

THE VARIETIES OF *RANUNCULUS FLAMMULA* L. AND THE STATUS
OF *R. SCOTICUS* E. S. MARSHALL AND OF *R. REPTANS* L.

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The great number of varieties of *R. flammula* L. which have been described gives an indication of the morphological diversity found within this species. There are, in addition, two closely related taxa which have been given specific rank, *Ranunculus reptans* and *Ranunculus scoticus*. An attempt has been made to elucidate the status of these, and to evaluate the named varieties by experimental means and by study of the literature. This investigation has been carried out almost entirely upon British material, although Scandinavian and Icelandic specimens were used whilst studying *R. reptans*.

NOMENCLATURE.

The brief Linnean description of *R. flammula* covers a considerable range of variation, but the specimen in the Linnean Herbarium fortunately represents one of the commonest and most widespread forms of this species. In addition to this variety, *R. flammula* subsp. *flammula* var. *flammula*, a considerable number of other forms and varieties have been described within subsp. *flammula*. Many of these can be reduced to synonymy by an examination of the literature.

The following infra-specific names need further consideration :

1. var. *tenuifolius* Wallr. (1822) (var. *pseudo-reptans* Syme (1856), var. *gracilis* Meyer (1890), var. *radicans* Nolte (1830), var. *reptans* Neilr. (1859), *R. reptans* Maly (non L.)).
2. var. *angustifolius* Wallr. (1822).
3. var. *ovatus* Pers. (1807) (var. *latifolius* Wallr. (1822)).
4. var. *serratus* DC. (1818).
5. var. *natans* Pers. (1807) (forma *natans* Glück (1911)).
6. forma *submersus* Glück (1911).
7. var. *major* Schult. It has not been possible to determine the precise date of this description but it is certainly much earlier than var. *alismifolius* Glaab (1911) with which it appears to be synonymous.
8. var. *pilifer* G. Beck (1890).
9. forma *minimus* A. Benn. (1904).

Most of these taxa are defined by characters of habit, leaf shape and serration, and petiole length, alone.

Field observations and transplant experiments demonstrate clearly the plasticity of habit and of leaf shape and serration and petiole length. Except in var. *major* and forma *minimus* there do not appear to be any other morphological or anatomical characters that are correlated with the diverse leaf forms that occur in various habitats. It is therefore evident that taxa within subsp. *flammula* which are based solely on leaf form have little significance.

Within subsp. *flammula* it appears only to be possible to recognise, if desired, several forms which are in fact phenotypes. Of the forms of var. *flammula*, the plant characteristic of stony lake-shores is common and widespread in the north ; it is small,

slender and prostrate, with stems that creep and root at most of the lower nodes. Plants of this type have a diploid chromosome number of 32 and fully fertile pollen. Specimens from a wide range of localities in the British Isles have been brought into cultivation; in all cases, the plants increased considerably in size and stoutness before dying down in the autumn, and the flowering axis produced in the following growing season was erect and showed no tendency towards nodal rooting. Field observations indicate that the small size and other characteristics are due to lack of nutrition, rather than to pH or drought. This phenotype will be referred to as forma *tenuifolius*.

Other distinct-looking phenotypes are forma *natans* (Pers.) Glück and forma *submersus* Glück.

Var. *major* Schult. is a strikingly large plant which has sometimes been confused with *R. lingua*. It was thought that this was essentially a southern plant, and that its large size was due to the milder climate of these areas; during the course of this investigation, however, specimens have been seen from most parts of the British Isles, the northernmost from Aberdeenshire. When cultivated, such plants retain the morphological characteristics which make them so conspicuous in the field.

Forma *minimus* A. Benn. has a number of inheritable characters which seem to justify its separation from subsp. *flammula* as a distinct subspecies. A description of it is given on p. 21

DESCRIPTIONS.

R. flammula L.

Perennial herb; stems (4 —) 8–55 (— 80) cm., erect or creeping and rooting at the nodes, uppermost part slightly branched. Laminae of basal leaves 0.5–4.0 (— 5.0) × 0.2–2.5 (— 3.0) cm., stalked, subulate or lanceolate to broadly ovate, base cordate to rounded. Laminae of cauline leaves 2.0–5.0 × 0.8–2.0 cm, stalked or sessile, ovate-

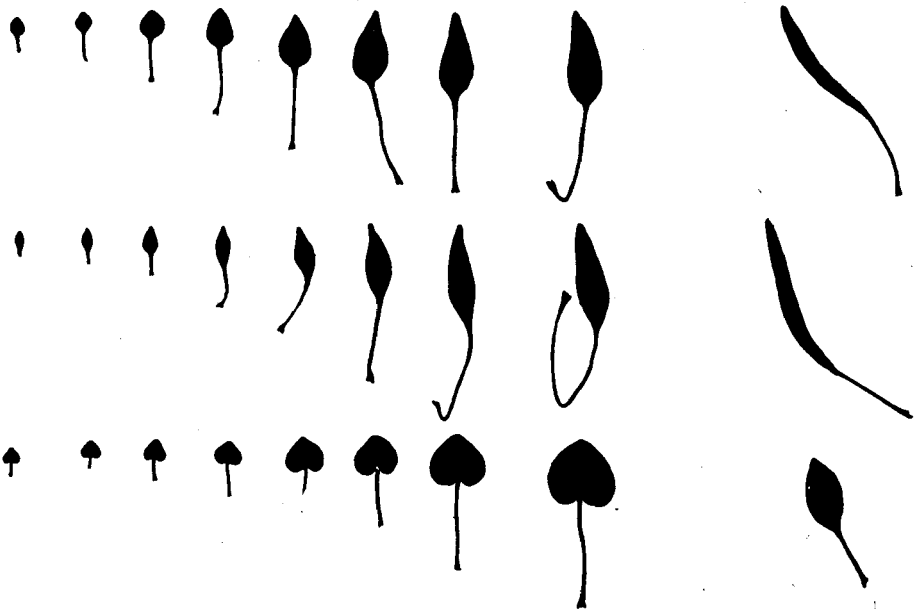


Fig. 1. Top and middle : Leaves 1-7, last basal leaf and leaf from second cauline internode of two plants of *R. flammula* subsp. *flammula*. Bottom : Corresponding leaves from a plant of *R. flammula* subsp. *minimus*.

lanceolate to linear-lanceolate. Leaf-margins subentire to strongly serrate. Flowers 0·8–2·0 (– 2·5) cm. diam. Sepals 5, greenish-yellow; petals 5, yellow, glossy, obovate. Achenes in a globose head of 20–50 (– 60), ovate, shortly beaked, 1·0–1·9 (– 2·2) mm. long (excluding beak). Ratio achene length : achene width = 1 : 1·4 (– 1·6); beak 0·05–0·39 (– 0·46) mm. long, slightly curved. Protandrous. Fl. 5–9. $2n = 32$.

Subsp. *flammula*.

Stem 8–55 (– 80) cm. long, erect or creeping and rooting at the lower nodes. Laminae of basal leaves 1·0–4·0 (– 5·0) × 0·8–2·5 (– 3·0) cm., stalked, lanceolate to broadly ovate. Ratio of achene length : achene width = 1 : 1·4.

Var. *flammula*.

Stem ascending or creeping and rooting. Plant fairly slender, flowers 0·8–2·0 cm. diam. 'Forma *tenuifolius*': stems creeping and rooting at the nodes; pollen fertile. 'Forma *natans*': basal leaves long-petioled, laminae floating; plants growing in running water. 'Forma *submersus*' is a deep-water state which has submerged, narrowly elliptical leaves and is always barren.

Var. *major* Schult.

Erect robust plant rarely rooting at even the lowermost nodes, 35–60 cm. high. Laminae of basal leaves 3·5–5·0 × 2·5–3·0 cm. Cauline leaves correspondingly large. Flowers 1·8–2·5 cm. diam.

Var. *pilifer* G. Beck is said to be more or less densely clothed with hairs and would seem to be a distinct entity which is absent from this country.

R. flammula subsp. **minimus** (A. Benn.) P. A. Padmore subsp. nov., based on *R. flammula* forma *minimus* A. Bennett, 1904, Ann. Scot. Nat. Hist., 1904, 227.

The distinguishing characters of this taxon as described by A. Bennett are its small size, short internodes and the fact that the laminae shorter in proportion to the petioles.

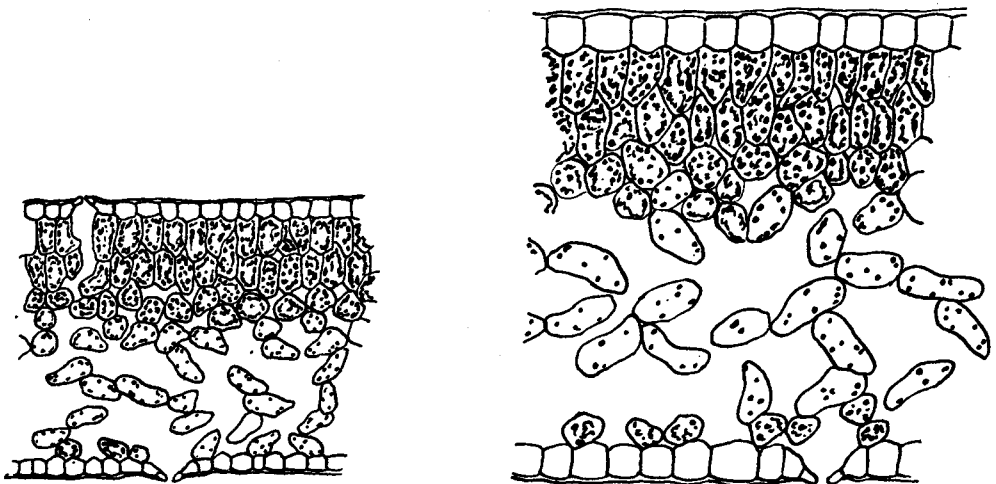


Fig. 2. T.S. leaf of *R. flammula* subsp. *minimus* (right) and subsp. *flammula* (left). × 38.

Stem semi-prostrate but not rooting at the nodes, 3–8 (–14) cm. long with very short internodes, 0.5–2.0 cm. long (those of subsp. *flammula* 4–7 cm.). Basal leaves shortly stalked, broader than long or at least orbicular, distinctly cordate at the base, thick and fleshy. Stem leaves broader in relation to length than in subsp. *flammula*. First flower at the second or third node (4th–7th in subsp. *flammula*). Flower diameter greater than 1.5 cm. Achenes 1.05 times as long as broad. The type specimen was collected from North Uist; other specimens labelled forma *minimus* by Bennett come from Holburn Head and the Cliffs of Kilkee.

Habitat: exposed situations by the sea, growing in short turf and often forming dense mats. Distribution: v.c. 109, Caithness, Holburn Head: v.c. 110, Outer Hebrides, North Uist: v.c. 111, Orkney, Yescanby and Skail Bay, v.c. 112, Zetland, Wick of Shuni: v.c. H9, Clare, Cliffs of Kilkee.

The most distinctive features of this plant are the short internodes, thick fleshy leaves and comparatively large flowers. The following table indicates the most important differences between these plants and normal *R. flammula*.

subsp. <i>minimus</i>	subsp. <i>flammula</i>
1. Basal leaves broader than long or at least orbicular.	Basal leaves longer than broad.
2. Basal leaves distinctly cordate at base.	Basal leaves cuneate, rounded or slightly cordate at base.
3. Leaves thick and fleshy.	Leaves thinner.
4. Internodes 0.5–2.0 cm. long.	Internodes 4–7 cm. long.
5. Height 3–8 (–14) cm.	Height usually considerably above 12 cm.
6. First flower from second or third node.	First flower from fourth to seventh node.
7. Flower diam. more than 1.5 cm. (large for the size of the plant).	Flower diam. 0.7–1.8 cm.
8. Achenes 1.05 times as long as broad.	Achenes 1.35 times as long as broad.

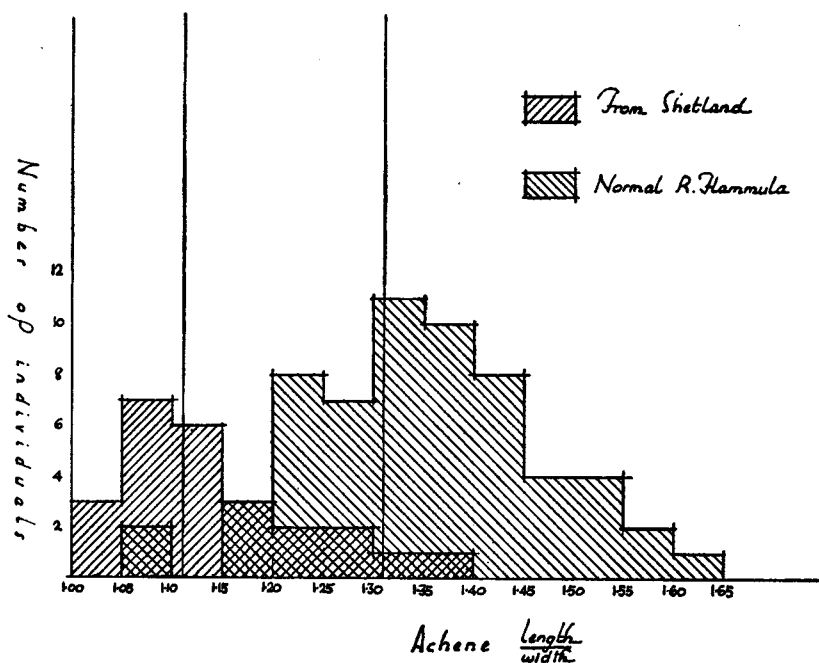


Fig. 3. Histogram of achene length : width ratio in normal *R. flammula* and the subsp. *minimus* from Shetland.

Plants from Orkney and Shetland were brought into cultivation in 1953; after 12 months they showed no morphological changes, apart from a slight increase in size which can be attributed to the richer soil conditions and reduced exposure. Seeds from these specimens were sown at the same time as seeds from two plants of normal *R. flammula*, and, as the leaves matured, they were removed in order and their silhouettes recorded. The results of this experiment are set out in Fig. 1 and indicate quite clearly that there is a marked difference between the two sets of seedlings. The plants were grown in artificial heat and light and their dimensions are therefore larger than they would be in the field.

Study of the leaf anatomy shows that the greater thickness of the leaves of subsp. *minimus* is due partly to larger cell size but mainly to an increase in the number of layers of cells (Fig. 2).

The accompanying histogram (Fig. 3) indicates that the mode of the ratio, achene length : achene width, is very much less in these plants (1.11) than in normal *R. flammula* (1.31). These results have been tested and found to be statistically significant.

While examining material in the British Museum, it was observed that some specimens collected by H. H. Johnston in Orkney had unusually large achenes. Even to the naked eye they appeared to fall outside the range of normal *R. flammula* achenes. This locality was visited in 1953 and live plants obtained which were brought into cultivation. The lengths of the achenes were measured under a dissecting microscope and the results plotted in the form of a histogram. This was compared with a similar histogram which had been prepared with the intention of obtaining a picture of the achene dimensions of the species as a whole, using achenes from a wide range of morphological types and from as many localities as possible. As can be seen from the accompanying diagram (Fig. 4) there is a marked difference between the two samples. These results have been tested and found to be statistically significant. There seem to be no other morphological characteristics to distinguish these plants from any other specimens of *R. flammula*. They are certainly above average size, but when the achene size of specimens of var. *major* was checked it was found to be in no way abnormal and indeed much smaller than in the Orkney plant. Cytological examination has shown a normal chromosome complement of $2n = 32$. No taxonomic status can be assigned to the plant until more is known about its morphology and distribution.

RANUNCULUS SCOTICUS

R. scoticus was first discovered by E. S. Marshall at Lochan Mathair Etive, Argyll (v.c. 98) in 1888. It was first described as *R. flammula* var. *petiolaris* Lange (Marshall, 1889), and then raised to specific rank as *R. petiolaris* (Marshall, 1892). This name was subsequently found to be pre-occupied and was therefore changed to *R. scoticus* (Marshall, 1898). The plant has subsequently been reported from numerous localities in N.W. Scotland and W. Ireland, but in many cases the identification has been incorrect.

The most striking character of this plant is the shape of the basal leaves. The lower leaves are reduced to a subulate petiole and are caducous. Later ones are sub-persistent, but always easily detached, with a slightly more pronounced short, blunt, linear-oblong blade. Other, less reliable, characters for identification are the rigid, slightly zigzag stem and the petals which have a cuneate base broadening upwards to a truncate top so that they appear to be distant from one another.

Cultivation experiments have shown that the morphology of the basal leaves remains unchanged when the plant is grown under terrestrial conditions; also that *R. flammula* subsp. *flammula* will not develop such leaves when grown in a few centimetres of water.

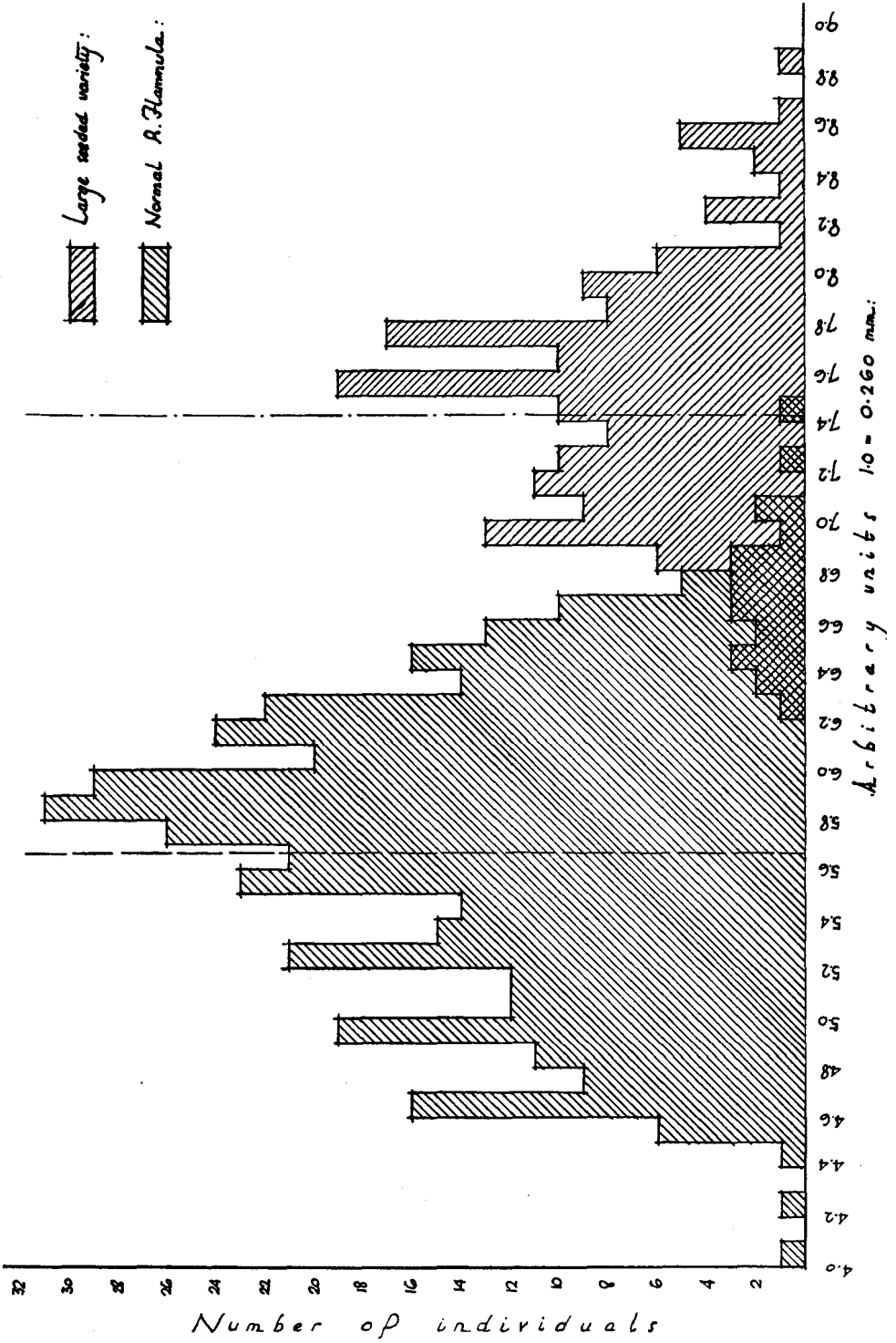


Fig. 4. Histogram of achene length in normal *R. flammula* and the variety from Orkney with large achenes.

There is therefore no doubt that this taxon is genetically distinct from *R. flammula*; it was reduced to a subspecies by Clapham (1952) and observations of plants both in the field and in cultivation indicate that this is probably the most appropriate category.

The distribution is difficult to determine from herbarium material, which rarely shows the basal leaves, since these usually drop off by the time flowering commences. It is, however, reasonably certain that it occurs in v.c. 98 (Argyll) and 104 (N. Ebudes) and also possibly H27 (W. Mayo); other records are probably erroneous.

RANUNCULUS REPTANS.

R. reptans is more common in Norway and Sweden than it is in the British Isles. Specimens from those two countries show a distinctive plant, extremely slender with arching internodes. Plants collected from the two best-known localities in Britain, Loch Leven and Ullswater, do not show such uniform morphology. Great variation in size and the degree of nodal rooting may be observed, the morphology varying according to the habitat. This variation has led to confusion with *R. flammula* 'forma tenuifolius,' and so, in an effort to establish a dividing line between the two, these localities were visited in 1952. The habitat in both was very similar. The plants occurring along the pebbly beach at the water line were very small and slender. Behind them, the plants became progressively stouter and less prostrate until, behind the high-water mark, there were populations of normal erect *R. flammula*. A representative selection of plants was brought into cultivation in June, 1952 and by the end of that growing season marked morphological changes could be seen in many of the plants. The most slender specimens which had been creeping along the water's edge remained prostrate; most of the intermediate forms, however, reverted to erect *R. flammula*, indicating that they should be assigned to *R. flammula* 'f. tenuifolius.' Clearly some method of distinguishing this form from *R. reptans* other than by cultural experiments was necessary and, in an attempt to discover some measurable characteristic, pollen grains were treated with lactophenol and cotton blue and examined. There were many shrunken and malformed grains and a survey was made to determine the percentage sterility. Using samples of not less than 300 grains from each plant it was found that the sterility varied from 10–90%. Values below 10% were not considered to be significantly subnormal. Although there was no absolute connection between percentage sterility and the type of morphology, nevertheless there was a distinct tendency for the more slender creeping plants to have the highest percentage sterility, while the closer the plants approached to *R. flammula* in their morphology the more fertile was the pollen. In no case was a plant of the slender type found to have fully fertile pollen (i.e. less than 10% sterile). These facts strongly suggest the possibility of introgressive hybridisation between *R. flammula* and *R. reptans* resulting in a hybrid swarm; the continual back-crossing with the most abundant species (*R. flammula*) having eliminated all genetically pure *R. reptans*.

Pollen from a collection of Swedish specimens was examined by the method described above, and it was found that in the north, where *R. flammula* is a great rarity, *R. reptans* had fully fertile pollen. Further south, however, the ranges of the two species overlap, and plants labelled *R. reptans* from this area showed varying degrees of sterility.

The only country from which *R. reptans* is reported, but where *R. flammula* is reputed to be absent, is Iceland. Herbarium material was obtained from Reykjavik and the pollen examined in the usual way; the majority of the plants were pure *R. reptans* with fully fertile pollen although there were a few specimens which were a rather dwarf semi-prostrate form of *R. flammula* which had been labelled *R. reptans* in error, probably owing to the fact they they showed a tendency to nodal rooting.

Although this cannot be regarded as conclusive proof, nevertheless it seems likely that the hypothesis of introgressive hybridisation is correct. It is probable that *R. reptans* was present in these islands in the Late-Glacial and that relict populations survived at Loch Leven and Ullswater and became modified at a later date by hybridisation and repeated back-crossing with *R. flammula*. If this is the case, it may be postulated that, so far as is known at the moment, there is no pure *R. reptans* remaining in the British Isles, and that the prostrate creeping forms to be found on northern lake shores are either:

- (a) *R. flammula* 'forma *tenuifolius*,' which will revert to normal *R. flammula* in cultivation, or (b) of hybrid origin.

As far as is at present known, these hybrids can only be certainly detected by examination of the pollen, which is more than 10% sterile.

SUMMARY

(a) Cultivation experiments and study of the literature have shown that the numerous described varieties of *R. flammula* may be reduced to the following taxa :—

R. flammula L.

subsp. *flammula*

var. *flammula*

var. *major* Schult.

subsp. *minimus* (A. Benn.) Padmore

subsp. *scoticus* (E. S. Marshall) Clapham

(b) The hypothesis is put forward that, on account of introgressive hybridisation there is no genetically pure *R. reptans* remaining in the British Isles; it is suggested that the small creeping forms of the northern lake shores are either *R. flammula* 'forma *tenuifolius*' or of hybrid origin. In the latter case the pollen is always more than 10% sterile. Subsp. *flammula* is widespread and common in Britain as a plant of damp places. Subsp. *minimus* is a plant of northern sea coasts which has a very characteristic leaf shape. Subsp. *scoticus* grows in shallow water and has certain morphological characteristics which are retained in cultivation. It occurs in the Highlands of Scotland and possibly also in north-western Ireland.

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REFERENCES

- ANDERSON, E., 1949, *Introgressive Hybridisation*; New York.
 ASCHERSON, P. & GRAEBNER, R., 1899, *Flora des Nordostdeutschen Flachlandes*; Berlin.
 BAILEY, C., 1887, *J. Bot.*, **25**, 135-138.
 BAUMANN, E., 1911, *Die Vegetation des Untersees*; Stuttgart.
 BECK, G. R. von, 1890-93, *Flora von Nieder-Oesterreich*; Vienna.
 BEEBY, W. H., 1887, *J. Bot.*, **25**, 370-372.
 BENNETT, A., 1904, *Annals of Scottish Natural History*, **1904**, 227.
 CLAPHAM, A. R., 1952, in Clapham, A. R., Tutin, T. G. & Warburg, E. F., *Flora of the British Isles*; Cambridge.

- DE CANDOLLE, A. P., 1818, *Regni vegetabilis Systema Naturale*; Paris.
- GLAAB, 1911, *Deutsche Bot. Monatschrift*, **11**, 76.
- GLÜCK, H., 1911, *Biologische und morphologische Untersuchungen über Wasser-und Sumpfgewächse*, **3**, 486-500; Jena.
- HEGI, G., 1912, *Flora von Mitteleuropa*, **3**; Munich.
- LINNAEUS, C., 1753, *Species Plantarum*, Stockholm.
- MARSHALL, E. S., 1889, *J. Bot.*, **27**, 230.
- , 1892, *J. Bot.*, **30**, 289.
- , 1898, *J. Bot.*, **36**, 103.
- NEILREICH, A., 1854, *Flora von Nieder-Oesterreich*; Vienna.
- PERSOON, C. H., 1807, *Synopsis Plantarum*; Paris.
- PRAHL, A., 1890, *Kritische Flora von Schleswig-Holstein*; Kiel.
- SYME, J. T. B., 1863, *English Botany*, Ed. 3, **1**; London.
- WALLROTH, K. F. W., 1822, *Schedulae criticae de Plantis Florae Halensis*; Halae.