

## FURTHER INTERSPECIFIC *SAXIFRAGA* HYBRIDS

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(With Eight Text-figures)

IN our experimental studies on the barriers separating morphologically defined species we made a number of crosses between British species of *Saxifraga*. Some of these did not "take". Three crosses between species placed in different sections by Engler and Irmischer gave, however,  $F_1$  families, and two of these gave  $F_2$  families, from one of which  $F_3$  families were raised. The three species used as parents were *S. granulata* L. (Sect. *Nephrophyllum*), *S. hypnoides* L. (Sect. *Dactyloides*), and *S. tridactylites* L. (Sect. *Tridactylites*).

### DESCRIPTIONS OF PARENT SPECIES

*S. granulata* L. Material from sandy grassy ground below the Hog's Back, Guildford district, Surrey, 1930, Stock Plants 6 and 9.

*Habit*: a perennial plant. A flowering stem arises from the centre of each rosette and has no sterile rosettes at its base. Numerous bulbils arise at the base of the flowering stem in the axils of the lowermost leaves at the soil level and even on rhizomes below the soil in the axils of scale leaves. Plants 2 and 3.1 dm. high.

*Rosette leaves*: with distinct lamina, petiole, and base; lamina oblate, cordate at base, the number, size, and depth of the lobes or crenulations vary, with a hydathode near the apex of each but no apical hairs, 15 mm. long, 20 mm. broad, with rather long white distinct hairs on both surfaces mixed with a few glands; petiole 15-35 cm. long, with spreading white hairs; base 3 mm. long and 5 mm. broad with long and dense white hairs (measurements from S.P. 9).

*Flowering stem*: erect, terete, purplish red, with dense long white non-glandular hairs below and with dense short glandular red-tipped hairs above.

*Stem leaves*: showing a gradual transition and simplification from rosette leaves to bracts, more deeply lobed than rosette leaves, and in upper ones only one to two lobes, as traced upwards they gradually become more glandular on both surfaces.

*Inflorescence branches*: as the top part of the stem, i.e. very densely glandular. Each stem up to 14-flowered.

*Calyx and receptacle*: densely glandular with short red-tipped hairs, sepals lanceolate-oblong, acute, 5 mm. long, 2 mm. broad, enlarging in young fruit.

*Corolla*: 18 mm. diam.; petals elongate-obovate, overlapping, 14 mm. long, 7 mm. broad, apex rounded to obtuse, slightly narrowed at base, five green veins, the three middle ones running up distinctly three-quarters the length of the petal. Stock-plant 9 bred true for petal shape.

*Androecium*: greenish yellow, becoming duller and red-tinged with age, glabrous; filaments up to 6.5 mm. long.

*Gynoecium*: with the two styles quite distinct, 5 mm. long (including stigma), at first parallel, later somewhat diverging; stigmas markedly oblique; ovary projecting 1 mm. above the receptacle.

*Fruit*: relatively long and narrow, projecting 6 mm. beyond the receptacle (including the persistent styles), 2.5 mm. diam.

*Seeds*: brownish black, ovoid-cylindric, 0.5 mm. long, papillose.

*Post-fruiting habit*: the aerial parts die right down after fruiting and new green shoots begin to appear about the middle of August.

*S. tridactylites* L. Material from wall-top, Box, near Bath, Wiltshire, 1932, Stock Plant 50.

*Habit*: an annual plant with no true basal rosette at the flowering stage. The flowering stem usually branches from the lowest base; the stems and branches all end in flowers.

*Flowering stems*: terete, deep brown-red, especially near the base, no long white hairs, very glandular with short red gland-tipped hairs; increasingly glandular upwards to the pedicels and receptacles.

*Leaves*: lowermost with three to five lobes, upper leaves increasingly smaller, shorter, and simpler, glandular on both surfaces, more sparingly above, medium below; a five-lobed leaf 1.4 cm. in total length, lamina with lobes 1.0 cm. broad, hydathodes inconspicuous and the lobes with no apical hairs.

*Inflorescence*: with up to about seven flowers on one main branch.

*Calyx*: with sepals triangular-ovate, acute, 1.25 mm. long, 1 mm. broad, somewhat enlarging in fruit.

*Corolla*: 3 mm. diam., petals obovate-oblong, not overlapping, apex rounded, 3 mm. long, 1.5 mm. broad, with three green veins.

*Filaments*: 1 mm. long.

*Gynoecium*: styles at first parallel, with stigmata about 0.5 mm. long, then very widely diverging and spreading out at right angles.

*Fruit*: projecting 1 mm. beyond the receptacle, 3 mm. diam.

*Seeds*: dark brown, ovoid-cylindric, 0.4 mm. long, papillose.

*Post-fruiting habit*: dies after fruiting.



Fig. 1. *S. tridactylites* S.P. 50 selfed (B. 113). Above seedlings. Seed sown 3. viii. 33, seedlings collected 16. i. 34.

*S. hypnoides* L. Material from Dovedale, Derbyshire, *R. W. Butcher*, 1928, Stock Plant 10.

*Habit*: a densely caespitose perennial plant with long slender stems, the lower parts of which are covered with dead leaves; many of the stems are sterile in any one season. There are no basal bulbils as there are in *S. granulata* but the leaves have axillary buds. Plants 9 cm. high.

*Lowest leaves*: five-lobed, those next above four- to three-lobed; 9 mm. long in total length, lamina 6 mm. broad including lobes, with a

hydathode near the apex of every lobe, and the apices hair-like, with scattered hairs and few glands on the upper surface, glabrous on the lower surface; petiole and base about 4-5 mm. long, with long white marginal hairs.

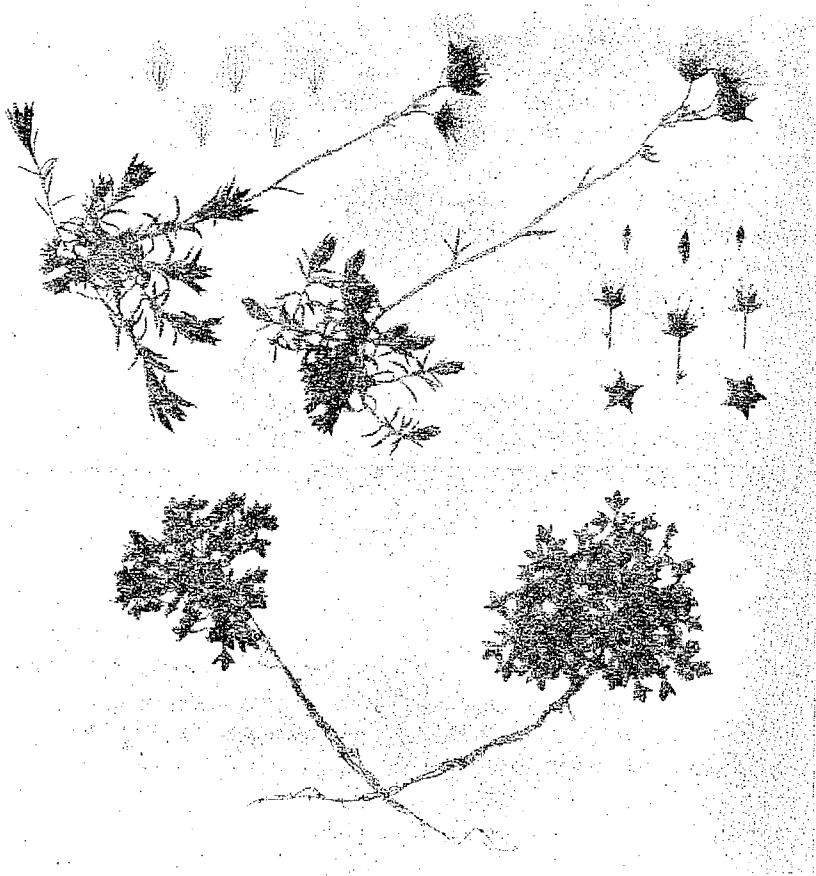


Fig. 2. *S. hypnoides* S.P. 10, 27. v. 37. Below seedlings from *S. hypnoides* S.P. 10 selfed (B. 147). Seeds sown 14. viii. 35, seedlings collected 22. ii. 36.

*Flowering stems:* erect, terete, purplish green, with long white hairs below, red-tipped glands start about 2 cm. above the base and become more numerous upwards, but are not dense until the inflorescence branches are reached.

*Stem leaves:* the highest are simple, linear, acuminate, 8 mm. long, 1.2 mm. broad, mostly with axillary buds.

*Inflorescence*: with up to 6 flowers per branch.

*Calyx and receptacle*: moderately glandular, sepals triangular, enlarging in young fruit up to 3 mm. long and 2 mm. broad.

*Corolla*: 15 mm. diam.; petals oblong-obovate, 8 mm. long, 5 mm. broad, with three green veins; young corolla buds tipped "Begonia Rose" (Ridgway, *Color Standards*, Pl. I).

*Androecium*: greenish yellow, glabrous, not colouring-up with increased age; filaments up to 3.5 mm. long.

*Gynoecium*: styles with stigmata 3 mm. long, at first erect, later spreading widely; colouring-up with age, but not strongly.

*Fruit*: projecting 3 mm. beyond the receptacle (including the persistent styles), 3 mm. diam.

*Seeds*: brownish black, ovoid-cylindric, up to 1 mm. long, papillose.

*Post-fruiting habit*: evergreen.

#### SELFINGS AND CROSSINGS

Successful selfings and crosses were made as follows:

- B. 131 = *S. granulata* S.P. 9, selfed.
- B. 113 = *S. tridactylites* S.P. 50, selfed.
- B. 147 = *S. hypnoides* S.P. 10, selfed.
- B. 125 = *S. tridactylites* × *S. granulata*.
- B. 171 = B. 125 plant 1 selfed.
- B. 173 = B. 125 plant 4 selfed.
- B. 174 = B. 125 plant 4 × B. 125 plant 1.
- B. 129 = *S. tridactylites* × *S. hypnoides*.
- B. 132 = *S. granulata* S.P. 9 × *S. hypnoides*.
- B. 135 = B. 132 plant 40 selfed.
- B. 183 = B. 135 plant 46 × B. 135 plant 9.
- B. 184 = B. 135 plant 9 selfed.
- B. 185 = B. 135 plant 46 selfed.
- B. 186 = B. 135 plant 69 selfed.
- B. 187 = B. 135 plant 92 selfed.
- B. 188 = B. 135 plant 93 selfed.

**B. 131.** *S. granulata* S.P. 9, selfed.

24 plants in family.

All uniform and as immediate parent for all characters, including petal shape.

**B. 113.** *S. tridactylites* S.P. 50, selfed.

50 plants in family.

All uniform and as immediate parent for all characters.

**B. 147.** *S. hypnoides* S.P. 10, selfed.

64 plants in family.

The plants were all as immediate parent, except for slight variation in petal shape. Flowering stems up to 16 cm. high. All plants with axillary buds to the leaves. Petal shape from narrowly to broadly obovate, 5 plants forming a narrow petal group.

**B. 125.** *S. tridactylites* (male parent) × *S. granulata* (pollen parent).

4 plants in family.

All uniform for all characters, except petal shape, and indistinguishable morphologically from the *S. granulata* pollen parent.

Petal shape: 2 obovate, 2 oblong-oblancoolate.

**B. 171.** = B. 125 plant 1 selfed, with obovate petals.

200 plants in family.

In all scorable phenotypic characters indistinguishable from the *S. granulata* grandparent, except for variations in the petal shape. Many plants did not flower. The petal shape of plants that flowered was scored as follows: 26 elongate-obovate: 28 obovate: 1 oblong-oblancoolate: 1 linear.

**B. 173.** = B. 125 plant 4 selfed, with obovate petals.

14 plants in family.

In all scorable phenotypic characters indistinguishable from the *S. granulata* grandparent, except for variation in the petal shape. Half the plants did not flower. The petal shape of the 7 plants that flowered was scored as oblong-oblancoolate.

**B. 174.** = B. 125 plant 4 × B. 125 plant 1.

149 plants in family.

In all scorable phenotypic characters indistinguishable from the *S. granulata* grandparent, except for variation in the petal shape. Many plants did not flower. The petal shape of plants that flowered was scored as follows: 5 elongate-obovate: 6 obovate: 3 oblong-oblancoolate.

In families B. 171, B. 173, and B. 174, germination was excellent, and the seedlings were uniform and indistinguishable from those of *S. granulata*.

**B. 129.** *S. tridactylites* (ovule parent) × *S. hypnoides* (pollen parent).

10 plants in family.

The plants all uniform to the following description:

*Seedlings*, 9 months old, not in flower: Plants of a low caespitose-adpressed habit; height above ground 2 cm.; diam. from 3.5 to 8.5 cm.; numerous non-flowering branches; leaves mostly simple, but with a fair number three-lobed though none five-lobed, long white hairs and some

glands on leaf margins, especially in the lower part, and a few glands on the upper and lower surfaces, lobes with acute apices and hydathodes, whole length of three-lobed leaf 1.4 cm., breadth (including lobed lamina) 6 mm., whole length of simple leaf 1 cm., breadth 2 mm.



◦ Fig. 3. *S. tridactylites* ♀ × *S. hypnoides* ♂  $F_1$  (B. 129).

Several plants flowered when about 12 months old. At 2 years of age all the plants had flowered.

*Plants*: 1 year 9 months old, in flower.

*Habit*: a low caespitose perennial with ascending branches; height above ground up to 3.2 cm.; diam. of plants 6-11 cm.; axillary buds were present and many branches were producing flowers or flower-buds.

*Leafy stems*: glabrous.

*Leaves*: simple or bi- or trilobed, the upper mostly simple, the lower simple or lobed, hairs and glands absent on upper and lower surfaces or very few indeed, white hairs and few glands on the margins, lobes with hydathodes and acute apices, total length of trilobed leaf 1.4 cm., breadth



Fig. 4. *S. tridactylites* S.P. 50 ♀ × *S. hypnoides* S. P. 10 ♂ (B. 129). Above seedling.  
Seed sown 3. viii. 33, seedling collected 16. i. 34.

(including lobed lamina) 6.5 mm., whole length of simple leaf 10 mm., breadth 2 mm.

*Flowering stems*: erect, terete, green with a slight tinge of purple, with a few long white hairs below, red-tipped glands start about a quarter of the total length above the base and become more numerous upwards.

*Inflorescence*: usually one- to three-flowered, but one stem with six flowers; flower-buds pendulous.



*Calyx and receptacle*: moderately glandular, sepals triangular, very acute, 2.5 mm. long and 1.4 mm. broad when in flower.

*Corolla*: 1.3–1.4 cm. diam., petals oblong-obovate, 6–7.5 mm. long, 3.5–4 mm. broad, with three green veins; young corolla buds slightly tinged with "Begonia Rose" and old petals also tinge up a little.

*Androecium*: greenish-yellow, glabrous; filaments up to 3 mm. long.

*Gynoecium*: style and stigma 2 mm. long, after pollination slightly spreading.

The plants were, in general appearance and in the majority of the morphological characters, nearer to *S. hypnoides* than to *S. tridactylites*. In spite of repeated self-pollination of several plants over a period of three years and back-cross pollinations with each parent, no fruit or seed was set. In our experience the plants were completely sterile both under controlled and with free open pollinations.

It is of interest to note that a hybrid with the putative parents *S. hypnoides* and *S. tridactylites* was discovered by Farrer on the western face of Ingleborough (Farrer, *The English Rock-Garden*, 2, 273, 1919) and was named by Druce (*B.E.C. 1907 Rep.* p. 256, 1908)  $\times$  *S. Farreri*.

B. 132. *S. granulata* (ovule parent)  $\times$  *S. hypnoides* (pollen parent).  
40 plants in family.

The plants were uniform in morphological characters, except for petal shape. They resembled the *S. granulata* parent more closely in appearance and in the details of the morphological characters than the *S. hypnoides* parent. The following comparative description records the more important characters:

*Habit*: a number of sterile rosettes occur around the base of the flowering stem or stems; average height of flowering plant 1.8 dm.; at anthesis most of the bulbils have grown out into the full leafy sterile rosettes, but a few bulbils which were narrower and more elongated than those of *S. granulata* were showing only green tips.

*Rosette leaves*: markedly heteromorphic, some simple with narrow-elliptic acute blades on petioles about 1.7 cm. long, others three- or five-lobed; hydathodes occurred near the apex of every lobe but there were no apical hairs; simple blades 1.2 cm. long, 6 mm. broad; five-lobed blades 1.2 cm. long, 1.7 cm. broad; leaf indumentum as in *S. granulata*.

*Flowering stems*: as in *S. granulata*, except that gland-tipped hairs extend five-sixths the total distance down the stem.

*Stem leaves*: rather heteromorphic.

*Inflorescence*: as in *S. granulata*, with up to sixteen flowers per branch.

*Calyx*: sepals as in *S. granulata*, at anthesis 4 mm. long and 2 mm. broad, enlarging in young fruit up to 5 mm. long and 4 mm. broad.

*Corolla*: 18 mm. diam.; petals more or less overlapping for about



Fig. 5. Top: *S. granulata* S.P. 9 ♀ × *S. hypnoides* S.P. 10 ♂ (B. 132). Seedlings. Seeds sown 3. viii. 33, seedlings collected 16. i. 34. Bottom: *S. granulata* S.P. 9 ♀ × *S. hypnoides* S. P. 10 ♂  $F_1$  plant 40 selfed (B. 135). Seedlings. Seeds sown 7. viii. 34, seedlings collected 12. xi. 34.

half their length, average 1.2 cm. long and 0.6–0.8 cm. broad, three- to five-veined (even on same plant). Petal shapes: 17 elongate-obovate: 7 obovate: 2 oblong-oblancoelate: 3 broadly obovate.

*Androecium*: filaments up to 5 mm. long.

*Gynoeceum*: styles and stigmata 3 mm. long, the stigmata colour with increasing age.

*Fruit*: projecting 5 mm. beyond the receptacle (including the persistent styles); 4.5 mm. diam.

*Seeds*: as in *S. granulata*.

*Post-fruiting habit*: as in *S. granulata*.

B. 135. One plant (No. 40) of the family B. 132 was selfed and produced an  $F_2$  family of 96 plants. There was no segregation for any vegetative character. The plants were uniform and like the immediate parent in all characters, except petal shape. The immediate parent (B. 132-40) had oblong-oblancoate petals. In B. 135 petal shape figures were—34 elongate-obovate: 36 obovate: 10 oblong-oblancoate: 10 broadly obovate.

B. 183-188. In all these families the seed germination was excellent, and in the total of 326 plants raised beyond the seedling stage there was no phenotypic segregation towards the *S. hypnoides* great-grandparent. The plants were essentially as those of B. 132. Many plants did not flower.

In the seedling stage B. 186, B. 187, and B. 188 were uniform, except for 5 variegated plants in B. 188. In B. 183, B. 184, and B. 185 a few plants showed from few to many malformed leaves which were thick, little lobed, and often asymmetrical.

B. 183 = B. 135 plant 46 × B. 135 plant 9.

75 plants in family, of which 24 did not flower. The petal shape for 51 plants was scored as follows: 11 elongate-obovate: 38 obovate: 3 oblong-oblancoate.

B. 184 = B. 135 plant 9 selfed, with elongate-obovate petals.

32 plants in family of which 4 did not flower.

The petal shape for 28 plants was scored as follows: 11 elongate-obovate: 12 obovate: 5 broadly obovate.

B. 185 = B. 135 plant 46 selfed, with obovate petals.

78 plants in family, of which 26 did not flower.

The petal shape for 52 plants was scored as follows: 28 elongate-obovate: 18 obovate: 3 oblong-oblancoate: 3 broadly obovate.

B. 186 = B. 135 plant 69 selfed, with oblong-oblancoate petals.

71 plants in family, of which 28 did not flower.

The petal shape for 43 plants was scored as follows: 25 elongate-obovate: 16 obovate: 2 oblong-oblancoate.

B. 187 = B. 135 plant 92 selfed, with obovate petals.

34 plants in family, of which 6 did not flower.

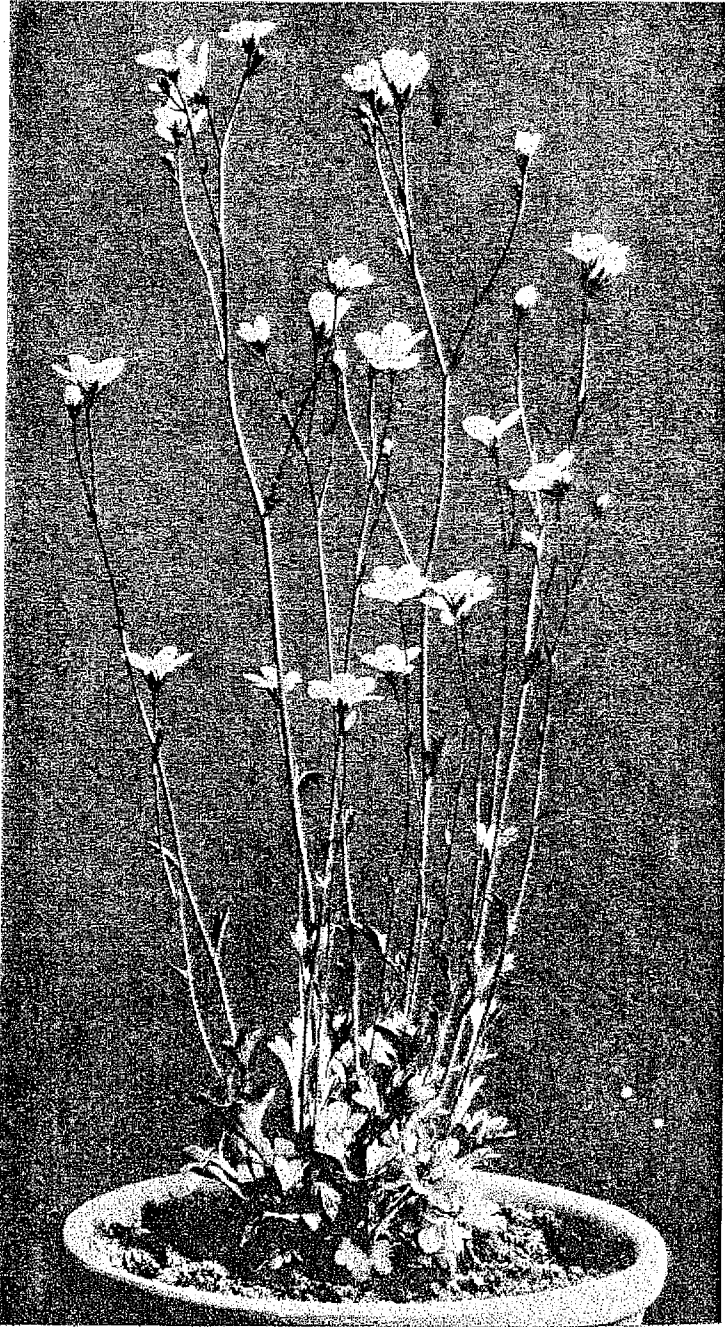


Fig. 6.  $F_3$  from the cross *S. granulata* S.P. 9 ♀ × *S. hypnoides* ♂ (B. 184, plant 27).

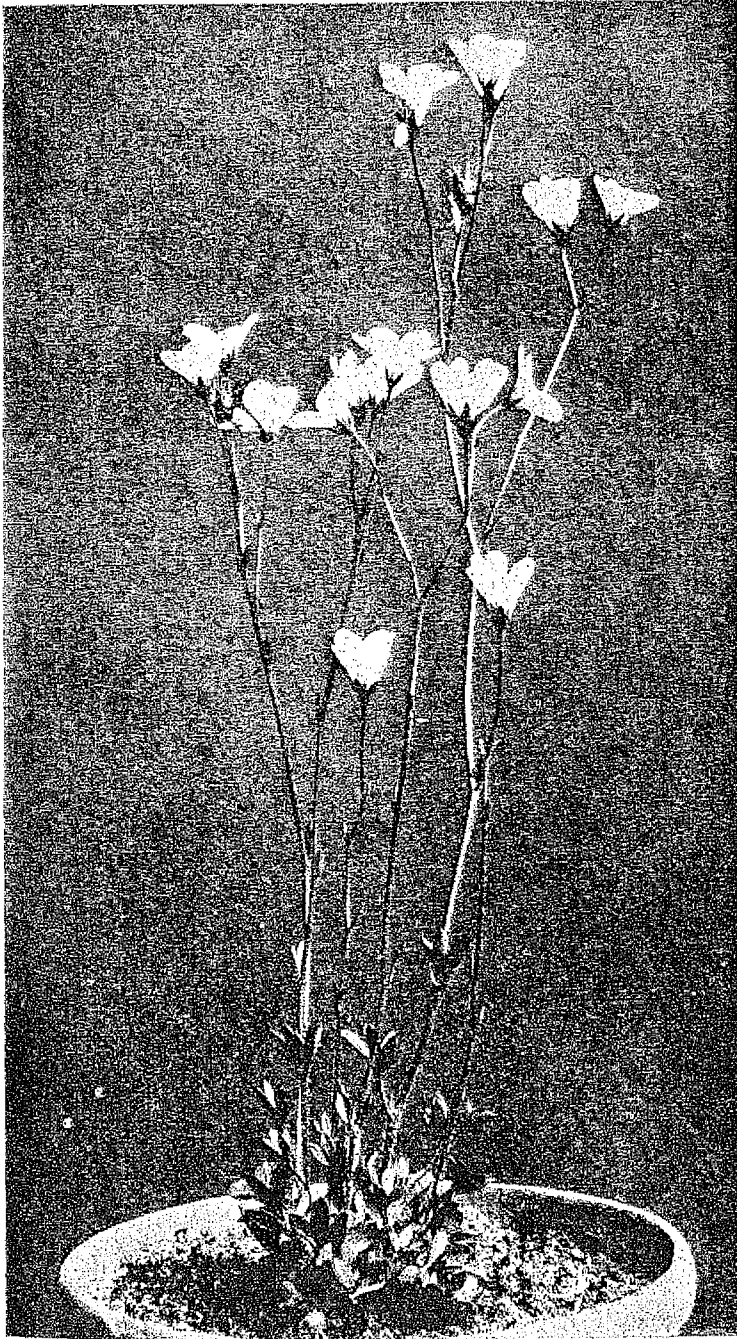


Fig. 7.  $F_3$  from the cross *S. granulata* S.P. ♀ × *S. hypnoides* ♂ (B. 186, plant 43).

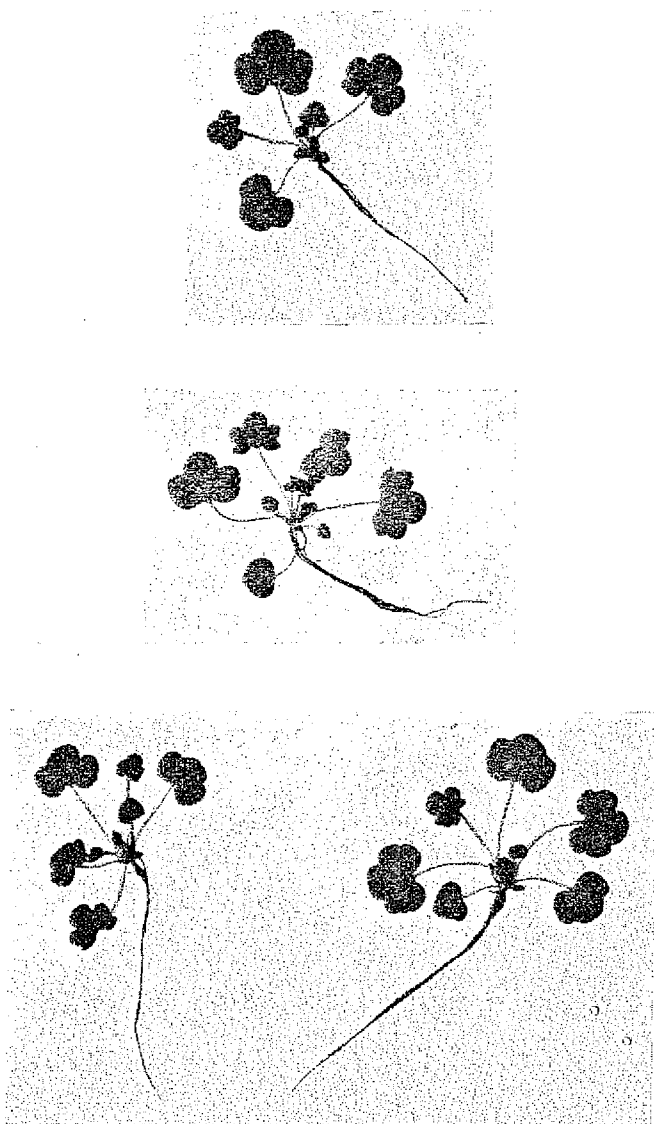


Fig. 8. Top: *S. granulata* S.P. 9 selfed (B. 131). Seedling. Seed sown 3. viii. 33, seedling collected 16. i. 34. Middle: *S. tridactylites* S.P. 50 ♀ × *S. granulata* S.P. 6 ♂ (B. 125). Seedling. Seed sown 3. viii. 33, seedling collected 16. i. 34. Bottom: *S. granulata* S.P. 6 selfed (B. 126). Seedlings. Seeds sown 3. viii. 33, seedlings collected 16. i. 34.

The petal shape for 28 plants was scored as follows: 13 elongate-obovate: 11 obovate: 1 oblong-oblancoelate: 3 broadly obovate.

B. 188 = B. 135 plant 93 selfed, with elongate-obovate petals.

36 plants in family, of which 1 did not flower.

The petal shape for 35 plants was scored as follows: 26 elongate-obovate: 7 obovate: 2 oblong-oblancoelate.

#### DISCUSSION

The experimental work recorded above has shown:

(1) That hybrids can be made between species of *Saxifraga* belonging to three different taxonomic sections of the genus.

(2) That in the cross *S. tridactylites* × *S. hypnoides* the  $F_1$  is completely sterile on both selfing and back-crossing, is much more like the pollen than the ovule parent, and that the perennial habit is completely dominant over the annual habit. Sterility has prevented any further genetical analysis of these characters.

(3) That in interspecific crosses with *S. granulata* used as either ovule or pollen parent, the characters of this species markedly predominate over characters of the other parent, *S. tridactylites* or *S. hypnoides* respectively.

(4) That in the  $F_1$  from the cross of *S. granulata* × *S. hypnoides*, though the majority of the characters were those of *S. granulata*, the ovule parent, certain characters showed the influence of *S. hypnoides*, such as the occurrence of simple leaves and variation in petal shape.

(5) That the  $F_2$  (96 plants) of the cross *S. granulata* × *S. hypnoides* showed no segregation for the characters scored, except for petal shape. In  $F_3$  a few plants showed malformed leaves.