THE MOSSY SAXIFRAGES OF THE BRITISH ISLES

By D. A. WEBB

The taxonomy of the Britannic species of the section Dactyloides of the genus Saxifraga has long been uncertain and confused. Marshall (1917; 1918), who died over thirty years ago, was the last man in these islands who was prepared to name a specimen with confidence, and this confidence was not always justified. Engler & Irmscher (1916-9) provided in the Pflanzenreich an exhaustive monograph of the genus, but valuable as much of this is, it has never been followed in the British Isles as far as the dactyloids were concerned, since it was very clear that the authors' knowledge of British and Irish forms was imperfect.

It was a realization of this situation, when I had occasion in 1943 to attempt to determine the saxifrages of the Galtee Mts., that induced me to proceed to a fairly thorough investigation and revision. This has now been published (Webb, 1948; 1950), but as the papers in question are rather bulky, and are perhaps not readily accessible to many readers of this journal, a summary of my principal conclusions is presented here for the benefit of British readers.

HISTORICAL SKETCH

The hey-day for species-making in the dactyloid saxifrages of western Europe was the early nineteenth century, and in the British Isles Haworth and David Don were particularly active, followed more cautiously by Smith. Haworth's work never carried much conviction to anyone but himself, but of the twelve species listed by Don (1821) as native to the British Isles the majority were generally accepted, and eight were illustrated in English Botany (S. cespitosa, palmata, incurvifolia, affinis, hirta, hypnoides, platypetala, elongella). By the middle of the century it had been discovered that specimens were constantly turning up which could not be located exactly in any of these species with their current definitions, and the attempt to correlate British with continental nomenclature ran into greater and greater difficulties. A reaction therefore set in; the supposed species were successively reduced to varieties and forms, till Bentham and Hooker recognized only two and Baker (1870) only one. The same tendency was at work in Central Europe, and there the matter rested till Marshall resuscitated most of the earlier species, added a few from continental authors (notably S. Sternbergii and S. sponhemica) and described a new one himself (S. Drucei). Engler and Irmscher recognized only two species in the British Isles, but manfully classified under these all the named plants in an imposing, if Procrustean, hierarchy of subspecies, varieties, subvarieties, forms and subforms.

Of these authors Marshall alone systematically cultivated specimens, and he seems to have been curiously blind to the phenotypic nature of many of the supposed specific distinctions which this cultivation should have made clear.

GENERAL PRINCIPLES.

The first step in mastering the taxonomy of a difficult group must always be the determination of the source from which the difficulty arises. Six years' experience of the study of these saxifrages in the field, the garden and the herbarium has led me to conclude that there are three factors which between them account for the difficulties in their taxonomy.

- (1) They are very plastic. Habit, leaf-form, length of flowering stem, size and shape of petals can all vary greatly in the same clone.
- (2) Apart from this phenotypic variability, a wide range of genetic variation (often reproducing or overlapping the former) may be found within a wholly or partly interfertile series. This may possibly be correlated with the high polyploidy of the group.
- (3) The group has a discontinuous and relict distribution. This obscures the distinction between species and subspecies.

The first of these difficulties can, of course, be allowed for by observation in garden culture, and even to some extent by noting in the field the degree of variation between different branches of a single clone (which can be very striking). The second makes it necessary to have regard continually to the interbreeding population and not the individual plant (still less the individual herbarium sheet) as the unit for taxonomic consideration. Brandon Mountain, for example, the reputed home of six species, is clearly occupied by a single convivium. To the third difficulty there is no real solution, and it means that the subjective elements of taste and judgment must enter into the decision whether each taxon must be given specific or subspecific rank.

RELATED CONTINENTAL FORMS.

Numerous species of dactyloid saxifrages are found in the Alps and Pyrenees, and some of these are taxonomically difficult; but fortunately they are quite clearly distinct from the British forms and need not be considered here. There are, however, in Iceland, the Faeroes, Scandinavia and Arctic Russia, Belgium and the Rhineland, Central and South Germany and Czechoslovakia, Eastern, Central and Southern France, and Northern Spain and Portugal, plants which have been or reasonably may be considered conspecific with those of the British Isles. A revision of the latter must, therefore, take cognizance of the dactyloids of all northern and western Europe except for the Alps and Pyrenees.

SPECIES RECOGNIZED

Baker (1870) maintained that the dactyloids of the British Isles presented a linear pattern of variation, ranging from the S. cespitosa of

the Cairngorms to the gemmiferous S. hypnoides of Cheddar and Dove Dale. This is in broad outline true, though in the central part of the series considerable reticulation of characters is found and a linear sequence cannot be recognized. If one reviews the European populations, however, it would seem that the pattern of variation is not quite continuous, and that there are five discontinuities, preserved by geographical or occasionally by ecological separation, which justify the discrimination of six species, of which four are found in the British Isles.

1. S. CESPITOSA L. (S. groenlandica L.)

Rather densely tufted, with short, nearly erect barren shoots which develop into small rosettes with usually incurved leaves. Leaves small, uniformly and densely clothed with short, glandular hairs, divided into 3 (seldom 5. never more) obtuse, somewhat parallel-sided lobes, which are never very divaricate. Flowers usually protogynous; petals rather small, dirty, creamy or greenish white; ovary more nearly inferior than in the other species. Seeds very finely tuberculate.

Distribution. Circumpolar. Throughout the Arctic, extending southwards in America to Oregon and perhaps to Arizona, in Asia to southern Siberia, and in Europe to Iceland, Scandinavia and Great Britain. Very rare in Great Britain, being restricted to the Cairngorms, the Ben Nevis area and Cwm Idwal. Unknown in Ireland.

Notes. A very variable species, especially in America, but in the Old World much of the variation seems to be phenotypic. There is no doubt at all as to the identity of the British with Scandinavian and Arctic plants. The glandular hairs, the flower-colour, and the protogyny are all constant and characteristic.

2. S. HARTH D. A. Webb (1950).

Loosely tufted, or somewhat straggling if growing among other plants. Barren shoots typically short, nearly erect, developing into flat rosettes with flattened, spreading leaves. Leaves medium-sized, uniformly and densely clothed with short glandular hairs, divided into 5 or more (up to 11 in robust cultivated plants) rather acute, somewhat triangular lobes. Flowers protandrous; petals fairly large, thick, pure dead white with conspicuous green veins. Seeds very finely tuber-culate.

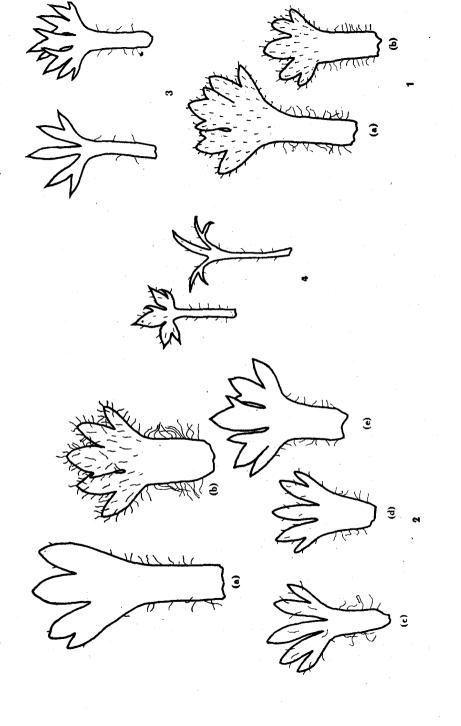
EXPLANATION OF FIGURES. ×2.5.

Leaves from the winter rosettes of cultivated plants of (a) Saxifraga Harlit.
(b) S. cespitosa.

^{2.} Leaves from the winter rosettes of cultivated plants of Saxifraga rosacea from different parts of Ireland: (a) from the Galtee Mts., (b) from Clare Island, Co. Mayo (c) from Brandon Mt., Co. Kerry, (d) from the Twelve Pins. Co. Galway, (e) from Black Head, Co. Clare.

^{3.} Leaves from the winter rosettes of cultivated plants of Saxifraga hypnoides

^{4.} Leaves from herbarium specimens of Saxifraga continentalis.



Distribution. Known only from Arranmore Island, off the west coast of Donegal, Ireland (not to be confused with the Aran Islands further south). It has been found here on four occasions, in at least three separate stations, and has been variously named S. hirta, S. Sternbergii and S. Drucei.

Notes. Intermediate between the foregoing and the following species, and very possibly the last relic of a hybrid population. But as it is now geographically isolated and does not fall within the variation-range of either of the supposed parents it seems best to give it specific rank. From S. cespitosa it differs in leaf-shape, protandrous habit, and size, texture and colour of the petals. From S. rosacea it is at once distinguished by the investment of glandular hairs. The form of S. rosacea which it most closely approaches is that which is geographically nearest—the hairy plant of Clare Island, Co. Mayo.

3. S. ROSACEA Moench (S. decipiens Ehrh., S. palmata Sm., S. Sternbergii Willd., S. hirta Sm., S. affinis Don, S. incurvifolia Don).

Very variable in habit, leaf-form and indumentum. Compact or straggling, but in plants with straggling or mat-like habit the prostrate barren shoots are stronger and coarser than in S. hypnoides. Leaves large or small, hairy or nearly glabrous, but with few or none of the hairs gland-tipped; divided into 3, 5, 7, or rarely up to 11 segments, which are very variable in form, but seldom as obtuse as in S. cespitosa, and never as distinctly apiculate-aristate as in S. hypnoides. Flowers protandrous, erect in bud; petals delicate, pure shining white. Seeds finely or coarsely tuberculate.

Distribution. (1) Iceland and the Faeroes. (2) Western Ireland and N. Wales. (3) South-central Germany and western Czechoslovakia, with an outlying station in the Vosges. In Ireland it is widespread in the Kerry mountains but very local elsewhere; it has been found in late-glacial deposits in Co. Dublin. It appears to be extinct in Caernaryonshire.

Notes. The most variable of all the species. Plants from Clare, Mayo, the Galtees and the summit of Brandon Mt. (Kerry) differ from each other widely and invite specific discrimination, but they are connected by a host of inter-breeding intermediates. In view of the disjunct distribution there is a curious lack of geographical subspeciation. The plants of Czechoslovakia on the one hand and western Germany on the other are hard to match exactly, but Irish plants may be very accurately matched with those from Iceland, the Faeroes, the Harz, Thuringia and Bavaria.

4. S. SPONHEMICA Gmelin (incl. S. condensata Gmelin; S. hirta Haworth non Smith; S. palmata Lejeune non Smith).

Loosely tufted or somewhat spreading, with weak but semi-erect or ascending barren shoots rather densely clothed with trifid leaves. Leaves and stem nearly glabrous. Rosette-leaves divided into 3 or 5 narrow, shortly but distinctly acuminate-aristate segments, which are never very divaricate. Dormant buds not present in axils of barren shoots. Flowers much as in *S. rosacea*; position of buds and ornamentation of seeds not noted.

Distribution. Rhineland and Palatinate, Luxembourg, south-east Belgium and the French Ardennes, with an outlying station in the French Jura.

Notes. It is possible that this should be reduced to a subspecies of S. rosacea which in Hesse manifests itself in a very acute-leaved form which is not easy to discriminate from S. sponhemica. The gap between the two populations, which now coincides with the valley of the Rhine, may be fairly recent, and there has doubtless been infiltration of sponhemica genes into the western populations of S. rosacea. The Rhineland plant certainly does not occur in the British Isles, and the identification of it with Smith's S. platypetala cannot be sustained.

5. S. HYPNOIDES L. emend. D. A. Webb.

Spreading, with usually long, prostrate barren shoots, rather sparsely clothed with leaves, which may be simple or trifid, and which sometimes hear dormant, but green and herbaceous, buds in their axils; frequently, however, these buds are absent. Leaves and stem nearly glabrous. Rosette-leaves with 3 to 9 narrow, acuminate-aristate, rather divaricate segments. Flowers nodding in bud, protandrous; petals delicate, pure shining white, rather narrower than is usual in S. rosacea. Seeds coarsely tuberculate.

Distribution. Iceland, the Faeroes and the British Isles, with outlying stations in western Norway and the Vosges. Widespread in Scotland, northern England, and much of Wales, with a few additional stations in western England; scattered through much of Ireland, especially the north and west.

Notes. The gemmiferous plant, which is usually considered the "typical" state of this species, shades off very gradually into the nongemmiferous forms that have been given various names, among which S. platypetala Sm. has been most widely used. The breadth of the petals seems to be of no taxonomic value. Gemmiferous forms usually have at least some of the leaves on the barren shoots undivided, but the exact correlation which has sometimes been postulated between dormant buds and undivided leaves, and between trifid leaves and absence of buds, certainly does not exist.

6. S. CONTINENTALIS (Engl. & Irmsch.) D. A. Webb (S. hypnoides, subsp. continentalis Engl. & Irmsch.).

Loosely tufted, with prostrate but rather short barren shoots. Leaves rather rigid, with 3 to 7 lobes, very variable in shape; segments acuminate-aristate. Dormant buds always present, very rigid, pointed, and silvery by virtue of the completely scarious bud-scales. Flowers much as in S. hypnoides.

Distribution. Central and southern France, northern Spain, northern Portugal.

Notes. The difference in habit and general appearance between this species and S. hypnoides is very striking, although it is not very easy to put into words, and there is never any difficulty in discriminating them. This constant morphological difference, coupled with a clearcut geographical separation without overlap, justifies specific rather than subspecific separation.

REJECTED SPECIES

The following names that have been used at one time or another for dactyloids of the British Isles are rejected in this revision.

- S. groenlandica L. Synonym of S. cespitosa (v. infra).
- S. decipiens Ehrh. Nomen nudum, to be rejected in favour of S. rosacea Moench (v. infra).
- S. incurvifolia D. Don
- S. affinis D. Don
- S. palmata Sm.
- S. Sternbergii Willd.
- S hirta Sm.
- S. Drucei E. S. Marshall
- S. elongella Sm. A phenotypic modification of S. hypnoides.
- S. platypetala Sm.
- S. laetevirens D. Don
- S. leptophylla D. Don
- S. spathulata Haw.
- S. angustifolia Haw.
- S. viscosa Haw.
- S. quinquefida Haw
- S. hirta Haw.
- S. sponhemica Gmel.

Forms or variants of S. rosacea, not worth taxonomic recognition.

Forms of S. hypnoides, in most cases not adequately diagnosed, and not worth taxonomic recognition.

Names given to foreign plants and transferred in error to the British list.

NOMENCLATURAL NOTES

Three nomenclatural problems arose in the course of this revision, which can only be very briefly summarized here.

- (1) S. groenlandica is widely used on the Continent for the species here named S. cespitosa. Linnaeus is responsible for both names, and for the eventual reduction of the former under the latter. If, therefore, it can be shown that S. cespitosa (1753) is valid, it is not necessary to decide whether S. groenlandica is or is not a nomen confusum. It is argued from the type-specimens and the description that S. cespitosa is valid, and the erroneous citation of synonyms by Linnaeus does not upset this conclusion.
- (2) S. decipiens is widely used for the species here named S. rosacea. The former is accompanied by no description, but by a reference to S. petraea of Roth. But in the volume of Roth's Tentamen to which Ehrhart makes reference there is no description of S. petraea. The

fact that in a later volume Roth adds a description is irrelevant; one cannot argue that Ehrhart's reference is a *lapsus calami*, since he was writing less than a year after Roth's second volume appeared and may well not have seen it.

(3) In splitting S. continentalis from S. hypnoides the choice of the northern plant as lectotype rather than the southern is justified by the fact that in the Linnaean herbarium (where both are present) it is against the northern plant that the serial number of the species in Species Plantarum has been written.

HYBRIDS

As far as is known all the Britannic species are to some extent interfertile. Occasional plants intermediate between S. hypnoides and S. rosacea have been found in Co. Clare and in the Galtees (the only regions of the British Isles where the two parents grow together) and are doubtless natural hybrids between the two. It is also perhaps significant that certain plants of S. hypnoides from Cwm Idwal deviate somewhat in the direction of S. rosacea (which once grew there), indicating perhaps some degree of introgressive hybridization.

The following hybrids (all fertile) have been artificially produced in culture:

 $S. hypnoides \times S. rosacea.$

S. Hartii × S. hypnoides.

S. Hartii × S. rosacea.

Difficulties experienced in maintaining S. cespitosa in cultivation, and in inducing it to flower at the same time as the other species, have so far prevented any attempt at crossing it with other species.

KEY TO THE BRITANNIC SPECIES

. cespitos

Leaves glabrous, or with woolly, eglandular hairs; glandular hairs few or absent: Leaf-segments obtuse or acute, but scarcely acuminate; flower-buds erect

s. rosace

Leaf-segments acuminate-aristate; flower-buds nodding S. hypnoides

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