ECOLOGY: *Boykinia jamesii* grows on the high peaks of the Colorado Front Range (Fig. 77), namely Pikes Peak and the mountains of the neighbouring Platte River drainage and Rocky Mountain National Park. It also occurs disjunctively in the Santa Fe mountains of New Mexico, although this station has never before been reported in the literature. The species occurs in crevices of granite outcrops and among stones of granite talus at elevations of 3000 m or more. The habitat can be an exceedingly dry one and this possibly explains the rather succulent leaves of the species. *Boykinia jamesii* is usually found in the open although there can sometimes be a partial canopy of coniferous tree species. There is evidence that the species is eaten by elk and deer (Craighead, Craighead & Davis, 1963).

Boykinia heucheriformis (Rydb.) C. Rosendahl, *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beibl., 83:* 62 (1905); (*"heucheri-forme"*).

SYNONYMS: *Therofon heucheraeforme* Rydberg, *Bulletin of the Torrey Botanical Club, 24:* 247, 248 (1897).
Telesonix heucheriformis Rydberg, *North American Flora, 22:* 126 (1905).
Boykinia Jamesii var. *heucheriformis* C. Rosendahl, *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beible., 83:* 34 (1905) *nomen nudum.*
Saxifraga heucheriforme M. E. Jones, *Bulletin of Biological Sciences of Montana State University, 15:* 32 (1910).
Boykinia Jamesii (Torrey) Engler var. *heucheriformis* Engler, in Engler & Irmscher, *Das Pflanzenreich, 69:* 674 (1919).
Telesonix Jamesii (Torrey) Raf. var. *heucheriforme* Bacigalupi, *Leaflets of Western Botany, 5:* 71 (1947).
Saxifraga Jamesii auct. non Torrey: W. J. Hooker, *Flora Boreali-Americana, 1:* 247, t. 84 (1832).

TYPE: Montana, Bozeman, *P. A. Rydberg 2677*, 23 vii 1895 (LECTOTYPE MIN!); Montana, Bridger Mountains, *Flodman 514*, 28 vii 1896 (SYNTYPE NY!); Montana, East Boulder, *F. Tweedy 255*, 1887 (SYNTYPE NY!).

STEMS 30–230 mm tall, densely glandular. PETIOLES of basal leaves (5–)10–50(–100) mm long, glandular. BASAL LEAVES glandular-pubescent on both sides, reniform (width about 1.3 times the length) occasionally varying to orbicular and cordate; 9–50 mm long by 13–70 mm wide, the margins 1 or 2 times crenate. STOMATA common on upper leaf surface. STIPULES a dilation of the petiole base 1–2 mm long, sometimes fringed with whitish subulate bristles, or occasionally larger and foliaceous. INFLORESCENCE composed of 1–3 flowered paracladia. CALYX campanulate 6–14 mm long divided about half its length into lanceolate, erect, glandular sepals 3–6 mm long. FREE HYPANTHIUM (1.5–)2.0–3.5 mm long. NECTARY green, inconspicuous. PETALS violet-purple, spatulate, 3–6 mm long and 1.0–3.5 mm wide at their widest point, shorter to only slightly longer than sepals, angle between the short claw and the lamina about 150°. STAMENS shorter than sepals, filaments about 0.6–1.5 times as long as the undehisced anthers. OVARY half inferior, styles united for about half their length. SEEDS 830–1355 μm long. $2n = 14$.

FLOWERING: June–August. Insect visitors Diptera–Empididae.

DISTRIBUTION AND ECOLOGY: *Boykinia heucheriformis* is found in the Rocky Mountains from Alberta south to Wyoming and disjunctively in the Black Hills of South Dakota(?) and the Charleston Mountains of southern Nevada (Fig. 77). Although presumably mostly eliminated from the Canadian Rockies by the Pleistocene glaciations there is some evidence that at least one population survived them in the Mountain Park area, near Jasper, Alberta (Packer & Vitt, 1974). A similar refugium may have existed for *B. heucheriformis* in the Waterton Lakes area of southern Alberta (Packer, 1971). The species is apparently restricted to calcareous substrates and is most frequently found at altitudes of between 2500 and 3500 m, although it can grow as low as 1500 m in the more northerly parts of its range and in places with suitably cold microclimates. Like *B. jamesii*, it usually grows in the open in rock crevices, although occasionally there is a partial canopy of pines or firs. It is eaten by elk and deer (Craighead *et al.*, 1963).

Boykinia section *Renifolium* C. Rosendahl ex Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien, ed. 2., 18a:* 120 (1930).

SYNONYM: section *Renifolium* C. Rosendahl, *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beibl., 83:* 62 (1905) *nomen nudum.*

TYPE SPECIES: *Boykinia richardsonii* (Hook.) Rothrock (LECTOTYPE).

LEAVES canaliculate on the upper surface, costate below. SHOOT uniformly clothed with prominent, glandular, trichomes. INFLORESCENCE spike-like with each first-order paracladium consisting of a terminal flower borne at or near the junction of a dichotomous branch pair, each branch bearing one flower only. CALYX green to purple. COROLLA white but often with veins flushed with a rose colour, sometimes deeply so. STAMENS 5, the anthers lacking an apical mucron. POLLEN 3-colporoidate. SEEDS brown, smooth at × 15.

Boykinia richardsonii (Hook.) Rothrock, *Annual Report of the Board of Regents, Smithsonian Institution, 1867:* 447 (1868).

SYNONYMS: *Saxifraga Richardsonii* W. J. Hooker, *Flora Boreali-Americana, 1: 247 (1832).*
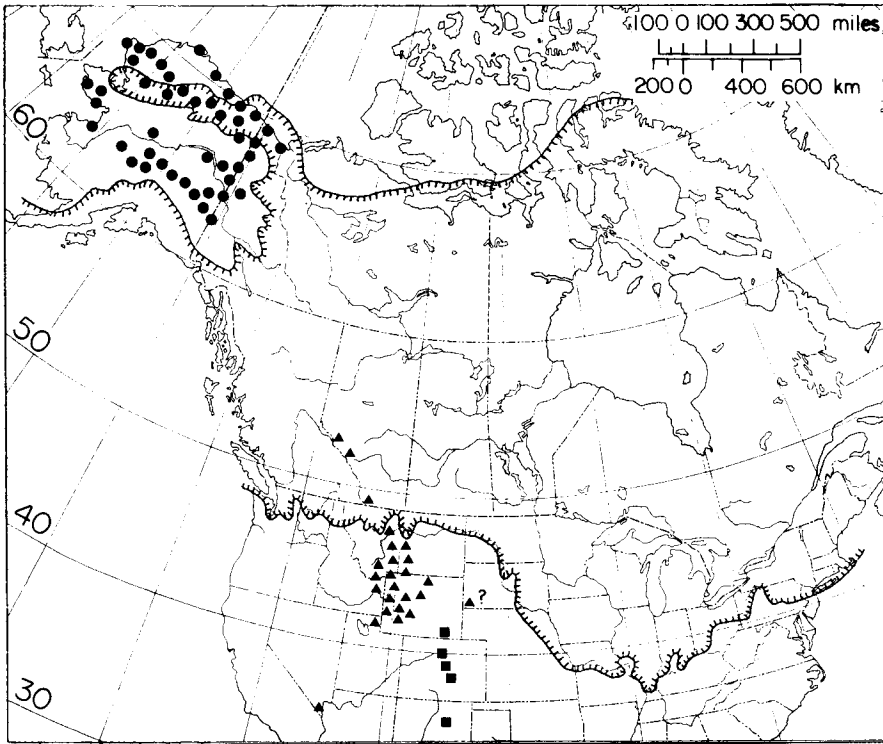
Figure 77. Distribution of *Boykinia jamesii* (■), *B. heucheriformis* (▲) and *B. richardsonii* (●).
Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

Hemieva richardsonii Rafinesque, *Flora Telluriana, 2:* 70 ("1836", 1837).
Therofon Richardsonii Kuntze, *Revisio Generum Plantarum, 1:* 227 (1891).
Saxifraga Nelsoniana auct. *non* D. Don: Hooker & Arnott, *The Botany of Captain
    Beechey's Voyage, 124, t. 29* (October –November 1832).

TYPE: Arctic Sea shore, *Dr Richardson* (LECTOTYPE K!); Imarook, Kotzebue's
Sound, *Lay & Collie s.n.* (ISOSYNTYPES GH, K!).

NOMENCLATURAL NOTES: Hooker (1832) stated that Richardson's specimen was
collected between the Mackenzie and Copper-mine Rivers. Lay and Collie's
specimen at K bears the name 'Beechey' rather than their own, but must have
been collected by them as they were the expedition's naturalists. Their collection
was made between July and September, 1826 (Hooker & Arnott, 1832).

STEMS stout 100–400(–600) mm tall, densely glandular with thick capitate
trichomes. PETIOLES of basal leaves 25–100(–225) mm long, glandular. BASAL
LEAVES glandular-pubescent below, glabrate above, reniform, width about 1.5
times the length, 20–70(–120) mm long and (30–)50–110(–150) mm wide, the
margins shallowly-lobed, 2–3 times dentate (very rarely 3-cleft). STOMATA
common on upper leaf surface. STIPULES a dilation of petiole base or foliaceous,
(1–)2–5 mm long, the smaller ones fringed with subulate bristles. INFLORESCENCE
composed of 3-flowered paracladia. CALYX campanulate, 6–14(–17) mm long,

divided about half its length into triangular to lanceolate, erect, usually sparsely glandular sepals 3–7 mm long. FREE HYPANTHIUM (1–)2–3 mm long. NECTARY greenish or deep purple. PETALS white, sometimes with rose veins, ovate with an acute apex and a cuneate to clawed base, 8–12(–15) mm long and 3–7 mm wide at the widest point, 2–3(–5) times as long as sepals. STAMENS shorter or equalling sepals, filaments 2–4 times as long as undehisced anthers. OVARY almost completely inferior, styles united about a quarter of their length. SEEDS 1355–1880 µm long. $2n = 84$ (Alaska Range), $2n = 36?$ (Brooks Range).

FLOWERING: June–August.

DISTRIBUTION AND ECOLOGY: *Boykinia richardsonii* has a U-shaped distribution in Alaska and the Yukon Territory (Fig. 77), inhabiting the Alaska Range at elevations of between 1000 and 1700 m, the Porcupine River drainage and east and northeast facing slopes of the Brooks Range at elevations from near sea level up to 400 m. Rydberg (1905) and Engler (1930) reported it from eastern Siberia; Hulten (1968) did not, although he considered its occurrence there "very probable". However, *B. richardsonii* is not listed in the *Flora of the U.S.S.R.* (Lozina-Lozinskaya, 1939) nor in the more recent Siberian Flora (Tolmachev, 1966). It is almost certainly a Tertiary relic, surviving the Pleistocene glaciations isolated in the unglaciated regions of Alaska and the Yukon (Fig. 77; Hulten, 1968).

The species grows in stream-side gullies and snow-bed grassland communities in protected depressions where snow lies frequently into mid-June. It can be found in the open or in the partial shade of various *Salix* species. Throughout its range it is a calcicole. Leaves and inflorescences are often eaten by grizzly bears (Murie, 1944; White, 1974), and we have observed that its capsules sometimes have holes in them, possibly indicating that they are robbed of their seeds (by birds?).

Plants from the arctic slope of the Brooks Range have been counted as $2n = 84$ (Johnson & Packer, 1968), and as $2n = c.$ 84 (Packer & McPherson, 1974). However, plants from the Alaska Range have been counted as $2n = 36$ (Knaben, 1968). This situation needs confirmation and deserves further study, especially with regard to glaciated vs. unglaciated retions. Plants from the two areas are indistinguishable except in that pollen equatorial diameters from Brooks Range plants are statistically larger than they are in plants from the Alaska Range.

Boykinia section *Boykinia*

SYNONYM: *Boykinia* subgenus *Therofon* Jepson, *A manual of the Flowering Plants of California*, 458–459 (1925), *nomen nudum*.

TYPE SPECIES: *Boykinia aconitifolia* Nuttall.

LEAVES canaliculate on the upper surface and costate below. SHOOT with at least the lower nodes, and especially the base, clothed with brown, chaffy, eglandular trichomes. INFLORESCENCE with usually one but up to two orders of paracladia, each paracladium consisting of a terminal flower (rarely absent) borne at, or near, the junction of a dichotomous branch pair, each branch bearing usually several flowers in a typically helicoid arrangement. CALYX green. COROLLA white or yellowish-green. STAMENS 5, the anthers mucronate. POLLEN 3-colporate. SEEDS black (rarely brown), minutely tuberculate.

Boykinia aconitifolia Nuttall, *Journal of the Academy of Natural Sciences of Philadelphia,* 7: 113, 114 (1834).

SYNONYMS: *Saxifraga aconitifolia* Fielding & Gardner, *Sertum Plantarum,* pl. 57 (1844).

Therofon aconitifolia Millspaugh, *Bulletin of the West Virginia University Agricultural Experimental Station, 2:* 361 (1892).

Therofon napelloides Rafinesque, *New Flora and Botany of North America IV. Neobotanon,* 66 ("1836", 1838). TYPE: Unaka or Iron Mountains of North Carolina, *Kin* (HOLOTYPE Herb. Collins, now possibly at P (Stuckey, 1971)).

Therophon turbinatum Rydberg, *North American Flora, 22:* 124 (1905).

Boykinia turbinata Fedde, *Just's botanischer Jahresbericht, 33:* 607 ("1905", 1906). TYPE: Banks of a stream among mountains, N Alabama, U.S.A., *S. B. Buckley s.n.,* September 1840 (HOLOTYPE NY!). The holotype has the generic name spelled "Therofon".

TYPE: Aus den Allaghanis bergh, *Kin 45* (HOLOTYPE PH!).

NOMENCLATURAL NOTES: Rafinesque (1838) cited a Kin specimen from North Carolina, labelled *Heuchera palmata,* in Collin's herbarium. Nuttall (1834) cited a Kin specimen from "Virginia or North Carolina", also labelled as a *Heuchera,* in Muhlenberg's herbarium (now at PH). It is known that Kin distributed his collections to Collins, as well as to Muhlenberg (Stuckey, 1971) and it is therefore entirely possible that Nuttall and Rafinesque based their descriptions on isotypes. The fact that both specimens are labelled as *Heuchera* could support such a view.

STEMS fairly stout, 150–800 mm tall, sparsely pilose below with brownish eglandular chaffy hairs and glandular trichomes, or glandular-pubescent only above. PETIOLES of basal leaves 30–180(–310) mm long, glabrate to pilose. BASAL LEAVES glandular-pubescent, reniform (width about 1.3 times the length), occasionally varying to orbicular-cordate, (25–)40–80(–120) mm long, (30–)50–130(–155) mm wide, 3–7 cleft up to three-quarters of their length, the margins 2–3 times dentate (occasionally crenate). STOMATA occasional on upper leaf surface. STIPULES a dilation of the petiole base up to 2 mm long and fringed with several brownish, subulate bristles or occasionally foliaceous up to 8 mm long. INFLORESCENCE with 5–20(–30) flowers per paracladium. CALYX turbinate to campanulate 3–6(–7) mm long, divided for a quarter to half its length into lanceolate to narrowly lanceolate densely glandular to usually sparsely glandular sepals 1–2(–2.5) mm long. FREE HYPANTHIUM 0.7–1.0 mm long. NECTARY green, inconspicuous. PETALS white, spatulate 3–6 mm long, 1–3 mm wide at their widest point, short clawed, 2–3(–4) times longer than sepals. STAMENS shorter or equalling the sepals, the filaments 1.3–2 times as long as the undehisced anthers. OVARY almost completely inferior. SEEDS 415–625 μm long. $2n = 14$.

FLOWERING: June–August.

DISTRIBUTION AND ECOLOGY: *Boykinia aconitifolia* ranges through the Appalachians from the Virginias south to Georgia and Alabama (Fig. 78). It grows in moist, woodland habitats along the margins of ponds, lakes and watercourses at elevations of between 300 and 1000 m.
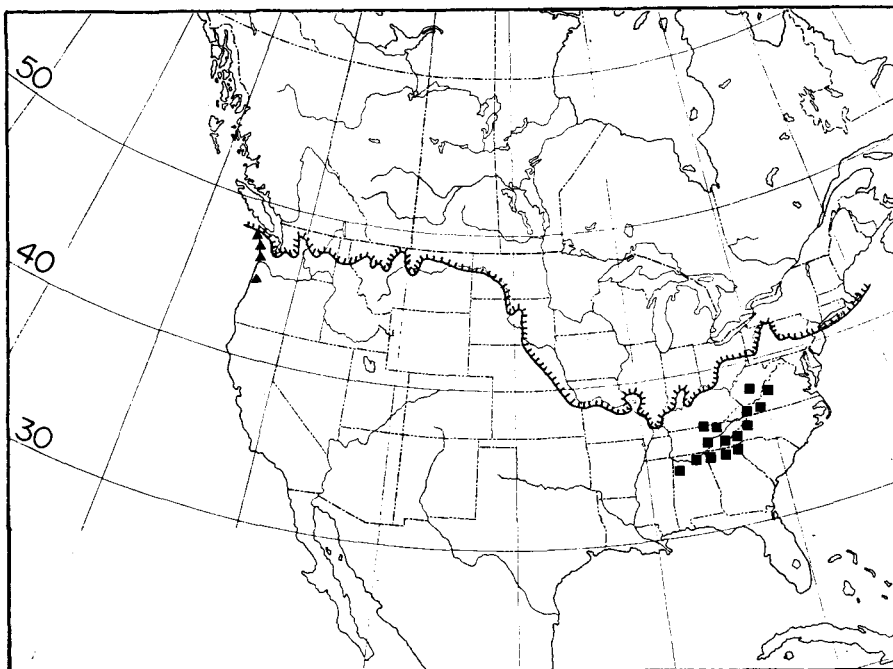
Figure 78. Distribution of *Boykinia aconitifolia* (■) and *B. intermedia* (▲). Toothed line indicates maximum limit of last glaciation. Only representative collections are shown.

Boykinia aconitifolia is variable in leaf shape and dentition in the same manner as many of the other species in section *Boykinia;* it also varies in the shape of its seed capsule, which may range from turbinate to urceolate. Rydberg (1905) described a new species from northern Alabama, *Therophon turbinatum*, based on this character and on the shape of the leaf teeth. *Therophon turbinatum* was described as having rounded-ovate leaf teeth and a turbinate capsule up to 8 mm long. *Boykinia aconitifolia* was distinguished by its lanceolate, ovate or triangular leaf teeth and a spherical or rounded capsule up to 4 mm long. However, measurement of a group of fruiting specimens for the relevant leaf and hypanthium characters showed that leaf and capsule shape are not closely correlated and that both characters show a continuous range of variation. Moreover although there is some tendency for plants having turbinate capsules to be found in Alabama and Georgia they occur also in North Carolina and Virginia. Similarly, plants with urceolate capsules can be found in Alabama and South Carolina. Variation in leaf shape was discussed earlier, and has been shown to have some developmental component. In view of these results, no recognition of a segregate taxon is warranted.

Boykinia intermedia (Piper) G. N. Jones, *University of Washington Publications in Biology, 5:* 168 (1936).

SYNONYMS: *Boykinia major intermedia* Piper, *Erythea, 7:* 172, 173 (1899).
    Therofon intermedium Heller, *Muhlenbergia, 1:* 53 (1904).

Therofon majus (A. Gray) Kuntze *intermedium* Piper, *Contributions from the United States National Herbarium, Smithsonian Institution, 11:* 311 (1906).

TYPE: New London, Chehalis Co., Washington, *Frank H. Lamb 1167*, 10 vi 1897 (HOLOTYPE US!, ISOTYPES DS! F! PH! UC!).

NOMENCLATURAL NOTES: Piper (1899) cited *F. H. Lamb 1267* as the type. The isotypes at DS, F and PH, however, are clearly marked "*Lamb 1167*", not "*1267*". On the holotype at US the collection number is ambiguous and could be interpreted either way; in view of the clear annotation on the isotypes, the number should be taken as "1167".

STEM 250–700 mm tall, sparsely pilose below with brownish (or reddish) eglandular chaff and glandular trichomes, or glandular pubescent only above. STOLONS present. BASAL LEAVES glandular/chaffy pubescent below, glabrate above, reniform (width about 1.3 times the length) (30–)50–110 mm long, (50–)80–140 mm wide, 3–7 cleft up to three-quarters of their length, the margins 2–3 times dentate. STOMATA absent or very rare on upper leaf surface. PETIOLES of basal leaves 30–150 mm long, glabrate to pilose. STIPULES usually foliaceous (2–)4–9 mm long, smaller ones often fringed with several brownish subulate bristles. INFLORESCENCE somewhat corymbiform, with (5–)9–13 flowers per paracladium. CALYX turbinate to campanulate 3–6 mm long, divided for half to three-quarters of its length into lanceolate, usually sparsely glandular sepals, (1.5–)2–3 mm long. FREE HYPANTHIUM 0.8–1.3 mm long. NECTARY greenish-yellow. PETALS white, spatulate, short clawed, 3–7 mm long, 1–3 mm wide at the widest, 2–3 times longer than sepals. STAMENS shorter or equalling the sepals, the filaments about 1.3 times as long as the undehisced anthers. OVARY almost completely inferior. SEEDS 490–640 µm long. $2n = 14$.

FLOWERING: June–August. Insect visitors Diptera–Empididae.

DISTRIBUTION AND ECOLOGY: *Boykinia intermedia* is restricted to the western side of the Olympic Peninsula in Washington and the Coast Range of northern Oregon (Fig. 78), areas where the rainfall exceeds 250 cm per annum. Reports of *B. intermedia* in northern Idaho (Bacigalupi, 1952; Johnson & Steele, 1978) are erroneous [as was the misquotation of the type locality as Idaho by Rydberg (1905)]. All collections from Idaho belong to *B. major*. *B. intermedia* is typically found in wet, woodland habitats along the margins of streams, rivers, ponds and lakes at elevations below 700 m. One population (*Gornall 24*) was found growing in running water.

Although originally described as an infraspecific taxon under *Boykinia major*, there is ample reason to follow Heller (1904) in recognizing *B. intermedia* as a distinct species. First, the chromosome number of *B. intermedia* is $2n = 14$ whereas that of *B. major* is $2n = 28$ (Gornall *et al.*, 1983). Secondly, *B. intermedia* has stolons, petals more spatulate than clawed, much smaller foliaceous stipules, a shorter free hypanthium, and a different inflorescence shape from *B. major*. Thirdly, it lacks the polymethylated flavonols typical of *B. major* (Gornall & Bohm, 1980).

Piper (1899) suggested that *B. intermedia* was the possible product of hybridization between *B. major* and *B. occidentalis*. Heller (1904) queried this view, and evidence from the comparative morphology, cytology and chemistry of the synthetic *B. major* × *B. occidentalis* hybrid combine emphatically to reject a

hybrid hypothesis (Gornall & Bohm, 1980; Gornall *et al.*, 1983; Gornall & Bohm, 1984).

Boykinia lycoctonifolia (Maxim.) Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien III. 2a:* 52 (1891).

SYNONYMS: *Saxifraga lycoctonifolia* Maximowicz, *Bulletin de l'Académie Impériale des Sciences de Saint-Pétersbourg, 31:* 41, 42 (1886).

Therophon lycoctonifolia Takeda, *Journal of Botany, British and Foreign, 49:* 114 (1911), *nom. invalid.* (Art. 34.1).

Neoboykinia lycoctonifolia H. Hara, *Botanical Magazine, Tokyo, 51:* 253 (1937).

TYPE: Japan, Prov. Senano, in Kinnaga-take, *R. Yatabe s.n.,* 2 viii 1882 (HOLOTYPE LE!).

STEM (150–)250–550(–750) mm tall, sparsely pilose below with brownish eglandular chaff and glandular trichomes, or glandular pubescent only above. STOLONS present. BASAL LEAVES glandular/chaffy pubescent below, glabrate above, reniform (width about 1.3 times the length), (30–)50–90 mm long, (40–)70–130 mm wide, 3–7 cleft to about half their length, the margins 3–4 times dentate. STOMATA absent or very rare on upper leaf surface. STIPULES usually foliaceous (2–)4–8 mm long, the smaller ones often fringed with several brownish, subulate bristles. INFLORESCENCE with (3–)5–13 flowers per paracladium. CALYX campanulate 3–7 mm long, divided about half its length into triangular, usually sparsely glandular sepals 2–3 mm long. FREE HYPANTHIUM 0.3–0.8 mm long. NECTARY green, inconspicuous. PETALS yellow-green, obovate, short clawed, up to 2 mm long and half as much wide, shorter than or about equalling the sepals. STAMENS shorter than or equalling the sepals, the filaments about 1.5 times as long as the undehisced anthers. OVARY almost completely inferior. SEEDS 425–565 μm long. $2n = ?$

FLOWERING: July–August.

DISTRIBUTION AND ECOLOGY: *Boykinia lycotonifolia,* a Japanese endemic (Fig. 79), inhabits seasonally wet, snow-bed grassland in the alpine zone of the mountains of central and northern Honshu and Hokkaido (Ohwi, 1965; Ishizuka, 1974), usually between 2000–2800 m, on volcanic soils (Hara, 1959).

Boykinia major A. Gray, *Botany of California, 1:* 196 (1876).

SYNONYM: *Therofon major* Kuntze, *Revisio Generum Plantarum, 1:* 227 (1891).

TYPE: Meadows, Big-tree Grove, Yosemite, California, *H. N. Bolander 4982,* 1866 (LECTOTYPE GH! ISOLECTOTYPES BM! F! GH! K! UC-two sheets!); Robinson's Flat, N California, 4000 ft, *W. H. Brewer 2166?* 1863 (ISOSYNTYPES GH! K!); California, *Thomas Bridges 126* (SYNTYPE GH!); In the rocky bed of Silver Creek or margins, Oregon, *Elihu Hall 158,* 1871 (ISOSYNTYPES BM! CAN! F-three sheets! GH! PH! POM!).

NOMENCLATURAL NOTES: in his protologue, Gray (1876) cited four specimens. Careful comparison of the description with these specimens shows that they were all used in its construction, although only *Bolander 4982* ("Yosemite") at GH is annotated "*Boykinia major* Gray n. sp.". There appear to be several isotypes of Bolander's collection, although the type locality is cited in different ways, and some of the specimens were identified as *Boykinia occidentalis* T. & G. The appearance of the specimens suggests that they do represent the same collection.
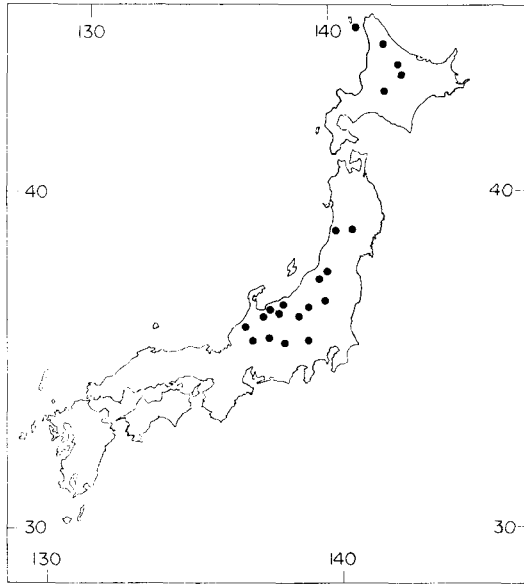
Figure 79. Distribution of *Boykinia lycoctonifolia*. Only representative collections are shown.

STEMS stout, (200-)500–1300 mm tall, sparsely pilose below with brownish eglandular chaffy hairs and glandular trichomes, or glandular pubescent only above. PETIOLES of basal leaves 50–250(–400) mm long, glabrate to pilose. BASAL LEAVES glandular/chaffy pubescent below, glabrate above, reniform (width about 1.3 times the length) varying occasionally to cordate, 50–150(–220) mm long, 70–180(–260) mm broad, 3–7 cleft about three-quarters of their length, the margins 2–3 times dentate. STOMATA absent or very rare on upper leaf surface. STIPULES foliaceous (2–)6–20(–35) mm long, smaller ones often fringed with several brownish subulate bristles. INFLORESCENCE corymbiform, with 8–15(–21) flowers per paracladium. CALYX cup-shaped (3–)4–7(–10) mm long, divided about half its length into triangular, spreading, usually sparsely glandular sepals 2–4 mm long. FREE HYPANTHIUM 1–2 mm long. NECTARY yellow, prominent. PETALS white, 4–7 mm long and 2–5 mm wide at their widest point, about twice as long as sepals, lamina orbicular with somewhat wavy margins and with a claw 0.5–3.0 mm long. STAMENS shorter or equalling the sepals, the filaments 1.3–2 times as long as the undehisced anthers. OVARY completely inferior. SEEDS 560–775 μm long. $2n = 28$.

FLOWERING: June–August(–September). Insect visitors mainly Hymenoptera-Halictidae, but also occasional Formicidae (*Myrmica*), Apidae (*Bombus*) and Coleoptera-Coccinellidae.

DISTRIBUTION AND ECOLOGY: *Boykinia major* grows on the western slopes of the Cascade–Sierra Nevada axis from central Oregon to central California, and disjunctively in the Bitterroot Mountains of Idaho and Montana. It also occurs in the Coast Ranges of northern California (Fig. 80). Reports of *B. major* from the Juneau area of the Alaska panhandle (Cooley, 1892) are erroneous. All of Cooley's specimens are *Heuchera glabra* Willd. In terms of habitat, *B. major* is a

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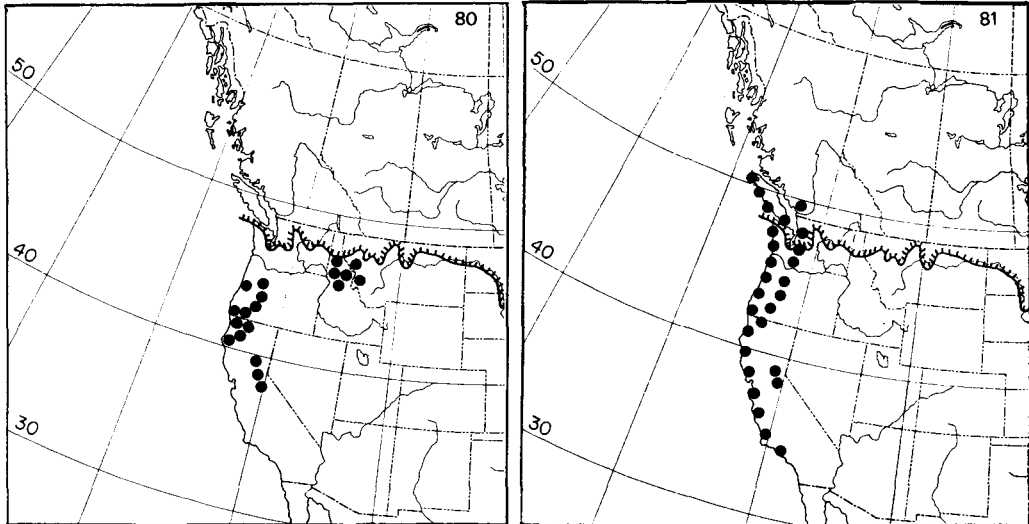
Figures 80 & 81. Fig. 80. Distribution of *Boykinia major*. Fig. 81. Distribution of *Boykinia occidentalis*. Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

plant of wet woodlands, growing along the margins of streams, rivers, ponds and lakes at elevations of between 1000 and 2200 m, being commonest at around 1700 m. *Boykinia major* is used for medicinal purposes by the Hupa Indians of northern California (fide *P. E. Goddard 12D*, UC).

Boykinia major is the largest species in the genus. Inflorescence structure can vary somewhat, rather as in *B. occidentalis*, with some populations having a regular cincinnate pattern and others having it less so. No infraspecific taxa have been described on this basis, nor are they warranted. In a few populations there is a polymorphism for entire vs. toothed petals (e.g. *Gornall 335* and *337*, Selway River, Idaho). Some plants also have flowers with purple blotches at the base of the petals (e.g. *Kruckeberg 3722*, Trinity Alps, California). Taxonomic recognition at the level of forma could be given, although one might merely be labelling single genes. We therefore prefer simply to record their existence rather than give them formal status. Putative hybrids with *B. occidentalis* have been collected from Lane Co., Oregon.

Boykinia occidentalis Torrey & Gray, *A Flora of North America, 1:* 577, 698 (1840).

SYNONYMS: *Therofon occidentalis* Kuntze, *Revisio Generum Plantarum, 1:* 227 (1891).
  Boykinia elata var. *occidentalis* C. Rosendahl, *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beibl., 83:* 36 (1905), *nomen nudum.*
  Boykinia elata occidentalis (Torrey & Gray) Nelson & Macbride, printed annotations on specimens of *Heuchera glabra* Willd. collected by *Walker & Walker* (nos. *718, 780, 852*) in 1915 (F! RM!).
  Boykinia elata (Nutt.) E. Greene var. *occidentalis* C. Rosendahl ex Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien, ed. 2, 18a:* 120 (1930).
  Saxifraga elata Nuttall in Torrey and Gray, *A Flora of North America, 1:* 575 (1840).
  Boykinia occidentalis Torrey & Gray var. *elata* A. Gray, *Proceedings of the American Academy of Arts and Sciences, 8:* 383 (1872).

Boykinia elata E. Greene, *Flora Franciscana:* 190 (1891).

Therofon elatum E. Greene, *Manual of the Botany of the Region of San Francisco Bay:* 121 (1894).

Boykinia Nuttallii J. M. Macoun, *Canadian Record of Science, 6:* 408 (1896). TYPE: Columbia River by Chinhook in very wet place, *Thomas Nuttall s.n.* (HOLOTYPE BM!). [The collection date may have been 4 vii 1835 (Graustein, 1967: 312), although Nuttall mentions June (no year cited) in the protologue.]

Therophon cincinnatum Rosendahl & Rydberg, *North American Flora, 22:* 124 (18 xii 1905).

Boykinia occidentalis Torrey & Gray var. *cincinnata* C. Rosendahl, *Botanischer Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beibl., 83:* 61 (22 xii 1905); ["var. *cincinnata* (Rydb. & Rosend.) n. comb."].

Boykinia cincinnata Fedde, *Just's botanischer Jahresbericht, 33:* 607 ("1905", 1906).

Boykinia elata (Nutt.) E. Greene var. *cincinnata* C. Rosendahl ex Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien, ed. 2, 18a:* 120 (1930). TYPE: Rocky banks of streams, Santa Cruz, California, *C. G. Pringle,* 11 vii 1882 (HOLOTYPE CAN!; ISOTYPES F-two sheets! MIN! PENN! PH! UC-fragment!). [The holotype has the specific epithet spelled "*circinnatum*".]

Therophon vancouverense Rydberg, *North American Flora, 22:* 125 (1905).

Boykinia vancouverensis Fedde, *Just's botanischer Jahresbericht, 33:* 607 ("1905", 1906). TYPE: Vancouver Island, *Harry Edwards s.n.,* 1 viii 1874 (HOLOTYPE NY! ISOTYPE UC-fragment!). [The generic name is spelled "*Therofon*" on the holotype.]

TYPE: California or Oregon, *Douglas s.n.* (HOLOTYPE GH!) [Torrey & Gray (1840) gave the collection locality as Oregon and the date as 1835, although Douglas died in 1834. At BM and K there are specimens, collected by Douglas in 1830, which may be isotypes.

NOMENCLATURAL NOTES: Regarding the correct name for the species, the earliest names were published simultaneously (Torrey & Gray, 1840): *Saxifraga elata* Nuttall and *Boykinia occidentalis* Torrey & Gray. In such cases the choice of epithet is up to the first author who combines the names (Art. 57). In the supplement to their flora, Torrey & Gray (1840) commented that Nuttall's *S. elata* "proves to be a true *Boykinia*" and strongly implied that it was conspecific with their *B. occidentalis*. Indeed, Gray (1842) stated that *S. elata* was referred to *B. occidentalis* in the supplement. However, it was not until 1872 that a formal combination was made, whereby *S. elata* Nutt. was given varietal status under *B. occidentalis* (Gray, 1872). Unhappily, the specimen cited (*Elihu Hall 158*) actually belongs to *Boykinia major*, a fact later recognized by Gray (1876). His difficulty stemmed from uncertainty over whether *B. major* graded into *B. occidentalis* in Oregon, and if so, he thought that plants there might be referrable to Nuttall's taxon (Gray, 1876). However, he continued to regard *S. elata* as "wholly or partly synonymous" with *B. occidentalis* (Gray, 1876). Macoun (1883) unequivocally reduced *S. elata* to complete synonymy under *B. occidentalis*, although he later changed his mind (Macoun, 1896) when he renamed Nuttall's *S. elata* as "*Boykinia Nuttallii*". The new name was deemed necessary because Greene (1891) had made the combination *Boykinia elata* with

B. occidentalis as a synonym. Therefore, although almost all recent treatments have used *Boykinia elata* (Nutt.) Greene (e.g. Hitchcock *et al.*, 1961), the correct name is *Boykinia occidentalis* Torr. & Gray.

STEMS somewhat slender, 150–600(–1000) mm tall, villous or pilose below with brownish or reddish (rarely whitish) eglandular chaffy hairs and glandular trichomes, or glandular-pubescent only above. PETIOLES of basal leaves (30–)60–180(–270) mm long, glabrate to villous. BASAL LEAVES glandular-pubescent, orbicular and cordate, about as long as wide, varying occasionally to reniform, (15–)20–80(–110) mm long, (15–)30–80(–120) mm broad, 3–9 cleft up to half their length, the margins 2–3 times crenate to dentate. STOMATA moderately common on upper leaf surface. STIPULES a dilation of the petiole base up to 2 mm long and fringed with brownish, subulate bristles. INFLORESCENCE with 5–10(–19) flowers per paracladium, sometimes wholly or partly reddish. CALYX turbinate-campanulate (2.5–)3–6(–8) mm long, divided for a quarter to half its length into lanceolate to narrowly lanceolate, densely glandular to glabrate sepals, 1.0–2.5 mm long. FREE HYPANTHIUM (0.7–)0.9–1.2(–1.8) mm long. NECTARY green, inconspicuous. PETALS white, spatulate, (2.5–)4–6(–7) mm long, 1–2 mm broad at their widest point, short clawed, 2–3 times longer than the sepals. STAMENS shorter than sepals, the filaments usually equalling the undehisced anthers. OVARY about three-quarters inferior. SEEDS 465–660 µm long. $2n = 14$.

FLOWERING: June–August. Insect visitors mainly Coleoptera–Staphylinidae, but also some Diptera–Empididae, Syrphidae, Otitidae and Muscidae, and Hymenoptera–Apidae (*Bombus*).

DISTRIBUTION AND ECOLOGY: *Boykinia occidentalis* is an essentially coastal element ranging from northern Vancouver Island to southern California (Fig. 81), growing on the western slopes of the Coast Ranges. It also occurs in the Cascade–Sierra Nevada axis chiefly in central Orégon, the Kalmath Ranges and from Plumas Co. to Amador Co., California. *B. occidentalis* grows in moist woodland habitats along the margins of streams and ponds and shows some preference for disturbed, bare soil, such as trail sides and mud slides. The species ranges from sea level to 1400 m, exceptionally to 1700 m.

The leaves of *Boykinia occidentalis* are eaten by the Quileute Indians of the Olympic Peninsula, Washington, as a treatment for tuberculosis (Gunther, 1973). The species is also used for medicinal purposes by the Hupa Indians of northern California (fide *P. E. Goddard 646*, UC).

Boykinia occidentalis is a very variable species, and Rydberg (1905) felt compelled to recognize four species, and Rosendahl (1905) two, one with two varieties. A comparison of these classifications and the distribution of supposedly diagnostic characters is shown in Table 8. Until now, experimental data on the species has been lacking. However, we describe below the observations we have made on these allegedly diagnostic characters.

Environmental modification of pubescence: Eight populations of plants, sampled from Vancouver Island to California, were grown under uniform environmental conditions (17–20°C, 16 h photoperiod) for 2 years. A series of measurements was then made:
    trichome density on the petioles of two basal leaves (one young and one old) of each plant;

length of three representative trichomes on each petiole examined;
trichome density on the hypanthium.

Since the impression of hairiness on the petioles owes much to the tangled
nature of the trichomes, a third parameter, petiole hairiness index, was
calculated by multiplying trichome density by the mean of trichome length. The
results are presented in Table 9.

The data show first that all measures of trichome density have completely
continuous distributions, and that there is no geographical correlation with this
variation. Second, young petioles are more pubescent than old petioles. This
demonstration of glabrescence vindicates the suspicion (Torrey & Gray, 1840)
that the "chaffy hairs", which were originally thought to distinguish Nuttall's
Saxifraga elata from their own *Boykinia occidentalis*, were deciduous. The results
support the recognition of a single species only.

Environmental modification of inflorescence morphology: Boykinia occidentalis is especially
variable in its inflorescence structure. Some individuals have paracladia
comprised of flowers with curved pedicels borne in highly regular (cincinnate)
helicoid cymes. In other individuals, the inflorescence structure is less cincinnate
and the flowers less secund, some even with straight pedicels. Intermediates are
common. Observation of individuals from the different cultivated populations
showed that the cincinnate condition becomes more apparent as the capsules
ripen. Examination of herbarium specimens also showed that the variation is
continuous, with no apparent geographical correlation.

Some attempts were made to alter experimentally both inflorescence structure
and pedicel curvature. In the first experiment, cloned individuals of each of
three populations (*Gornall 22, 256, Straley 1753*) were given conditions of drought.
In each case they developed very small basal leaves and produced a highly
depauperate and irregular shoot system when compared with their well-watered
counterparts with identical genotypes (Fig. 82). In the second experiment, we
found that pedicel curvature was also phenotypically plastic and depended, at
least in part, on the orientation of the stem. The great variation in both pedicel
curvature and inflorescence structure in *B. occidentalis* makes it impossible to

Table 8. Characters supposedly diagnostic of taxa segregated from *Boykinia
occidentalis* Torr. & Gray, including a comparison of the classifications of
Rydberg (1905) and Rosendahl (1905). The key is based on Rydberg (1905)

		Rydberg	Rosendahl
1.	Inflorescence cincinnate-cymose, pedicels curved	 2	
1!	Inflorescence irregularly cymose, pedicels straight .	 3	
2.	Hypanthium densely glandular, purplish; leaf blades firm; petioles hirsute	*B. cincinnata*	*B. occidentalis* var. *cincinnata*
2!	Hypanthium sparingly glandular, green; leaf blades thin; petioles glabrous or with a few scattered hairs	*B. occidentalis*	*B. occidentalis*
3.	Sepals in fruit reflexed or spreading; inflorescence puberulent, green	*B. vancouverense*	*B. elata*
3!	Sepals in fruit erect or ascending; inflorescence densely glandular, purplish	*B. elata*	*B. elata*

Table 9. Variation in trichome density among eight populations of *Boykinia*
occidentalis grown in a growth chamber

Population*		Mean petiole trichome density (mm^{-2}) (a)		Mean petiole trichome length (mm) (b)		Mean petiole hairiness index (a × b)		Mean hypanthium trichome density (mm^{-2})
		Young	Old	Young	Old	Young	Old	
G8 (3)	Vancouver Is.	10.3	4.7	2.3	1.5	23.5	7.4	35.0 ± 12.3
	British Columbia	(1.2)†	(2.3)	(0.1)	(0.3)	(3.2)	(4.4)	
G2 (4)	Vancouver	14.8	7.0	2.2	1.9	30.5	13.6	28.0 ± 11.8
	British Columbia	(2.2)	(0.8	(1.1)	(1.1)	(11.2)	(9.8)	
G22 (2)	Jefferson Co.	16.0	8.5	2.9	1.9	46.2	15.6	19.0 ± 9.9
	Washington	(2.8)	(3.5)	(0.1)	(0.1)	(5.9)	(5.9)	
G216 (2)	King Co.	14.5	6.0	1.9	1.2	26.2	6.6	29.0 ± 1.4
	Washington	(6.4)	(2.8)	(0.2)	(0.2)	(8.7)	(2.0)	
G255 (2)	Lincoln Co.	12.5	4.0	3.1	1.6	39.8	7.0	25.7 ± 2.5
	Oregon	(3.5)	(1.4)	(0.9)	(0.9)	(22.3)	(5.7)	
G256 (3)	Curry Co.	13.3	10.3	3.5	3.2	46.8	33.2	11.0 ± 2.7
	Oregon	(4.0)	(2.1)	(0.4)	(1.7)	(13.2)	(21.6)	
S1753 (5)	Del Norte Co.	17.8	8.2	3.5	2.5	61.2	21.1	47.6 ± 21.8
	California	(5.5)	(1.6)	(1.2)	(0.7)	(22.6)	(9.2)	
G86 (8)	Humboldt Co.	9.8	3.9	2.4	1.7	24.5	6.7	12.8 ± 8.1
	California	(3.5)	(1.3)	(0.8)	(0.4)	(14.1)	(2.8)	

*Collection numbers are those of Gornall (G) or Straley (S). The number of plants is shown in parentheses.
†Standard deviations are shown in parentheses.

recognize discreet groups. The comment (Piper, 1906) that the variant
cincinnatum is only "feebly distinguishable" is endorsed here.

The colouring of the inflorescence branches and hypanthium is also variable,
sometimes even within an individual and often between plants in the same
population, and there is a complete intergradation from red to green. The
redness is caused by anthocyanins whose concentration in a plant is greatly
affected by both environment and age.

Variation in other characters: In terms of leaf thickness, it is common for shaded
plants to have thinner leaves than those growing in brighter light, and for this
character to be phenotypically plastic (Givnish, 1978). Sepal reflexion is
continuous in its variation and no other significant differences could be found
between populations in terms of seed or pollen morphology, flavonoid profile
(Gornall & Bohm, 1980) or chromosome number (Gornall, Bohm & Taylor,
1983). All crosses between populations were successful (Gornall & Bohm, 1984)
and the progeny were fertile.

We propose to recognize a single variable species, *B. occidentalis*. The
occurrence of hybrids with *B. major* has been described in the notes under that
species. Particularly aberrant plants from Butte County, California, are very
hairy and their gross morphology suggests the result of hybridization with
B. rotundifolia. This is most unlikely on geographic criteria, and until they can be
investigated experimentally we prefer to treat them as an extreme variant of
B. occidentalis.

Boykinia rotundifolia Parry in A. Gray, *Proceedings of the American Academy of Arts
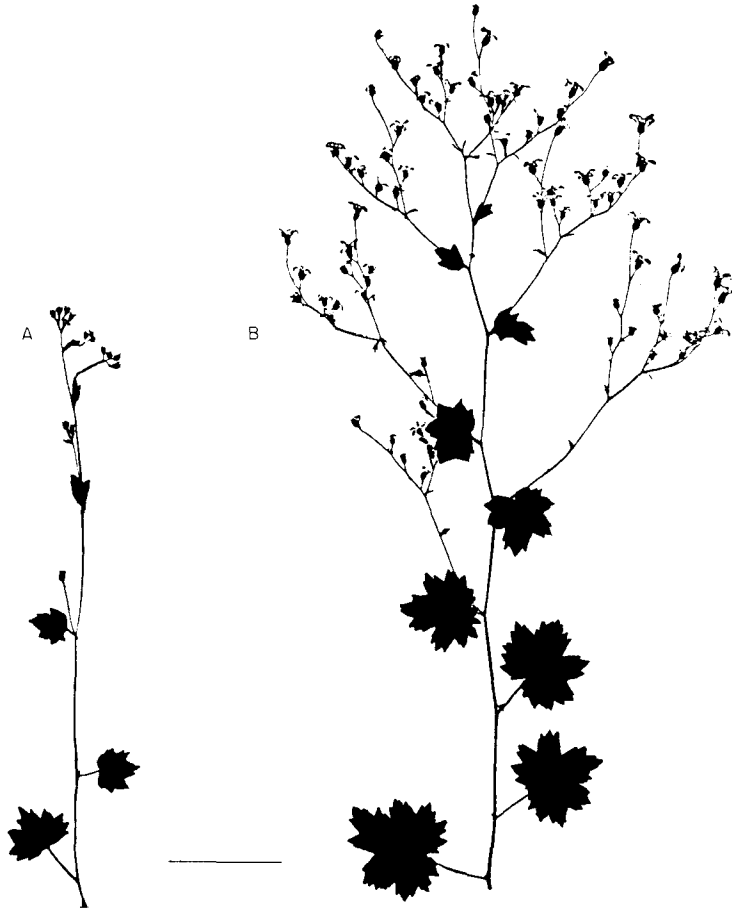and Sciences*, *13:* 371 (1878).

Figure 82. Inflorescences of droughted (A) and watered (B) clones of *Boykinia occidentalis*. Scale bar = 40 mm.

SYNONYM: *Therofon rotundifolium* Wheelock, *Bulletin of the Torrey Botanical Club*, *23*: 70 (1896).

TYPE: Along water courses, San Bernardino Range, Crafton, San Bernardino Co., California, *C. C. Parry and J. G. Lemmon 113*, 1876 (HOLOTYPE GH!).

NOMENCLATURAL NOTES: The type locality is apparently in Waterman Canon on the southern slopes of the San Bernardino Mountains (fide *Parish 7147*, 8 vii 1909, specimens at OSC! and CAN!).

STEMS fairly stout, (300–)500–800(–1300) mm tall, hirsute below with whitish eglandular chaffy hairs and glandular trichomes. PETIOLES of basal leaves 50–220 mm long, hirsute-glandular. BASAL LEAVES glandular pubescent, orbicular and cordate (about as long as wide) varying occasionally to reniform, (35–)70–160 mm long, (40–)90–180 mm wide, the margins shallowly lobed, 2–3 times serrate. STOMATA moderately common on upper leaf surface. STIPULES a dilation of the petiole base up to 2 mm long and fringed with brownish subulate bristles. INFLORESCENCE with (10–)15–25 flowers per paracladium, prominently

cincinnate. CALYX campanulate 4–7 mm long divided about one-third of its length into triangular to lanceolate, glandular sepals 1.5–2.0 mm long. FREE HYPANTHIUM 1–2 mm long. NECTARY green, inconspicuous. PETALS white, narrowly spatulate, 2–3 mm long and *c*. 1 mm broad at their widest point, equalling or up to 1.5 times longer than the sepals. STAMENS shorter than the sepals, filaments often only half as long as the undehisced anthers. OVARY one-half to two-thirds inferior. SEEDS 445–595 μm long. $2n = 14$.

FLOWERING: June–July.

DISTRIBUTION AND ECOLOGY: *Boykinia rotundifolia* is a narrow endemic, virtually restricted to the Sierra Madre Mountains and the southern slopes of the Transverse ranges of southern California (Fig. 83). An exceptional plant was discovered in San Diego County, about 130 km further south; its origin may have been due to long distance dispersal, although there is an old and unconfirmed record from "Lower California" (*Williamson*, 24 vii 1901, PH!) which might indicate a formerly continuous distribution. The species occurs at elevations of between 800–2000 m in wet woodland habitats along the margins of streams, rivers and lakes.

Excluded or doubtful species

Boykiana humilis Rafinesque, *Neogenyton*, 2 (1825) = *Ammannia humilis* A. Michx (Lythraceae)

Boykinia trispora Nutt. ex Arnott, *Hooker's Journal of Botany, 3:* 276 (1841), *nomen nudum = Cayaponia boykinii* (Torrey & Gray) Cogn. (Cucurbitaceae).

Boykinia Purpusii T. S. Brandegee, *Coulter's Botanical Gazette, 27:* 447, 448 (1899). *Therofon Purpusii* (T. S. Brandegee) Heller, *Catalogue of North American Plants*
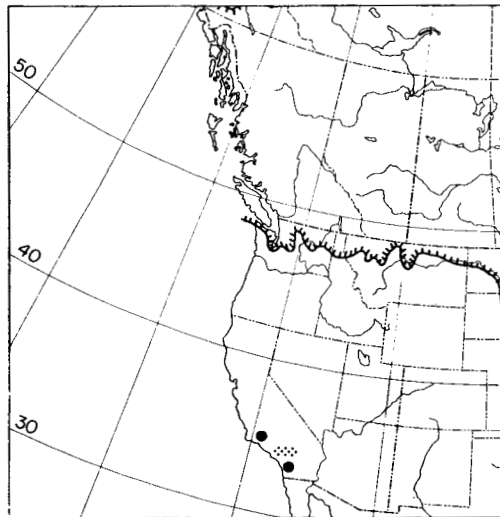

Figure 83. Distribution of *Boykinia rotundifolia*. Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

North of Mexico, exclusive of the Lower Cryptogams, ed. 2: 5 (1900) = *Sullivantia Purpusii* (T. S. Brandegee) C. Rosendahl (Saxifragaceae).

Boykinia minor Farrer, *The English Rock Garden, 1:* 147 (1919), *nomen nudum*. The identity of this plant is unclear, although Farrer listed it along with *Boykinia aconitifolia, B. major* and *B. occidentalis,* the four species being "all pretty much alike". We therefore think it may be a synonym of *B. rotundifolia,* the epithet *minor* referring to the inconspicuous flowers.

Bolandra A. Gray

Bolandra A. Gray, *Proceedings of the American Academy of Arts and Sciences, 7:* 341, 342 (1867).

TYPE SPECIES: *Bolandra californica* A. Gray.

PERENNIAL HERBS, leafy stemmed, glandular-pubescent. RHIZOMES bulbiliferous. LEAVES alternate in a 3/8 phyllotactic spiral, basal leaves orbicular to reniform in outline, long petioled, shallowly crenately-lobed to deeply cleft, early caducous, margins incised with mucronate or acute teeth, each tooth terminating in a Rosid-type hydathode, venation actinodromous; cauline leaves becoming reduced, short petiolate to sessile upwards. LEAF TEXTURE canaliculate-smooth on upper surface, somewhat ribbed on lower surface. STOMATA anomocytic, development unknown, occasional on upper surface, common on lower leaf surface. STIPULES foliaceous, often adnate to cauline leaves. TRICHOMES multiseriate, with multicellular glandular heads which often have 2–3 distinct papillae; occasional trichomes transitional to uniseriate condition; present throughout the plant and especially common on inflorescence branches but not hypanthia. INFLORESCENCE monotelic with up to two orders of paracladia, congested initially but spreading following anthesis and especially during fruiting; each paracladium consisting of a terminal flower (rarely absent) borne at or near the junction of a dichotomous branch-pair, each branch bearing from one to a few flowers. FLOWERS perfect, actinomorphic or occasionally slightly irregular. CALYX of 5 sepals, connate below to form a glabrate tubular-campanulate floral cup, subulate lobes erect to reflexed. COROLLA of 5 red and/or green, subulate petals inserted on rim of floral cup, truncate, glabrous, marcescent, with a single vascular trace entering each petal base, margins entire. NECTARY of green, glandular tissue in a band around the base of the interior of floral cup. STAMENS 5 in a single anti-sepalous whorl, inserted on rim of floral cup; filaments single-veined, slender-conical; anthers 2-locular, yellow, cordate at the base, dehiscing longitudinally, marcescent. MICROSPOROGENESIS with simultaneous cytokinesis. POLLEN binucleate, isopolar, 3-colporate, tectum reticulate with prominent luminae. GYNOECIUM of 2 follicle-like carpels, connate below. OVARY superior, 2 loculate, with numerous bitegmic, crassinucellate anatropous ovules on axile placentae, the placentation restricted to connate portion of carpels. STYLES free, erect, becoming divergent in fruit, stylar canals lined with transmitting tissue; stigmata capitate, 'wet Group III'-type. FRUIT a septicidal capsule, each carpel dehiscing ventrally in the stylar region, styles spreading widely. SEEDS numerous, narrowly elipsoid, brown, with an inconspicuous raphe, testa minutely tuberculate. EMBRYOLOGY and EMBRYOGENY unknown. GERMINATION epigeal. ROOT TIPS pigmented red with

anthocyanins. CHROMOSOME base number $x = 7$. FLAVONOID profile a complex array of flavonol glycosides, including myricetin and a set of polymethylated flavonols.

GENERIC LIMITS: *Bolandra* shows great similarities with *Suksdorfia* and a case could be made in favour of uniting the two genera. However, striking differences in general appearance, various aspects of floral morphology, seed shape and flavonoid chemistry (Table 7) outweigh the array of similarities. In many respects *Bolandra* is intermediate between *Boykinia* and *Suksdorfia*.

Key to the species of Bolandra

1. Lobes and teeth of leaves rounded, mucronulate; sepals 3–5 mm
    long; carpels connate for one-third of their length . . . *B. californica*
1′. Lobes and teeth of leaves triangular, acute; sepals 4–10 mm
    long; carpels connate for at most one-quarter of their length . *B. oregana*

Bolandra californica A. Gray, *Proceedings of the American Academy of Arts and Sciences,*
    7: 341, 342 (1867).

TYPE: On rocks, Mariposa trail, Yosemite Valley, California, *H. N. Bolander 4898,* 1 vii 1866 (HOLOTYPE GH! ISOTYPES UC-two sheets!); Foothills of the Sierra Nevada, *Torrey s.n.* (PARATYPE NY?).

STEMS 150–300(–410) mm tall. PETIOLES of basal leaves 25–65(–110) mm long. BASAL LEAVES reniform (width about 1.3 times the length) varying to orbicular and cordate, (10–)15–40(–45) mm long, 15–35(–55) mm wide, 3–5 cleft at least half their length, the margins of the lobes 1–2 times crenate-dentate usually with rounded teeth. STIPULES foliaceous 4–10 mm long, sometimes adnate to cauline leaves. INFLORESCENCE with up to 12 flowers per plant, and 1–3 flowers per paracladium. CALYX 7–10 mm long divided about half its length into sepal lobes (2–)3–5 mm long. FREE HYPANTHIUM 3.0–4.5 mm long. PETALS 5–8 mm long, *c.* 1.0–1.3 times as long as the sepal lobes. STAMENS shorter than or equalling sepal lobes, filaments about 3 times as long as undehisced anthers. STYLES free for two-thirds of their length. SEEDS 580–750 μm long. $2n = ?$

FLOWERING: June–July.

DISTRIBUTION AND ECOLOGY: *Bolandra californica* is restricted to the western slopes of the cental Sierra Nevada in California (Fig. 84), at elevations of between 1600 and 2800 m. It grows on mossy rocks in shaded, humid places in woodland habitats, usually close to a water course. The micro-habitat is typically well-drained and can be quite dry between rainfalls, a condition especially marked in summer months. *Bolandra californica* always occurs on granite (Jepson, 1936).

Bolandra oregana S. Watson, *Proceedings of the American Academy of Arts and Sciences,*
    14: 292 (1879).

SYNONYMS: *Hemieva oregana* Nelson & Macbride, printed annotation on specimen
    collected by *Henderson s.n.,* 29 vii 1896 (RM!).
    Bolandra imnahaensis Peck, *Rhodora, 36:* 266 (1934).
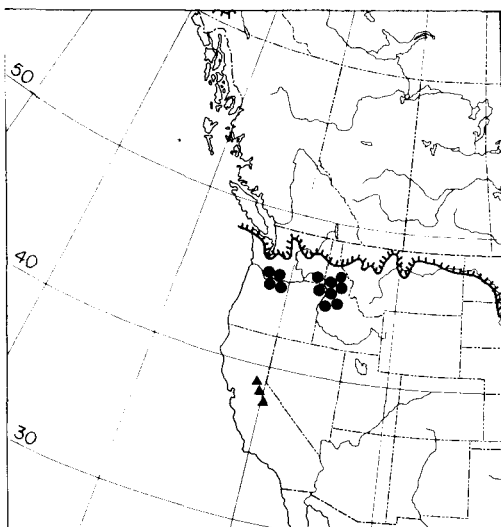   *Bolandra oregana* Wats. var. *imnahaensis* Peck, *Manual of the Higher Plants of*

Figure 84. Distribution of Bolandra oregana (●) and B. californica (▲). Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

Oregon: 371 (1941). TYPE: Wet cliff in small canyon along Imnaha River, 3 miles above Imnaha, Wallowa Co., Oregon, *Peck 17495*, 4 vii 1933 (ISOTYPES GH-two sheets! MIN! UC! WS!).

TYPE: Wet rocks, Milwaukee, Oregon, *J. Howell s.n.*, vi 1877 (HOLOTYPE GH!). [The protologue gives the precise locality as "Willamette River, near Oregon City, Oregon".]

STEMS (185–)220–400(–500) mm tall. PETIOLES of basal leaves 70–150(–200) mm long. BASAL LEAVES reniform (width about 1.3 times the length) varying to orbicular and cordate, 20–55(–75) mm long, 30–70(–100) mm wide, 5–14 cleft for one-third to half of their length, the margins of the lobes 1–2 times dentate, the teeth usually acute but occasionally rounded. STIPULES foliaceous 5–25 mm long, often adnate to the cauline leaves. INFLORESCENCE with up to 40 flowers per plant, and 1–5 flowers per paracladium. CALYX 8–16 mm long, divided about half its length into sepal lobes 4–7(–10) mm long. FREE HYPANTHIUM 3–6 mm long. PETALS 5–12 mm long, up to about 1.5 times as long as the sepal lobes. STAMENS about half as long as the sepal lobes, the filaments up to 3 times as long as the undehisced anthers. STYLES free for about three-quarters of their length. SEEDS 625–815 μm long. $2n = 14$.

FLOWERING: May–June.

DISTRIBUTION AND ECOLOGY: *Bolandra oregana* occurs disjunctively in the Columbia River Gorge and in the Snake and Salmon River drainages of the Wallowa and Bitterroot Mountains in eastern Oregon, Washington and northern Idaho (Fig. 84). It occurs at elevations from about sea level in the Gorge to about 1400 m in the Bitterroots, and is found primarily on basaltic rocks. The habitat is very similar to that of *B. californica*—shaded, humid, mossy, well-drained rocks in woodland, usually close to a water course.

Peck (1934) believed that *Bolandra imnahaensis* was closely related to *B. oregana* but claimed that it differed in its "more numerous flowers, a narrower calyx tube not becoming urceolate, and in the nearly separate carpels". However, variation in these and other characters is continuous with *B. oregana*, populations of which from Idaho and eastern Oregon are more variable than from elsewhere, and even varietal status is unwarranted.

Suksdorfia A. Gray

Suksdorfia A. Gray (*nom. cons.*), *Proceedings of the American Academy of Arts and Sciences, 15:* 41, 42 (1879).

SYNONYMS: *Hemieva* Rafinesque, *Flora Telluriana 2*, 70 ("1836", 1837).

    Hieronymusia Engler, *Notizblatt des Königlichen Botanischen Gartens und Museums zu Berlin-Dahlem 7:* 265–267 (1918).

    Boykinia subgenus *Hemieva* Jepson, *A Manual of the Flowering Plants of California*, 458–459 (1925), nomen nudum.

TYPE SPECIES: *Suksdorfia violacea* A. Gray.

NOMENCLATURAL NOTES: The name *Suksdorfia* was conserved against the earlier-published Hemieva at Vienna (Briquet, 1906).

PERENNIAL HERBS, leafy stemmed, glandular-pubescent. RHIZOMES bulbiliferous. LEAVES alternate in a 3/8 phyllotactic spiral, basal ones orbicular to reniform in outline, long petiolate, shallowly crenately lobed to deeply divided, early caducous, margins incised with mucronate teeth, each tooth terminating in a Rosid-type hydathode; venation actinodromóus; cauline leaves becoming reduced, short-petiolate or sessile upwards. LEAF TEXTURE somewhat succulent, canaliculate-smooth on upper surface, somewhat ribbed on lower surface. STOMATA anomocytic, common on both upper and lower leaf surfaces. STIPULES foliaceous, often adnate to cauline leaves, or represented by basal dilations of petioles. TRICHOMES multiseriate, with multicellular, glandular heads which often have two or three distinct papillae; present throughout the plant, but especially common on inflorescence; occasional forms transitional to uniseriate condition; unicellular, eglandular trichomes on pedicels and calyces in *S. violacea* and *S. alchemilloides*; uniseriate, eglandular trichomes on anthers and stigmata in *S. alchemilloides*. INFLORESCENCE monotelic with usually one, but up to two, orders of paracladia, highly congested initially but spreading following anthesis and especially during fruiting; each paracladium consisting of a terminal flower (rarely absent) with one lateral flower, or of a terminal flower (rarely absent) borne at or near the junction of a dichotomous branch pair, each branch bearing from one to many flowers in a typically helicoid arrangement. FLOWERS perfect, actinomorphic or occasionally slightly irregular. CALYX of 5 sepals, connate below and forming a campanulate to turbinate floral cup, the ovary portion densely glandular-pubescent, lobes sparsely pubescent to glabrate, erect or spreading, their apices acute. COROLLA of 5 white, rose or violet petals inserted on rim of floral cup, truncate to long-clawed, marcescent, with a single vascular trace entering each petal base, margins entire. NECTARY of prominent, yellow glandular tissue, or green and inconspicuous, in a band around the base of the carpels inside floral cup. STAMENS 5 in a single anti-sepalous whirl, inserted on rim of floral cup; filaments single-veined, slender-conical (in one species

highly reduced); anthers 2-locular, yellow, cordate at base, often mucronate, dehiscing longitudinally, marcescent (in *S. alchemilloides* bearing minute, multicellular, uniseriate, eglandular trichomes). MICROSPOROGENESIS with simultaneous cytokinesis. POLLEN binucleate, isopolar, 3-colporate, tectum reticulate with prominent luminae. GYNOECIUM of 2 follicle-like carpels, connate below. OVARY two-thirds to completely inferior, 2-loculate with numerous bitegmic, crassinucellate, anatropous ovules on axile placentae, placentation usually restricted to connate portion of carpels. STYLES free, erect, becoming divergent in fruit, stylar canals lined with transmitting tissue; stigmata capitate to truncate, 'wet group III'-type (in *S. alchemilloides* bearing minute, red, multicellular, uniseriate, eglandular trichomes). FRUIT a septicidal capsule formed by urceolate floral cup, each carpel dehiscing ventrally in stylar region, styles spreading widely. SEEDS numerous, small, ovoid, brown, with an inconspicuous raphe, testa minutely tuberculate. EMBRYOLOGY and EMBRYOGENY unknown. GERMINATION epigeal. ROOT TIPS pigmented red with anthocyanins. CHROMOSOME base number $x = 7$. FLAVONOID profile mainly an array of flavone and flavonol glycosides, poly-O-methylated aglycones sometimes present, charged compounds rare.

GENERIC LIMITS: *Suksdorfia*, as circumscribed here, is composed of three, formerly segregated, monotypic genera: *Hemieva*, *Suksdorfia* and *Hieronymusia*. Is there any justification for the recognition of these genera? Historically they have been separated on the basis of floral characters alone (compare descriptions). These characters are the same ones which are used to separate different species of *Boykinia*, and indeed the trends in floral variation are similar in the two genera. Strong evidence of a close relationship between the three species emerges if vegetative characters are considered. All three species possess a bulbiliferous rhizome; all three also possess multiseriate, glandular trichomes, sometimes with distinctive papillate heads. In addition, both *S. violacea* and *S. alchemilloides* have the unicellular trichomes so common in *Boykinia*. The species share similar pollen and seed morphologies, and ecological preferences. Cytologically only the N American species are known, both with $2n = 14$ chromosomes (Gornall *et al.*, 1983). In terms of flavonoid profile (Gornall & Bohm, 1980), *S. ranunculifolia* and *S. violacea* are very similar, possessing flavones and polymethylated flavonols. *Suksdorfia alchemilloides* is somewhat distinct in lacking flavones, 3-O- and 4'-O-methylation and 4'-O-glycosides. However, it shares 7-O-methylation and an array of triglycosides similar to those in *S. violacea*. Similar total variation is found in *Boykinia*. The three species have a uniform habit: slender, with crenate to deeply-divided, cordate to reniform basal leaves (similar variation occurs in *Boykinia*) and foliaceous stipules which are often adnate to the cauline leaves. In the inflorescence there is a progression from the complex structure with paracladia of dichasia helicoid cymes in *S. ranunculifolia*, to simpler versions in *S. alchemilloides* and *S. violacea*. The variation again parallels that in *Boykinia*.

   The relationships between *S. alchemilloides*, *S. ranunculifolia* and *S. violacea* are therefore best expressed by a single genus, *Suksdorfia*. In view of the variation within *Suksdorfia*, three monotypic sections could be recognized, commensurate with the treatment of similar variation in *Boykinia*. However, rather than clutter the nomenclature, it seems sufficient to realize that the three species are distinct. Distinguishing characteristics of the genus are given in Table 7.

5

Key to the species of Suksdorfia

1. Basal leaves ternately divided; pedicels usually lacking
   unicellular trichomes; flowers white, sometimes purplish at the
   base, with a prominent yellow nectary disc; ovary about one-half
   inferior; anthers without mucros . . . . *. S. ranunculifolia*
1′. Basal leaves 1–2 times crenate; pedicels with unicellular
   trichomes; flowers usually pink or rose, without a prominent
   nectary; ovary more than one-half inferior; anthers mucronate . . . 2
   2. Petals oval, clawless, equalling or shorter than sepals;
      anthers and stigmata with uniseriate eglandular hairs;
      anthers shorter or equalling filaments . . . . . . *. S. alchemilloides*
   2′. Petals spatulate, clawed, about twice as long as sepals;
      anthers and stigmata lacking uniseriate eglandular hairs;
      anthers much longer than filaments . . . . *S. violacea*

Suksdorfia violacea A. Gray, *Proceedings of the American Academy of Arts and Sciences,*
   15: 41, 42 (1879).

SYNONYM: *Hemieva violacea* Wheelock, *Bulletin of the Torrey Botanical Club, 23:* 71
   (1896).

TYPE: Wet rocks on the Columbia, Washington Territory, *Suksdorf 19,* iv 1878
(HOLOTYPE GH! photographs at POM! & WS!); Wasco Co., Oregon, near the
Columbia, *Howell s.n.,* vi 1879 (ISOPARATYPES GH! F! photographs at POM! &
WS!). [The protologue gives the exact type locality as "near the junction of the
White Salmon River".]

STEMS (50–)100–250(–300) mm tall. PETIOLES of basal leaves (10–)25–60
(–140) mm long. BASAL LEAVES reniform (width about 1.3 times the length),
(5–)10–20 mm long and (5–)10–30 mm wide, 3–5 cleft for one-third to half
their length, margins broadly crenate with rounded teeth. STIPULES foliaceous,
(2–)4–10 mm long, sometimes adnate to cauline leaves. INFLORESCENCE few-
flowered, each paracladium with a terminal flower and 1–2 lateral flowers;
unicellular, eglandular trichomes present on pedicels and calyces. CALYX
4–8 mm long, divided about half its length into narrowly lanceolate sepal lobes,
2–4 mm long. FREE HYPANTHIUM 0.5–1.0 mm long. NECTARY green,
inconspicuous (not a disc). PETALS violet to pink (rarely white), spatulate, long-
clawed, 5–10 mm long, about 2–3(–4) times as long as the sepal lobes. STAMENS
half as long as the sepal lobes, the filaments 0.1–0.3 times length of undehisced
anthers which are frequently slightly mucronate at apex. OVARY two-thirds or
more inferior. SEEDS 415–525 μm long. $2n = 14$.

FLOWERING: (March–)May–June. Insect visitors Diptera–Syrphidae.

DISTRIBUTION AND ECOLOGY: *Suksdorfia violacea* has its main area of distribution in
the Monashee, Selkirk and Purcell ranges of British Columbia and their
extensions in adjacent Washington, Idaho and Montana (Fig. 85); it also occurs
disjunctively in the Columbia River Gorge. The species can only have survived
the ice ages south of the glacial boundary in Idaho and Washington and there is
some evidence that refugia, separated by valley glaciers, may have existed in the
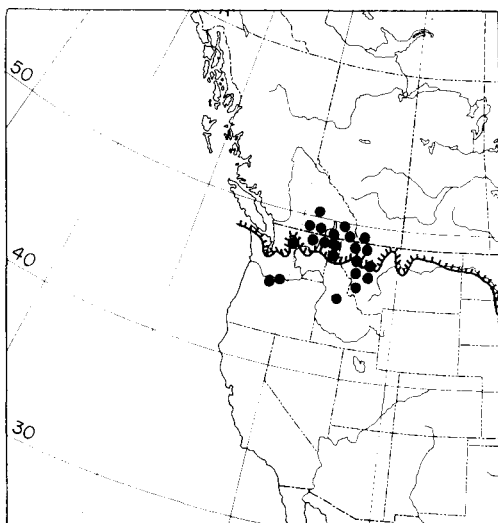Wenatchee Mountains of the northern Washington Cascades (Calder & Savile,

Figure 85. Distribution of *Suksdorfia violacea*. Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

1959). The species grows in the rain shadow of the eastern slopes of the mountains at elevations from near sea level to 3000 m, where the habitats are seepy, wet places in early spring from the heavy rains and snow-melt, but become dry by summer. It grows on mossy, rocky outcrops (both acidic and basic), avoiding those which face north. Although *S. violacea* is often found in the open, it can also be found under a partial canopy of *Pinus ponderosa* or *Pseudotsuga menziesii*, growing up through layers of duff.

Suksdorfia alchemilloides (Griseb.) Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien III. 2a:* 52 (1891).

SYNONYMS: *Saxifraga alchemilloides* Grisebach, *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen, 24:* 142, 143 (1879).
    Hieronymusia alchemilloides Engler, *Notizblatt des Königlichen Botanischen Gartens und Museums zu Berlin-Dahlem, 7:* 265–267 (1918).

TYPE: Sierra de Tucuman, Argentina, *G. Hieronymus & P. G. Lorentz 586*, 10–17 i 1874 (LECTOTYPE K! ISOTYPES GOET! US!). [The protologue gives the precise locality as "Cienega".]

STEMS 35–85(–115) mm tall. PETIOLES of basal leaves (10–)20–60 mm long. BASAL LEAVES reniform (width about 1.3 times length), 10–35 mm long and 15–40 mm wide, 5–7 cleft up to one-third of their length, margins broadly crenate with rounded teeth. STIPULES usually foliaceous (occasionally a dilation of petiole base), (0.5–)2–3(–5) mm long, smaller stipules fringed with subulate bristles, larger ones sometimes adnate to cauline leaves. INFLORESCENCE few-flowered, each paracladium with a terminal flower and 1–2(–5) lateral flowers; unicellular, eglandular trichomes present on pedicels and calyces. CALYX 2–4 mm long, divided about half its length into triangular sepal lobes, 1–2 mm long. FREE HYPANTHIUM up to 0.5 mm long. NECTARY green, inconspicuous (not
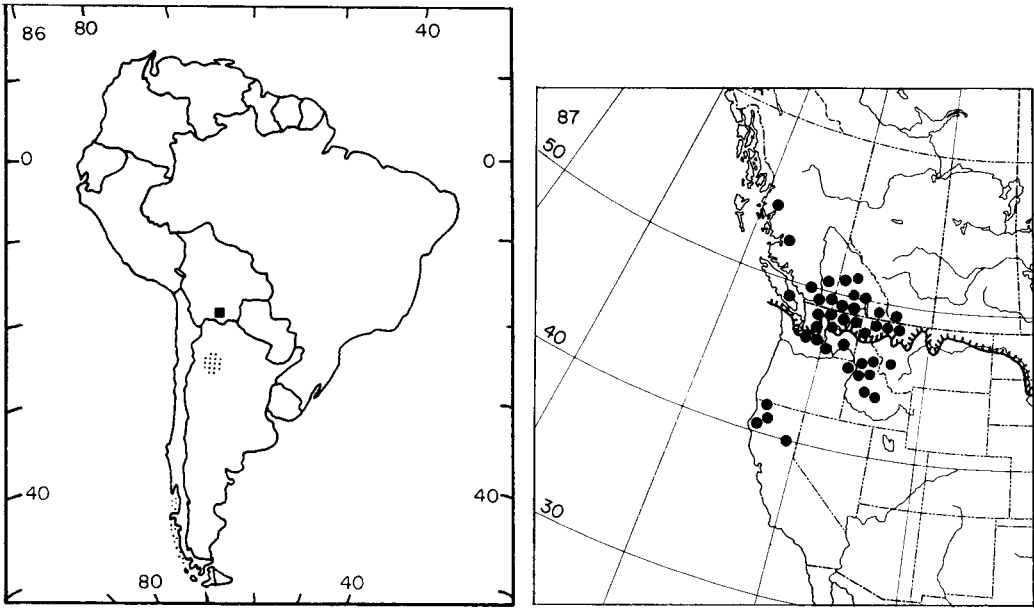
Figures 86 & 87. Fig. 86. Distribution of *Suksdorfia alchemilloides*. Fig. 87. Distribution of *Suksdorfia ranunculfolia*. Only representative collections are shown. Toothed line indicates maximum limit of last glaciation.

a disc). PETALS rose or white, oval, base truncate, 1–2 mm long, shorter than or barely exceeding the sepal lobes. STAMENS nearly equalling the sepal lobes, the filaments 1.3–2.0 times the length of the undehisced anthers which have a mucronate apex and minute, red, uniseriate, eglandular trichomes; the latter also occuring on the stigmata. OVARY fully inferior. SEEDS 385–460 μm long. $2n = ?$

FLOWERING: January–April.

DISTRIBUTION AND ECOLOGY: *Suksdorfia alchemilloides* inhabits the high eastern slopes of the Andean Cordillera in northern Argentina and southern Bolivia (Fig. 86), at elevations of between 3000 and 3800 m. This habitat is spring-wet but summer-dry. Herbarium label data indicate that the species grows on wet, rocky bluffs, sometimes in association with *Araucaria* species.

Suksdorfia ranunculifolia (Hooker) Engler, in Engler & Prantl, *Die naturlichen Pflanzenfamilien III. 2a:* 52 (1891).

SYNONYMS: *Saxifraga ranunculifolia* W. J. Hooker, *Flora Boreali-Americana, 1:* 246, 247, t. 83 (1832).
   Hemieva ranunculifolia Rafinesque, *Flora Telluriana, 2:* 70 ("1836", 1837).
   Boykinia ranunculifolia E. Greene, *Flora Franciscana:* 190, 191 (1891).

TYPE: Wet rocks on the mountain near Kettle Falls on the Columbia, *Douglas s.n.,* 1826 (HOLOTYPE BM!).

NOMENCLATURAL NOTES: In his journal, Douglas (1914) described collecting a plant, which was very probably the type of *S. ranunculifolia,* from near the Kettle Falls on 19 v 1826. It was assigned the number 68.

STEMS (100–)150–350(–375) mm tall. PETIOLES of basal leaves (30–)40–100(–150) mm long. BASAL LEAVES reniform (width about 1.3 times the length) varying occasionally to cordate, 10–40 mm long and 15–40 mm wide, ternately divided more than three-quarters of their length into cuneate, obovate lobes, margins entire to crenate or serrate. STIPULES foliaceous or formed by expanded petiole base, 3–8 mm long. INFLORESCENCE usually of first order paracladia, each consisting of a terminal flower (rarely absent) borne at or near the junction of a dichotomous branch pair, each branch bearing 3–15 flowers in a near-helicoid arrangement. CALYX 3–5 mm long, divided about half its length into triangular to lanceolate sepal lobes, 2–3 mm long. FREE HYPANTHIUM 0.5–1.0 mm long. PETALS white fading to cream, sometimes purplish at the base, ovate, clawed, 3–6 mm long, about twice as long as the sepal lobes. NECTARY a prominent yellow disc. STAMENS about one-half as long as the sepal lobes, the filaments 1.3–2.0 times length of the anthers, anthers rounded at the apex. OVARY about half inferior. SEEDS 625–980 µm long. $2n = 14$.

FLOWERING: May–June(–August). Insect visitors mainly Diptera-Empididae but also some Trichoptera-Phryganeidae.

DISTRIBUTION AND ECOLOGY: *Suksdorfia ranunculifolia* is sympatric with *S. violacea* over much of its range (Fig. 87), namely in the Monashee, Selkirk and Purcell Ranges of British Columbia and their extensions south into Washington, Idaho and Montana. Although absent from the Columbia River Gorge, it does occur in the Snake-Salmon drainages of central and southern Idaho. *Suksdorfia ranunculifolia* also occurs disjunctively in isolated populations along the coastal belt from the Skeena river in northern British Columbia to the Klamath Ranges in northern California. The species probably survived the glaciations south of the ice sheets in the same way as did *S. violacea*. Edaphically, *S. ranunculifolia* is found in the same open, spring-wet, summer-dry, mossy, rocky outcrops as *S. violacea*; indeed mixed populations with both species can sometimes be found. It occurs on both acidic and basic soils and, at its Bella Coola station in coastal British Columbia, is found very close to the sea shore (Kermode, 1918).

EVOLUTION

The habitats of the genera monographed here, together with those of the related genera *Jepsonia* and *Sullivantia,* can be grouped into seven general categories:

riparian woodland, becoming snow-bed grassland above the tree line . . . . *Boykinia* sections *Boykinia* and *Renifolium*
alpine rock faces and talus. . . . . . *Boykinia* section *Telesonix*
open, spring-wet, summer-dry bluffs . . . .*Suksdorfia*
humid rocks in woodland, often summer-dry . . . . . *Bolandra*
forest floor . . . .*Peltoboykinia*
dripping wet cliffs . . . . *Sullivantia*
winter-wet, summer-dry, maritime areas . . . . *Jepsonia*

These groups largely correlate with generic limits, and the possibility of evolution from a common ancestral stock by adaptive radiation into different

habitats is an attractive proposition. Savile (1961) proposed that evolution in the family was linked to a series of radiations following delayed and limited penetration of physiographic or climatic barriers. He recognized that most genera have differentiated through adaptation to particular habitats, and he related this to seed dispersal and pollination mechanisms, although each genus often has a characteristic vegetative facies as well.

Savile (1975) also suggested a scenario for the evolution and biogeography of the Saxifraginae using information from the rust parasites. He proposed an origin in eastern Asia during the Oligocene or later, and then early migrations into the Himalayas and western N America. The latter migration was suggested to have given rise to the various N American genera by extensive radiation. *Saxifraga* was considered to have begun life in N America as a 'proto-*Saxifraga*' which re-crossed the Bering Straits back into Japan before becoming differentiated. Radiations occurred from here partly into the Himalayas (again) and on into Europe, and partly back into N America across Beringia. The chief problem with this scenario lies in reconciling the timing of all this saxifragaceous traffic with the timing of orogenic and climatic events.

Peltoboykinia: Peltoboykinia is a Japanese endemic and Hara (1959) suggested it shared a common Miocene ancestor (a *Saxifraga*-like plant?) with *Boykinia*. Differentiation could have accompanied the middle Miocene phase of orogenic activity in eastern Asia which coincided with the invasion by the sea of the Japan peninsula, splitting the land mass into small islands (Maekawa, 1974). Certainly, *Peltoboykinia* occupies an intermediate position between *Saxifraga* (with which it shares a similar trichome complement and chromosome base number) and *Boykinia* (with which it shares similar pollen and floral morphologies).

Speciation in *Peltoboykinia* possibly accompanied the Pleistocene formation of the Seto (Inland) Sea which created isolated, island populations. Hara (1959) suggested that the climatic fluctuations and topographic changes of the Pleistocene stimulated speciation in many Japanese plant groups.

Boykinia: As mentioned, *Boykinia* may have had an Asian origin with *Peltoboykinia*; on the other hand, the most primitive species of Boykinia (with a simple inflorescence, coloporoidate pollen, 10 stamens and smooth seeds) occur in section *Telesonix* which is distributed through the Rocky Mountains of N America. The next most primitive section, section *Renifolium* (with a slightly more complex inflorescence and five stamens), contains only *B. richardsonii*, which is endemic to Alaska and the Yukon. Only the most advanced section, section *Boykinia* (with a complex inflorescence, colporate pollen, five stamens and tuberculate seeds), has a Japanese representative and is disjunct between Japan and N America. This would suggest that the genus evolved in N America rather than in Japan, although a relict status cannot be ruled out.

Boykinia, together with genera like *Tiarella, Mitella* and some sections of *Saxifraga,* shows a disjunct distribution between the Appalachians, the Western Cordillera and Japan. This and similar disjunctions (Wood, 1971; 1972) probably resulted from the disruption of the widespread, Miocene, mixed mesophytic forest by climatic change, vulcanism and orogenic events (Graham, 1972). Thus these genera of the Saxifraginae had probably evolved at least by late Miocene times when the forest became disjunct between eastern Asia and N

America. The fact that the advanced section *Boykinia* shows this disjunction suggests that the genus *Boykinia* probably originated rather earlier than the late Miocene. *Boykinia lycoctonifolia* in Japan has therefore probably been isolated from the rest of the genus since this time. Its closest relatives on morphologial grounds are *B. intermedia* in the Olympic Peninsula, and *B. aconitifolia* in the Appalachians. The three species probably constitute the remnants of the formerly wide-ranging ancestral stock of section *Boykinia,* and can be considered to be vicariads. *Boykinia aconitifolia* presumably became isolated from its relatives by the drying of the Great Plains and by Pleistocene extinctions.

In western N America, speciation in *Boykinia,* as well as in *Bolandra, Suksdorfia, Sullivantia* and *Jepsonia,* was probably stimulated by Pliocene Mountain building and the Pleistocene glaciations. The tetraploid *Boykinia major (2n = 28)* may have had a segmental allotetraploid origin during the differentiation of the other three western N American members of section *Boykinia.*

Sullivantia, Bolandra and *Suksdorfia: Sullivantia, Bolandra* and *Suksdorfia* are clearly most closely related to *Boykinia* and probably evolved in N America from a *Boykinia*-like ancestor. The present distribution of *Sullivantia* as a series of highly disjunct populations across the U.S.A. suggests a formerly continuous distribution, disrupted by the drying of the Great Plains and by Pleistocene extinctions. *Suksdorfia* and *Bolandra* most probably evolved in the Pliocene in response to the new summer-dry climate in the Pacific Northwest and the new habitats created by the uplift of the Coast and Sierra Nevada-Cascade Ranges. Their bulbiliferous rhizomes may be seen as adaptations to the drier environments.

Suksdorfia shows a remarkable disjunction between the Cordilleras of N and S America. *Suksdorfia alchemilloides* is presently found on the high eastern slopes of the Andean Cordillera in northern Argentina and southern Bolivia, whereas its two congeners are confined to western N America. According to Raven (1963) many such amphitropical disjunctions can be attributed to long-distance dispersal. Although he was concerned primarily with coastal and desert plant species, his generalizations nevertheless seem to be applicable to *Suksdorfia.* The evidence is as follows:

  The closest relative of *S. alchemilloides* is the N American *S. violacea* (both have similar leaf shapes and inflorescence structures, pink petals and unicellular trichomes).

  The close juxtaposition of anthers and stigmata in *S. alchemilloides* suggests that it is self-compatible and possibly autogamous; *Suksdorfia violacea* is both (Gornall & Bohm, 1984). Establishment after long-distance dispersal would thus be facilitated (Baker 1955).

  The primary associations of subtribe Saxifraginae are with the Northern Hemisphere.

  Both *Suksdorfia* species are found in open, spring-wet habitats, not in dense woodland.

  The floras of N and S America have been distinct at least since the middle Cretaceous and are still very different at present.

It is possible, therefore, that the common ancestor of the two species was transported by birds (Raven 1963; Cruden 1966) from the Rocky Mountains sometime in the late Pliocene or early Pleistocene, just after the Pliocene uplift of

the Andes (Raven 1972), and became established in the Bolivian and Argentinian Andes where it has evolved in isolation for the last 2–4 million years, and is currently recognized as *S. alchemilloides*. A more gradual dispersal, by 'mountain hopping', is of course also entirely possible. It is interesting that *Suksdorfia* is a better candidate for dispersal than some other genera because it can be transported both as seeds and as bulbils. As testimony to its mobility, it is also the only genus which has colonized formerly glaciated territory to any great extent; compare also the similarly bulbiliferous, but woodland-inhabiting, *Bolandra*, which has not (Figs 84–87).

The present, largely sympatric distribution of the two N American *Suksdorfia* species probably results from southward migrations during the Pleistocene and from subsequent northward invasions of formerly glaciated territory in post-Pleistocene times.

Jepsonia: Jepsonia shares a number of primitive characteristics (simple inflorescence, colporoidate pollen, ten stamens and smooth seeds) with *Boykinia* section *Telesonix,* and a common origin, possibly from a *Saxifraga*-like plant, followed by a long and independent evolutionary history, seems likely. The starchy caudex probably dates from the Pliocene, arising as an adaptation to the drier environments (Ornduff, 1969b). *Jepsonia* also has some affinities (e.g. scapose inflorescence and precocious flowering) with *Darmera* (from western N America) and with *Mukdenia* and *Oresitrophe* (from eastern Asia).

REFERENCES

BACIGALUPI, R., 1944. Saxifragaceae. In *Abram's Illustrated Flora of the Pacific States, 2:* 349–384. California: Stanford University Press.
BACIGALUPI, R., 1947. A new combination in the genus *Telesonix. Leaflets of Western Botany, 5:* 71.
BACIGALUPI, R., 1952. Saxifragaceae. In R. J. Davis (Ed.), *Flora of Idaho:* 361–388. Dubuque, Iowa: W. C. Brown Co.
BAKER, H. G., 1955. Self-compatibility and establishment after "long distance" dispersal. *Evolution, 9:* 347–348.

BENSEL, C. R. & PALSER, B. F., 1975. Floral anatomy in the Saxifragaceae sensu lat. II. Saxifragoideae and Iteoideae. *American Journal of Botany, 62:* 661–675.

BRIQUET, J., 1906. *Règles internationales de la nomenclature botanique adoptées par le congrès international de botanique de Vienne 1905.* Jena: Verlag von G. Fischer.

BURTT, B. L., 1964. Angiosperm taxonomy in practice. In V. H. Heywood & J. McNeill (Eds), *Phenetic and Phylogenetic Classification:* 5–16. Systematics Association Publication No. 6.

CALDER, J. A. & SAVILE, D. B. O., 1959. Studies in Saxifragaceae. 1. The *Heuchera cylindrica* complex in and adjacent to British Columbia. *Brittonia, 11:* 459–467.

CONOLLY, A. P., 1976. Use of the scanning electron microscope for the identification of seeds with special reference to *Saxifraga* and *Papaver. Folia Quaternaria, 47:* 759–768.

COOLEY, G. W., 1892. Impressions of Alaska. *Bulletin of the Torrey Botanical Club, 19:* 178–189.

CRAIGHEAD, J. J., CRAIGHEAD, F. C. & DAVIS, R. J. 1963. *A Field Guide to Rocky Mountain Wildflowers.* Boston: Houghton Mifflin Co.

CRUDEN, R. W., 1966. Birds as agents of long distance dispersal for disjunct plant groups of the temperate western hemisphere. *Evolution, 20:* 517–532.

DAHLGREN, K. V. O., 1930. Zur embryologie der Saxifragoideen. *Svensk Botanisk Tidskrift, 24:* 429–448.

DANDY, J. E., 1927. The genera of Saxifragaceae. In J. Hutchinson (Ed.), Contributions towards a phylogenetic classification of flowering plants, VI. *Bulletin of Miscellaneous Information. Royal Botanic Gardens, Kew, 1927:* 100–118.

DANDY, J. E., 1935. *Boykinia.* In J. S. L. Gilmour *et al.* (Eds), Additions and ammendments to the international rules of botanical nomenclature: 87. *Bulletin of Miscellaneous Information. Royal Botanic Gardens, Kew, 1935:* 65–92.

DAVIS, G. L., 1966. *Systematic Embryology of the Angiosperms.* New York: Wiley.

DAVIS, P. H., 1978. The moving staircase: a discussion of taxonomic rank and affinity. *Notes from the Royal Botanic Garden, Edinburgh, 36:* 325–340.

DOUGLAS, D., 1914. *Journal kept by David Douglas During his Travels in North America 1823–1827.* London: Wesley & Son.

ENGLER, A., 1891. Saxifragaceae. In A. Engler & K. Prantl (Eds), *Die naturlichen Pflanzenfamilien III. 2a:* 41–93. Leipzig: Engelmann.

ENGLER, A., 1918. *Hieronymusia* Engl., eine neue Gattung der Saxifragaceen. *Notizblatt des Königlichen Botanischen Gartens und Museums zu Berlin–Dahlem, 7:* 265–267.

ENGLER, A., 1919. Species sub titulo Saxifragarum descriptae, e genere *Saxifraga* excludendae. In A. Engler & E. Irmscher, *Das Pflanzenerich, 69:* 673–675. Leipzig: Enggelmann.

ENGLER, A., 1930. Saxifragaceae. In A. Engler & K. Prantl (Eds), *Die naturlichen Pflanzenfamilien, 18a,* 2nd edition: 74–226. Leipzig: Engelmann.

ERDTMAN, G., 1960. The acetolysis method. A revised description. *Svensk Botanisk Tidskrift, 54:* 561–564.

FAVARGER, C., 1957. Sur deux critères nouveaux utilisables dan la taxinomie des Saxifragacées. *Revue de Cytologie et de Biologie Végétales, 18:* 125–137.

GIVNISH, T. J., 1978. Ecological aspects of plant morphology: leaf form in relation to environment. *Acta Biotheoretica 27 Supplement, Folia Biotheoretica No. 7:* 83–142.

GORNALL, R. J. & BOHM, B. A., 1980. The use of flavonoids in the taxonomy of *Boykinia* and allies (Saxifragaceae). *Canadian Journal of Botany, 58:* 1768–1779.

GORNALL, R. J. & BOHM, B. A., 1984. Breeding systems and relationships among species of *Boykinia* and related genera (Saxifragaceae). *Canadian Journal of Botany 62:* 33–37.

GORNALL, R. J., BOHM, B. A. & TAYLOR, R. L., 1983. Chromosome numbers in *Boykinia* and allies (Saxifragaceae). *Candian Journal of Botany, 61:* 1979–1982.

GRAHAM, A., 1972. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. In A. Graham (Ed.), *Floristics and Palaeofloristics of Asia and Eastern North America:* 1–18. New York: Elsevier.

GRANT, V., 1971. *Plant Speciation.* New York: Columbia University Press.

GRAUSTEIN, J. E., 1967. *Thomas Nuttall, naturalist: explorations in America* 1808–1841. Cambridge: Harvard University Press.

GRAY, A., 1842. Notes of a botanical excursion to the mountains of North Carolina etc; with some remarks on the botany of the higher Alleghany Mountains. *American Journal of Science, 42:* 1–49.

GRAY, A., 1872. Botanical contributions II. Determination of a collection of plants made in Oregon by Elihu Hall during the summer of 1871, with characters of some new species and various notes. *Proceedings of the American Academy of Arts and Sciences, 8:* 365–412.

GRAY, A., 1876. *Botany of California,* Vol. 1. Cambridge, Massachusetts: University Press.

GREEN, M. L., 1940. Additional nomina generica conservanda (Pteridophyta and phanerogamae). *Bulletin of Miscellaneous Information. Royal Botanic Gardens, Kew, 1940:* 81–132.

GREENE, E. L., 1891. *Flora Franscistana.* San Francisco.

GRISEBACH, A. H. R., 1879. Symbolae ad floram argentinam. Zweite bearbeitung argentinischer pflanzen. *Abhandlungen ser Königlichen Gesellschaft der Wissenschaften zu Göttingen, 24:* 3–345.

GUNTHER, E., 1973. *Ethnobotany of western Washington. The knowledge and use of indigenous plants by native Americans* (revised edition.) Seattle: University of Washington Press.

HARA, H., 1937. Two new genera of Saxifragaceae in Japan. *Botanical Magazine, Tokyo, 51:* 250–253.

HARA, H., 1957. Synopsis of the genus *Chrysosplenium* L. *Journal of the Faculty of Science, Tokyo University, III, 7:* 1–90.

HARA, H., 1958. *Distribution Maps of Flowering Plants in Japan,* Vol. I. Tokyo: Inoue Book Co.

HARA, H., 1959. An outline of the phytogeography of Japan. In H. Hara, *Distribution Maps of Flowering Plants in Japan,* Vol. 2: 1–96. Tokyo: Inoue Book Co.

HARRINGTON, H. D., 1954. *Manual of the Plants of Colorado.* Denver: Sage Books.

HELLER, A. A., 1904. Western species, new and old—II. *Muhlenbergia, 1:* 47–62.

HESLOP-HARRISON, J., 1975. Incompatibility and the pollen-stigma interaction. *Annual Review of Plant Physiology, 26:* 403–425.

HICKEY, L. F., 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany, 60:* 17–33.

HIDEUX, M. J. & FERGUSON, I. K., 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae sensu lato. In I. K. Ferguson & J. Muller (Eds), *The Evolutionary Significance of the Exine, Linnean Society Symposium Series No. 1:* 327–378. London: Academic Press.

HITCHCOCK, C. L., CRONQUIST, A., OWNBEY, M. & THOMPSON, J. W., 1961. *Vascular Plants of the Pacific Northwest,* Vol. 3. Seattle: University of Washington Press.

HOLMGREN, P. K., KEUKEN, W. & SCHOFIELD, E. K., 1981. *Index Herbariorum I.* (7th Edition) *Regnum Vegetabile, 106:* 1–452.

HOOKER, W. J., 1832. *Flora Boreali-Americana,* Vol. 1. London.

HOOKER, W. J. & ARNOTT, G. A. W., 1832. *The Botany of Captain Beechey's Voyage.* "1841". Weinheim: J. Cramer (reprint 1965).

HULTEN, E., 1968. *Flora of Alaska and Neighbouring Territories.* California: Stanford University Press.

IKUSE, M., 1956. *Pollen Grains of Japan.* Tokyo: Hirokawa Publishing Co.

ISHIZUKA, K., 1974. Mountain vegetation. In M. Numata (Ed.), *The Flora and Vegetation of Japan:* 173–210. New York: Elsevier.

JEPSON, W. L., 1936. *A Flora of California,* Vol. 2. San Francisco: California School Book Depository.

JOHANSEN, D. A., 1950. *Plant Embryology.* Waltham, Massachusetts: Chronica Botanica.

JOHNSON, A. W. & PACKER, J. G., 1968. Chromosome numbers in the flora of Ogotoruk Creek, N.W. Alaska. *Botaniska Notiser, 121:* 403–456.

JOHNSON, F. D. & STEELE, R., 1978. New plant records for Idaho from Pacific coastal refugia. *Northwest Science, 52:* 205–211.

JONES, G. N., 1938. The flowering plants and ferns of Mount Rainier. *University of Washington Publications in Biology, 7:* 1–192.

KAPLAN, K., 1976. Zur Embryologie und Systematik der Gattung *Saxifraga. Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie, 97:* 61–71.

KAPLAN, K., 1981. Embryologische pollen- und samen-morphologische Untersuchungen zur Systematik von *Saxifraga* (Saxifragaceae). *Bibliotheca Botanica, 134:* 1–56.

KERMODE, F., 1918. Botany. *Report of the Provincial Museum of Natural History and Anthropology, Province of British Columbia, 1917:* 15–28.

KLOPFER, K., 1973. Florale Morphogenese und Taxonomie der Saxifragaceae sensu lato. *Feddes Repertorium, 84:* 475–516.

KNABEN, G., 1968. Chromosome numbers of flowering plants from Central Alaska. *Nytt Magasin for Botanikk, 15:* 240–254.

KRACH, J. E., 1976. Samenanatomie der Rosifloren 1. Die Samen der Saxifragaceae. *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie, 97:* 1–60.

KUNTZE, O., 1891. *Revisio Genera Plantarum,* Vol. 1. London: Dulau & Co.

LEBEGUE, A., 1952. Recherches embrogéniques sur quelques dicotylédones dialypétales. *Annales des Sciences Naturelles, Botanique XI., 13:* 1–160.

LEVIN, D. A., 1973. The role of trichomes in plant defense. *Quarterly Review of Biology, 48:* 3–15.

LOZINA-LOZINSKAYA, A. S., 1939. Saxifragoideae. In V. L. Komarov (Ed.), *Flora of the U.S.S.R., 9:* 106–169. Moscow: Izdaniya Akademii Nauk SSSR.

MACOUN, J. M., 1883. *Catalogue of Canadian plants. Part 1: Polypetalae.* Montreal: Dawson Bros.

MACOUN, J. M., 1896. Contributions to Canadian botany. *Canadian Record of Science, 6:* 405–415.

MAEKAWA, F., 1974. Origin and characteristics of Japan's flora. In M. Numata (Ed.), *The Flora and Vegetation of Japan:* 33–86. New York, Elsevier.

MAXIMOWICZ, C. J., 1871. *Saxifraga tellimoides. Bulletin de l'Académie Impériale des Sciences de Saint-Pétersbourg, 16:* 215–216.

METCALFE, C. R. & CHALK, L., 1950. *Anatomy of the Dicotyledons,* Vol. 2. Oxford: Clarendon Press.

MILLER, N. G. & THOMPSON, G. G., 1979. Boreal and western North American plants in the late Pleistocene of Vermont. *Journal of the Arnold Arboretum, 60:* 167–218.

MOREAU, F., 1976. Types stomatiques et trichome foliaire des Saxifragoidées Saxifragacées). *Revue de Cytologie et de Biologie Végétales, 39:* 329–341.

MURIE, A., 1944. *The Wolves of Mount McKinley.* Fauna of the National Parks of the U.S., Fauna Series No. 5; Washington: U.S. Government Printing Office.

NEW, J. K. & HERRIOTT, J. C., 1981. Moisture for germination as a factor affecting the distribution of the seed coat morphs of *Spergula arvensis* L. *Watsonia, 13:* 323–324.

NUTTALL, T., 1834. *Boykinia. Journal of the Academy of Natural Sciences of Philadelphia, 7:* 113–114.

OHWI, J., 1965. *Flora of Japan.* Washington: Smithsonian Institution.

ORNDUFF, R., 1969a. Reproductive biology in relation to systematics. *Taxon, 18:* 121–133.

ORNDUFF, R., 1969b. Ecology, morphology, and systematics of *Jepsonia* (Saxifragaceae). *Brittonia, 21:* 286–298.

OSTERHOUT, G. E., 1920. Rocky Mountain botany and the Long Expedition of 1820. *Bulletin of the Torrey Botanical Club, 47:* 555–562.

PACKER, J. G., 1971. Endemism in the flora of western Canada. *Naturaliste Canadienne, 98:* 131–144.

PACKER, J. G. & McPHERSON, G. D., 1974. Chromosome numbers in some vascular plants from northern Alaska. *Canadian Journal of Botany, 52:* 1095–1099.

PACKER, J. G. & VITT, D. H., 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. *Canadian Journal of Botany, 52:* 1393–1409.

PAYNE, W. W., 1969. A quick method for clearing leaves. *Ward's Bulletin, 8:* 4–5.

PECK, M. E., 1934. Three interesting new plants from Wallowa County, Oregon. *Rhodora, 36:* 266–268.

PIPER, C. V., 1899. New and noteworthy northwestern plants—III. *Erythea, 7:* 171–174.

PIPER, C. V., 1906. Flora of the state of Washington. *Contributions from the United States National Herbarium, 11:* 1 637.

RAFINESQUE, C. S., 1837. *Flora Telluriana.* Part 2. "1836". Philadelphia.

RAFINESQUE, C. S., 1838. *New Flora and Botany of North America. IV. Neobotanon* 1. "1836". Philadelphia.

RAFINESQUE, C. S. 1840. *Autikon Botanikon.* Philadelphia.

RAVEN, P. H., 1963. Amphitropical relationships in the floras of North and South America. *Quarterly Review of Biology, 38:* 151–177.

RAVEN, P. H., 1972. Plant species disjunctions: a summary. *Annals of the Missouri Botanical Garden, 59:* 234–246.

ROSENDAHL, C. O., 1905. Die nordamerikanischen Saxifraginae und ihre Verwandtschafts-verhaltnisse in Beziehung zu ihrer geographischen Verbreitung. *Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 37, Beibl. 83:* 1–87.

ROSENDAHL, C. O., 1927. A revision of the genus *Sullivantia. Research Publications of the University of Minnesota, Studies in Biological Science, 6:* 401–427.

ROSENDAHL, C. O., BUTTERS, F. K. & LAKELA, O., 1936. A monograph on the genus *Heuchera. Minnesota Studies in Plant Science, 2:* 1–180.

RYDBERG, P. A., 1897. Rarities from Montana—II. *Bulletin of the Torrey Botanical Club, 24:* 243–258.

RYDBERG, P. A., 1905. Saxifragaceae (pars). *North American Flora, 22:* 81–158.

SAVILE, D. B. O., 1961. Evolution of Saxifragaceae from a mycologist's viewpoint. *Recent Advances in Botany, 1:* 169–172.

SAVILE, D. B. O., 1975. Evolution and biogeography of Saxifragaceae with guidance from their rust parasites. *Annals of the Missouri Botanical Garden, 62:* 354–361.

SAVILE, D. B. O. 1976. *Conimitella* (Saxifragaceae) and its rust. *Canadian Journal of Botany, 54:* 1977–1978.

SCOGGAN, H. J., 1978. *The Flora of Canada,* Vol. 3. Ottawa: National Museum of Canada.

SOLTIS, D. E., 1980. Flavonoids of *Sullivantia:* taxonomic implications at the generic level within the Saxifraginae. *Biochemical Systematics and Ecology, 8:* 149–151.

SOLTIS, D. E., 1981a. Variation in hybrid fertility among the disjunct populations and species of *Sullivantia* (Saxifragaceae). *Canadian Journal of Botany, 59:* 1174–1180.

SOLTIS, D. E., 1981b. Heterochromatin banding in *Boykinia, Heuchera, Mitella, Sullivantia, Tiarella* and *Tolmiea* (Saxifragaceae). *American Journal of Botany, 69:* 108–115.

SPONGBERG, S. A., 1972. The genera of Saxifragaceae in the southeastern United States. *Journal of the Arnold Arboretum, 53:* 409–498.

STUCKEY, R. L., 1971. The first public auction of an American herbarium including an account of the fate of the Baldwin, Collins and Rafinesque herbaria. *Taxon, 20:* 433–459.

TAYLOR, R. L., 1965. The genus *Lithophragma* (Saxifragaceae). *University of California Publications in Botany, 37:* 1–122.

TOLMACHEV, A. I. (Ed.), 1966. *Vascular Plants of the Siberian North and the Northern Far East.* Moscow: Izdaniya Nauk [1969, Jerusalem: Israel Program for Scientific Translations].

TORREY, J. & GRAY, A., 1840. *A Flora of North America,* Vol. 1. New York: Carvill & Co.

WATARI, S., 1939. Anatomical studies on the leaves of some Saxifragaceous plants, with special reference to the vascular system. *Journal of the Faculty of Science, Imperial University of Tokyo, section III, Botany, 5:* 195–316.

WHITE, H. A. (Ed.), 1974. *The Alaska-Yukon Wild Flowers Guide.* Anchorage: Alaska N.W. Publishing Co.

WOOD, C. E., 1971. Some floristic relationships between the southern Appalachians and western North America. In P. C. Holt (Ed.), *The Distributional History of the Biota of the Southern Appalachians. II. Flora:* 331–404. Research Division Monograph No. 2. Blacksburg, Virginia: Virginia Polytechnic Institute of the State University.

WOOD, C. E., 1972. Morphology and phytogeography: the classical approach to the study of plant disjunctions. *Annals of the Missouri Botanical Garden, 59:* 107–124.