

SYSTEMATICS OF
THE RANUNCULUS ACRIS L. sens. lat. COMPLEX
IN EUROPE

Being a thesis submitted for the
degree of Ph.D. in the Faculty
of Science. 1968.

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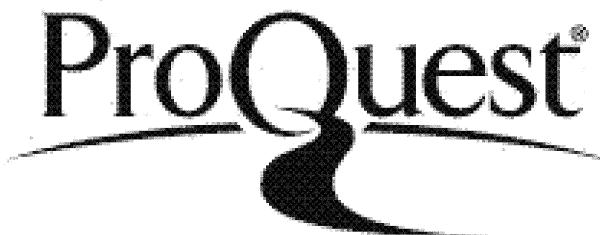


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ABSTRACT

The Ranunculus acris L.s.l. complex was examined within Europe, to investigate the geographical variation, and to see how this correlates with previous nomenclature assigned to the group.

Most of the work was carried out on herbarium specimens, but this was supplemented by cultivated material of known origin. Characters were investigated from as many parts of the plant as possible. Much variation was found to be due to the time of year or relative position of the organ on the plant. Graphical and mapping techniques were used, so that continuous variation would not be masked, but discontinuities would still show up.

Many of the numerous names previously applied to parts of the complex, were applied to parts of a continuous cline or even to seasonal variations. The following taxa are recognised in the present work.

R.granatensis Boiss.;Diag.ser 2(1):8(1853)

(syn. R.acris subsp.granatensis (Boiss.)Nyman;Consp:12(1878))

R.strigulosus Schur;Enum.Pl.Transs.:17(1866)

(syn. R.acris subsp.strigulosus (Schur)Hyl.;Symb.Bot.Upsal.

7:1(1943))

R.acris L.s.s.;Sp.Pl.:554(1753)

subsp.acris

(syn. R.boreanus Jord.;Obs.Pl.Crit.6:19(1847)

R.tomophyllus Jord.;Diag.:71(1864))

var.villosus (Drabble)Comb.nov.

(syn. f.villosus Drabble;Rep.B.E.C.9(3)(1930))

var. pumilus Wahlenb.; Flora Lapp.(1812)

subsp.friesanus (Jordan) Rouy & Fouc.; Fl. Fr. 1:103(1893)

(syn. R.friesanus Jordan: Obs. Pl. Crit. 6:17(1847))

var. pyrenaeus nom.nov.

subsp.borealis (Trautv.) Nyman; Consp.:12(1878)

(syn. R.borealis Trautv.; in Bull. Soc. Nat. Mos. 33:72(1860))

R.granatensis Boiss. and R.strigulosus Schur have a restricted distribution and are relatively uniform in appearance. R.acris L.s.s. occurs over most of Europe and is a very variable plant.

Breeding experiments showed R.acris L.s.s. to be an obligate outbreeder, and all the plants tested, even from places as far apart as Finland, Austria and England, were found to be freely interfertile. Pollen fertility could not be used to detect any decrease in fertility of the hybrids due to the high but variable pollen infertility found in a large percentage of the parent plants. That much of the geographic variation within R.acris L.s.s. could not be split into separate infra-specific taxa could be attributed to its being an obligate outbreeder with no apparent geographical or ecological barriers within its distribution.

The main clinal variation in R.acris s.s. is in a West-East direction; a further cline occurs in a South-North direction in the North West of its distribution. R.acris subsp. friesanus (Jord.) Rouy & Fouc. forms no part of this variation pattern, although its

distribution is completely overlapped by that of subsp. acris. It appears likely that it has previously been at least ecologically isolated from subsp. acris.

ACKNOWLEDGEMENTS

I should like to offer to Professor T.G. Tutin, my supervisor, my sincere thanks for his help and encouragement during this work.

I am very grateful to the many people who collected seed or plants from different parts of Europe for me; and to the directors of the following institutions who either allowed me to examine material at their herbaria or who sent loans of material: British Museum, Kew, Copenhagen, Vienna, Stockholm, Paris, Leningrad, Florence, Liverpool, Cambridge, Edinburgh.

My thanks go to the Laboratory Staff of the Botany Department, University of Leicester, especially to Mr. E. Singer for the photographic work he undertook.

This work was carried out during the tenure of a post graduate grant from S.R.C., to whom I am much indebted.

Chapter 1

INTRODUCTION

The Ranunculus acris L.s.l. complex belongs to the subgenus Ranunculus (subgenus Euranunculus (Gren. & Godr. / A.Gray), section Ranunculus (or to the section Chrysanthé (Spach) L.Benson in the classification of the genus according to Benson (1940)). It is held to be Linnaeus' nomenclatural type for the genus.

No satisfactory classification of the genus Ranunculus, at the sectional level has yet been produced. There is an obvious need for the whole genus to be revised, taking into account a wider range of characters than has previously been used. Previous classifications have frequently been based on too few characters, often with a single character having a very heavy bias. Benson (1940), for example, pays especial attention to the nectary scale.

The species in section Ranunculus are characterised by having caducous yellow petals, with the nectary covered by a flap which is more or less free laterally; they have distinctly beaked, compressed glabrous achenes; and the receptacle in fruit is not more than three times its length in flower.

R.acris is separable from most other European members of section Ranunculus in having a terete pedicel, patent sepals, and a glabrous receptacle. Those species which are similar in these characters may

be distinguished from R.acris s.l. as follows: R.lanuginosus L. has orangy-yellow petals, rather than golden-yellow ones, has larger achenes (4 mm and over) and has leaves usually only 3-lobed. R.serbicus Vis. and R.brutius Ten. are both distinguishable by having the beaks of their achenes at least half as long as their achenes; in R.acris the beak seldom reaches such dimensions.

Plants within the R.acris complex possess vertical or oblique premorse, or short horizontal rhizomatous rootstocks. Davis (1960) when considering Turkish species belonging to subgenus Ranunculus found that he could separate them into two distinct groups chiefly on the presence or absence of a premorse or of a rhizomatous rootstock. But he realised that if he had extended this classification to include European species, R.acris would have cut across the classification, although on the basis of other characters it ought to have belonged to the group characterised by the possession of a premorse rootstock.

The basal leaves of R.acris are divided in a palmate rather than in a biternate manner. The degree of lobing of the leaf varies greatly. The inflorescence is usually a much branched bracteate cyme. The pedicels are terete and are pubescent.

R.acris is among the Ranunculus species possessing $2n=14$ chromosomes (see chapter 9). Within the genus a basic number of 8 is more common than one of 7. Gregory (1941) concluded from a consideration of the rest of the family possessing Ranunculus-type chromosomes and especially from the similar situation in Anemone, that

7 was probably a derived number.

Both Larter (1932) and Coonen (1939) found a remarkable resemblance in the karyotypes throughout the genus. Larter found that in the species he investigated which possessed a basic number of 7, ($2n=14$ in R.acris, R.chius DC. and R.nelsonii A.Gray, $2n=28$ in R.serbicus Vis.) all differed in the composition of their chromosomes. If he is correct this would show that the basic number of 7 has probably arisen independently in each case. The difference, if correct, between the karyotype of R.acris and R.serbicus is interesting as they have generally been held to be closely related species.

Distribution

A summary of the distribution of R.acris s.l. is given by Harper (1957). It is generally distributed over Europe, where it is commonly found right up to the North Coast. To the West it reaches the British Isles, The Faeroes and Iceland. It also occurs in Greenland, but there has been some dispute as to whether it is truly native there. It is introduced in Svalbard and has been reported in Jan Mayen.

Its distribution in the South of Europe is more limited. It is absent in Portugal, and in Spain only occurs in the north, east and south-east; it also extends into Morocco. Harper states that it is present in Corsica and Sardinia; but all the herbarium material from these islands, labelled as R.acris, has proved to be referable to other

species. He states that in Italy it does not extend much further south than Florence. Herbarium material has been seen from localities in the Apennines as far south as lat. 42° N.

In the Balkan Peninsula it extends as far south as the Macedonia region of Greece. Material has been seen from Albania, a country in which it had been stated not to occur.

The distribution of the complex extends eastwards through Siberia and a series of types is to be found in E.Asia.

R.acris has been introduced to America where it forms a continuous distributional belt including the Great Lakes and spreading as far south as Baltimore, Indiana and Illinois. It is also widely distributed in discrete communities over America mainly between 30° N and 50° N. It spreads as far westwards as the Eastern Aleutian Islands (Hultén 1944 and 1960). Benson (1948) states that in places such as Washington it has spread into new territory with amazing rapidity; and that it has spread more rapidly in the Pacific and Northern forest, than into the Rocky Mountains, the deciduous forests and the Prairies.

It has also been introduced into S.Africa, and New Zealand (Fisher 1966) and has been reported from Abyssinia.

Ecology

R.acris is a species tolerant of a wide range of habitats and it is widespread over most of its range. The variety of habitats in which it occurs include grazed and mown grasslands (including

lawns, where it is able to maintain itself but not to flower) and mountain habitats, including snow-patch habitats in the Northern European countries, also woodlands, fenlands and sand dunes. A summary of the habitats in which it occurs in Britain is given by Harper (1957).

One of its main limiting factors appears to be that of the water content of the soil. It is absent from areas permanently water-logged and from those which experience serious summer droughts. Its peak of flowering is before any possible periods of summer drought.

Its absence over large areas of chalk-grassland, such as in S.England, appears to be due to lack of moisture rather than to the chemical composition of the soil, as it will grow in similar grassland where there is sufficient moisture (Hope-Simpson in Harper 1957). In some chalk-grassland regions, as was observed in the Chilterns, R.acris may only occur in a narrow band of vegetation round a wood, where the rain-drip off the trees provides sufficient moisture.

R.acris is not markedly calcicole or calcifuge, although it does appear to be limited by a very low base status. McVean and Ratcliffe (1962) list R.acris as a species indicative of a better base-status in Agrostis-Festuca grassland and as a good differential species in separating species-rich and species-poor Nardus sub-alpinum, Alpine Deschampsia caespitosa and Deschampsieto-Rhytidadelphetum. In mountain habitats it is also associated with even more calcareous habitats such as Saxifraga aizoides banks, which are held by McVean and Ratcliffe to be the most reliable community indicating the presence of highly calcareous rocks.

The competition between the other common species of Ranunculus occurring in British meadows is largely prevented by the precisely determined conditions required by each species for germination. R.acris requires more moisture than R.bulbosus but less than R.repens (Harper 1957).

Aims and General Methods

The European range of R.acris s.l. was examined to find the type of variational patterns occurring, and to see how these patterns related to previous classifications of the group.

Most of the work was carried out on herbarium material, since this was the only way in which a wide coverage of the total European distribution could be examined. This was supplemented wherever possible by living material, both in the wild and in cultivation.

Using the material available, a broadly morphological classification was the only possible one. As many characters as were possible, from as many parts of the plant as possible, were investigated. A classification based on the morphological affinities of present-day organisms, even found from a wide range of characters, will not necessarily be a phylogenetic classification, as fossil evidence is needed before a truly phylogenetic classification can be produced. Even if a phylogenetic classification was possible, it would not necessarily be the most useful classification for a group of organisms in the form in which they occur in the present-day.

From the literature on R.acris and from the disparity in the

classifications of the group, it was obvious that the group contained many local variations, and that these variations, in a reportedly widespread and outbreeding plant, would seldom be likely to be of a disjunct nature. It was therefore felt that a purely numerical method of investigating the affinities of plants within the group was not applicable, and that variation, where continuous, would be better shown up by graphical and mapping techniques, which would still show up any discontinuities.

A numerical method forms a sound basis for comparing affinities of disjunct groups, but would not show up the geographical variational pattern. Where there is continuous variation a statistical analysis of character types within localities is applicable, but too few localities within the total range could have been sampled in the time available to have made such an approach worthwhile.

More 'good' characters than were found would have been needed for a numerical method. The plants were found to be all fairly closely related; nearly all the characters showed great variation in plants from a single locality and also great variation due to environmental conditions and due to time of year. The number of plants which had to be examined before much of the continuous variation was recognisable, would have been impossibly large for a numerical method. Sokal and Sneath (1963) state that matrices of formidable size would have to be processed if numerous individuals of each of several apparent taxonomic groups were used when computing a classificatory hierarchy.

The cultivated material was used to find the range of variation from localities in different regions, when the plants were growing under the same conditions. Measurements of the plants were not made until the plants had been in cultivation for at least a year. The cultivated material was also used to find the seasonal variation within the plants and to compare the reactions of plants from widely differing regions, when growing under the same conditions. Transplant experiments were carried out to try and find some of the effects of environment on the plants. Experiments were also carried out to investigate the breeding mechanisms in force in the complex, which might account for the patterns of variation found.

The breeding experiments were carried out on plants growing in a greenhouse, but otherwise the plants were grown in the open. The plot of ground used, varied in dampness. Using several types of plants, clonal tests were made to find the effect of this variation in soil conditions on the plants. It was found that in some plants the flowering stems were slightly shorter at the drier end and the plants very slightly hairier. These differences were in all cases however negligible in comparison with the differences between separate plants from the same locality. Thus it was felt that the extra labour involved in growing the plants from the same locality in different parts of the plot, to make allowance for the variation in soil conditions, was not justified.

In the following chapters the characters of different parts of the plant and their variations are considered separately. The variational patterns of the plant types as a whole is discussed in Chapter 10.

Chapter 2

ABNORMALITIES AND OTHER WIDESPREAD CHARACTERS OF SCATTERED OCCURRENCE

Gynodimorphism of the flowers

The frequent occurrence of R.acris plants bearing flowers which are functionally only female has been noted by many authors. It occurs more commonly than in R.repens or R.bulbosus, and differs from these two species in that the stamens are further reduced in form being either completely absent or scale like (Whitelegge 1878).

However, all grades from the functionally only-female to the normal hermaphrodite flower occur (Marsden-Jones and Turrill 1929b and 1935). Among the names given to the extreme female forms are § parviflorus Mort. (H.Mortensis, herbarium sheet 1873), and var., subvar., or forma minutiflorus Druce (1916). Such names reflect the appearance of the flower, which always has very small petals. The size of petal, according to Marsden-Jones and Turrill (1935), can also be correlated to the degree of femaleness in intermediate flowers even where these occur on the same plant.

Although there seems to be genetical control of these flower types, fluctuations of types within a single plant are common. Even plants which have been totally female for years may revert back and produce some viable pollen (Marsden-Jones and Turrill 1935).

Plants failing to produce either pollen or ovaries have also occasionally been reported, but only a single record of a plant producing only pollen has been seen. This functionally male plant differed from the former types in being malformed, both in its flowers and in its vegetative parts (Parkin 1929a & b and 1932, Marsden-Jones and Turrill 1935). Male flowers have been seen on plants damaged by spray and a single plant in cultivation produced such flowers in 1967, but not in 1966; in both these cases they resembled the previously reported male plant in having small very narrow petals, reminiscent of R.ficaria, but were vegetatively normal.

Whyte (1929a and 1929b) investigating these female types cytologically, found that the degree of femaleness could be correlated with the degree of overlap in the timing of the 'anther phase', (marked by commencement of physiological activity of the tapetum and continuing until the formation of mature pollen grains), and the 'ovule phase' (commencing with the growth of the ovules and continuing until formation of mature embryo sacs). In normal hermaphrodite flowers these formed two distinct and successive phases: in totally female flowers there was a complete coincidence; whereas in intermediate flowers, the commencement of growth in the ovules is associated with the sudden failure of the tapetum in the anthers of the same flower with cessation of pollen development as a sequel.

It has been suggested that R.acris is showing possible evolution to a true gynodioecious condition as found in some labiates. Gynodimorphism appeared relatively common throughout the complex and was not found to be correlated with any decrease in seed production.

Colour variants of the petals

Marsden-Jones and Turrill (1929) described a series of colour variants of paler colours in the petals. As such variants only occurred on solitary plants or only on small numbers of plants within any population, Marsden-Jones and Turrill concluded that they arose as mutations in different localities. A pale colour of the petals was found to be correlated with reduced vigor of the plants (Marsden-Jones and Turrill 1952). Such colour variants have only very rarely been seen in any of the natural populations examined.

Brown pigmentation of the vegetative parts

Brown pigmentation of the stem, leaves and sepals is due to suffusion with red anthocyanin of a single layer of cells immediately below the colourless epidermis. From breeding experiments with plants showing various grades of the pigmentation, Marsden-Jones and Turrill (1952) concluded that it was due to a genetical factor.

A low percentage of all types of R.acris plants from all the regions represented in cultivation showed this character. No geographical trends in percentage of occurrence were visible, and as it is a character

not visible in pressed material, it was ignored.

Vegetative abnormalities

Abnormalities of the vegetative parts which have been seen, have included varying degrees of fasciation of stems and abnormalities of the leaves, such as duplication of one of the major lobes. Plants have also been seen in which the leaves are distorted and in which the veins approach a parallel condition; it is possible that this might have been due to a virus infection.

Both abnormalities of vegetative and floral parts have often been found to occur only within a sector of a plant and subsequently they often revert back to a normal condition.

Abnormalities of the floral organs

Abnormalities of the floral organs appear to be very numerous in the Ranunculaceae. Meyer (1966) reports for the genus Ranunculus, phylloid calyx, corolla and carpels, petaloid calyx, stamens and carpels and carpelloid stamens. Petaloidy is reported as the commonest abnormality in flowers, whereas sepaloidy is relatively uncommon. Sepaloid carpels were reported from other genera of the Ranunculaceae.

Many abnormalities have been seen in the flowers of R.acris. Some of these have transformed characters usually held as safe diagnostic

characteristics of the R.acris complex.

The habit of the sepals, whether spreading or reflexed, forms a reliable diagnostic character segregating a number of species; so does the presence or absence of hairs on the receptacle. The constancy of this latter character within the genus is considerably greater than that of the pubescence on the vegetative parts (Benson 1948).

The R.acris complex is characterised by having spreading sepals. However Harper (1957) reports a colony of plants in Norway having reflexed sepals, and among the plants which have been grown in a greenhouse, many had deflexed sepals and some truly reflexed sepals. Benson (1948) comments on the fact that when flowers open indoors, those of some species which have a reflexed calyx, frequently have spreading sepals.

The R.acris complex is characterised by having glabrous receptacles. In several cases, in otherwise normal flowers, including ones in cultivation, some plants were found to have a tuft of a few hairs at the apex of the receptacle.

The complex is also characterised by having glabrous achenes, but four cases of achenes bearing hairs have been seen. In two of these cases such achenes were associated with further abnormalities. In one of these the 'corolla' was of the form of hairy cotyledons and the filaments were densely hairy for their whole length. The other such case of achenes bearing hairs occurred on a plant in cultivation from England (loc. 62a). At the beginning of the flowering season in 1966,

this plant produced two sorts of abnormal flowers, some showing petaloidy of the stamens and the others sepaloidy of the carpels. Where the carpels were seploid in form, the ovules were borne naked. In the latter situation some of the 'normal' achenes bore hairs. It is suggested that in the other cases the presence of hairs on the achenes is also a sign of incipient sepaloidy of the achenes.

Chapter 3

THE ROOTSTOCK

In previous works the type of rootstock in R.acris, whether premorse and erect or rhizomatous and horizontal, has been held to be a character of primary importance. Davis and Heywood (1963) state that 'the presence or absence of a horizontal rootstock is a critical feature in the recognition of the subspecies of Ranunculus acris in Europe and is as important as achene morphology.'

When examining herbarium material, the extent of elongation of the rootstock appeared to be the only character on which the types of rootstock could be divided. Using this single character only, rarely was any difficulty found in deciding whether a rootstock was rhizomatous or not. Thus there seemed to be a clear distinction between the two types, but the few intermediate plants seen seemed to show that the only difference was in degree of elongation.

Clear geographical groupings of the rhizomatous plants were apparent from the herbarium studies. There is an E.European group centred mainly in Rumania but also occurring in Hungary, S.W.Ukraine, Yugoslavia and Bulgaria; a group with its centre of distribution in S.Spain and N.Morocco; and a third group with its main centre of distribution in E.France, W.Switzerland and neighbouring regions, but also occurring further afield, e.g., Austria and Sweden, where it is held to be introduced. The plants occurring in the Pyrenees and N.E.Spain are

similar in most ways to the rhizomatous plants of E.France. (For distributions see Map 1 or 2).

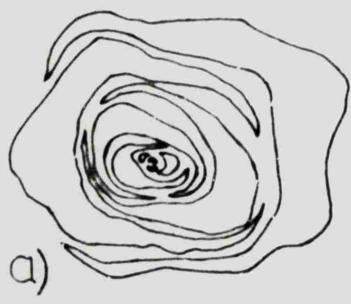
The rootstocks of the plants in cultivation were examined to find if there were any other characteristics of the rootstock form, other than just the extent of elongation, separating the two types of rootstock. In cultivation there was an array of types ranging from E.French plants with long rhizomes, to plants intermediate between these and the premorse types, and plants with premorse bases of varying degrees of elongation.

It was found that whereas the leaves on a premorse rootstock were borne in a spiral arrangement, those on a rhizome had an alternate two-ranked phyllotaxy. Fig. 1a shows sections of buds to show these two types of phyllotaxy.

Plants from localities 39 and 41 (E.France - see appendix) had the longest rhizomes. Plants from loc. 33 (Germany) had shorter rhizomes, the leaves in the buds still maintained a distinct, alternating two-ranked phyllotaxy, but this was less evident in the mature leaves (fig. 2).

From the examination of further intermediate plants it was apparent that although the rate of elongation of the rootstock was primarily under genetical control it varied during the life cycle of the plant. The phyllotaxy was found to be linked to the rate of elongation and a certain type was therefore not invariably displayed by a plant of a certain genetical composition. This was well illustrated

A



a)

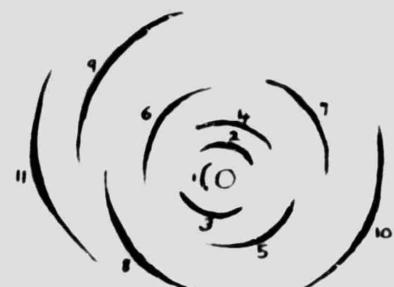


b)

Sections of buds to show

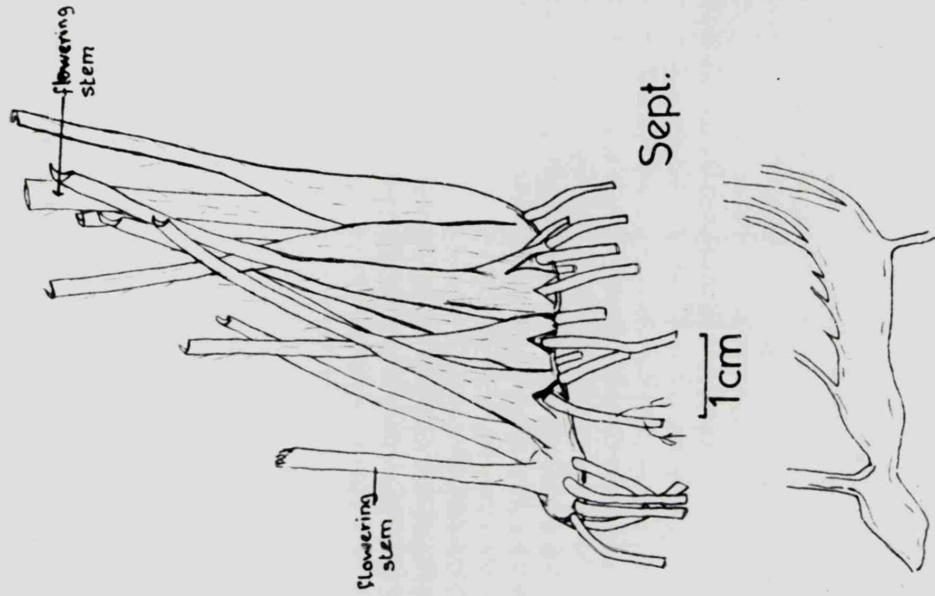
a)Spiral phyllotaxy b)two ranked phyllotaxy

B



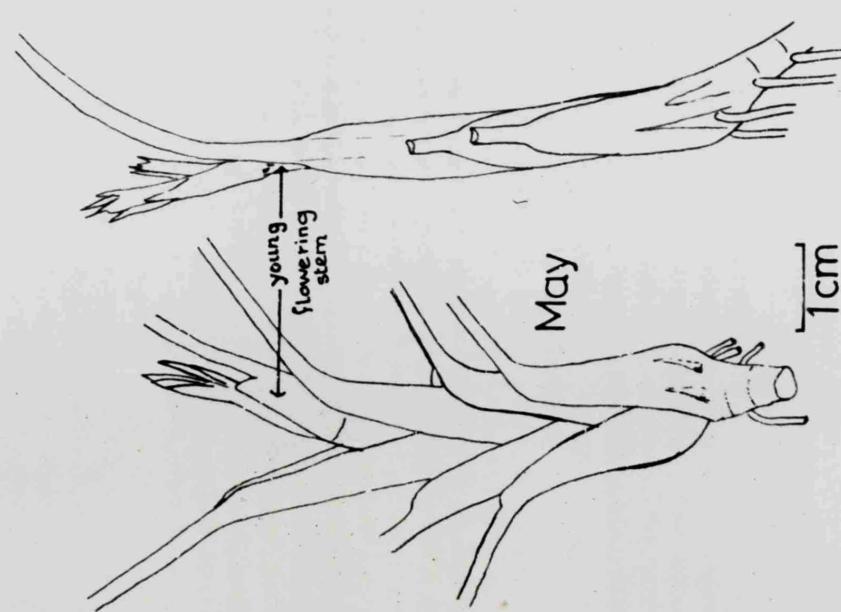
Diagrams to show various phyllotaxies found within a single plant from loc. 44.

FIG.1



Sept.

1cm



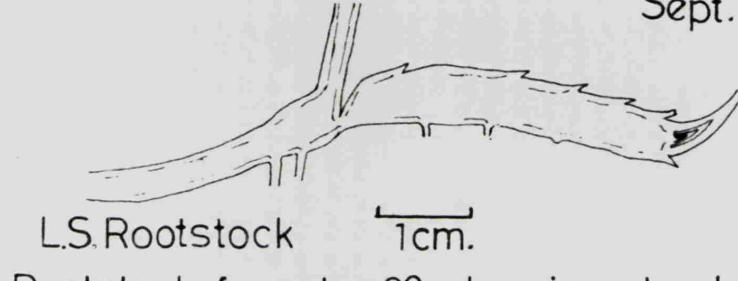
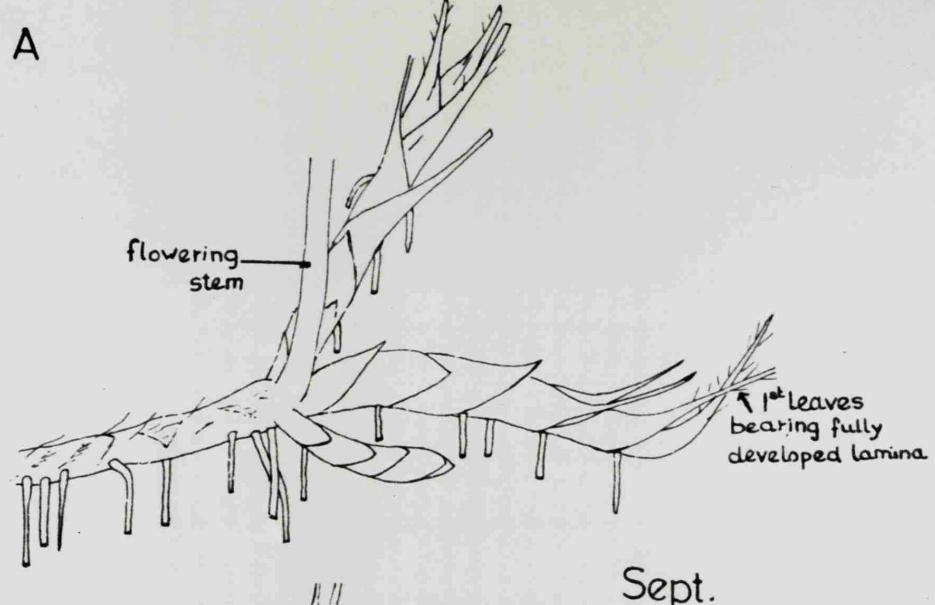
May

1cm

Loc.39 Rhizomes very elongated, two ranked phyllotaxy still obvious in mature leaves.

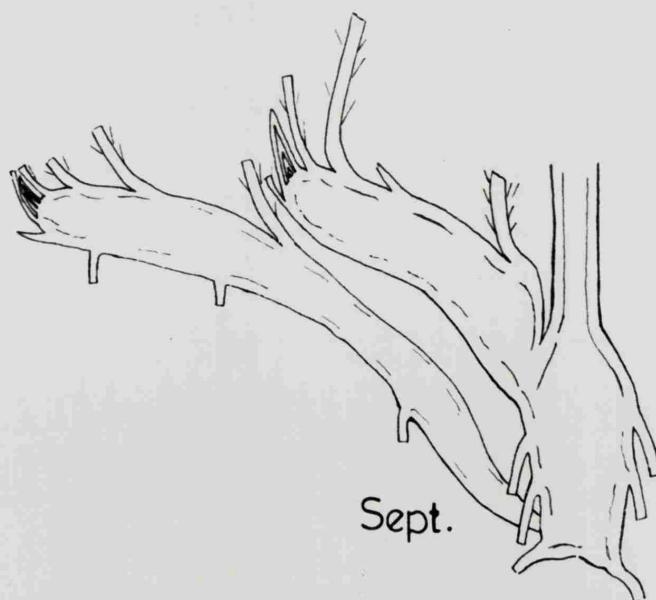
Loc.33 Rhizomes less elongated than in loc.39 and two ranked phyllotaxy less obvious in mature leaves.

FIG. 2



Rootstock from loc. 39 showing development of young rhizomes

B



L.S. of 1st year rootstock from loc. 39 showing production of rhizomes from a 'premorse' rootstock

FIG. 3

by plants from loc. 44 (Italy). These had rhizomes slightly shorter than those from loc. 33; in leaf-shape they, like those from loc. 33, appeared intermediate between such plants as those from loc. 39 and truly premorse plants. In a single plant from loc. 44 actively elongating vegetative shoots showed a two-ranked phyllotaxy, but rootstocks which had stopped elongating due to the production of a flowering shoot showed various transitions in phyllotaxy, which in the larger buds approached a perfect spiral arrangement (see fig. 1B). Occasional examples of a few leaves showing such a reversal, associated with a flowering stalk, were even found in rhizomes of plants from loc. 39.

A further reason for believing that the type of phyllotaxy is linked to the type of elongation is that in their first year the E.French rhizomatous plants were often identical to all the other plants, in having a premorse rootstock and perfect spiral phyllotaxy, although at times a two-ranked phyllotaxy was produced before the production of the first flowering stem. In these plants rhizomes were first produced by the growth of the lateral buds (see fig. 3B). The same situation was found to occur in R.serbicus Vis. It may be concluded that such a situation probably occurs throughout all the rhizomatous types of the R.acris complex. A herbarium specimen was seen of a plant which agreed in all other characters with the E.European rhizomatous type, except for the possession of a premorse rootstock. This discrepancy in rootstock type could well be explained, as was corroborated by the leaf-shape, by the plant being in its first year.

Plants from loc. 22 (Sweden) showed a relationship to E. French rhizomatous types, not only in morphological characters, but also in such biological aspects as their reaction to winter conditions; they had short horizontal rhizomes, much less elongated than those in plants from loc. 33 or 44. The leaves were always spirally arranged. The extent of elongation of the rootstock in these plants was still much greater than that seen in all but four or five plants (large plants from damp habitats) among the material of the premorse types examined, with the exception of plants from Foula (Shetlands).

All the plants in two separate collections of live material which were received from Foula had rootstocks as elongated as those from loc. 22 (see Fig. 4B). They similarly had a spiral phyllotaxy. Unlike the plants from loc. 22 they show no traces of any relationship to true rhizomatous types. Foula is a very isolated island and this appears to be yet a further example of divergence from the mainland types, as has occurred in other organisms living on this island.

The type of phyllotaxy seems to be a useful character in assessing the extent of elongation, but does not appear to be a satisfactory criterion for distinguishing a rhizome from a premorse base. A further such character was found to be the form of the first leaves produced on a new lateral rhizome. In very elongated rhizomes only the sheath part of these leaves developed. Several such scale leaves were produced on the rhizomes of plants from loc. 39 (see fig. 3A). In plants from loc. 41, which possessed slightly shorter rhizomes only one or two of

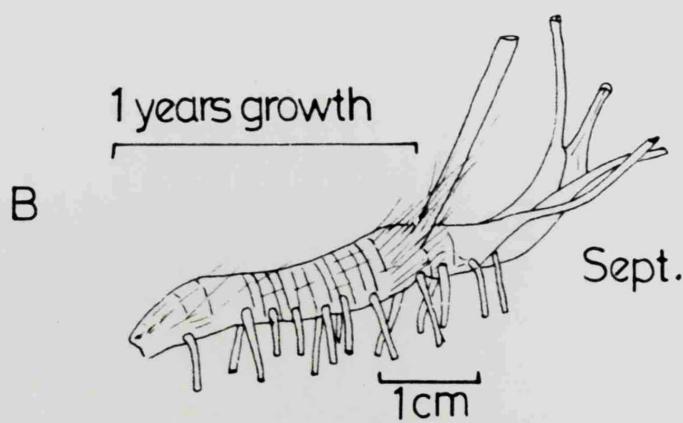
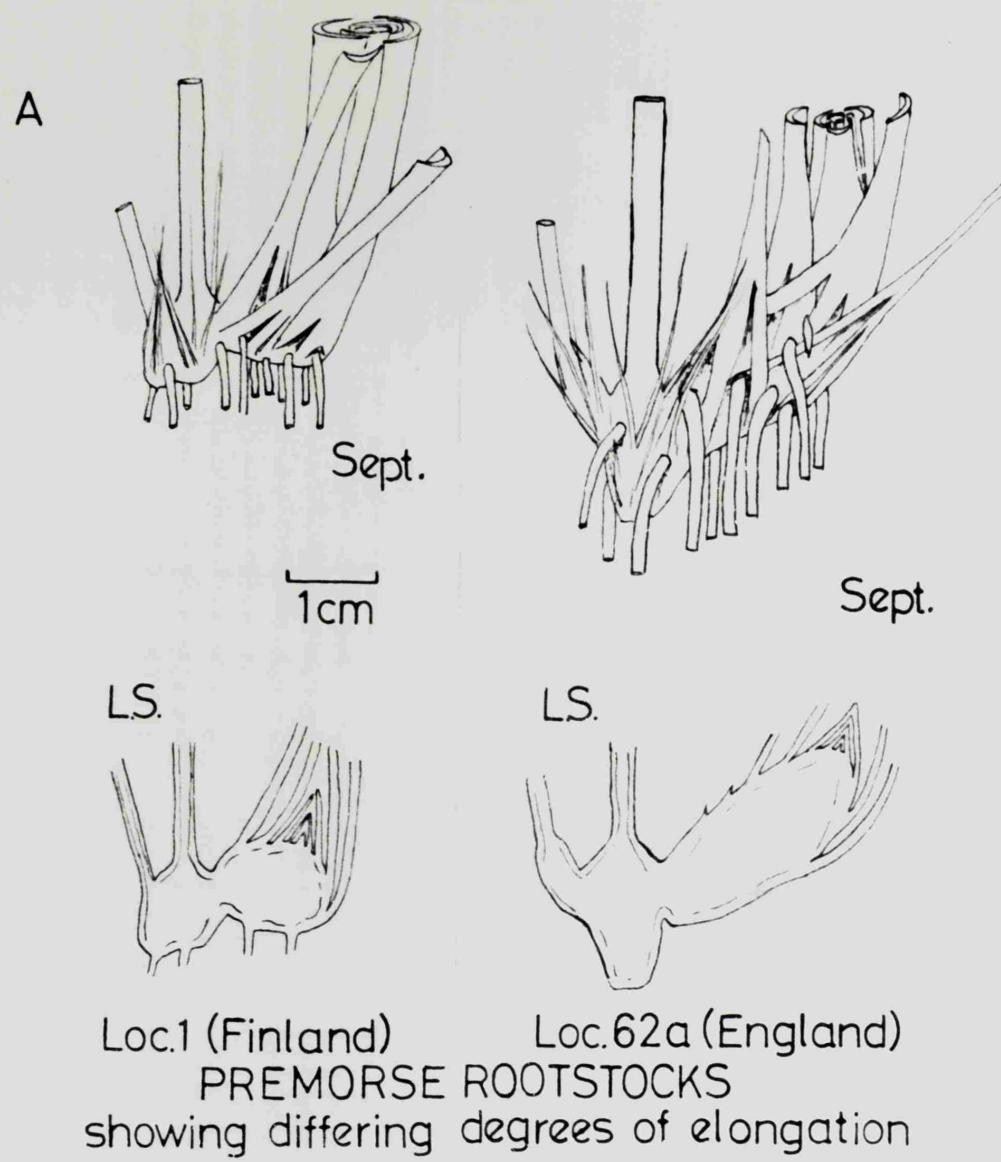
these scale leaves were produced on each rhizome. In plants from locs. 33 and 44 with even shorter rhizomes, leaves approaching this state were only rarely seen.

Importance has been placed by some authors on the direction of growth of the rootstock, whether horizontal, inclined or vertical. Rhizomes usually grow horizontally and premorse rootstocks usually vertically, but ~~in~~ the more elongated premorse types are inclined.

Premorse rootstocks to the West of Europe are said to be more elongated than those from the East (Jordan 1864), and this was found to be generally true (see fig. 4A). But such differences were not constant enough or easy enough to measure, to be used as a diagnostic character.

Drabble (1930), quoted in Harper (1957), when studying British plants and trying to differentiate between premorse and rhizomatous types, stated that growth direction and length of rootstock, being more or less dependent on rate of decomposition, are at least partly determined by soil conditions. This indeed seems to be partly true for the premorse types which occur in Britain. Drabble was unaware that true rhizomatous types were not represented in Britain.

A test was made to see if the type of phyllotaxy could in any way be linked with the direction of growth. Plants from loc. 39 (possessing long rhizomes) and ones from loc. 62a (England) (possessing a premorse rootstock) were planted in pots. Once established the entire



Loc.107, Foula Shetlands.
Rootstock elongated
phyllotaxy still spiral.

FIG.4

plants were covered by a thick layer of sand. In both plants upward growth occurred by extensive elongation of the internodes, but in neither was the phyllotaxy at all affected (see fig. 5). Also in a plant from loc. 44 (Italy) there was no difference in appearance, length or phyllotaxy, between an abnormal rhizome, which had grown in a perfectly vertical direction for 10cm., and the rest, which had grown in the normal horizontal direction.

In the majority of material there seems little difficulty in distinguishing between a rhizomatous and a premorse rootstock. This appears mainly to be due to the lack of intermediates between the rhizomatous groups and premorse plants. Where intermediates do occur, as with the E.French rhizomatous plants, such a division must be purely arbitrary as all degrees of elongation are found.

Plants from localities 33, 44, and 22 are such intermediate plants. It might be argued that rootstocks always showing a spiral phyllotaxy, as in plants from loc. 22, ought to be termed premorse, but such rootstocks are far more elongated than truly premorse bases, and phyllotaxy can only rarely be determined from herbarium material.

In the artificially produced hybrids it was found that rootstocks intermediate between those of the parent plants were produced. Hybrid plants, with plants from loc. 39 as one of the parents and a premorse based plant as the other, had well developed but shortish rhizomes. Hybrid plants, with plants from loc. 33 (possessing shorter rhizomes than those from loc. 39) as one of their parents had rootstocks showing two ranked phyllotaxy but with relatively little elongation.

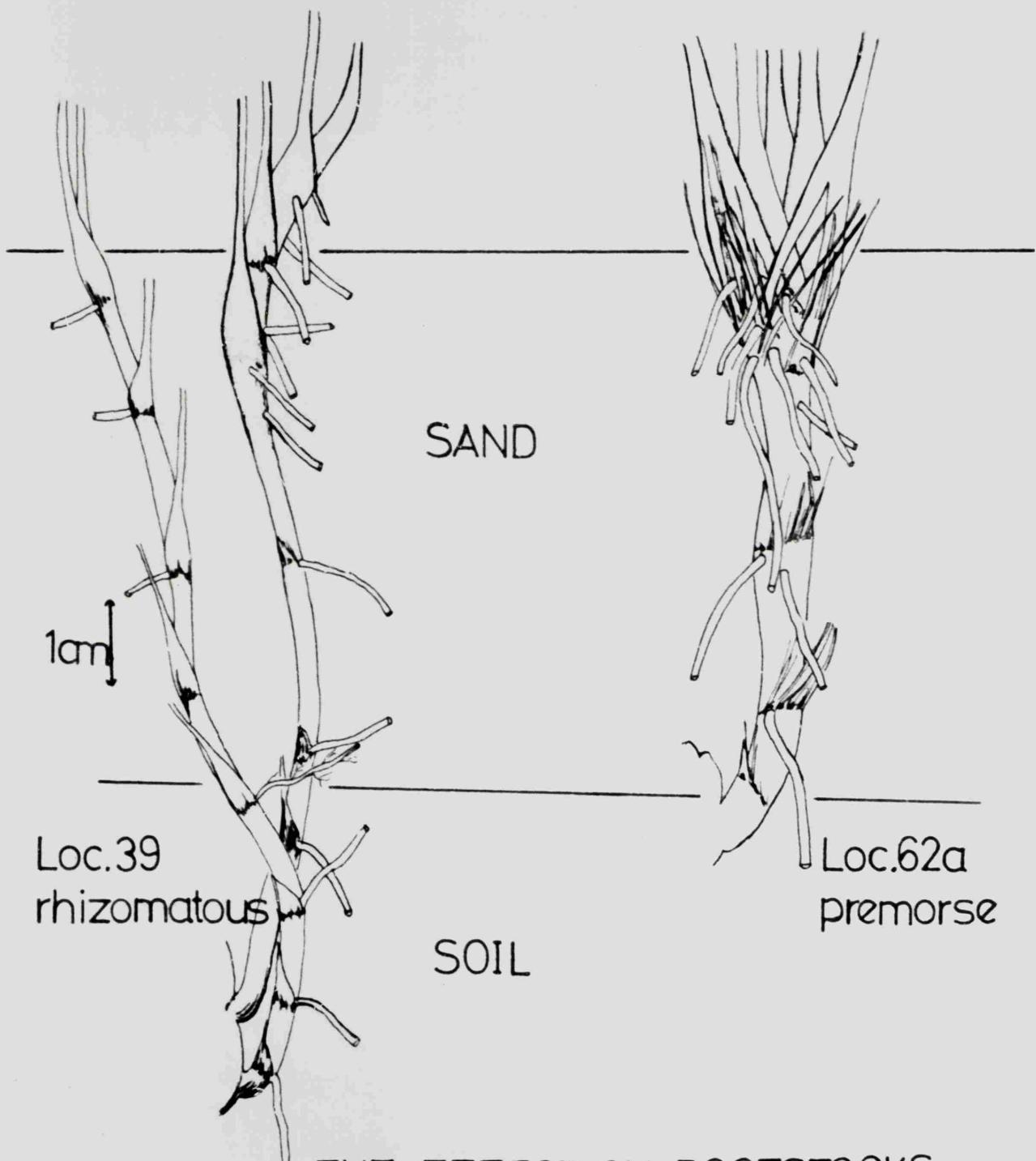


FIG. 5

THE EFFECT ON ROOTSTOCKS
OF INUNDATION BY SAND

Chapter 4

THE LEAF

The leaf of Ranunculus acris L.s.l. is palmate in shape and is primarily three lobed. These lobes or 'segments' may either be shortly stalked or joined for a short distance. Descriptions often refer to the leaf being 3,5 or 7 lobed; this is due to the lateral segments being deeply 2-lobed and the median segment 3-lobed in the more finely dissected leaves. These secondary lobes are always joined to one another for part of their length. These principal divisions are then usually further lobed and the lobes toothed.

To make terminology easier the term 'segment' will only be used when referring to the three main divisions of the leaf, and the term 'lobe' to further divisions of the segments.

Different methods of measuring the leaf, including a consideration of those used by other authors, were tried, to find which measurements would most accurately define the shapes involved.

Due to the type of variation found in leaf-shape within the group, no two leaves can be said to be of the same basic shape without the correlation of several ratios. This excludes the possibility of finding any relatively simple mathematical transformation relating the shapes as Fisher (1960) found in R.insignis Hook.f.; where, similarity in only a single ratio, was paralleled by similarity in actual shape. This species, however, had the advantage of having simple leaves and in

showing negligible seasonal variation.

The method of finding the degree of lobing in leaves as used in the study of Talbert and Holch (1957) again appeared inapplicable, as in this case shape and degree of lobing were directly correlated.

Melville (1960) suggests the use of polar co-ordinates for defining leaf-shape in palmate leaves, his method of rectangular co-ordinates (1937) being 'cumbersome for very complex shapes.' The use of polar co-ordinates, however, does not seem to be the easiest and most direct method of measuring the leaf, and a series of linear measurements were devised which appear to define the leaf-shape adequately.

The shape of the leaf as a whole can be defined by measurements made on the median segment only, as the degree and form of the dissection of a leaf is similar throughout. A variation does occur in the ratio of the length of the median segment to that of the lateral segments, but this in no way appears to be correlated with shape type.

The measurements used are shown in fig.6, which shows their application to two extreme shapes of leaf.

They are as follows:-

l-length of the median segment.

x-length of 'fusion' between the median and lateral segment; or

the length of the stalk of the median segment (x').

w-width of the median lobe of the median segment, measured immediately above the major division of the segment.

z -distance from the base of the median segment to the major division of this segment.

q -distance between the tips of the lateral lobes of the median segment.

d -height of these tips above the base of the median segment.

The ratios x/l , z/l , and w/l were calculated, giving comparable values for the dissection of the leaf and fineness of the segments. It was felt that ratios in this form gave the most easily comparable mental-pictures of the leaf-shapes involved. These values have been turned into percentage values, for ease of plotting. A comparable value for the angle of divergence of the two side lobes is given by the ratio q/d , this being $2 \tan. \frac{1}{2}$ this angle.

Correlation between these ratios, even for plants from the same locality, is frequently lacking: they have therefore not been combined to form any sort of composite leaf index. Lewis (1965) in measuring leaf dissection in R.acris s.s. has as an index $l-w/\text{width of central lobe}$. This may be satisfactory for giving a rough estimate of the degree of dissection over a limited range of the complex, but not for defining leaf shape throughout the complex.

The two sides of a leaf are frequently dissimilar. Where this dissimilarity is slight, an average of the two measurements has been taken, but where one side is obviously abnormal in nature, this side has been ignored. Abnormal leaves, such as those with two median lobes have been completely ignored.

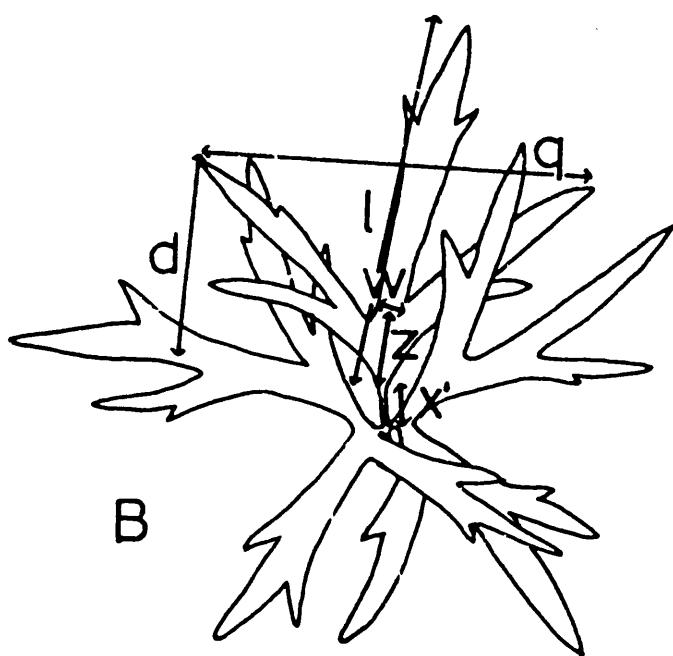
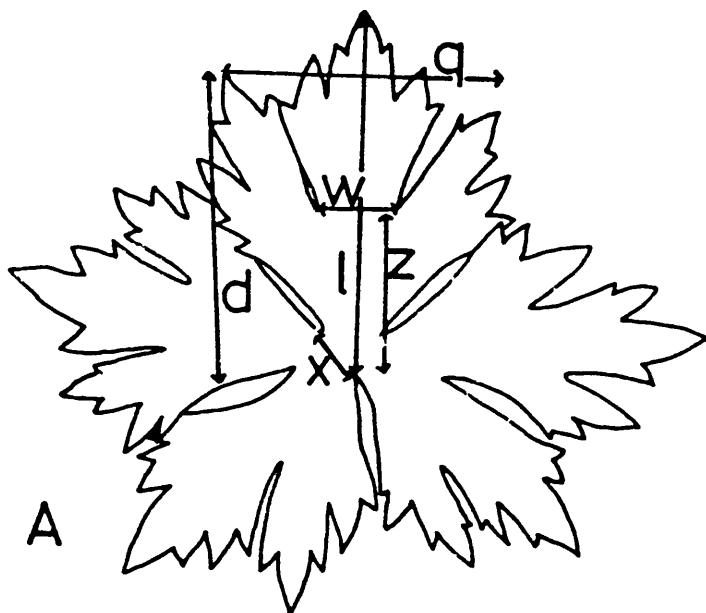


FIG. 6 LEAF-MEASUREMENTS

Measurements have been made to the nearest millimeter, except in the case of shorter lengths, where they have been made to the nearest $\frac{1}{2}$ millimeter.

The total lobing of the median segment has been recorded as the number of points per group or 'major lobe': no division can be drawn between 'teeth' and small 'lobes'. Leaf A in fig. 6 thus has 1:2:6 'teeth', leaf B 1:2. An average between the two sides is used and 'immature teeth' have been ignored.

Choice of leaves

Comparison of leaf-shape using herbarium material has been restricted to the innermost leaves of a rosette which has overwintered and produced a flowering stem. This restriction has been made as investigations using cultivated material have revealed great seasonal variation; the following outline of this is given to show the reasons for such a choice.

The successive leaves of a rosette in spring show increasing dissection. The change in shape between two successive leaves may be very great, especially in some montane plants. The leaves formed by the buds in the axils of these leaves, after the first flowering stem has been produced, are almost always strikingly different in shape, showing resemblances to the leaves produced by seedlings in their first season. These 'autumn' leaves have broader lobes and are less deeply divided than are the 'spring' leaves. The 'autumn' leaves also show

greater variation due to environment, and variation in their shape is due to the time of year of their production rather than to their position on the plant relative to the production of a flowering stem. However another reason for ignoring these 'autumn' leaves is that greater similarity between these leaves from different groups in the R.acris complex is shown, than between 'spring' leaves of the same groups. Seasonal variation in leaf-shape is discussed further in a later section of this chapter.

Fortunately among herbarium material the majority of plants have been collected with 'spring' leaves. R.acris is a 'common weed' over much of its distribution and seems to receive little attention except when it is at its peak of flowering, when fortunately it is associated with its 'spring' leaves. However it is unfortunate that it usually has only later type leaves during the major holiday period, when much collecting is done, and collections from some of the more interesting areas of its distribution have suffered in this respect.

Results

Leaf-shape, as recorded by the percentage values of x , z and w to the length of the median segment is shown diagrammatically in Map 1. This is drawn to give an idea of the distribution of different leaf-shapes. The ratio q/d has not been included, for although it is necessary in defining the shape of any individual leaf, it shows no definite

distributional trends. Both extremes of variation in this ratio are to be found among the more finely divided leaves. This is especially so at the upper end of the scale, where the lobes tend to curve outwards: thus the ratio is no longer a true measure of the initial angle of divergence of the lateral lobes. Curving inwards also occurs, but only rarely.

Direct comparisons of more than two characters in a graphical manner are impractical except for relatively small samples. In figs. 7 and 8 w/l has been plotted against z/l . These two ratios have been chosen as being those which most closely define the major characteristics of any leaf shape under observation.

If all results from the whole of Europe were plotted together it would show that no discontinuous variation of leaf shape occurs. Even if leaf-shape of plants possessing rhizomes were plotted against plants with premorse rootstocks it would be found that complete overlap of types would occur; with both extremes of variation being occupied by plants with premorse rootstocks. But by comparing plants from adjacent regions it has been possible to demonstrate the geographical trends that occur. For simplicity, division of regions has been mainly based on countries. Graphs have only been drawn up for those regions where fairly large samples have been examined.

In fig. 7A it can be seen that plants from France with a premorse rootstock and those with rhizomes, whose main centre of distribution is

E.France, show continuous variation. However, there is little overlap in leaf-shape between these two types of plants. Plants from Switzerland, Austria and Sweden, which possess rhizomes are seen to show the same type of variation as those from E.France. However, those plants possessing rhizomes, whose centre of distribution is the Pyrenees do not conform to this pattern of variation.

Fig.7B shows that there is a similar pattern and range of variation when plants with premorse rootstocks in E.European countries are compared with plants possessing rhizomes, whose centre of distribution is E.Europe. The leaf-shape of the premorse based plants is indeed similar to that of such plants in France, but although that of the two sets of plants with rhizomes appears similar on comparison of these two ratios alone, their general appearance rarely coincides. Fig.7B also shows the similarity in the variation of these ratios in the leaves of rhizomatous plants from southern Spain to those of E.Europe.

Fig.8B shows the range of variation in England and Wales compared with that of Scotland, Iceland and The Faeroes: all these plants are premorse. The range of variation is much greater than that of such plants occurring in France or E.Europe. A higher percentage of plants from Scotland have broadly lobed leaves than do those from England. The Scottish variational pattern is paralleled by that of Iceland and the Faeroes.

The variational pattern of leaf-shape of Scandinavian plants (fig.8A) appears somewhat similar to that of Great Britain, but the

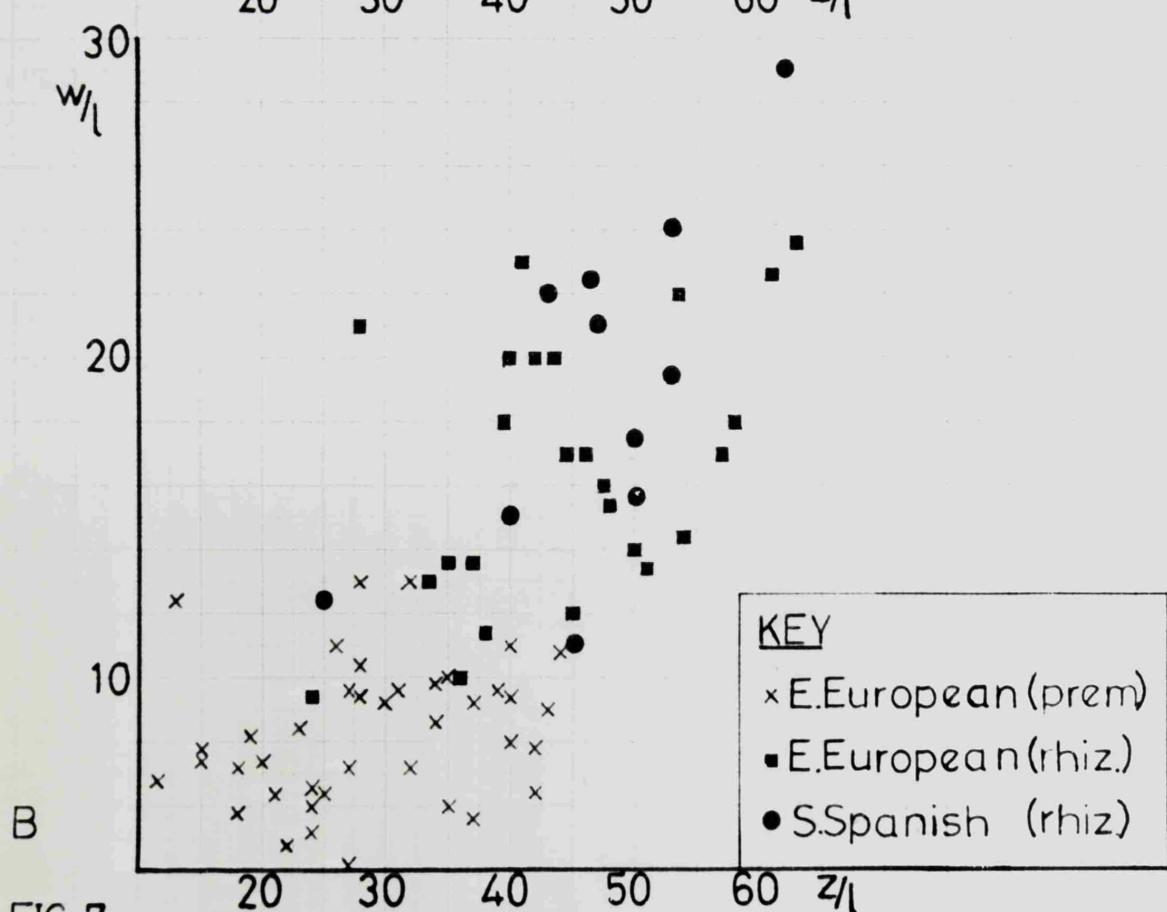
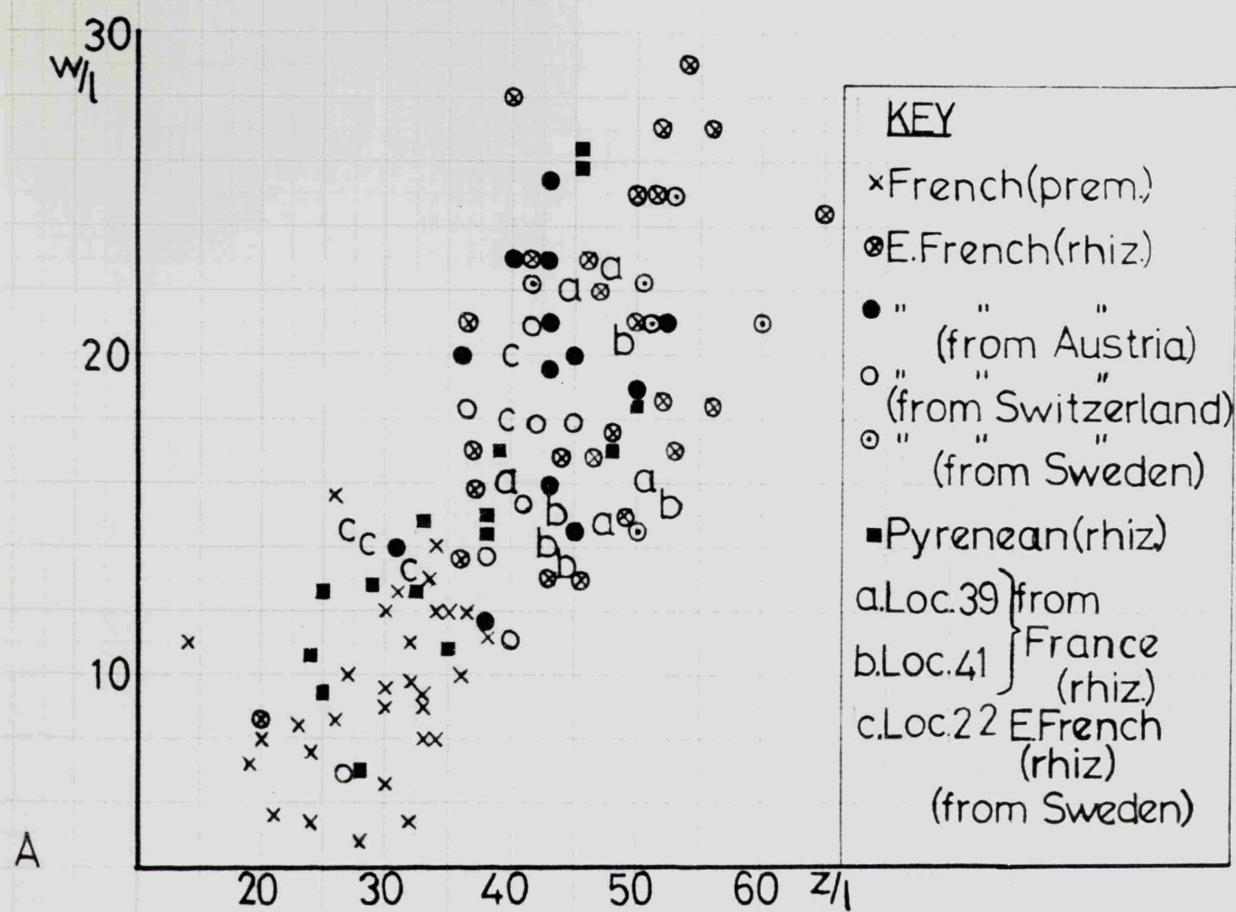


FIG. 7

GRAPHICAL COMPARISONS OF LEAF-SHAPE.

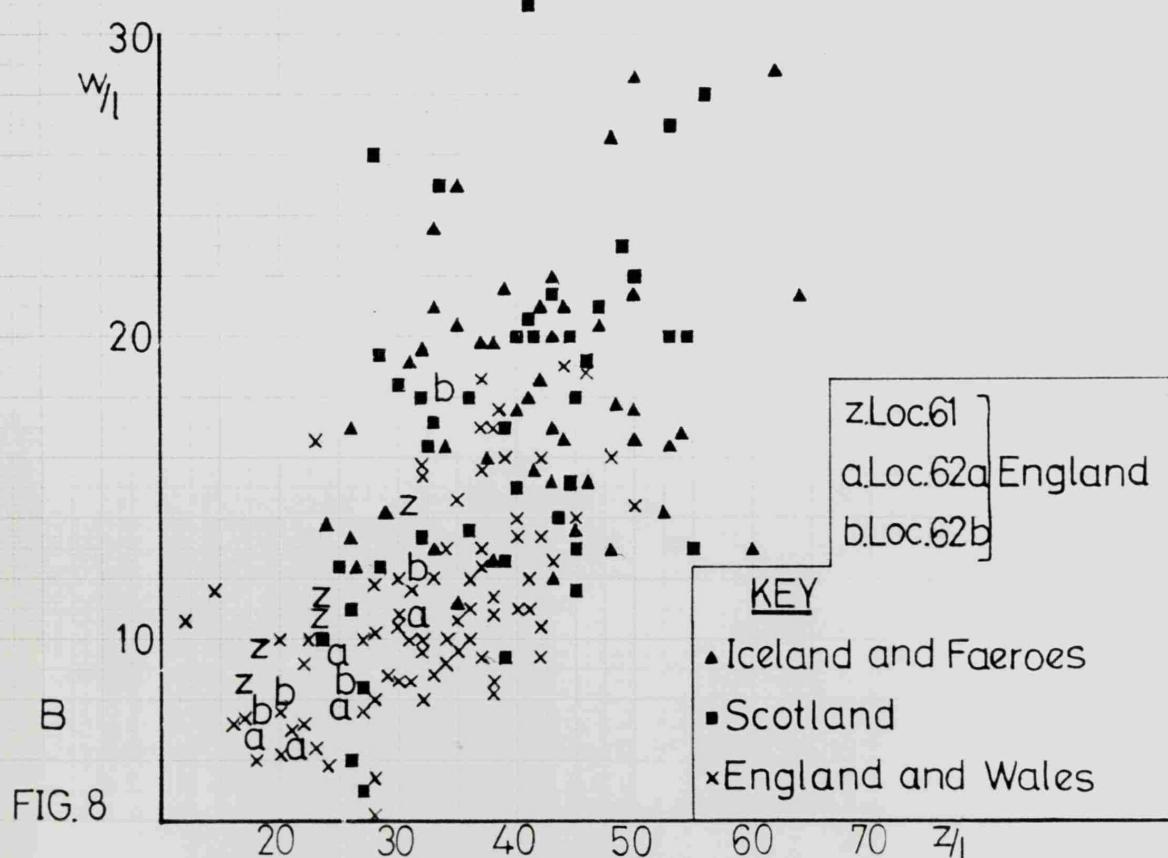
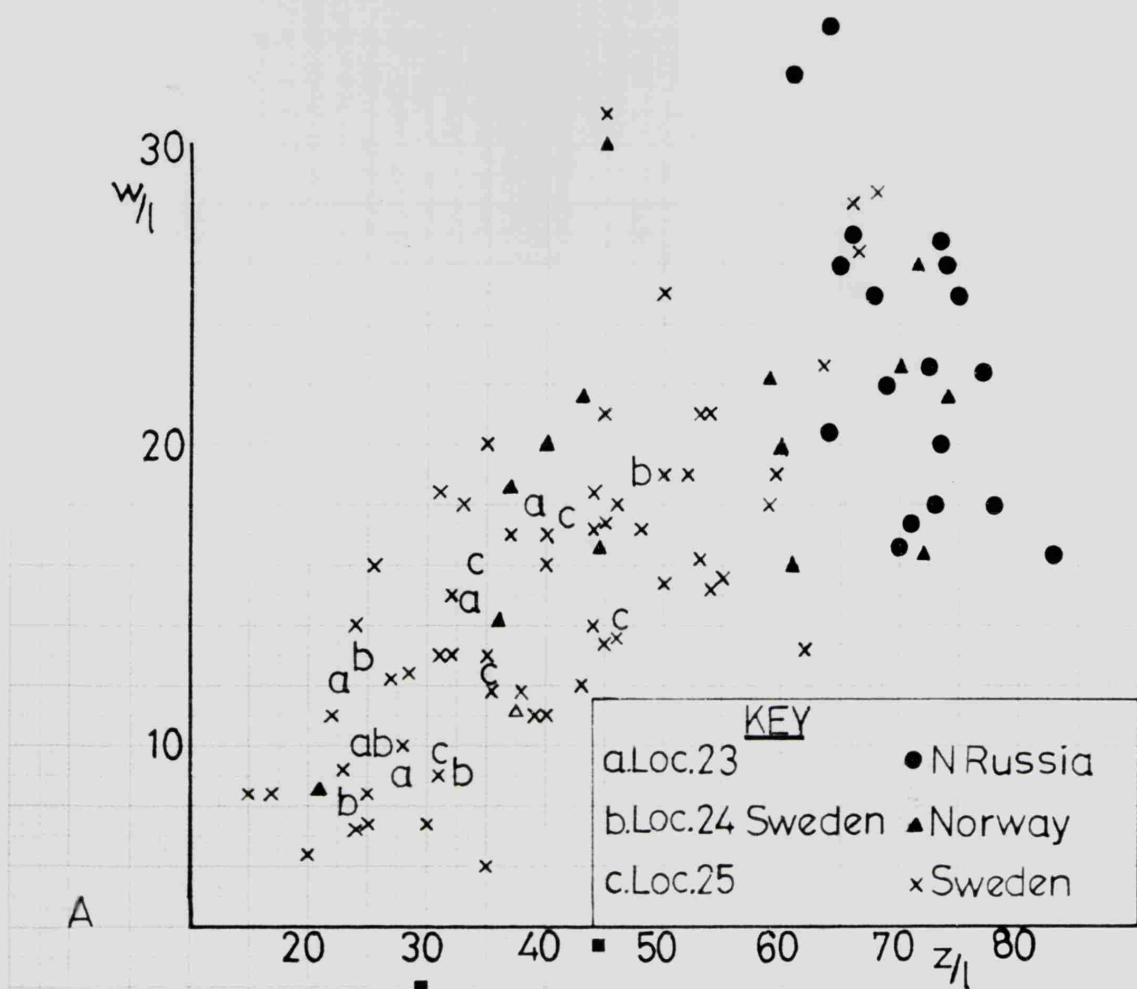


FIG. 8

GRAPHICAL COMPARISONS OF LEAF-SHAPE

plants from these two regions with the same leaf-shapes differ in other morphological characters.

The leaf-shape of plants from arctic Russia can be seen to be different from that of other groups. There is only a relatively small amount of overlap in leaf-shape between this group and the extremes of variation of other groups. This overlap is found to occur mainly in the plants from the north coast of Norway, which are also in other ways, those most similar to the artic Russian plants.

All graduations from highly divided leaves to ones approximating to those from the north coast have been seen from some Scandinavian montane localities. Similar variation in leaf-shape was also found among southern lowland plants; they show a much greater variational range than those in France.

Variation in leaf-shape, in the cultivated plants corresponds well with that of the herbarium material. But it was found that almost the total range of variation for a whole country, as found from herbarium specimens, often occurred in plants from a single locality, even where the plants had been originally collected from an area of only a few square feet. Relevant examples have been added to figs.7 and 8 (see also fig.10).

Among the samples of 'spring' leaves taken from cultivated plants originally from the same locality, it has often been found that the shortest leaves are also the leaves which are broadest and least divided. Thus in fig.8A the length of this leaf for locality 23 is 28mm, the

second shortest being 49mm; and for locality 25 it is 40mm; then 52mm. Such a correlation does not always apply, as in locality 24 where the broadest leaf is 42mm, but there are two leaves much shorter than this from this locality, one being only 30mm. long. Similarly among herbarium material examined, the broadest type of leaf for any region, has often been among the shortest, this is especially true of the premorse based plants. Allowance for this has not been made, when comparing leaf shapes from different regions, as it is not a sufficiently constant rule.

Dwarfing, which produces this type of leaf, can be due to genotype or environment. These 'spring' leaves in being broader and less divided, show less divergence from the leaf shape occurring in autumn and on first year plants. In extreme cases, where dwarfing is very severe, as in some montane plants, the leaves are similar to the early seedling leaves.

The degree of fusion of the lobes

The wide variation in correlation as found between z/l and w/l in leaves from all geographical groups is also found when x/l is compared with either of these ratios.

In fig. 9 x/l is plotted in a) against z/l and in b) against w/l , using the same leaves for both graphs. The leaves used are a random sample from groups which cover all the major leaf-shapes. It can be seen from the graphs that the bulk of these groups are inseparable on this basis, only individual plants showing any trends which might characterize a group.

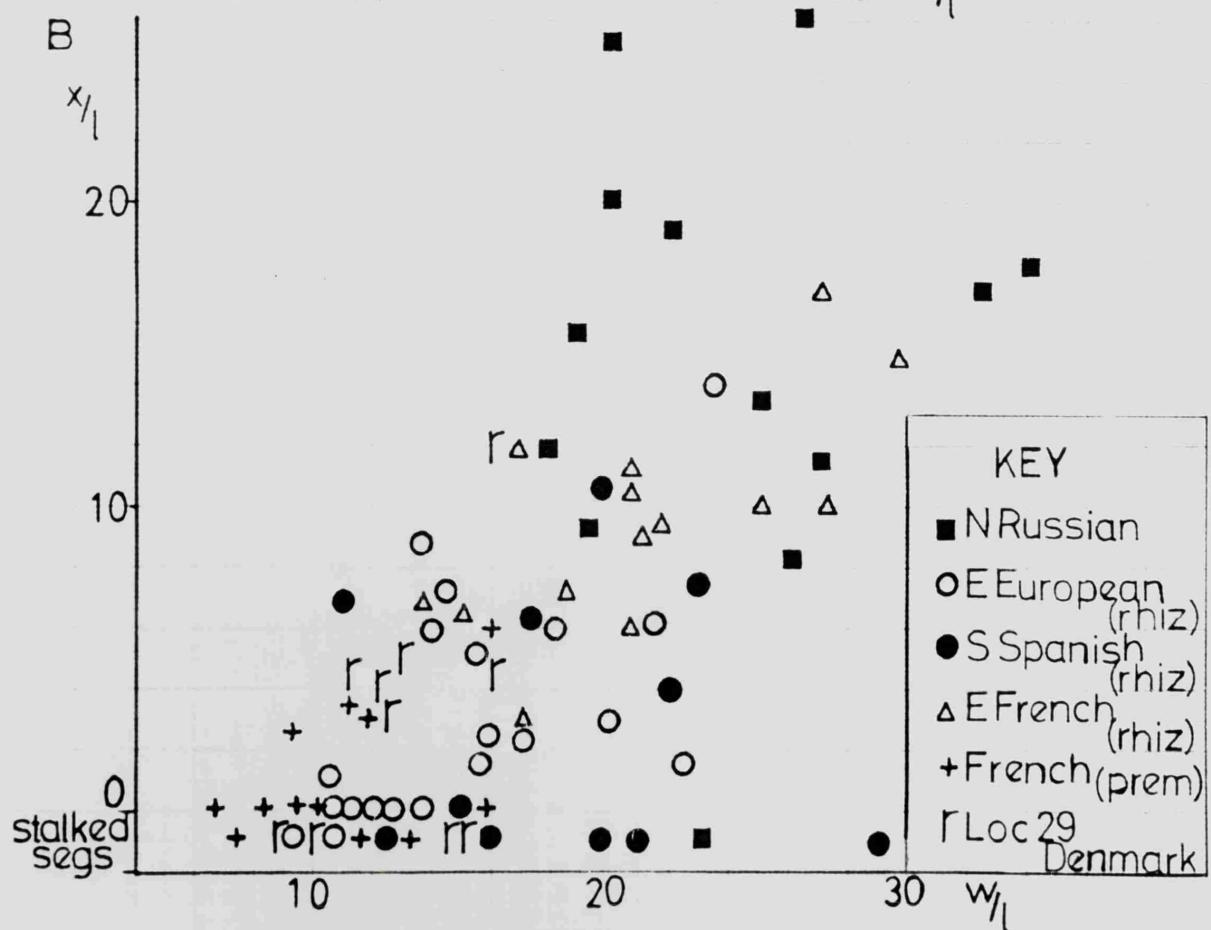
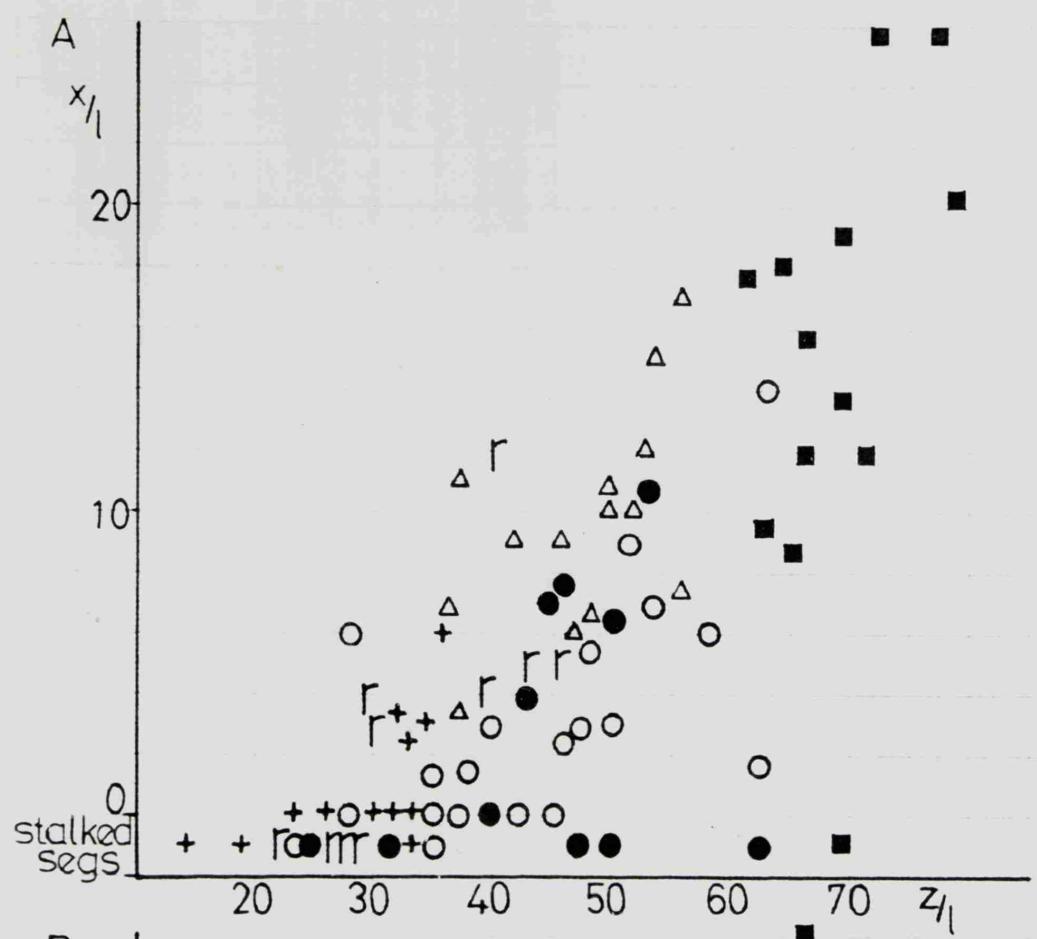


FIG.9 GRAPHICAL COMPARISONS OF LEAF-SHAPE.

The segments of most groups are only stalked or completely divided in the more finely divided leaves. The main exceptions to this rule are found in the E.European and S.Spanish rhizomatous groups, this is especially true of the latter group where actually stalked segments are found among some of the broadest lobed leaves of the group. Among the E.European types stalked segments are rare and only found among very narrow lobed and fairly finely dissected leaves; leaves showing fusion of the segments are common even among some of the longest leaves measured. In some localities of the S.Spanish plants it was found that whereas the larger leaves had stalked segments, the smaller leaves had fused segments. This appears to be a further case of slight juvenility of leaf-shape being associated with dwarfing. Such a trend in leaf-shape is one of the disadvantages of the all too frequent occurrence of collectors chosing small specimens which will more easily fit onto herbarium sheets.

Juvenility of leaf-shape in association with dwarfing appeared especially prevalent in the arctic Russian plants. Leaves having very high x/l values were from dwarfed plants. Leaves showing little fusion of the segments, or even with stalked segments, occurred on plants showing no signs of dwarfing.

Shape of the sinuses

The angles made by the sides of the main sinuses of the leaf are roughly correlated with the width of the lobes. The angles tend to be

greater the narrower the lobes. This is often accentuated in narrow lobed leaves by the sides of the sinuses curving, making the sinus initially much wider, but curving back again so that the lobes overlap. Overlapping of the lobes tends to occur rarely in wide lobed leaves, except where they are so wide that the subtended angles of the segments exceeds 360° .

The nature of the variation of the shape and size of the sinuses was such that measurement could have only been by divisions into arbitrary groups of types. This was tried, but found to be very unsatisfactory, and it was also felt that it would add little of value to the information about the leaf-shape as recorded by the measurements already discussed.

Further lobing and toothing of the segments

The following observations have been made from comparisons of the relationship between the number of teeth and the length and width of the lobes of the leaf.

Using the British material it was found that an increase in number of teeth was more closely correlated with the length rather than the width of the lobe. Thus, using clonal material from locality 62 it was found that the increase in the number of teeth on a leaf due to increase in the length of the leaf under more favourable environmental conditions, was often greater than the difference in number between plants of differing leaf width grown under the same conditions. The wider 'autumn' leaves seldom varied much in tooth number from the narrower

'spring' leaves, and indeed a larger number of teeth on the 'spring' leaves was more frequent than the reverse situation.

The broad leaves of East French rhizomatous plants typically have a large number of teeth, but it is certainly not the exception for narrow lobed premorse plants from the same country to have as many or even more teeth. When one of the broad leaves, possessing a large number of teeth is compared with one of the narrow leaves, possessing a similar number of teeth, it is found that in the broad lobed leaf there are fewer groups of teeth, but each of these groups contains a larger number of teeth.

It was found that certain groups of plants are characterised by having a small number of teeth in comparison to their length. This is even more pronounced in the E.European rhizomatous plants than in the S.Spanish rhizomatous plants. In the E.European rhizomatous plants only two sets of teeth occurred, except in very rare cases, nearly all of which appeared to be of possible hybrid origin. Three sets of teeth were common on the leaves of the S.Spanish plants. A reduction in number of teeth was also commonly found among lowland premorse plants from the east of Europe. In one plant this reduction was so great that the median segment was of a simple linear form without teeth, similar to the upper bracts of most plants.

SEASONAL VARIATION IN LEAF-SHAPE

Seasonal variation in leaf-shape was examined in the cultivated plants. The main part of this investigation was carried out on plants from those localities which were in cultivation from 1965 and which are asterisked in the locality list.

These plants had been planted out in the botanic gardens in October 1965. From February 1966 to February 1967 inclusive, leaf samples were picked and pressed from each of five plants per locality, during the forth week of each month. Due to the size of the plants, the number of leaves per plant collected each month had to be cut down to one, which was chosen as being the most representative leaf present, of those which had most recently reached maturity. A time interval of less than a month would have been more satisfactory, but this was also impossible due to the size of the plants.

The leaves produced in the winter of 1965-66 were, except in their decreased size, very similar to those which had been produced in the autumn of the plant's first year.

With the increase in leaf length in the spring there was a marked increase in dissection, producing leaves which were much finer than any produced by the seedling plants in their first season.

The leaves arising in the axils of these 'spring' leaves, after the overwintering rosettes had produced a flowering stem, showed a marked discontinuity in shape. The very first leaves were frequently

very small and similar to the early seedling leaves. Otherwise all these leaves were similar to the mature leaves produced by the plants in their first season.

These broader 'autumn' leaves were then produced for the remainder of the year, during which time they showed a gradual increase in dissection, the sequence of which seemed unaffected by the production of further flowering stems. The winter foliage differed greatly in size, but showed little if any increase in dissection.

Thus it was shown that there was a regular sequence of increasing dissection from early summer of one year to early summer of the next year, with a marked discontinuity of leaf shape after the first flowering stem had been produced.

A similar discontinuity in leaf-shape was found, from herbarium material, to occur throughout the whole complex of R.acris and also in R.serbius.

The 'autumn' leaves, with only rare exceptions were found to show an increase in all the ratios, z/l , w/l and x/l , when compared with the 'spring' leaves of the same plant. They were also characterised by having a smaller angle of divergence of the side lobes of the median segment.

Figure 10 shows a comparison of the shape of the 'spring' leaves (collected in May) and that of the 'autumn' leaves (collected in September), as defined by the ratios z/l and w/l , for a selection of the localities. The leaves collected in September were chosen, although

they are more finely divided than the first produced 'autumn' leaves, as some plants produce few leaves during the summer period. This coincides with the resting period, after the main flowering season, which occurs especially in plants from districts with a continental climate; where this occurs there is often a long time lag between the maturing of the last 'spring' leaves and the production of the first 'autumn' leaves. The only group of plants where any 'autumn' leaves persistently did not show an increase in the ratios occurred among the Finnish plants, but this was only in certain plants from each locality sample.

From fig.10 it can be seen that the relationship between each pair of leaves is roughly the same. It also shows that although the 'spring' and 'autumn' leaves from any one plant can be easily distinguished from one another, within the whole sample of leaves from a locality, it may, in the case of certain leaves be impossible to tell from their shape alone whether they were produced before or after the first flowering stems.

It was found that the shape of the 'autumn' leaves is much affected by transplantation. Transplantation in late autumn or early spring had little effect, but if it occurred during the spring flush of leaf production, the 'autumn' leaves subsequently produced were much wider than usual. The remainder of the 'spring' leaves produced were not affected, probably due to the fact that the leaf and flower initials are formed at an early stage, often by February. (See plate 5).

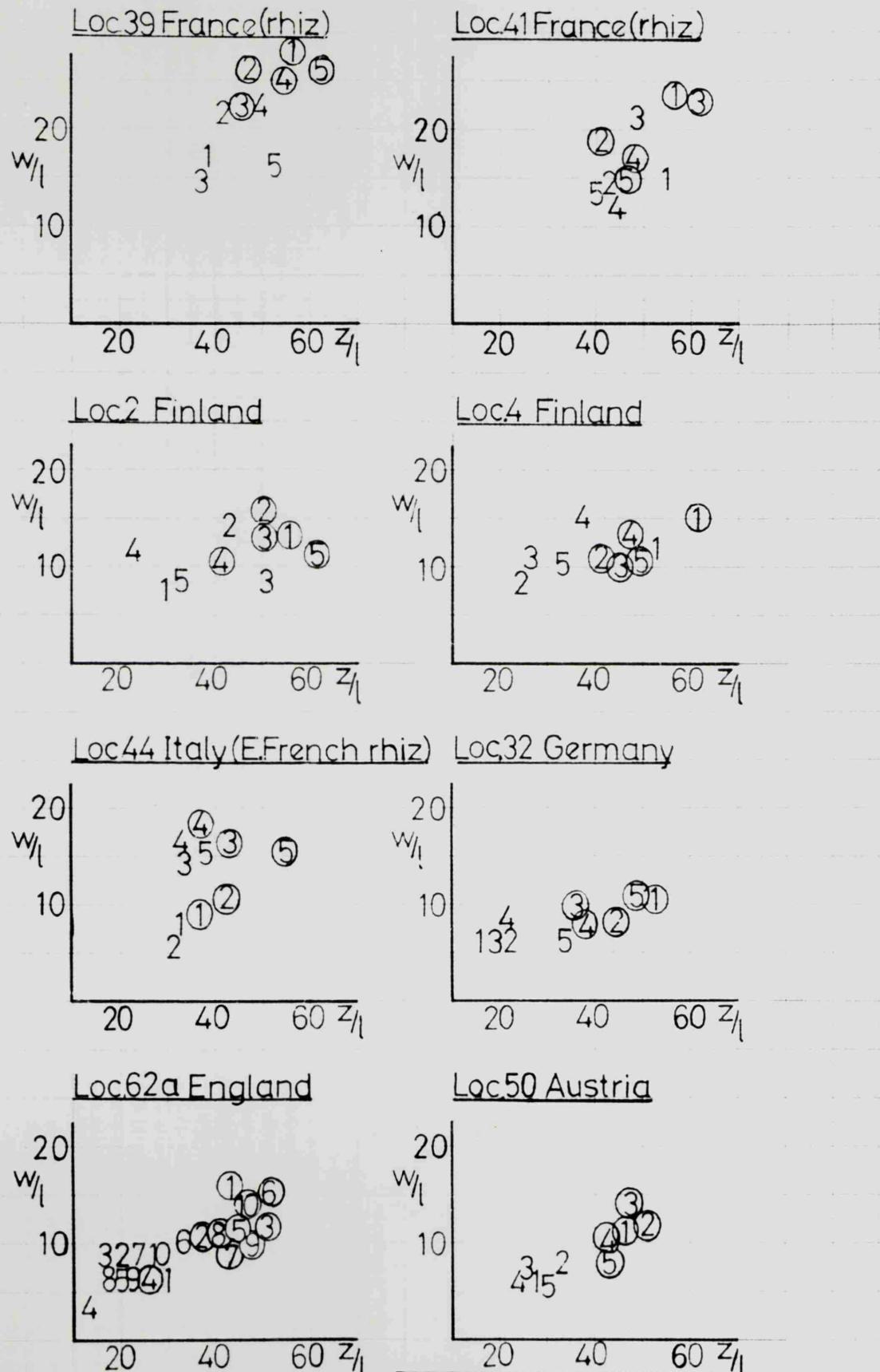


FIG.10

1-Spring (May) leaf } same
 ①-Autumn (Sept) leaf } plant

GRAPHICAL COMPARISONS OF 'SPRING' AND 'AUTUMN'
LEAF-SHAPES IN SOME CULTIVATED PLANTS.

From the examination of herbarium material it seemed that other factors could also produce abnormally broad 'autumn' leaves. The main factor appeared to be the removal of the foliage, as in the cutting of hay. This was tested and found to be true.

It is to be remembered that 'autumn' leaves are identical to those produced by a plant in its first year just before the production of the first flowering stem. The abnormally broad 'autumn' leaves produced by certain factors are reminiscent of some of the very early seedling leaves, and can thus be said to have reverted to a juvenile shape.

It was often found that the maximum length of leaf produced during the year was not produced until the autumn. This was particularly found to occur in the Finnish and Swedish plants, but was less pronounced in premorse plants from further south. It did not occur in the E.French rhizomatous plants, where the 'autumn' leaves at times did not even reach the maximum lengths obtained by the 'spring' leaves. (See fig.11).

THE REACTION TO WINTER, OF THE PLANTS IN CULTIVATION

During the winter the plants did not die back, but continued to produce small leaves. Variation was found in the timing of the initiation and of the size and hairiness of the winter foliage. (See fig.11 for examples).

The plants were found to be divisible into two main groups in respect to the initiation of winter foliage. In the first group were

plants from the localities in Finland, loc. 8 (Russia) and loc. 25 (Sweden). These had all been producing full sized leaves in September (see fig. 11), but by October they had shown an abrupt decrease in leaf-length. The leaves produced in October were well under 20mm in length.

The rest of the plants showed a more gradual decrease in leaf-length and even by November some of these plants still had leaves over 20mm in length. Such leaves in November were found to occur mainly in the British premorse plants and the rhizomatous plants (including loc. 22 from Sweden). Plants from Sweden, Denmark and Austria nearly all had leaves under 20mm long by November.

The length of the leaf in the first group remained more or less constant from November to February or even March. But in the second group the minimum winter length only occurred in December and January, or even only in January in the case of the rhizomatous and some British plants.

Associated with the decrease in size of the leaves in winter is a decrease in density of hairs, often resulting in completely glabrous leaves. The petiole is more frequently glabrous than the leaf-blade, but it is rare for both to be hairy during mid winter.

The following observations are based on leaves collected in January. Completely glabrous leaves are the dominant type found in the Finnish, Swedish and Scottish plants, but only rarely occur among the others. Leaves with both petiole and blade hairy are absent among

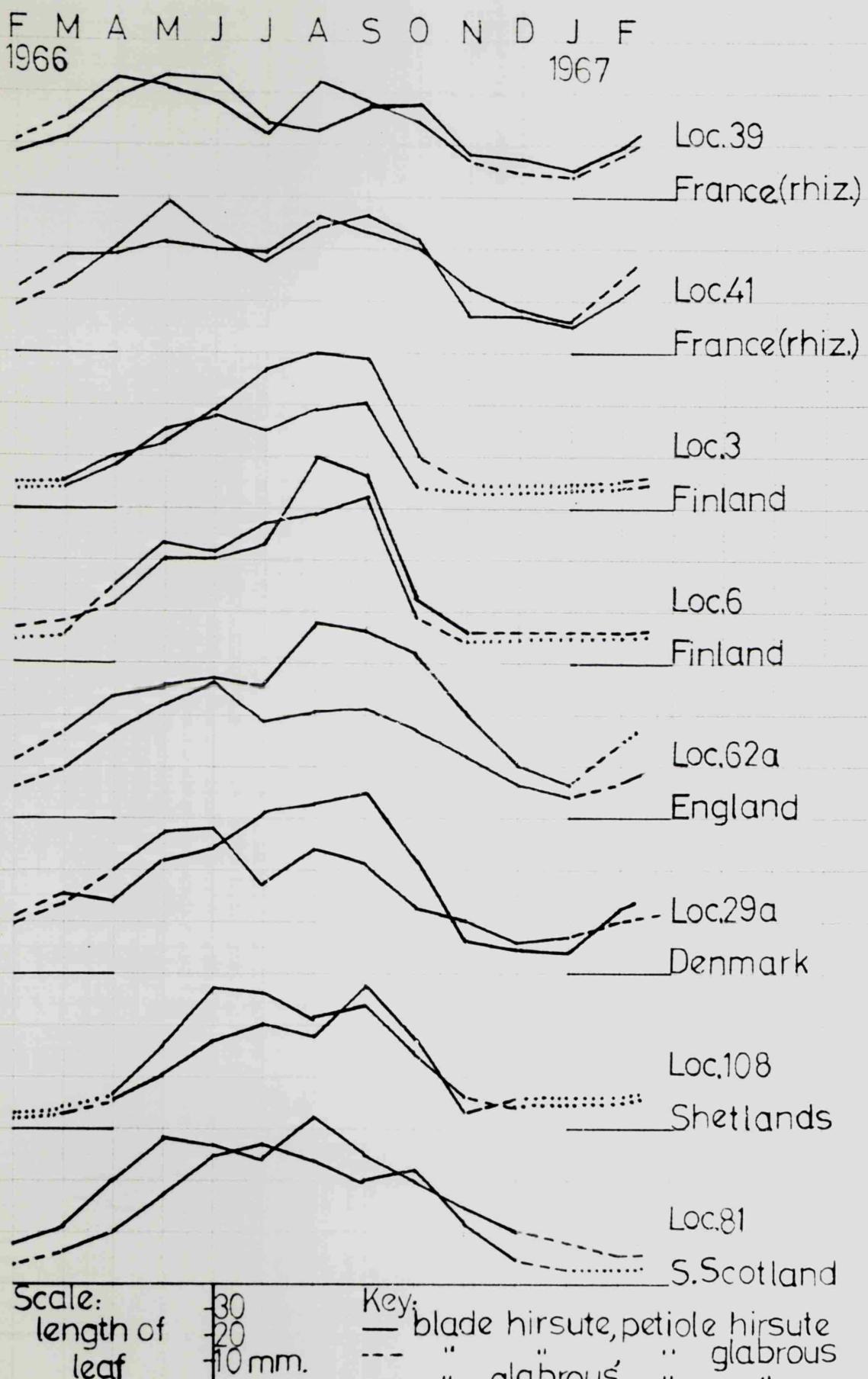
this group, although leaves with just the blade hairy are fairly common.

Completely hairy leaves are commonest among the rhizomatous plants and are also found in some Danish and English premorse plants. This is the dominant type in most of the rhizomatous plants, but leaves with glabrous petioles are the dominant type in the Danish and English plants. Completely glabrous leaves are very rare in both these groups.

In plants from several Danish localities the leaves produced in January ranged from very small, completely glabrous leaves to largish completely hairy ones. But although so much variation can be found among plants from the same locality, from the results based on the monthly collections of leaves and from general observations on all the plants in cultivation, it has been possible to show that the winter reaction can be correlated with the climatic conditions of the original habitats of the plants.

Thus the most extreme reaction was found in plants from Finland and other N.Baltic regions. South Swedish, west coast Norwegian and Scottish plants produced similar winter leaves, but their initiation was slightly later, especially in the case of S.Scottish plants. Danish plants had a similar timing of winter foliage initiation, but the winter leaves were generally of a hairier type. E.European plants were similar to Danish ones. English and Welsh plants showed an even later initiation of winter leaves.

Plants of the E.French rhizomatous type showed least reaction. This was less than might have been expected from the reaction shown by



VARIATION IN LEAF-LENGTH THROUGH THE YEAR
FIG.11 as shown for 2 plants/locality.

premorse plants from localities of somewhat similar climates.

Sørensen (1941) found a difference in the winter reaction of plants in cultivation from differing ecological habitats in Denmark. Shore-line plants showed the greatest reaction and woodland plants the least. The plants from Denmark and S. Sweden under investigation in this study came from just as wide a range of habitats. But no such difference was found in the reactions of plants from differing ecological habitats, and as has already been stated plants from the same locality, showed great variations in their reaction to winter, although often having originally been growing within only a few feet of one another.

The plants which were grown throughout the year in a heated greenhouse produced winter foliage. Winter foliage is therefore presumably produced in response to day length rather ^{than} _^ to temperature change.

Tests on the effect of environment on leaf-shape

The effect of different environments on leaf-shape was tested in two ways. Firstly plants from the same locality (62, England) but growing under different conditions, were transplanted and grown under similar conditions; and secondly plants of clonal origin were grown under different conditions.

In the first test one set of plants came from a marshy area and the other from a dry field. The first set were characterised by having finely divided leaves and the second set by having leaves with broader lobes. After a year in cultivation it was found that only the leaves of about half the plants from each set had changed in shape. Those from the wet habitat which changed produced leaves with broader lobes and those from the dry habitat produced leaves with narrower lobes.

The clonal material was used to test the separate effect of availability of water and of temperature. The former tests failed as the plants under very wet conditions died during the winter. The leaf shape of the plants grown in a heated greenhouse with no winter frosts differed from that of those grown in a cold greenhouse by being less divided with broader lobes (see Plate 6). Fisher (1960) found when growing R.hirtus B.&S. under conditions of high temperatures that there was a reversion of the leaf-shape to the undivided juvenile type.

Cotyledons

Variation in cotyledon shape and size was examined in pickled seedlings, which had been grown from seed samples of wild origin. The cotyledons on first emergence are narrowly ovate, but soon broaden. Measurements were made on mature cotyledons, that was after several leaves had been produced.

There appeared to be no correlation between the type of cotyledon and the type of mature plant. The seedlings from some localities produced cotyledons of a rather uniform shape, whereas in those from other localities the variation in shape, as defined by the greatest width/length, covered almost the whole range of shapes found. Thus in loc. 4 (Finland) w/l was from 0.57 to 1.0 and in loc. 25 (Sweden) w/l was from 0.669 to 1.16.

Seedling-leaves

Successive seedling-leaves, up to the time of the production of their first flowering stems, were collected and pressed from five plants per locality (for those localities which are asterisked in the locality list). The plants had been growing in a cool greenhouse.

The successive leaves produced by a seedling showed a gradual increase in dissection. The first seedling-leaves were often only three lobed, or were at most five lobed due to the lateral lobes being further divided. These leaves and frequently also later produced leaves are glabrous. The first seedling-leaves of R.serbicus were always found to have a greater degree of lobing than were those of R.acris s.s.

It was found that no particular shape of the first seedling-leaf could be correlated with the leaf-shape of the mature plant. An idea of the mature leaf shape was shown by subsequent seedling-

leaves, but only in as far as whether the mature leaf would have very broad lobes or very narrow ones.

It was found that seedlings could not provide any useful characters for determining the affinities of the plants, as differences at this stage are so much less pronounced than when the plants are mature.

Chapter 5

THE STEM

The flowers of R.acris are borne on an erect stem, which arises from the centre of the basal rosette. The inflorescence takes the form of an irregular cyme. The pedicels are terete and pubescent.

Foliar organs on the stem

A variable number of foliar organs occur on the stem, the lower are stalked and similar to the basal leaves, but higher up they become sessile and simpler in form. The sessile organs, 'bracts', usually subtend the branches of the primary cyme, and the stalked organs, 'stem-leaves', usually subtend later flowering branches in their axils. However no clear distinction can be drawn either between the type of foliar organ or the type of branch; there is often an almost negligible time lag between the development of the lower branches of the cyme and that of the lateral shoots.

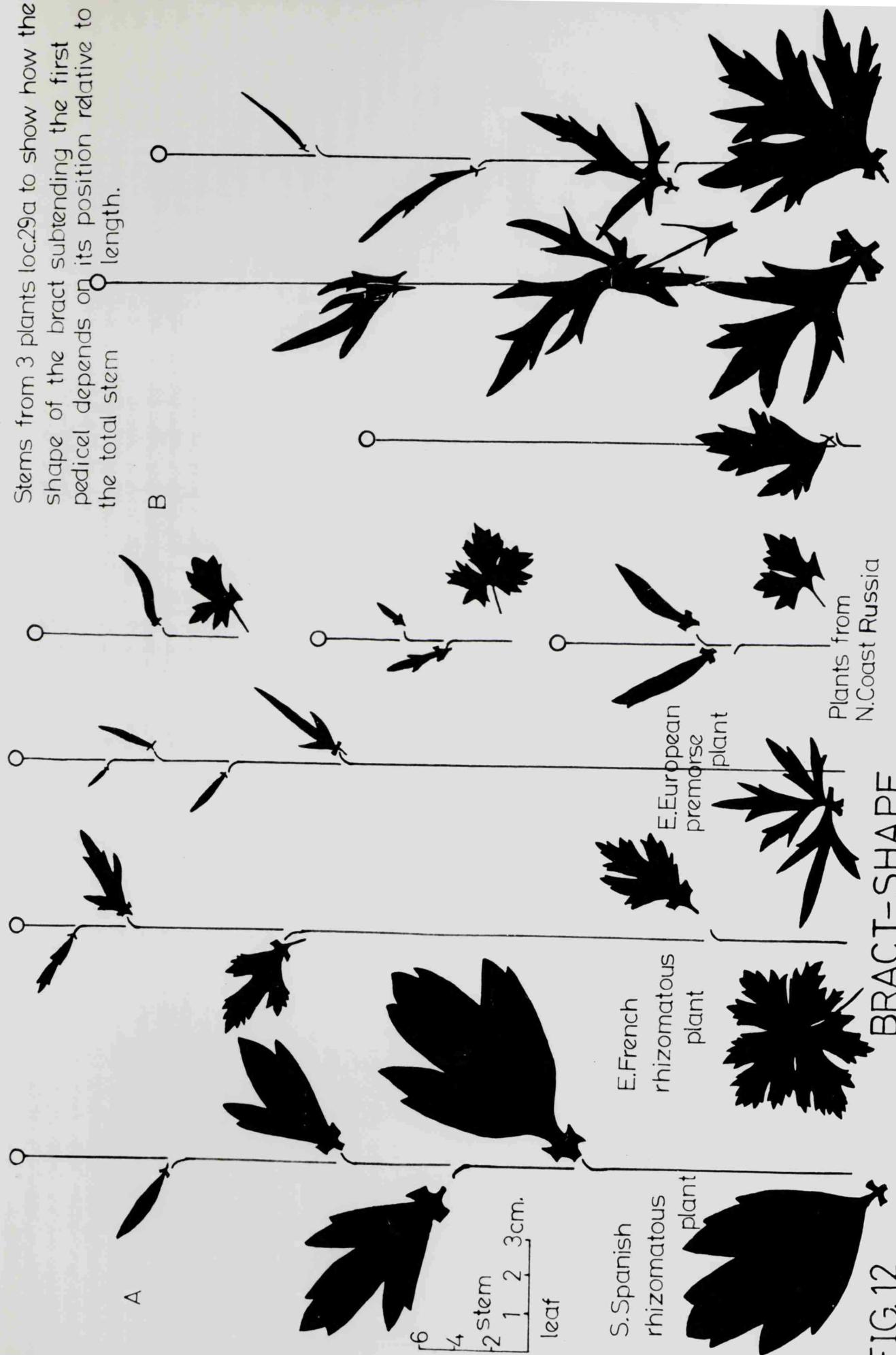
The change in shape in these organs with their relative height on the stem is not affected by their relative frequency; but as there are no fixed relative heights on the stem at which these organs occur, no comparison of the shape of those occurring on differing stems can be made. The number and position of these organs differ no more between stems of different geographical groups, than they do among successive stems produced by the same plant. Fig. 12B shows how the shape of the

bract subtending the first flower differs, with the relationship of the length of the pedicel to the total height of the stem, on stems taken from plants from the same locality.

The shapes and sizes of these organs are nearly always directly correlated with those of the basal leaves, and would therefore not give additional evidence about the relationships of the plants. Fig. 12A shows some examples of the bracts in plants with different types of basal leaf. Where the basal leaves are broad and have many teeth the stem-leaves and bracts will appear to be more 'leaf-like' to a greater height of the stem. Whereas when the basal leaf is narrowly lobed with few teeth the stem-leaves and bracts will become simple and linear at a much lower level. The decrease in number of teeth on a bract at increasing heights on the stem is primarily by a decrease in the number of teeth per lobe rather than by a decrease in number of lobes.

The exception to this correlation of bract types with basal leaf-shape occurs in many arctic and north western plants. These are plants with broad little-divided leaves and in these the transition to simple linear bracts is often abrupt. (See fig. 12A). The bracts in these plants are usually as long as the basal leaves. Only in rare cases, in lowland and southern plants, are the bracts as long as the basal leaves.

Stems from 3 plants loc. 29a to show how the shape of the bract subtending the first pedicel depends on its position relative to the total stem length.



Plants from
N. Coast Russia

BRACT-SHAPE

FIG. 12

The height of the stem and degree of branching

The height of the stem and degree of branching and hence the number of flowers, are very variable and much affected by environment. Herbarium and fieldwork have proved these characters to be of little value, and actual measurements have only been compared in the case of cultivated material.

Height

The cyme as a whole varies in height with its age, successive flowers being borne at ever increasing levels. For consistency in method of measurement, the height of the stem has been taken as the distance from ground level to the level of the earliest flower. The level of the earliest flowers in cymes of the same final height (i.e. when flowering has finished) vary very little, although the lengths of the pedicels bearing the first flowers may vary considerably (see fig. 12B).

It has been found from the plants in cultivation that premorse based plants from N.W. Europe often have the pedicel of the earliest stems arising at a much lower level than do those of subsequent stems. This tendency was never so marked among the plants from S. and E. Europe.

The height of the stem has at times been used as a diagnostic character: an example of this is to be found in the key in *Flora Europaea* (Tutin, 1964). Plants referable to subsp. borealis (Trautv.) Nyman, do indeed seem to be uniformly short, but the frequency of

dwarfed plants in the other groups, due to both genotype and environment, make it a diagnostic character of dubious value.

Also from an examination of herbarium material, no correlation was found between the length of the stem and the type of rootstock. Plants with rhizomes were stated to have longer stems than plants with premorse bases (Tutin 1964). Plants under cultivated conditions showed a slight correlation, but only in as much as the longest stems occurred among the rhizomatous plants (the maximum length was 68cm), and that all these plants had stems of 40cm and over, and they were frequently over 50cm. But some premorse based plants from nearly all the localities had stems of over 40cm and lengths of over 50cm were not infrequent. Great variation occurred in the stem lengths from nearly every locality, the greatest was in plants from loc. 24 (Sweden), where the minimum length was 18cm and the maximum 41cm.

Degree of branching

The most satisfactory method of measuring the degree of branching has been found to be that of a count of the number of flowers produced by the primary cyme. This method, as would any other, runs up against the difficulties that the primary cyme can not be delimited from later developing lateral branches: also a cyme can theoretically produce flowers, and therefore branches, to an infinite number, but in practice the flowers become progressively smaller until production is either terminated by imperfect flowers or by buds which do not develop.

No consistent differences in the degree of branching were found between any of the types of plants in cultivation. The previously reported characteristic of the E.French rhizomatous plants in having branches more spreading than in the other groups was not verified. The type of plant from arctic Russia has previously been characterised by having only very few flowers (only 1-3 according to Tutin 1964). Although this was found to be true of most herbarium specimens examined, some had highly branched stems (see plate 14) and it is suggested that this might be a character governed mainly by environment.

Chapter 6

HAIRS

Ranunculus acris s.l. is generally a rather hairy plant, except in its winter state. Plants approaching a completely glabrous state during the flowering season have only been seen among the northern montane plants and as extremely rare individuals of more southern, lowland plants; even in these extreme cases both pedicels and sepals have a normal hair complement.

The hairs are single-celled and are all similar in form (see Fig. 14). They are smooth-walled and generally parallel-sided for the greater part of their length, tapering at their tip to a fairly fine point. Spindle-shaped hairs are not infrequently encountered, but never found to the exclusion of the former type.

The following regions of the plant have been examined in respect to the length and density of the hairs; the lower part of the stem, the petioles of the basal leaves, the leaf-blade, the sepals.

Stem and petiolesLength

Hairs of a wide range of lengths are found on any area covered by hairs. Measurements based on the maximum length found in the samples of hairs has been found to show variational patterns of a geographical

nature. The maximum lengths are based on hair lengths which are frequent and not those only rarely found on the organ concerned.

Hair length has been divided into five groups by arbitrary divisions and these are as follows.

A-up to 0.4mm

B-over 0.4mm to 0.8mm

C-over 0.8mm to 1.2mm

D-over 1.2mm to 1.6mm

E-over 1.6mm

Density

The density of hair cover on both the petiole and stem has been scored by using 4 arbitrary categories, viz very dense, continuous, scattered, glabrous. Actual numbers of hairs in a set area, as used for leaves, were found to be impracticable due to the small diameter of many of the organs involved. These divisions seemed adequate in showing the major trends in hair density, although a slight underestimate of density in plants with short hairs may probably have occurred.

Measurements of hair densities have only been made on 'spring' organs, as the hair density is greater on the 'autumn' ones.

Types

As well as varying in density and length, the hairs on both these organs vary in their relative position to the organ. For scoring,

three categories, appressed, spreading, and deflexed have been used; deflexed including those hairs which are at an angle of 90° or over, to the surface of the organ above the base of the hair.

The type of hair on the petiole and stem of the same plant are commonly the same, but if they differ, it is the hairs on the petioles which are usually, but not invariably, the more strongly spreading or deflexed. The hairs on the sheath and lower parts of the petiole are frequently more strongly spreading than are those higher up. The lower half of the petiole, excluding the sheath, has been used for scoring the type of hair present on the petiole.

The lower part of the stem is frequently less densely hairy than are the petioles. Glabrous stems are common among nearly all groups, whereas glabrous petioles are almost totally confined to the northern montane plants. Despite the type of hair cover occurring on the lower part of the stem, usually by at least half way up the stem, before the level of the bracts is reached there is a gradual change over to continuous appressed hairs. However where there are nodes in the lower part of the stem there may be noticeable discontinuities in both hair density and type from one internodal region to the next. The length as well as the density of the hairs on the upper parts of the stem, especially on the pedicel is rather uniform throughout the complex. Therefore in measuring the density and length of the stem hairs, only the lower part of the stem has been considered. The extreme basal part of the stem and any very short first internodes have also been ignored

as these are often very much hairier than the rest of the basal part of the stem.

Results.

In Map 2 geographical distribution of hair types, densities and lengths is shown for stems and petioles.

From this it can be seen that density shows no clear trends. But very dense hair cover is commonest among those plants of the western oceanic regions. Glabrousness of the stem is associated mainly with plants growing in the more continental type climates and on northern mountains, whereas hairiness is associated with more oceanic climates and southern European mountains.

Deflexed hairs are found among all the rhizomatous groups excepting the Pyrenean type, in which all plants examined had appressed hairs. Among the premorse plants deflexed hairs are rarely found except in the western oceanic districts, where they are found to be most frequent in Britain, the more northerly islands, W.Norway and W.France.

In the premorse plants there is a general trend of long hairs in the W. of Europe and shorter types in the East. This trend shows a rough correlation with longitude. The French rhizomatous plants have hairs of similar length to those of other plants occurring in France; but they differ from one another in that some plants of the East French type have hairs of the D and even E group, whereas although C group is common in the Pyrenean type longer hair types were not found.

The other two rhizomatous groups, those occurring in E.Europe and S.Spain, are alike in having mainly very long hairs, D and E types being far more common than in any other group of plants, and B type hairs only occur on plants of rare occurrence, which appear to be hybrids between the E.European rhizomatous plants and premorse plants.

Width of hairs

The degree of difference in hair width between plants was found to be the same when comparisons of hairs from any particular organ were made. Organs for which such tests were made included stem, petiole, upper and lower leaf-surfaces, pedicels and sepals.

Measurement of the degree of difference in the hair width is easiest when using hairs from that part of the plant on which they reach their maximum dimensions. This occurs on the lower part of the stem, but as it is so frequently glabrous, the petiole was chosen; the dimensions of hairs on these being only slightly less than those on the stem.

The width and length of the hairs was measured microscopically using an ocular micrometer. A sl^vipper of petiole with hairs attached was mounted in phloroglucin and hydrochloric acid. This stain had the advantage of clearing the material more quickly than water and in staining the hairs red in contrast to the unchanging colour of the epidermis. A check was made to see that this stain had no adverse effect on the shape of the hair: one sample was left in stain and one in water for two hours, both were measured immediately before and after the two hour

period. Measurements of those in the stain remained unchanged, whereas those in the water showed a variation due to the hairs initially being difficult to delimit.

In the majority of cases measurements were made on hairs taken from the petioles of 'spring' leaves, but some were from those of 'autumn' leaves. The variation in hair type, as opposed to density, between petioles of 'spring' and 'autumn' leaves, was found to be negligible. Samples were taken from about one third of the way up the petiole, that is shortly above the sheathing region, which was avoided as it often has longer hairs on it than does the rest of the petiole.

Although usually a gradual increase in width was associated with an increase in length frequent exceptions were found. In many samples of hairs occasional hairs were found which although longer were barely half the width of a neighbouring hair (see fig.14), and seldom was any constancy in the ratio of length to width encountered.

Due to this variation it was found that a hair index, unless based on an impossibly large number of measurements was of little value. Instead, maximum widths were recorded, in the same way as those of length. The widths were grouped into the following arbitrary categories;

1. up to 0.02mm
2. over 0.02mm to 0.03mm
3. over 0.03mm to 0.04mm
4. over 0.04mm to 0.05mm
5. over 0.05mm

From measurements made, variations in the thickness of the wall were found to be fairly well correlated with the diameter of the hairs, and was therefore not considered as a separate character.

Results (see Map 3)

Among those plants with premorse rootstocks, hairs of the narrowest category were only found in the artic Russian type of plants and on occasional plants in the N.W. of Europe. The hairs of the montane plants of Scandinavia were always relatively narrow; but through the rest of the distribution of the premorse based plants a wide variation in width occurred in all regions and no geographical variational trends were apparent.

The E.French rhizomatous plants were unique among the rhizomatous plants in that many of them had very fine hairs. Most of these plants had hairs belonging to width groups 1 and 2, although much wider hairs were also found. All the Pyrenean plants had hairs of groups 3 and 4.

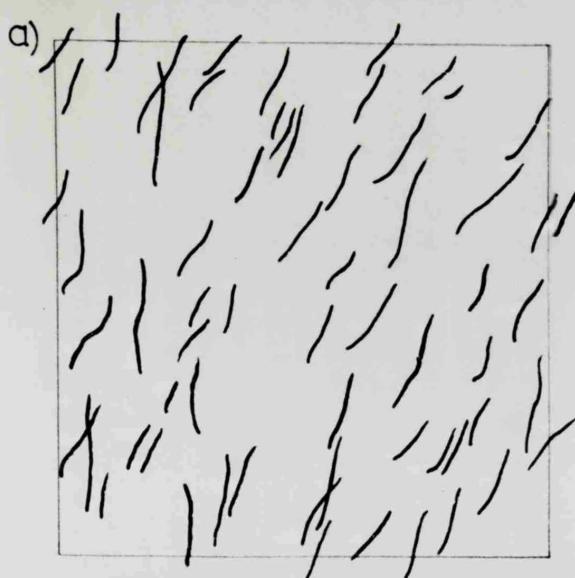
The other rhizomatous plants, those of S.Spain and E.Europe were alike in usually having very broad hairs. Although such broad hairs are found in some premorse plants they occur much more rarely. Among these rhizomatous plants group 3 type hairs rarely occur, those of group 4 or 5 being the normal type. In the premorse based plants group 2 or 3 are the more usual types, with some of group 4 and only very rarely those of group 5.

Hairs on the upper surface of the leaf

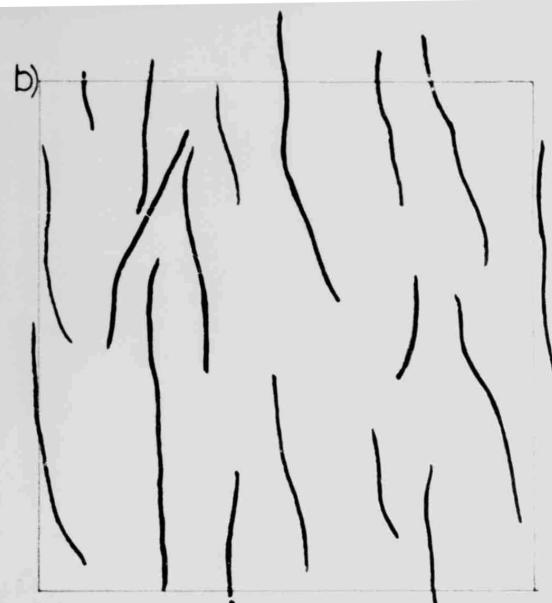
The lengths of the hairs on the upper surfaces of the leaves are similar to those on the petioles. The only exception to this was found among the premorse plants where only certain plants having hairs of over 1.2mm on their petioles also had hairs of such lengths, in any numbers, on their leaves. The possession of these long hairs on leaves of premorse based plants was found to be characteristic of a type of plant found in N.Scotland, parts of Ireland, The Faeroes and Iceland. In figure 13 are some examples of the hair lengths found within 4 sq. mm. of leaf surface, on different types of plants. Fig. 13c) and d) are from English plants with hairs of group D on their petioles, but which do not have the long hairs on their leaves, as is characteristic of a plant type occurring in parts of N.Scotland, (see fig.13e) and f)).

The density of the hairs was measured by counting the number of hairs in 4 sq. mm. of leaf surface. The density was much affected by environment and by the age of the leaf. The results were similar to those for the densities of hairs on the petioles, with generally no clear geographic trends.

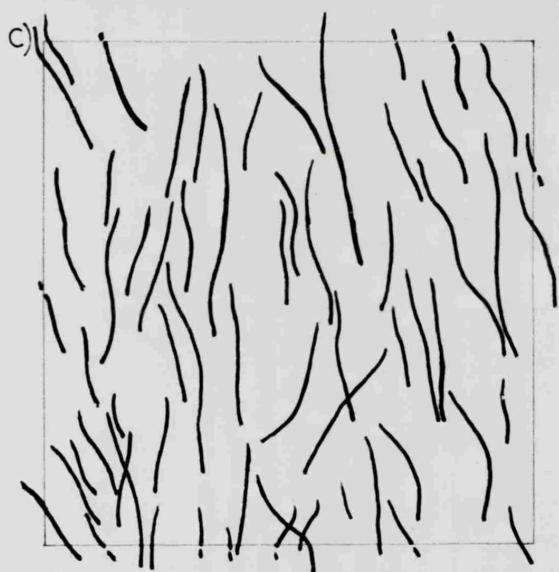
The hairs on the upper surfaces of the leaves were only found to be appressed to the leaf in plants from the extreme E. of Europe (loc. 58, loc. 59, and loc. 50). This character could only be observed in fresh material.



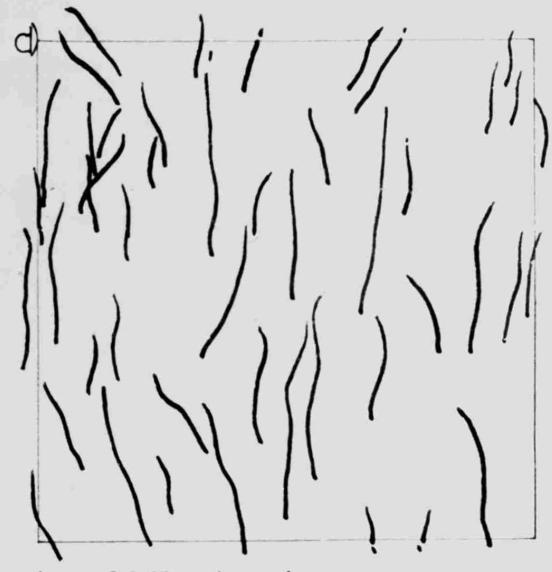
Loc 50, Austria.



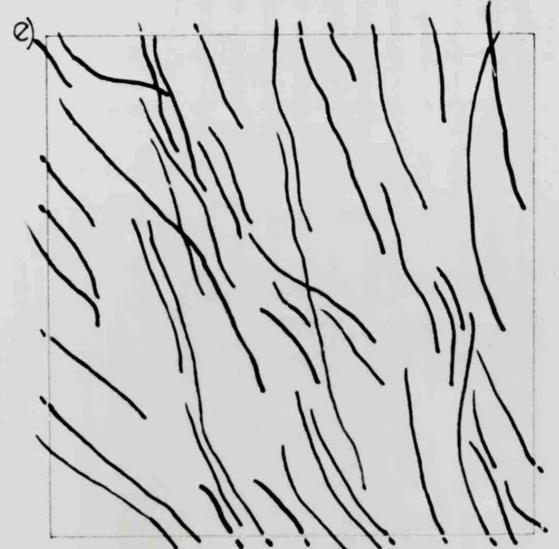
Sierra Nevada, Spain (rhiz.).



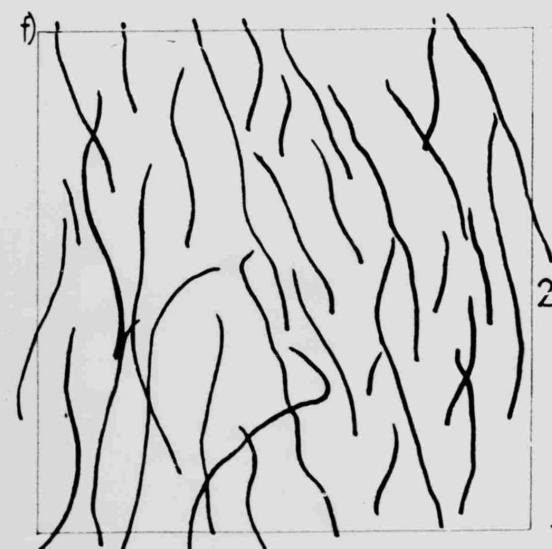
Kent, England.



Loc 60, England.



Rockfield, Ross & Crom, Scotland.



Melvich, Sutherland, Scotland.

LEAF-HAIRS within 4 sq mm of upper leaf surface
to show the relative lengths of the hairs

FIG. 13

Hairs on the lower surface of the leaf

The hairs on the lower surfaces of the leaves are very much finer than are those on the upper surface or on the petiole. A difference in width between these hairs on different plants still occurred. The variations in length of these hairs could be correlated with that of the hairs on the upper surface.

Many variations in the hair cover of the lower surface of the leaf are so affected by the age of the leaf that direct comparisons could only be made on leaves of the same maturity. This proved impossible for the majority of the material, but from general observations certain trends were visible. The density of hairs on the lower surface is generally greater in all the rhizomatous groups, than in the premorse based plants. Hairs on the main veins are appressed, except in old leaves, in the E. European and S. Spanish rhizomatous plants. The hairs on the main veins spread away from them, except in young leaves, in all the other groups, including the French rhizomatous group.

Hairs on the sepals

The lengths and densities of the hairs on the sepals could be correlated with those occurring on other parts of the plant. Tufts of hair exceeding the tip of the sepal were generally only found on plants with hairs of over 1.2mm on their petioles.

The general appearance of the sepal-hairs, that is whether they lie tidily or had a more fuzzy appearance, was found to be closely

correlated with the width of the hairs. An extremely fuzzy appearance especially occurring in plants of the arctic Russian group, was found to be due to the walls of fine hairs collapsing on drying and consequently twisting and bending the hairs.

On most sepals hairs of different lengths were more or less evenly distributed over the sepal, although a small zone at the base of the sepal was usually devoid of the longest hairs. However, in the S.Spanish and E.European rhizomatous plants the longest hairs rarely occurred on at least the lower third of the sepal. This zone was usually larger and more distinct in the S.Spanish plants where there were often few hairs of intermediate length and the long hairs were often of a much greater width than were the rest of the hairs. The E.European plants more frequently had a long tuft of hairs exceeding the tip of the sepal than did those from the S.Spanish plants, but within this former group sepals without hairs exceeding the tip were not uncommon.

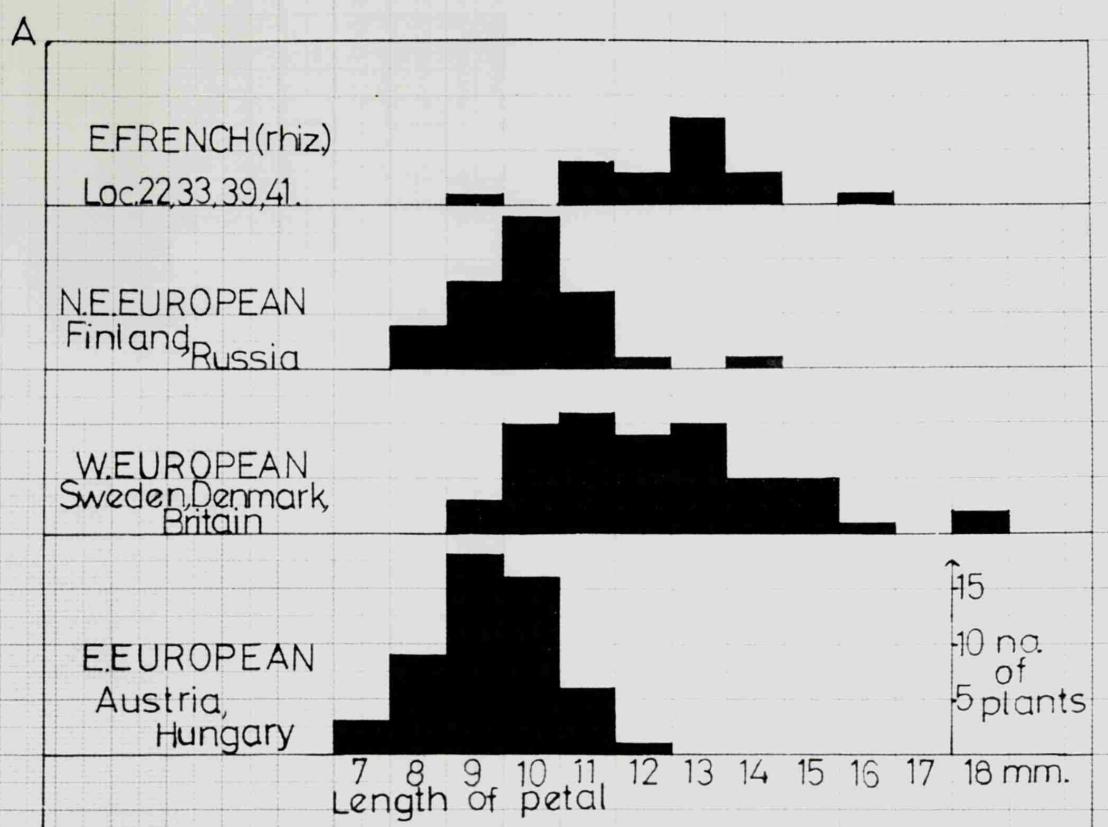
Colour of the hairs

The colour of the hairs has frequently been used as a diagnostic character by various authors. The colour ranges from a rusty-red, to a paler orange-brown, and through increasingly paler shades of fawn to white. In this present investigation hair colour was not found to be a good diagnostic character of any geographical grouping. In most cases colour appeared correlated with hair width, and the variational pattern was therefore almost exactly parallel to that of hair width.

Hairs of a really bright rust-red have a very sporadic occurrence, they have been seen to occur mostly among north western oceanic plants, and even then were restricted to the very base of the stem; they have also been seen on the rhizome of an E.French plant.

Hairs of an orange-brown hue are commonest in N.W.Britain and the more northerly islands, and E.Europe among both rhizomatous and some premorse based plants. All these are plants with broad hairs. The possession of hairs of this colour has previously been used as a diagnostic character to separate the rhizomatous plants of E.Europe from those of S.Spain (Tutin 1964). It was found that such hairs only occurred in the E.European group, but that many of these plants had a hair colour similar to that of the S.Spanish group, being some shade of fawn.

Very narrow hairs, such as those occurring in the E.French rhizomatous plants and some premorse plants are white. Increasingly broader types among these plants are increasingly deeper shades of fawn.



HISTOGRAMS OF PETAL-LENGTH FOR GROUPS OF CULTIVATED PLANTS.

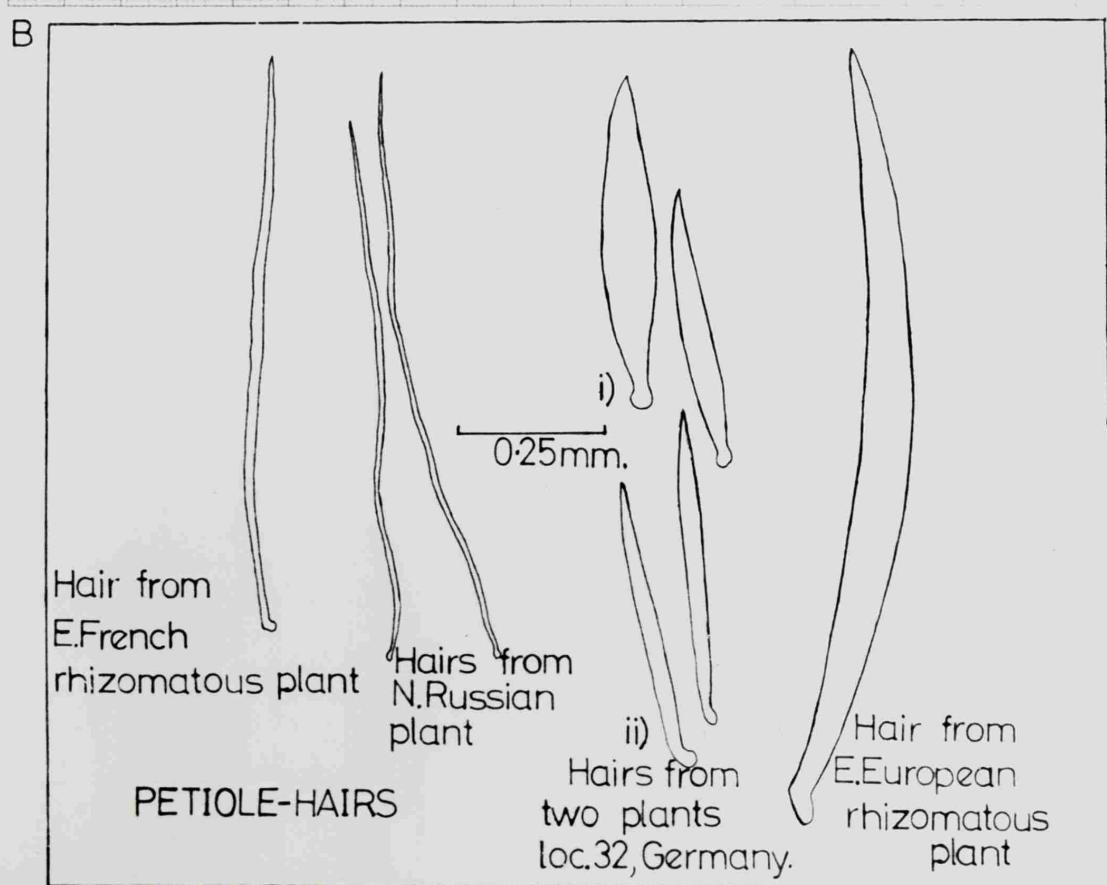


FIG. 14

Chapter 7

THE FLOWER

The parts of a Ranunculus flower are usually five sepals, five petals (sometimes termed honey-leaves) and numerous spirally arranged stamens and carpels. The number of sepals does not vary as often as does that of the petals. The number of stamens and carpels varies greatly.

Riley (1923) investigated the aestivation of R.acris flowers. He found that in pentamerous whorls four overlapping arrangements were possible; and in a sample of 1,000 flowers he found that these arrangements for the petals were present in the following percentages - quincuncial 33.8%, apotactous 27.5%, paratactous 32.1% and convolute 6.1%. He found that usually two or three of these arrangements occurred on the same plant, but that the aestivation of the calyx was normally quincuncial. This was verified by the examination of the flowers on a single stem. According to Payer (see Riley 1923) the primordia of the petals arise simultaneously whereas those of the sepals arise successively. The percentage values which Riley found for the petals are those which might be expected if they were arranged cyclically, whereas if they arose in a spiral, only a quincuncial arrangement would be expected.

The sepals

Except for the hair cover on the sepals (see chapter 6) no characters of the sepals have been found which could have been used to differentiate between different morphological types.

The relative widths of the membranous margins of the sepals, have frequently been used as diagnostic characters by other authors, but no allowance ever appears to have been made for the great variation occurring in a single flower. In sepals which are not overlapped by other sepals the margin is narrow, but where they are overlapped the margin is broad. In sepals where only one side is overlapped, on one side the margin is broad and on the other narrow.

The petals

The shape and size of the petals were examined in both herbarium and cultivated material. The following measurements were made; the length of the petal, the greatest width of the petal, and the distance of this position from the end of the petal.

Measurements were made on the petals from the earliest flowers of a cyme, since flower size decreases in the later produced flowers. This decrease in petal length in plants from loc. 61 (England) was found to be as great as from 15mm to 7mm and from loc. 50 (Austria) from 10mm to 6mm.

Length - Petal-length was chosen as being an easier and more accurate measurement of flower size, than is flower diameter as used by most other authors.

From an examination of herbarium material, petal-length of over 11mm was found to be common in the western and northern oceanic countries, including Britain, France, Belgium, Holland, Scandinavia and the N. coast of Russia. The highest incidence of very long petals, that is over 13mm, was found to be in N.Scotland, The Faeroes, Iceland and the extreme N. of Scandinavia and Russia.

Petals of even 11mm in length were found to be rare in E.Europe, that is in an area including N.Russia (excluding the coastal region) and S.Finland, and further south, east of a line approximately Berlin-Basle-Marseilles.

The lengths of the petals in the E.European and S.Spanish rhizomatous plants were found to be similar to those of the E.European premorse based plants, whereas the lengths of the petals of the French rhizomatous plants were similar to those of W.European premorse plants.

The petal-lengths of the plants in cultivation paralleled those found in the herbarium material. The results are given in fig.14, which shows that although long petals are commoner in plants from the west of Europe, such lengths are no more common among these plants than are the lengths found in E.European and Finnish plants.

Shape - The most common petal shape was broadly obovate. The only real exceptions to this basic shape were found among northern plants, where several greatly differing shapes occurred even in the same locality, but where the obovate shape still appeared most frequent.

Examples of petal shape are shown in fig.15. The range of values for the ratio of greatest width/length of petal was found to be very similar for all regions.

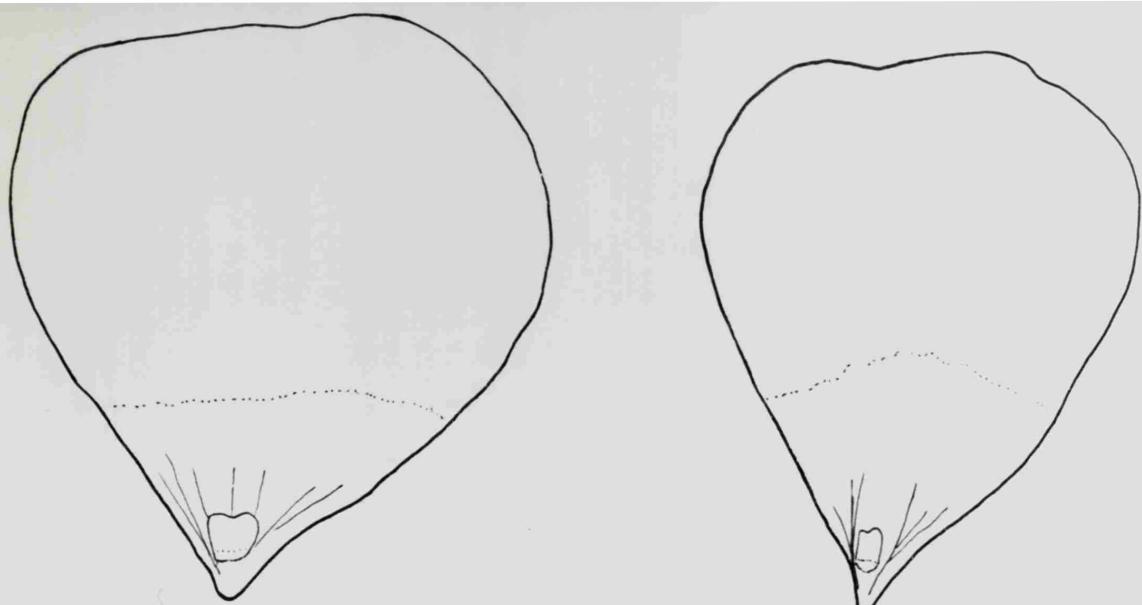
Many of the petals showed irregular notching on their upper edge. This was found to be more frequent among the longer petals. It is due to the petals while in bud not overlapping one another but their ends growing against each other. Flowers with petals showing various degrees of notching and ones with entire petals were found to occur on the same stems.

Colour of petals

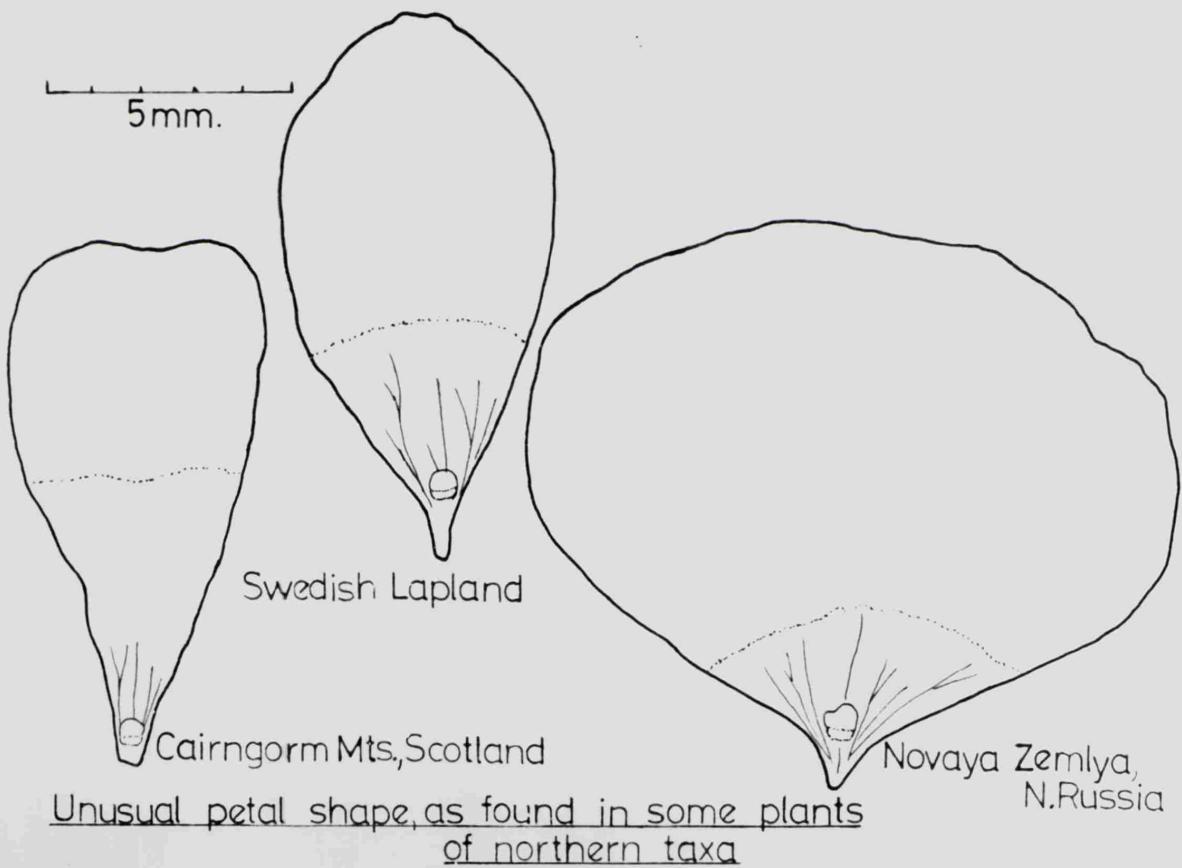
No differences between the colour of the petals of any of the groups in cultivation were noted. The only colour differences ever recorded appear to be local mutations (see chapter 2). The occurrence of brown-veined petals in the northern montane plants (Tutin 1964) was not upheld; it only appeared to be a feature of any petals which are dried too slowly.

Nectary-scales

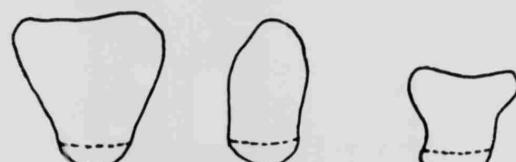
The shapes and sizes of the nectary-scales showed very great variation even within the same flower. The only geographic trend in type of scale was that of short nectary scales occurring among northern montane and artic plants, but not to the exclusion of other types.



Hants, England
Vaigach Is., N.Russia
Normal petal shape



Swedish Lapland
Cairngorm Mts, Scotland
Novaya Zemlya,
N.Russia
Unusual petal shape, as found in some plants
of northern taxa



Nectary scales showing the range of shapes
found in the plants from Austria

Examples of shapes encountered are given in fig. 15.

The nectary scales of the E.Asian taxon, R.acris var.frigidus

Regel, differ from those of the European plants as they are as broad as the basal part of the petal, whereas those of the latter are always much narrower.

Stamens

The lengths of the filaments and the size of the anthers have been used by some authors (e.g. Jordan 1864) as diagnostic characters. However, these were found to be far too variable, even within a single flower, to be of any value; also they are characters much affected even by slight femaleness of the flowers.

Hylander (1943) reported the presence of hairs on at least the basal parts of the inner filaments of the E.European rhizomatous plants: this had previously only been noted in the S.Spanish rhizomatous plants of the complex. Hylander stated that such hairs were absent in the French rhizomatous plants and in all the premorse based plants of the complex, thus serving as a clear diagnostic character between these groups and the former rhizomatous groups.

Although nearly all the flowers from plants of the E.European rhizomatous group were found to have filaments with such hairs, flowers were examined in which no such hairs appeared present. Such hairs were also commonly found in flowers from E.European premorse based plants, occasionally found in plants from W.Europe and even once or

twice found in flowers from French rhizomatous plants. The hair density in these plants was often as great as that occurring in the E. European rhizomatous plants.

The number of hairs on the filaments of the S. Spanish rhizomatous plants was found to be much greater than that occurring in any other plants of the complex. It was usually in the range of well over thirty hairs on at least some of the filaments: it did not exceed twenty in other plants. The plants in Morocco similar in other characters to the S. Spanish plants were not found to have so many hairs, but the material examined was very poor and this needs further investigation.

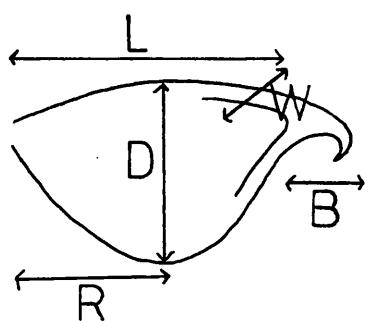
THE ACHENE

The shape and size of the achenes together with the number per flower head have previously been held to be characters of prime importance.

Using cultivated material the number of achenes per flower head on any one plant was found to be very variable. The larger numbers occurred in the earlier flowers of a cyme, and there was a considerable decrease in numbers in the later developed flowers. Even using the numbers of achenes in the first flowers of a cyme no correlation between numbers of achenes and the plant's geographical origin or morphological type was found.

The size and shape of an achene were recorded by the following

measurements -



L-length of achene without beak
 B-length of beak
 W-maximum width of achene
 D-maximum depth of achene
 R-distance of D from point of attachment of achene

In the cultivated material measurements were made on five mature achenes per plant, these achenes were picked at random.

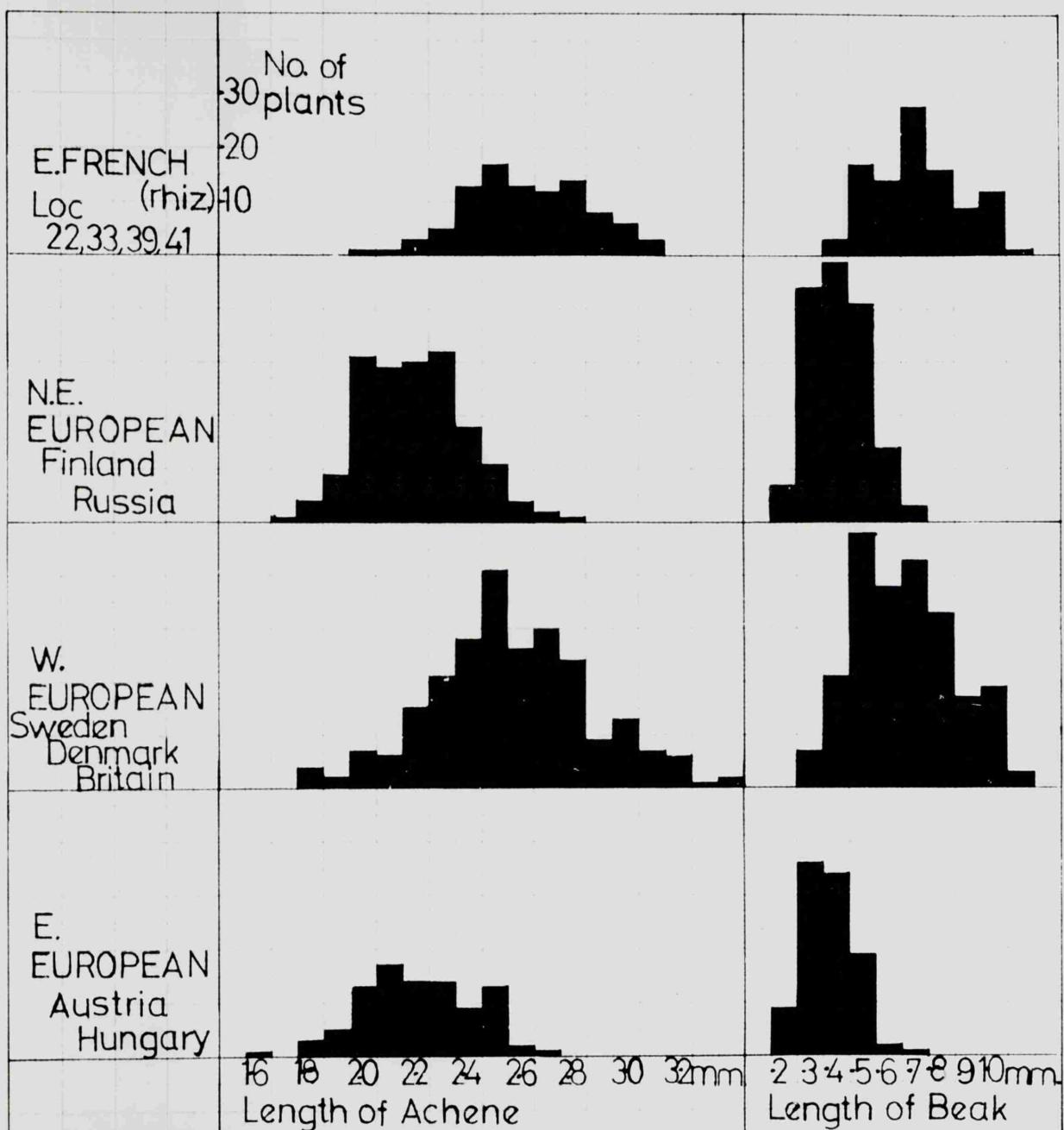
Results using the cultivated plants

Length of achenes and beaks-

Longer achenes and beaks occurred among the plants from W.Europe and the E.French rhizomatous types than occurred among the E.European and N.Baltic plants, although lengths similar to those of the latter group were common among the W.European and rhizomatous plants. (See fig.16).

Depth of achenes-

Great variation was found in the depth of the achenes. The ratio of depth over length for achenes from the same plant was found to vary very little, but the extremes of variational range were frequently



HISTOGRAMS OF ACHENE-AND BEAK-LENGTH
FOR GROUPS OF CULTIVATED PLANTS

FIG.16

found in plants from the same locality. (See fig. 17). No geographical trends in this character, even in frequency of types could be found in the premorse based plants. In the rhizomatous plants great variation was also found, but the lower values of D/L were absent.

The position of maximum depth was more constant among plants from the same locality, than was the ratio of D/L. But still no geographical mode of variation was apparent.

Width of achenes-

This appeared to be correlated with the length and depth of the achenes.

Degree of curvature of the beaks-

This was found to be fairly constant for any given locality, but no geographical trends were apparent among the plants in cultivation. Only a few beaks were found which approached a straight condition, and in nearly every case this was found to be due to the fragile curved tip having broken off. In the few cases where straight beaks occurred, and no such breakage could be detected, other achenes from the same plant were seen to show some hooking of the beak.

Results from herbarium material

Measurements of achenes from herbarium material were very few due to the rare occurrence of mature achenes. An attempt was made to estimate the beak length of herbarium material only possessing immature achenes, using as a guide comparisons made of immature and mature

achenes from cultivated plants. An accurate estimation was difficult as in immature achenes the beak is so much larger in proportion to the body of the achene, than it is in mature fruits. Recording of such estimates was by three arbitrary categories-

short-corresponding roughly to lengths up to 4mm.

medium- " " " over 4mm. and up to 8mm.

long- " " " over 8mm.

Among the premorse based plants it was found that 'long' beaks almost exclusively occurred in the W.oceanic regions, but even in these regions beaks of 'medium' length were more common. In S.Europe east of the Alps the beaks were predominantly 'short' in length with only a few of 'medium' length. West of the Alps 'medium' length beaks are predominant, but 'short' beaks do occur sporadically even in the west coast regions of Europe.

All the premorse plants had hooked beaks, except for certain plants in the E. of Europe and the N.E.Baltic region. These plants had beaks which were merely short points, too short in fact for them ever to be hooked.

The E.French rhizomatous plants had hooked beaks of at least 'medium' length and often of 'long' length. The Pyrenean rhizomatous plants had similar beaks but 'short' ones were common and 'long' ones appeared absent.

The E.European rhizomatous group was found to be characterised by having straight beaks or at the most with the tips of the beaks only

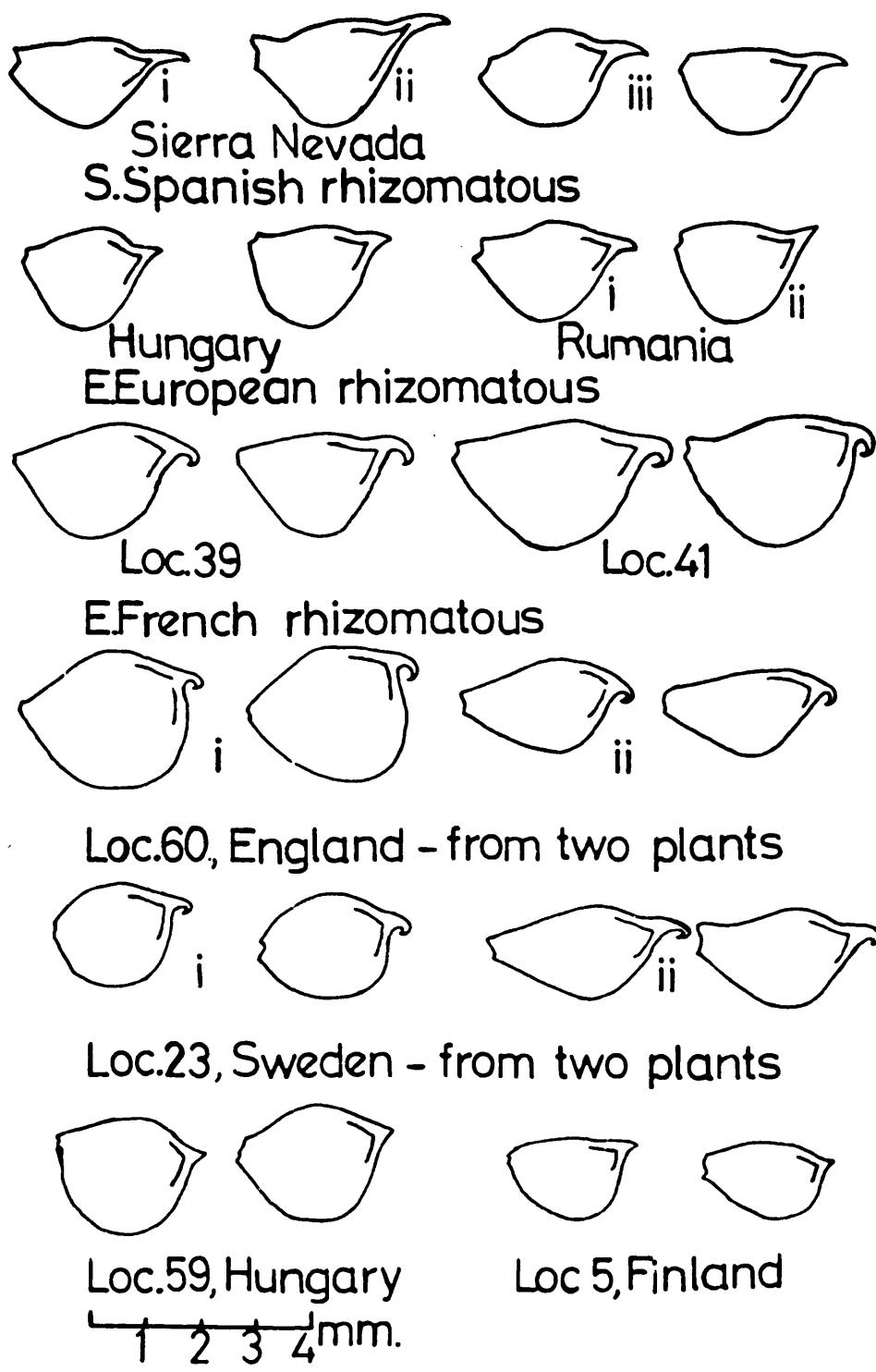


FIG. 17

slightly curving, and the beaks were about 0.6mm to 0.7mm in length. None of the short pointed beaks of the E.European premorse types ever reached such dimensions, although these two types of achenes were otherwise very similar.

The achenes of the S.Spanish rhizomatous plants were similar to those of the E.European rhizomatous plants, having straight or only slightly curving beaks, but the beaks were much longer being from 0.9mm to 1.2mm in length. These two rhizomatous groups appeared distinct from the other groups and from each other on the character of their beaks. No other disjunct variations in achene form occurred among the complex.

THE TIME OF FLOWERING IN CULTIVATED PLANTS

In the summer of 1966 the total number of flowers from five plants from each locality (for those localities which are asterisked in the locality list) was counted at regular intervals. Individual plants from the same locality showed little variation in the timing of their peak of flowering, but did show variation in the total length of their flowering season.

The flowering season of all groups was found to be very similar. Examples of the chief variations are shown in fig.18.

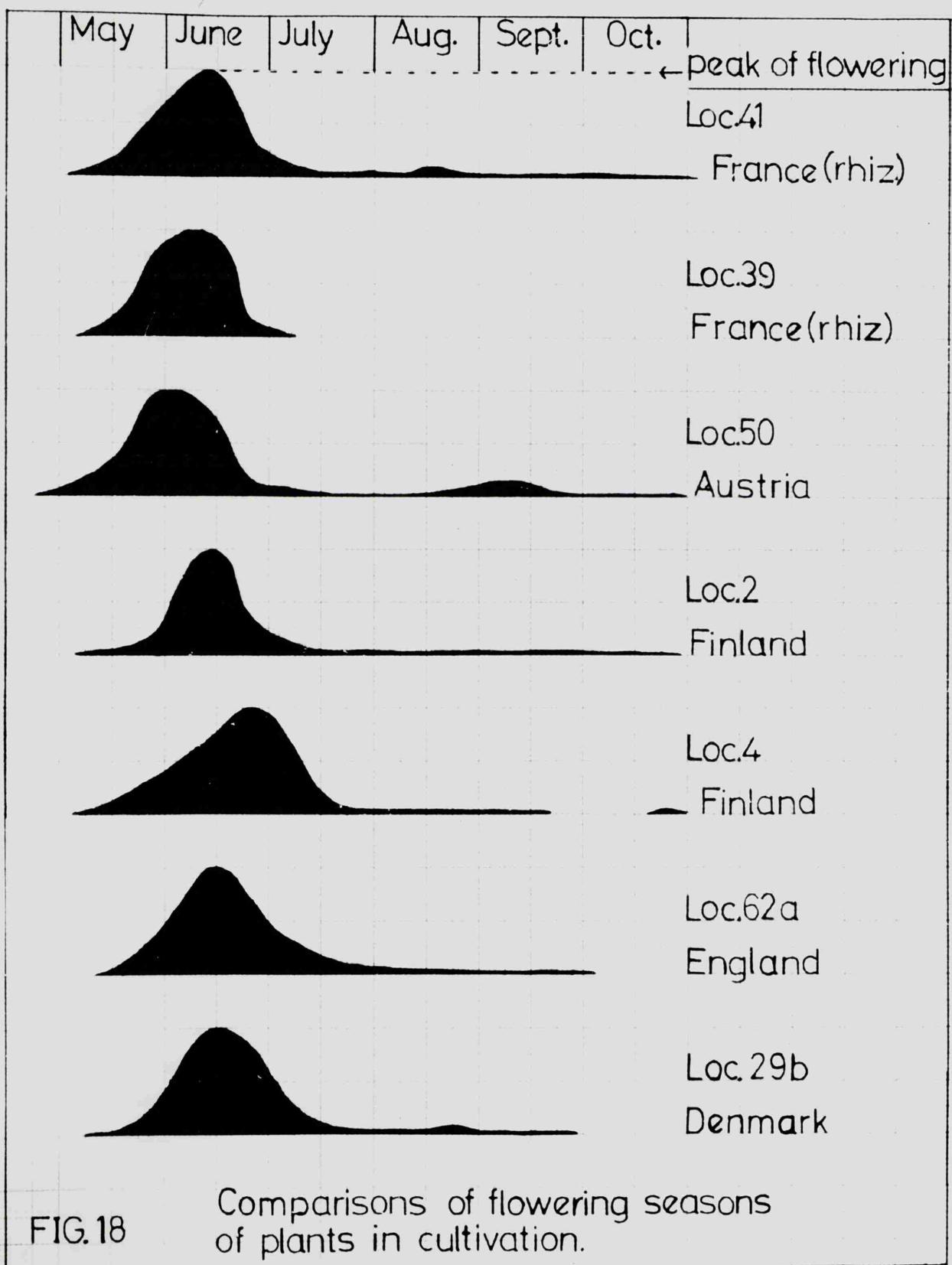
The first plants to start flowering were from locality 50 (Austria). However in 1967 plants from locs. 47 and 48 (Italy, planted

in 1966) started flowering in early April, long before any Austrian plants. Plants from S.Europe were also the first to reach their peak of flowering. The next group to reach their peak were the rhizomatous plants from locs. 39, 41 (E.France) and 33 (Germany), although they had not started flowering any earlier than some of the other groups. All the others had reached their peak of flowering by mid June, except for a few Finnish localities, which were only at the most about a week later. Some of the British plants were the last to start flowering, but this did not affect the timing of their peak.

After the first peak of flowering in early summer very few flowers were produced, but although few in number, in most plants there was an uninterrupted production of flowers until autumn. Loc.39 was the only group not to keep flowering until at least well into August; but a plant from this locality which had been transplanted in the spring of 1966 flowered until late November; the plants which were tested, which had overwintered in situ finished flowering in early July. Transplanting was found to have a similar effect on all plants.

Some plants occasionally produced buds during the winter, but these were usually killed off by frost. These mainly occurred on the Finnish and S.European plants, but never among those from Britain and Denmark.

The only localities to show any sort of secondary peak of flowering were 50 (Austria), 32 and 33 (Germany); these are plants from districts



with a continental climate and this secondary peak can be correlated with the fact that in their natural environment such plants more or less die down after the first peak of flowering, that is during the hot dry summer, and start flowering again when the autumn comes.

Böcher (1945) found that R.acris only flowered after being subjected to long day conditions. He also found that a certain amount of cold was needed to promote flowering. This appeared true in the case of mature plants, as the plants which overwintered in a warm greenhouse did not flower during the following season. This factor may be one of the chief reasons for the scarcity of R.acris in S.Europe; and that its most southerly locations are at high altitudes would corroborate this suggestion. But the plants grown in the warm greenhouse did not include any from the most southerly ecotypes.

Chapter 8

ANATOMYThe stem

The vascular tissue in the stem of R.acris is composed of a ring of various sized bundles which are usually embedded in a band of lignified cortex. Each bundle is surrounded by a sclerenchymatous sheath, which on the side of the phloem takes the form of a well developed fibrous cap. A small amount of secondary growth occurs within the bundles and the phloem is of the monocotyledonous type. (See fig. 19).

No consistent differences in the anatomy of the stem were found among any of the main European groups of R.acris s.l.. The vascular bundles of R.seroticus Vis. were very similar, but the fibrous cap tended to be larger in relation to the size of the bundle.

Bergman (1944) found that the nature of the interfascicular tissue and pericyclic sclerenchyma afforded valuable characters for the identification of Ranunculus species; but similarly found no significant differences between the vascular bundles of R.steveni (referable to the E.French rhizomatous type) and R.acris s.s..

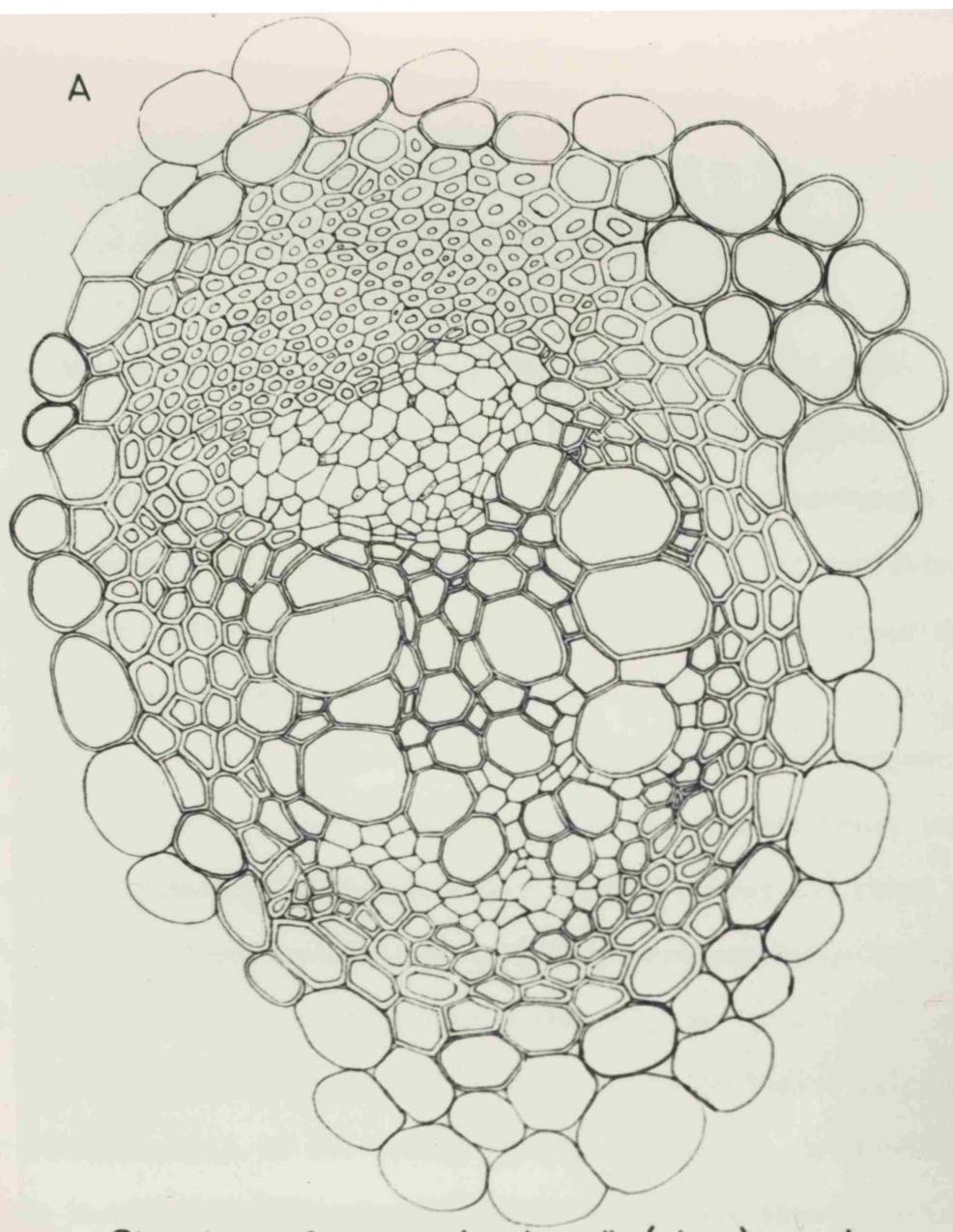
The stem anatomy of the E.Asian R.acris var. nipponicus Hara (see chapter 13) was found to be similar to that of the European R.acris. But that of R.acris var. frigidus Regel was distinct, due to the sclerenchyma sheath not being continuous on the xylem side of the bundle, and in the cells of the cap not being distinguishable from those of the rest of the sheath.

The root

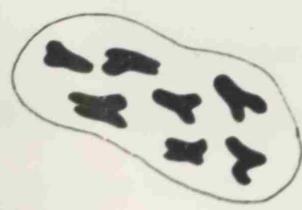
The anatomy of the root similarly showed no consistent variations within the European members of the complex. Well developed, regularly arranged intercellular spaces in the cortex were found to occur sporadically in all the groups and in R. serbicus, presumably due to the conditions under which the plants had been growing.

Leaf

The thickness of the leaf has been used as a diagnostic character separating the S.Spanish and E.European rhizomatous plants from the E.French rhizomatous plants, (Hylander 1943), the leaves of the former plants being thicker than those of the latter. This character, from the general appearance of the herbarium material, appeared to hold true for all but a few plants of the former group. A few sections of leaves from herbarium material were cut, and it was found that the difference in thickness was due to the size of the cells rather than to an increase in the number of cells.



B



Loc. 33

7 bivalents



Loc. 1

3 bivalents
8 monovalents

FIG. 19

Chapter 9

CHROMOSOMES AND BREEDING EXPERIMENTS

The chromosomes of R.acris s.s. have had more attention than have those of most other species of Ranunculus. Comprehensive lists of the earlier counts are given by Gregory (1941) and Coonen (1939).

Gregory (1941) states that R.acris shows great variation in chromosome number, which is not characteristic of the other species. However it is to be noted that the majority of the variations in chromosome number are from counts made by Sorokin and Senjaninova (see Gregory 1941); and except for other rare occurrences, such as the tetraploid ($2n=28$) found by Langlet (1932), almost all other numbers ever reported were $2n=14$. Whyte (1929) when examining hermaphrodite, female and male forms of R.acris found only $2n=14$.

$2n=14$ can thus be taken as the typical number. This was the only number found in the counts made on the plants in cultivation.

The only plant types for which counts have been reported are the European premorse types and the E.French rhizomatous types. Unfortunately no living material of the E.European or S.Spanish rhizomatous plants could be obtained during this investigation.

Stomatal length and pollen grain diameter, which in certain instances in other species have been found to provide diagnostic characters separating diploid and tetraploid races, were examined in

R.serbicus Vis., a species which is generally held to be closely related to R.acris and which has $2n=28$ chromosomes. These measurements were compared with those from herbarium material of premorse and E.French rhizomatous types of R.acris. It was found that seldom was there any overlap in the average values of these measurements, those of R.serbicus being the greater. Measurements from herbarium material of E.European and S.Spanish rhizomatous plants were of the same order of those of R.serbicus. However an anomaly was found in the pollen grain diameters of the cultivated plants examined, as they were of the same order as those of R.serbicus rather than being similar to those from herbarium material of the same type. Although no conclusions can be drawn from these measurements they do not rule out the possibility that the E.European and S.Spanish rhizomatous types might be tetraploid plants.

Although actual chromosome number could not be used in providing evidence for the affinities of the different morphological types, such evidence may well be provided by the karyotypes of the plants, but these were not examined in this present investigation.

Experiments to investigate the breeding mechanisms

Most of the breeding experiments were carried out on plants from the localities which are asterisked in the locality list. Five plants per locality were used so that there would be sufficient buds at the right stage at the same time. The plants were grown in a cold greenhouse. The plants were regularly sprayed with systemic insecticide to

stop contamination by greenfly and other insects.

Emasculation of flowers was carried out while they were still in the bud stage, when the petals were just visible but before any of the anthers had burst. The stamens were removed with a fine pair of forceps which had previously been sterilised in alcohol. Fisher's (1954) method of using an iris diaphragm to simplify the emasculation technique in Ranunculus flowers was abandoned, as it was found too difficult to manipulate without damaging the carpels as the filaments while still in the bud are so short. The flowers were covered by small cellophane bags. Crosses between plants were made by copiously dusting the pollen from the male parent onto the carpels of an emasculated flower so that a visible layer of pollen remained on the stigmas. Pollination was usually carried out shortly after the flowers opened. The time of application did not matter as the stigmas appeared receptive for sometime before the flower would have naturally opened until shortly after the petals had fallen.

Tests for self-compatibility and apomixis

Compatibility of selfing was tested on at least four flowers per locality. The flowers were allowed to open naturally under a bag and were dusted with their own pollen.

Apomixis was tested on at least three flowers, and often on many more, by emasculating them while still in the bud stage.

In these tests, excepting cases where contamination could be attributed to the presence of greenfly, out of the over 3,500 carpels from emasculated buds only 29 seeds were set and of the 4,500 carpels which had been selfed only 3 seeds were set. That these were probably also due to contamination is likely, due to the following facts. Seed set was more common in the plants which had been emasculated, and therefore more liable to contamination, which is suggested by these achenes only occurring on four flower heads. The achenes set after selfing were at a time when there were greenfly in the greenhouse which had contaminated other flowers, but were not seen in the bags in question; that only single achenes were set in each case was typical of contamination by greenfly.

Other authors report finding selfing and apomixis occurring in some plants of R.acris. James and Clapham (1935) state 'in some localities the flowers are self-sterile, but this does not seem to be general'. They further describe the method of dehiscence of the anthers, which they concluded should make cross-pollination rather more probable than self-pollination. Others say that cross-pollination is achieved by the protogyny of the flowers. Marsden-Jones and Turrill (1935 and 1952) report both selfing and apomixis, but the latter only occurring in under 1%, a figure that can hardly be said to be significant and which could easily be due to contamination. They only mention the use of an insect-proof breeding house, and not to having bagged the individual flowers; this would seem necessary as the copiously produced pollen

is easily scattered.

From the tests carried out, despite previous reports, it is thought highly probable that all the plants of R.acris s.s. are obligate outbreeders.

Tests to find the self-incompatibility mechanism

The Ranunculaceae has previously been reported to contain species which are self-incompatible but no investigations appear to have been made into which type of mechanism is in operation (Bateman 1954). A relationship between certain factors and the type of self-incompatibility mechanism has been found; and by the Ranunculaceae having binucleate pollen when shed, and in having simultaneous cytokinesis, it has been deduced that such plants should have a homomorphic gametophytic system (Pandey 1960).

A series of crosses between plants from the same localities were made. When the parent plants were crossed with pollen from 'hybrid' F₁ plants, good seed set was obtained in all cases. Back crosses to the parent plants are always compatible in the case of a gametophytic incompatibility system, but only occasionally so in sporophytic systems (Bateman 1954). When plants were selfed it was found that the pollen did in fact germinate and the pollen tubes enter the style. The point of inhibition of the pollen in a gametophytic system is usually in the style (Pandey 1960, Bateman 1954). It would appear from

these preliminary tests that incompatibility mechanism in R.acris is gametophytic.

Interlocality crosses

A series of test crosses was made consisting mainly of those between plants from each locality and plants from localities 5 (Finland), 50 (Austria) and 39 (E.France-rhizomatous). These localities were chosen as representatives of the geographically most distant and morphologically dissimilar plants.

The results are given on the following page as the percentage seed set per flower head. All the plants tested were found to be freely interfertile. Generally as good or sometimes better seed set was produced between geographically remote and morphologically dissimilar plants as was between morphologically similar plants from the same country or even the same locality.

The percentage of seed set depended on the general fertility of the mother plant rather than on the origin of the pollen. In cases of poor seed set, in crosses between certain parent plants, repeats using a more copious application of pollen, produced results as good as those obtained using pollen from plants of other localities. The percentage of seed set was not affected even when pollen containing a high percentage of infertile grains was used.

♂ Parents

Parents
of

Locality numbers	Locality numbers													
	5	50	39	1	2	4	6	24	22	62b	32	33	41	40
1	79;68	82;91;76	61;67;95					92				94	94	
2	54;96 76	69;61;60	85;63					85						
3	92;96	93;90	96;92					46						
4	54;91 86	54;86	88;21;87					34	22					
5		87;79;61	70;73;64					29						
6	0; 8	94;29;50 61	94;29;28 43;68											
8	78;83	90;79	78;91											
25	66;59	88;90	73;72											
23	76;81	72;89	91;67											
24	73;58	90;77;65	43;47				59							
22	63;61	65;67	78;73											
62b	12;17	9;11;32 17;27	12; 01 6 17											
50	86;84		78;74;35 23;94;83 92;88;87	93	4	19	94	77		70	90	91		85
				83						87	61			
58	56;67	48;82	81;90							53				
										72				
48	95;84	84;73	94;89							85				
										77				
44	42;21	28;23	29;10;47 21							38				
32	83;72 78	63;84;91	98;95;80 91;89;79	74 46 86							90			
											75			
33	41;37	52;93;24	41; 0145		23	66								
				69										
39	63;87	36;14; 0 0;68;63												
41	52;36	54;65	39;48							28				
40	63;65	48;74;41 85	57;54;56 73;75							70				
										64				

Test crosses between plants from localities in cultivation.
 Results, given as percentage seed set per flower head.

♀ Parent		♂ Parent	Percentage seed set per flower head	
(5 x 50)	x	39	51	52
(5 x 50)	x	62b	56	
(50 x 39)	x	5	31	35
(33 x 2)	x	50	29	47
(5 x 39)	x	50	59	73
(5 x 39)	x	62b	80	
(33 x 50)	x	33	70	
(33 x 50)	x	5	79	76

Results of test crosses between hybrid plants and plants from further localities.

That truly hybrid rather than apomictically produced seed was obtained from such crosses was proven by the intermediate character of the F.1 generation plants. The shape of the 'spring' leaves of thirty of such hybrids, in their second year, was compared with that of their parents. In only a couple of cases was the shape, although intermediate in character, nearer the shape of the leaves of the maternal parent than to that of the paternal parent. Some examples of leaf-shape of the parent and hybrid plants are shown in plate 6.

The interfertility between some of these hybrids and a third parental type was tested. It was found to be as good as between any of the original parental plants. The hybrid plants still remained totally self-incompatible.

Germination of achenes from interlocality crosses

The achenes obtained from the crosses were sown in a cold greenhouse in the autumn or following spring. In both cases germination of the achenes from a single flower was found to spread over several months.

Poor germination was obtained from the achenes harvested in 1965. The pots of achenes had been allowed free drainage, whereas in 1966 they stood in an inch of water and relatively good germination percentages were obtained in nearly all cases.

The germination percentages seemed to indicate no differences in the interfertility of plants from the different localities. Good

germination percentages were as common from achenes whose parents were geographically distant and morphologically dissimilar as they were from crosses between plants from the same localities.

Fertility of the hybrid plants from interlocality crosses

Fertility of the hybrid plants was first investigated by an examination of meiotic divisions of pollen mother cells. Squashes of young anthers were stained in acetic-orcine. However it was found that irregularities in the pairing of the chromosomes were found as frequently in the parent plants as in the hybrids. (See fig.19).

The fertility of the pollen produced by the hybrids compared with that produced by the parent plants was investigated. Pollen from a young flower was stained in cotton blue, which shows up grains possessing cytoplasmic contents. An estimate of fertility was given by the percentage of full sized grains with cytoplasmic contents: this is only an estimate of fertility as it is a count of morphologically good pollen and not of the percentage of grains capable of germination.

The percentage of 'good' pollen was found from a well mixed sample of pollen taken from all the anthers of the flower. Whyte (1929) stated that 'good' and 'bad' pollen occurred in separate pollen sacs: the 'good' in the older ones and the 'bad' in the younger ones. This was not found to be completely accurate as a mixture of both was found in nearly every pollen sac, but with a higher percentage of 'bad' being

found in the inner pollen sacs. It was felt that the relationships of the percentages from different plants, as found in the above manner, would be the same as those from either inner or outer anthers only.

Even in parental plants of normal appearance, percentages of 'good' pollen as low as 20% were not uncommon. Whyte (1929b) commenting on the large percentage of 'bad' pollen often encountered in R.acris stated that plants, which on superficial observation appear normal hermaphrodite plants, are not actually normal but have traces of incipient sterility which are manifest in plants showing differing degrees of femaleness.

Plants with obviously female flowers were avoided when making the pollen counts, but a few were checked and some of these had as high percentages of 'good' pollen as did some flowers of normal appearance.

It was, however, found that comparisons between the percentages of 'good' pollen in the parent plants compared with that in the hybrids were impossible. No method of standardising the flowers sampled could be found. The percentage values from different flowers from the same plant, collected at the same time or in different years, frequently gave widely differing results. In 1966 a count from one of the hybrid plants was 83% whereas a repeat count in 1967 gave only 31%. It is to be remembered that fluctuations of femaleness in a single plant are common (Marsden-Jones and Turrill 1935).

The following table gives an idea of the range of the percentage values of 'good' pollen found in plants in cultivation. Similar results were obtained from flowers collected in the wild.

Loc. 62a (England)	56%	Loc. 62b	40%	Loc. 39 (E. France)	91%
76		24		89	
59		18		70	
83		27		73	
56		28		67	
46		Loc. 33	47%	Loc. 22	79%
60		(Germany)	42	(Sweden)	53
75			35		80
70			39		79
54			21		75

All the methods which have been tried to estimate the degree of fertility between the plants from different localities, have proved useless. Before a satisfactory method can be found more needs to be known about the causes of the high infertility which was found to occur in all but a few individual plants. This infertility has been manifest in the high occurrence of univalents at meiosis, in the high percentage of bad pollen and in the poor seed set of some plants even when pollinated by plants from the same localities.

Interfertility with other species

Six crosses were made between R.acris and R.ser比cus. In all cases good seed was obtained, but no achenes ever germinated.

Crosses between R.acris and R.lanuginosus have not yet been tried; but a plant of intermediate appearance between these two species was found in Austria.

Lewis (1954) reported the breaking down of self incompatibility in some species of plants by the addition of pollen from a closely related species, but one not capable of crossing with the parent plant. Crosses between R.acris and R.bulbosus never produced any seed: neither was any seed set when pollen of R.bulbosus was added to selfing flowers of R.acris. If pollen from other species of Ranunculus does break down the self incompatibility mechanism of R.acris, it might have important implications, as insect visitors do not appear to discriminate between some species of Ranunculus (Harper 1957).

Chapter 10

SUMMARY OF THE VARIATIONAL PATTERNS

The morphological types, as discussed in the previous chapters, show differing degrees of distinctness. No intermediate plants have ever been seen between any of the rhizomatous types probably because they are geographically isolated from each other. However intermediates between some of these groups and neighbouring premorse plants occur. All the premorse types are linked by a series of intermediates. In some districts these premorse based plants form a continuous cline, and in all regions appear at least to be linked by a range of intermediates which are not of a hybrid nature. There appear to be no land regions of any size which are devoid of R.acris within the distributional range of the premorse based types.

The S.Spanish and E.European rhizomatous groups

The S.Spanish group is more or less completely geographically isolated from all the other groups and no intermediates have ever been seen between these plants and those of any other group. Morphologically they are closest to the E.European rhizomatous group. Only very few intermediates between the E.European rhizomatous group and any others have been seen. These occurred in S.W. Ukraine and were intermediate with the E.European premorse plants: this conclusion as to the origin of these plants is in agreement with that of Hylander (1943). The

distribution of this rhizomatous group is almost completely overlapped by that of the E.European premorse plants.

The S.Spanish and E.European rhizomatous groups are similar in the following respects: they have rhizomatous rootstocks; broad lobed leaves in which the three main segments of the leaf are often completely divided or even stalked, and the segments of the leaves are relatively little divided and have few teeth; the thickness of the leaves is generally greater than in the other groups; the hairs on the petioles are at least of group C in length, but often of group D or E, and are rarely of group 3 in width, widths of group 4 or 5 being more normal; the beaks of the achenes are straight or only slightly curving, never hooked; the lower third of the sepal is devoid of long hairs.

These two groups differ in that the segments of the leaves of the S.Spanish plants are more frequently stalked than are those of the E.European rhizomatous plants, and the median segment of the former group often bears three pairs of lobes, whereas that of the latter group only bears two pairs of lobes. The hair type in both groups is similar, but orange-brown petiole and stem hairs only occur in the E.European plants. The beaks of the achenes of the S.Spanish group are longer, being 0.9mm-1.2mm in length, those of the E.European plants are only 0.5mm-0.7mm long. The filaments of the stamens in the S.Spanish plants are often densely hairy, bearing over thirty hairs per filament, but in the E.European plants the number of hairs was never found to exceed twenty. The zone of long hairs on the sepals of the

S.Spanish plants is often more distinct than that on the sepals of the E.European plants, due to a distinction in widths as well as lengths of hairs.

The E.French rhizomatous group

This group as a whole has a well defined geographical distribution. But a complete array of intermediate plants was found between these rhizomatous plants and the neighbouring premorse plants. Such intermediate plants were relatively rare in the main distributional range of this rhizomatous type, but were common in the extremes of its distribution.

The extreme forms of this group are characterised in addition to the possession of a distinct rhizome, by having very broadly lobed leaves and fine hairs. Plants intermediate in character vary in width of lobes and hairs. Although occasional plants could be said to have shorter rhizomes than those found in the more extreme plants, using herbarium material it was usually only possible to say if a rhizome was present or absent, and positive scoring usually meant that the rhizome was well developed. Well developed rhizomes were found in occasional plants which in no other respects could be said to approach this group of plants. But generally little overlap was found in leaf-shape of rhizomatous plants and neighbouring French premorse plants, showing that there is a definite correlation between these characters.

Correlation between hair width type and leaf type was found to be very variable. Very fine hair cover (that is of group 1) was found always to be associated with the broadest lobed leaves. But such leaves were also found to be associated with broad hairs: this was found to be especially true in the Vosges region where fine hairs appeared absent. Both fine (group 2) and broad hairs were also to be found associated with the narrower lobed leaves.

In the range of variation of hair lengths, hair cover, petal lengths and of achene form, no differences were found between these E.French rhizomatous plants and the premorse plants of W.Europe.

These rhizomatous plants are reported as introduced into other parts of Europe. Numerous examples of such plants from Sweden and Austria have been examined. In most of the localities they have remained distinct but in both these countries examples have been seen of plants showing that hybridisation has occurred with the native premorse types.

The Pyrenean rhizomatous group

In previous taxonomic treatments of the R.acris complex this group has been included as belonging to the previous group. In this present investigation it has been found to differ from the other French group in the following ways. No plants approaching the E.French rhizomatous type in its extreme form occur. Wide lobed plants occur,

but a far greater percentage of narrow leaved plants occur (see fig. 7A) than do in the E.French group. In the Pyrenean group these narrow lobed leaves are not referable to plants intermediate to premorse types as they are in the E.French group. Pyrenean plants all have hairs corresponding to at least group 3 in width, whereas in E.French plants narrower hairs are common. The hairs on the stems and petioles of the Pyrenean plants are always appressed, whereas in the E.French group spreading and deflexed hairs are very common. The beaks of the achenes of the Pyrenean plants are generally shorter than those of the E.French plants.

From the herbarium material examined it has been impossible to tell whether the Pyrenean group is distinct from the adjacent premorse types, if there are indeed adjacent plants, or whether there is continual variation from one type to the other. It is the only type occurring in Spain other than the distinct S.Spanish rhizomatous type.

The premorse based plants

The main cline of variation in the premorse based plants is from west to east. Plants in the west of this cline are characterised by having long hairs (over 0.8mm) which spread or are deflexed on the lower part of the stem and on the petioles. Their achenes are often larger and the beaks of the achenes longer than those of eastern plants. Their petals are often over 11mm, and the premorse rootstock is more elongated than those of the eastern plants. The leaves may be broadly lobed but

are often as finely divided as those of the plants in the east.

In the extreme west, N.Scotland, Ireland, The Faeroes and Iceland, there are plants characterised by having broadly lobed leaves, broad simple bracts and in having on the upper surfaces of the leaves many hairs over 1.2mm. The hairs on these plants are usually orange-brown. One or two plants approaching this condition have been seen from the W.Coast of Norway, but plants typical of this group have not been seen from the mainland of Europe.

In central France and further eastwards the plants have hairs which are nearly always under 0.8mm in length and which are normally appressed. The petals rarely exceed 11mm and the beaks of the achenes rarely exceed 0.5mm.

To the east of the central European mountains the plants have achenes with beaks usually even shorter, which may be hooked or only mere points. The hairs on the petioles in some cases are under 0.4mm and the hairs may even be appressed on the upper surfaces of the leaves. The leaves are narrowly lobed, but not more so than occurs in some western plants: however the extreme eastern plants are characterised by having leaves with relatively few teeth.

In the E. of Europe the E.European types, extend up to S.Finland and N.Russia. The achenes of the plants from such localities still have very short beaks, often only mere points. The hairs on the petioles and stems are short and usually appressed. The leaves are still characterised by having few teeth, but are often much more broadly lobed than those from S.E. Europe. Although these plants are

somewhat morphologically similar it was found that they differed greatly in the biological reactions for which they were tested.

In the tundra and montane regions of Scandinavia there occurs a form of plant characterised by having leaves which are only relatively shallowly lobed, and by having 'spring' leaves and petioles which are glabrous, only the 'autumn' leaves and petioles bearing hairs. This type of plant appears to be associated with distinct ecological conditions. The normal hairy lowland plant is to be found right to the North coast of Norway and intermediates between this and the glabrous type are common. In Britain this montane type occurs only at high altitudes in the Cairngorms, plants from other mountains in Scotland (e.g. Ben Eighe) have also been referred to the same taxon by some botanists, but such plants have always proved to have fairly finely divided hairy 'spring' leaves. A few plants of the glabrous form have also been seen from Iceland.

On the N.coast of Russia are plants distinct from other groups by having their lobes little divided, less than those of the Scandinavian plants (see plate 2), from which they also differ by their 'spring' leaves and petioles usually being covered by hairs which are always very narrow (group 1). This was the only type seen along this north coast, and no intermediates between these plants and the 'northern E.European' plants were seen. Intermediates between the N.coast Russian type and the Scandinavian type occur on the north coast region of Norway, but only a few such plants have been seen.

Chapter 11

TAXONOMIC CONCEPTS

Botanical categories are subjective concepts, expressing the level of groups assigned to them. It is difficult if not impossible to define any category in terms other than in those of its relationships in rank to other categories.

The impossibility of defining the categories and the non-conformity in their usage can be said to be due to the disparity between the continuity of evolution and the rigidly discrete steps of the taxonomic system. From the types of variational patterns produced by evolution it seems evident that there can be no absolute system of classification arranged on a structure of clearly defined and precisely evaluated categories, although many attempts have been made to do so.

The needs of the taxonomist are best served if the categories are elastic and relative so that they have as wide a use as possible.

Mason (1959) stated that 'the wisdom of past experience has dictated that the taxonomist purposely refrain from defining these categories in any way that will impose restrictions on the freedom with which he may express the interrelationships that he construes to exist.'

Lewis (1963) similarly states, 'to make it precise would be to destroy its general usefulness.' The system as it stands at present has proved adaptable to the diverse patterns of discontinuity in all groups of organisms.

The seemingly impossible task of grouping organisms in what appear to be purely subjective categories of varying ranks is said by some to be resolved by there being some biological reality in the species, and by the fixing of this category the rest can be placed accordingly.

The Species

In the zoological context the species has often been defined purely on breeding potential, with no consideration being made of morphological distinctions. Thus Mayr et al. (1953) define a species as 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.'

In plants there are many groups which are isolated geographically or ecologically, which are morphologically distinct but are still capable of freely interbreeding. On the other hand, there are frequently reproductive gaps of various kinds and degrees between populations which are morphologically indistinguishable. The former situation is particularly common among woody plants, but not exclusively so, and the latter among herbaceous plants (Mosquin 1966). Mosquin pointed out that 'if the criterion of reproductive isolation were applied without any measure of consistency, the taxonomic units so created would not only have less biological meaning and consequently be less useful but would often be far more arbitrary than the present groupings based principally on morphology.'

The species category when applied to plants appears most applicable where there are distinct morphological discontinuities. The criterion of the existence or non-existence of reproductive isolation should be used where there is not a conflict with the morphological evidence, and provided it does not cause great practical difficulties.

Such attributes as interfertility and chromosome number are particularly important at a specific level of differentiation, although this is not true in all cases.

The degree of morphological distinction needed between groups of populations for the species category to be applicable is open to debate. Gilmour's (1940) definition of a species seems to be the one most generally applicable to the situation as found in plants. 'A species is a group of individuals which, in the sum total of their attributes, resemble each other to a degree usually accepted as specific, the exact degree being ultimately determined by the more or less arbitrary judgment of taxonomists.'

Infra-specific categories

The concept of a subspecies varies as greatly as does that of a species.

An extreme point of view is held by Fisher (1965), who claims that taxonomic recognition is ruled out where groups of plants show even slight overlap in morphological features. In the case of a subspecies, he considers that there should not only be no overlap but

that there should also be a firm geographic basis. The morphological differences between his subspecies may only involve single characters. The groups he recognises as species differ from subspecies only in the accumulation of further morphological differences. Such an arbitrary distinction between subspecies and species is unfortunate when using the binomial system of classification in its present form.

Most botanists advocate the use of the subspecies category where there is slight overlapping of the groups, and some even permit such a situation for species. Walters (in Meikle 1957) suggested that when only 90% of specimens could be assigned to one taxa or another, then the taxa should be given specific rank!

The groups for which the subspecies category is most frequently employed are those illustrated in the definition proposed by Tutin (in Meikle 1957); 'taxa differing from one another in minor morphological characters, occupying distinct areas (though sometimes with a zone of overlap) or else isolated ecologically, but potentially capable of interbreeding without substantial reduction in fertility.'

Löve (1964) argues for the inclusion in infraspecific categories of all groups which are theoretically capable of introgressive hybridisation, including those which are geographically isolated and very distinct, but, as has been already argued, these are more conveniently referred to as species.

However, there seems to be a case for modifying the above definition to include among the taxa most appropriately allocated to the

subspecific category, those which differ in major morphological characters, but where there is a naturally occurring zone of intermediate plants, which on grounds of fertility are not recognisable as hybrids, and for the exclusion of groups having a similar intermediate zone, and showing only very minor morphological differences. This latter case seems more appropriately allocated to the category variety, where the plants still occupy a distinct area or ecological niche.

There seems to be little taxonomic value in categories below that of variety. Agreement is found with Melville's (in Meikle 1957) use of the term 'form'; he suggests that it should be applied to such variants as albino flowers and pendulous variants of trees, which may only be due to a single gene change. The obvious disadvantage of such a category is that several forms may occur within only one population and may be combined in differing combinations.

The many subdivisions of the infraspecific categories already discussed appear redundant, at least in the case of describing the variations in outbreeding species.

The choice of category must depend on an assessment of each situation and be at the discretion of the individual taxonomist. Even when using numerical methods the choice of the affinity levels for each category are arbitrarily chosen within each study (Sokal and Sneath 1963).

The justification of such arbitrary decisions in the choice of categories is that a more generally useful classification is provided by the use of a few categories, than would be by the use of a vast array of categories that would be needed to cover each type of variational pattern created by evolution. To quote Walters (in Meikle 1957) 'As with the use of 'species' it was neither necessary nor desirable that subspecies should be genetically or in any other way be strictly comparable units. The chief consideration in taxonomy should be convenience, and taxonomists should aim at providing useful, general-purpose classifications.'

Where there is continuous or more or less continuous variation, although the mass of variation may seem too great to be lumped into a single taxon, it is advisable that no taxonomic recognition be made; the categories are inclusive in form and would mask the continuous variation.

The geographic origin of the majority of the material within a cline can still be correctly diagnosed. And it is unfortunate that only categorised groups are usually described in floras. Although the description of a taxon may include the extremes of variation often no indication is given concerning the type of plant that might be expected to occur in any district.

Many of the names previously applied to the R.acris complex cover parts of a more or less continuous cline. It is felt that

especially in local floristic works there might be a place for such categories, which by definition would not be inclusive in form. A suitable name for such a category is 'cline-form' (Pryor in Davis and Heywood 1963). The main disadvantage would of course be that such groups would have no stability as no diagnostic boundaries would exist.

Chapter 12

PREVIOUS NOMENCLATURE APPLIED TO THE COMPLEX

Even at the specific level, the names referable to the R.acris complex, are so numerous that reference to the original descriptions has only been made in certain cases. These have included all but two of the names listed in Index Kewensis, of which there are over forty, and other names which have frequently occurred in literature or in herbarium determinations.

The majority of the original descriptions are too brief to be able to tell to which plants they were originally applied, and it has only proved possible to examine type material in relatively few cases.

Plants labelled as R.acris in the Linnaean herbarium include both the lowland Swedish types and the montane dwarf types with broad lobed leaves. But Linnaeus' description in Species Plantarum (1753) clearly refers to the former type, having leaves with narrow lobes and many flowered stems.

The majority of the names in Index Kewensis are due to the notorious species makers Jordan and Schur.

Jordan in 1847 described the following species which are referable to the R.acris complex, R.acris, R.friesanus and R.boraeanus. Type material has been seen of all these. R.boraeanus (see plate 11) refers to those plants of France which have premorse rootstocks, appressed

usually fairly short hairs, and finely divided leaves.

R.friesanus (see plate 16) (later spelt R.friesianus or frieseanus by some authors) is referable to the distinct rhizomatous plants of E.France. His R.acris is also referable to this group, but to plants with slightly narrower lobed leaves.

In addition Jordan in 1864 described the species R.tomophyllus, R.stipatus, R.pascuicolus and R.vulgatus. He also changed the name friesanus to nemorivagus and equated his R.acris to R.steveni Andrz.

He stated that R.tomophyllus is similar to and replaces R.boreaeanus in N.W. France, differing from it in having dense long hair on the calyx and petioles, and in having longer beaked achenes and a less compact rootstock. It has been found that these are all characters typical of premorse plants in the extreme west of Europe, and such plants are commoner in the N.W. than in any other part of France.

R.vulgatus has, from material determined by Jordan, been seen to refer to an intermediate between the extreme E.French rhizomatous plants and premorse plants, showing more characters of intermediate state than Jordan's R.acris, although still with a well defined rhizome and it is not so very different from the extreme E.French types.

R.stipatus and R.pascuicolus he described as smaller plants of the Alps region, which have broadish lobed leaves. From the descriptions it has been difficult to tell if these were true premorse based plants from this region or whether they were plants intermediate between rhizomatous and premorse types. Dwarf intermediate plants showing

little rhizome have been seen from both E. France and the Tyrol. He described R.pascuicolus as differing from R.stipatus in having smaller flowers, smaller and less numerous carpels with a slightly differing beak form. These are all characters which have been found to vary greatly even within the same plant. Other characters used by Jordan in distinguishing his species, such as the colour of the leaves, difference in size of anthers, size and shape of nectary scale, overlapping of the leaf lobes, petal size and shape of cotyledons, have all been found to be characters of dubious value, often varying greatly within a single plant.

Bureau's R.rectus (1857) and his R.franchetianus (1868) both appear to refer to plants intermediate between the French premorse and the E. French rhizomatous plants. Material of the latter, as determined by Bureau, has been examined.

Schur described a large number of species referable to the R.acris complex as it occurs in E. Europe. He recognised the difference between the E. European rhizomatous and the premorse types, but further divided them. He retained the name R.acris L. for the premorse group. He described this group as extremely variable and found that the numerous forms that he recognised were difficult to delimit due to the frequency of transitional forms. In 1876 he described ten major forms, to some of these he listed as synonymous R.barthii,

R.subtilis, R.trachyticus, and R.subalpinus Schur. He also described R.kladnii as a separate species but as synonymous to one of the four forms of R.acris which he described in 1867. The name R.orbiculatus Schur, as seen in a determination by Schur, was applied to a plant of this group, but he has been seen to have applied one of his R.acris form names to a plant belonging to the R.auricomus group.

As Schur (1867) stated, and as has been seen on material determined by him, in the first instance he called the E.European rhizomatous plants R.steveni Bess. (i.e. Andrz. in Bess.). He changed the name of such plants to R.strigulosus Schur, and applied the name R.steveni to another type, but it has been impossible to tell to which plants he then applied it. In 1876 he described two forms of R.strigulosus, (R.eustrigulosus Schur he states as being synonymous to one of these) which he stated could often be found growing side by side.

In 1866 he also described R.malocophyllus (synonyms of which he gives are R.constantinopolitanus Schur and R.macrophyllus Schur), to which he stated R.friesanus Jord. was synonymous, but he applied this latter name to a separate species in 1876. R.malocophyllus from his description appears applicable to broad leaved plants of the E.European rhizomatous type. This name has been applied by other botanists to such plants from the type localities and from the basal remains of a type specimen it appears to be the right interpretation.

A further species described in 1876, referable to the rhizomatous group, was R.csatoi, which Schur admitted was difficult to delimit. He

held R.malocophyllus to be an intermediate form between R.csatoi and R.frieseanus.

Schur's R.kayseri appears referable to R.serbus Vis.

Schur gave the same type localities for many of his species, and many of the distinguishing features which he used could easily have been due to seasonal variations and to environmental conditions.

He described R.malocophyllus as being later flowering than R.strigulosus, which suggests that the broad leaves of the former might well have been due in many cases to their having been 'autumn' leaves.

R.steveni Andrz. is a species referred to by most authors, but which has had many interpretations. It has been applied to plants in most regions, including all the rhizomatous forms and broad leaved premorse plants in districts where rhizomatous plants do not occur.

From the original description of R.steveni Andrz. (Besser 1822) and from the district in which it was said to grow, it has been impossible to tell to which type of plants it referred. The description does not fit either the E.European rhizomatous plants which grow in S.W.Russia or the E.French rhizomatous plants which appear to have been introduced into this region. Hylander (1943) suggested that the plants originally described might have been intermediate forms between premorse plants and E.European rhizomatous plants or might, from poor doubtful type material, only be premorse plants with elongated rootstocks as occurs when a rootstock is buried.

The description of R.borealis Trautvetter (1860) corresponds to the plants examined from arctic Russia. Trautvetter's varieties however appear to be referable to environmental differences only.

Wahlenberg's description of his R.acris β pumilus is referable to the montane types to be found in Scandinavia. Trautvetter's species does not appear to cover such plants for he states that it usually has patent pubescence and only rarely is glabrous, a condition which is characteristic of the former plants for the main part of the year.

Part of R.lanuginosus Ledeb (1841) corresponds to R.borealis Trautv., but from the description and range of distribution given it may well include species other than R.acris s.l. R.lanuginosaeformis Selin (Fellm 1864) appears to correspond to R.borealis in its western form.

R.propinquus C.A. Meyer from Ledeb's description in his Fl. Altaica (1830) appears very similar to R.borealis, except that the former has appressed hairs. The plants examined from N.Russia have shown great consistency in possessing deflexed hairs, but no material from east of the Urals has been seen. Hara (1952) states that R.propinquus is closely allied to R.japonicus Thunb. of E.Asia. It may therefore be the form linking R.borealis and the E.Asian forms, but no recent revision of the forms occurring in Siberia has been made.

Boissier's description of his R.granatensis (1853) refers without doubt to the S.Spanish rhizomatous plants. R.atlanticus Ball (1873) refers to such plants as they occur in Morocco: this name was reduced to a variety of R.acris by Maire (1964).

No name has been found which refers solely to the type of plant found to occur in the Pyrenees. Lapeyrouse's description of his R.tuberosus appears to fit this part of the R.acris complex, but Jordan (1864) pointed out that there had been contradictions^{as}_^ to the true identity of the type material. And Lapeyrouse's description of R.acris adequately covers the form occurring in the Pyrenees (Lapeyrouse 1813). The Pyrenean plants are included in R.steveni Andrz. by Willkomm and Lange (1880). Their R.acris corresponds to R.nemorosus DC.

The description of R.silvaticus Villars (1779) (of which R.sylvaticus Thuillier, 1799, is only a variation in spelling) is too brief to tell which type of plant was referred to. Most authors use it as synonymous to part of the E.French rhizomatous group.

Such names as R.major Dumontier (1827), R.siculus Presl (1822) and R.paradoxus Weihe (1835-36) seem only to refer to local variants and have never been seen applied to any herbarium material.

De Candolle's (1817) R.acris f.multifidus refers to plants of the R.boraeanus Jordan type.

Dwarf forms of R.acris from the Alps have been termed R.parvulus Clairville and R.acris var.subalpinus Strobl. Turesson (1925) tested such plants in cultivation, and concluded that the dwarfness was due to environment only.

Type material of Laestadius' varieties, based on material from Swedish Lapland, has been examined. His var.squarrosus was mentioned by Nyman (1878). The varieties can be divided into the following categories: var.lacinatus, var.acutilobus and α nothus, applying to plants with finely divided 'spring' leaves; var.agrarius and β squarrosus to similar plants but with juvenile or 'autumn' leaves; and var.collinus equivalent to Wahlenberg's var.pumilus, a name which Laestadius also used.

K.Wiinstedt applied his name, var.latilobum to Danish plants with wide lobed 'autumn' leaves. The names var.balticus Krause and var.velutinus Lindb. have also been applied to similar plants.

R.granatensis Boiss. and R.borealis Trauvt. were reduced to subspecies by Nyman (1878), R.strigulosus Schur was reduced to a subspecies by Hylander (1943) and R.friesanus to a subspecies by Rouy and Foucaud (1893).

Chapter 13

PROPOSED TAXONOMIC TREATMENT OF THE COMPLEX IN EUROPE

The S.Spanish and E.European rhizomatous types would both appear to warrant specific status. They are distinct in morphological characters and show no array of intermediates with neighbouring types of plants. Intermediate plants have only been seen between the E.European plants and premorse plants; and in being morphologically midway between the two presumed parents would appear to be of a 'hybrid' origin. The 'hybrid' plants were from a single locality (S.W.Ukraine) near the limit of distribution of the E.European rhizomatous plants; although the distribution of this group is largely overlapped by that of E.European premorse plants, and there appears to be no clear ecological separation of the two types.

No breeding experiments have been carried out on these two groups of plants as no living material was obtainable. They may well prove to be freely interfertile with other plants of the complex. Even if this were the case specific status would still be suitable. Groups which are isolated from one another in ways other than by incompatibility, e.g. geographically or ecologically, are often best still treated as species, as this will generally produce the most practical classification. The correct names for these groups are for the S.Spanish rhizomatous group R.granatensis Boiss. (1853), and for the E.European

rhizomatous group R. strigulosus Schur (1866).

There are many intermediate plants between the E.French rhizomatous plants and premorse plants; but in the extreme form the E.French rhizomatous plants are morphologically very distinct from any of the premorse plants. Also in no way is it part of the West-East cline of variation found in the premorse plants, which completely overlaps the E.French rhizomatous plants in distribution. The E.French rhizomatous plants are plants of woodlands and alpine meadows (Jordan 1847), and it appears likely that the abundance of intermediate forms with the premorse types is due to the breaking down of its ecological isolation by modern farming methods together with the distribution of premorse plants as weed seeds. Due to the ease with which the E.French rhizomatous plants cross with the premorse plants in the wild, resulting in a continuous array of plants from one form to the other, they cannot be satisfactorily classified as a separate species but would seem to merit subspecific status. The correct name for these plants is R.acris subsp.friesanus (Jord.) Rouy & Fouc. Except in the possession of a rhizome, these plants show no close affiliations to R.strigulosus Schur or R.granatensis Boiss.; in morphological features, especially those of the flower, they are closest to the W.European premorse plants.

Examination of further material is required before an opinion on the true affinity of the Pyrenean rhizomatous plants can be given. Except for the presence of a rhizome, many of the Pyrenean plants

resemble some forms of the West-Central European premorse plants, but are more uniform in characters such as hair-type than are the premorse plants. They are similar to some of the intermediates between the E.French rhizomatous plants and the premorse plants, but not to the extreme E.French rhizomatous plants.

How significant is the rhizomatous rootstock in indicating relationships between different members of the complex? From distributional data and variational patterns it would seem most likely that the rhizomatous rootstock arose from a premorse based type than vice versa. Davis (1960) in classifying the genus Ranunculus in Turkey found that the R.acris complex had closer affinities to Turkish species with premorse bases than to those with rhizomatous bases; this would again suggest that the premorse rootstock has an older origin in the complex than does the rhizomatous rootstock. This being the case, the rhizomatous rootstock in the complex appears to have arisen at least twice viz. in the R.strigulosus and R.granatensis groups, which are similar in many morphological features and in the R.acris subsp. friesanus group. Also a stage towards the production of a true rhizome is to be found in plants from the Island of Foula, Shetlands, ^h_A were the rootstock is horizontally elongated. The presence of a rhizome on its own would therefore not be evidence of close affinity.

The Pyrenean group could have arisen from a premorse based type or be a split off subsp.friesanus. This subsp. does show local variations; plants in the Vosges were found to differ from the rest in

never having the fine hairs characteristic of the extreme types in the Savoie region, although they still had extremely broad leaves not characteristic of intermediate plants. The Pyrenean group is here tentatively called R.acris subsp.friesanus var.pyrenaeus. Further investigation could prove that it should be placed as a subspecies in its own right or as a var. of subsp.acris.

The only distinct group within the premorse plants of the R.acris complex are the plants occurring on the N.coast of Russia. These can be easily distinguished from the other plants as their leaves are only very shallowly lobed and their hairs very fine. No intermediates between these plants and the N.E. premorse plants have been seen, but a few intermediates between them and the Scandinavian montane plants occur on the N.E. coast of Scandinavia. This group of plants would appear to warrant subspecific status. The correct name for them is R.acris subsp.borealis (Trautv.) Nyman. This status might well have to be revised if the array of Siberian forms, which links the European complex to that of E.Asia, was considered, but no material from this region was examined.

The majority of the remainder of the premorse plants form a continuous cline, which cannot be split up into separate taxa even at the varietal level, as the intergrading of the morphological types within the cline is so gradual. The only groups of plants which appear to warrant varietal status are the Scandinavian montane plants and the

group of plants in N.Scotland, Ireland, The Faeroes and Iceland.

The Scandinavian montane plants have often been included in the same taxon as the plants belonging to subsp.*borealis*, but they differ in having more deeply divided leaves, in having the 'spring' leaves and petioles glabrous and in usually having thicker hairs. These plants are an ecological race restricted to high mountains and tundra habitats. Intermediates with the 'lowland' premorse plants are very numerous. They correspond to the R.*acris* var.*pumilus* of Wahlenberg (1812).

The other plants which warrant varietal status are those occurring in N.Scotland, Ireland, The Faeroes and Iceland, which are characterised by having broadly lobed leaves with many long hairs (over 1.2mm.) on their upper surfaces, and long orange-brown deflexed hairs on their petioles. The presence of long hairs on the petioles is not rare in other premorse plants of the same districts but such plants do not have long hairs in any numbers on the upper surfaces of their leaves. Extremes of this group are also characterised by having their bracts simpler and larger than do the other plants of these areas.

The extremes of the group occur in the remoter areas untouched by cultivation. These plants, from the localities in which they are found, would appear to be relics of a population which is being obliterated by breeding with plants which have arrived from further east. It could be that they are a relic of the form present during the last interglacial or early post-glacial, and the other forms were later

arrivals, whose rapid spread was aided by agriculture. R.acris is readily dispersed as a weed seed; a plant corresponding to the E. European premorse type was seen from the Hebrides. It has also been found that in other parts of Britain the longer - haired more densely covered plants often occur in uncultivated areas e.g. shores of St. Mary's Loch, Selkirk and Teesdale. This may indicate that such plants were previously much more widespread but have now mostly lost their identity due to the advance of other types.

The only description of this N.W. group is by Drabble (1930), the plants correspond to his form villosus. Intermediates between this group and the other premorse plants of the area are very numerous. Plants of this group are in all the regions in which it occurs in the minority, and from fieldwork in the N^o Scotland it was found that they are much rarer than is suggested by their frequency in herbarium collections.

Although only two groups appeared to warrant varietal status, more intensive work in some of the under-collected areas would probably uncover similar ecological or local geographical groupings.

Chapter 14

R.ACRIS IN BRITAINPrevious classification of the British forms of R.acris

The descriptions of R.acris and its varieties in British floras, up to a few years ago, were based on classifications which were adaptations of continental systems to British material. This approach to British material is well illustrated by that of White and Bucknall (White 1907), who working in the Bristol district tried to identify the forms of R.acris 'with the idea of arranging them under segregates described by Jordan and other continental botanists.' These continental systems were produced during a period when the naming of trivial variants was in vogue and the accompanying nomenclatural ^{ao}chôas of many groups was rife in R.acris. The position in Britain was even more ridiculous as these continental names were applied to British material which does not include all the continental types to which the names were first applied.

The main classifications of the British material have been those of Townsend (1900) and Drabble (1930).

Townsend's classification is mainly an adaptation of Jordan's classification of French material, and parts of Townsend's descriptions are word for word translations of Jordan's works.

The subspecies and forms Townsend recognised were as follows.

Subsp. I R.boreanus

Form I. R.boreanus Jord.

Form 2. R.rectus Bor.

subvar. pumilus

Form 3. R.stipatus Jord.

Form 4. R.pascuicolus Jord.

Subsp. II R.steveni Andrz.

Subsp. III R.friesianus

Form I. R.vulgatus Jord.

Form 2. R.friesianus Jord.

Form 3. R.nemorivagus Jord.

The only forms for which Townsend gives no British localities are R.stipatus, R.pascuicolus and R.nemorivagus.

Townsend's classification was critically reviewed by Drabble (1930) who put forward the following classification.

Var. multifidus DC. (R.boreanus Jordan) (common throughout Britain)

Forma stipatus (several scattered localities given)

Forma tomophyllus (common throughout Britain)

Var. steveni Andrz. (common throughout Britain)

Var. friesianus Jordan (including R.vulgatus Jord.)
(much less common, though widely distributed)

Forma villosus Drabble (N.Scotland only)

Var. pumilus Wahlenb. (Cairngorms)

Both Townsend and Drabble delimit their varieties chiefly on the character of the rootstock and on the width of the leaf-lobes. Their descriptions of such varieties as R.friesianus and R.steveni agree with those of the continental botanists who applied them to true rhizomatous plants. To which British plants then, were they applying such names? Drabble gave himself away by stating that in the Isle of Wight var. multifidus flowers in early summer and spring and var. steveni and var. friesianus in late summer and autumn. From an examination of herbarium material determined by Drabble, the almost complete correlation between plants with 'autumn' leaves being termed var. steveni and var. friesianus, and plants with 'spring' leaves being termed var. boreanus (syn.var. multifidus) was verified. He only used the name var. friesianus for plants with exceptionally broad lobes. No justification could be found in his calling some rootstocks rhizomatous and others premorse.

The names boreanus and tomophyllus have been used in much the same way as they were used by Jordan in France. These types of plants are similar in both countries.

Only the two varieties of Drabble's with a restricted geographical range, seem to have any validity. His name f. villosus for the type found in N.Scotland and Ireland, of which type material has been seen, was the only one found which applied to these plants in particular.

Present conclusions

All the plants in Britain do in fact correspond to R.acris subsp. acris; such names as steveni and friesianus having been mostly

applied to plants in their 'autumn' state. Not even introduced plants of R.acris subsp.friesanus (Jordan) Rouy & Fouc. have been seen, although they have been introduced to many other parts of Europe.

The general cline of morphological characters among the premorse plants in Europe is visible even within the British Isles. The plants in the east, especially in East Anglia, tend to have more narrowly divided leaves and shorter appressed hairs on their petioles and stems (see Maps 1 and 2). Whereas those plants in the west and north generally have longer, spreading or deflexed hairs and broadly lobed leaves are commoner in these regions.

Both of the recognised varieties occur in Britain.

Var. villosus (Drabble) in N.Scotland and Ireland and var.pumilus Wahlenb. in the Cairngorm Mts., Scotland. Cultivated plants of the latter variety from the Cairngorms tended to have more finely divided leaves than was generally seen among Scandinavian plants, but the character of glabrous 'spring' leaves was found to be stable. No plants from any other British Mountains were found to correspond to this variety.

R.ACRIS IN AMERICA

A series of plants from both the west and east of the N.American continent were examined. R.acris has been introduced into N.America. All the plants were found to be similar to the premorse types found in the West of France or England, with spreading or deflexed hairs.

THE STATUS OF R.ACRIS IN GREENLAND

There has been controversy as to whether R.acris is truly native in Greenland. It has a peculiar distribution within Greenland. It is commonly found on the south coast but only at a few very scattered localities on both the west and east coasts (Böcher 1938 and 1963). Böcher holds that these scattered localities are pre-glacial relicts and not recent introductions. His main evidence is that these localities also contain a number of other rare species with sporadic distribution, the localities show only signs of local glaciation during the last ice age and show no signs of human settlement. Examination of herbarium material from both the south and east coasts has shown that Greenland material cannot be distinguished from plants such as are found in England and they do not appear to show any relationship to the type of plant typical of Iceland or Scandinavia. They are similar in type to the introduced plants occurring in Spitzbergen near the mining settlements.

THE STATUS OF R.ACRIS IN THE FAEROES

Benson (1962) states that R.acris was probably introduced to the Faeroes in prehistoric times from the European mainland and is restricted to areas about villages. He regards the disappearance of the species away from human habitation as due to the lack of flies. This reason seems highly improbable as R.acris is frequently found far from human habitation, as in the northern Greenland localities (Böcher 1963) and it is pollinated by a very wide range of insects. The plants in

The Faeroes from the range of types present appear as native as do those in Iceland and N.Scotland. The apparent restriction to villages could be due to cultivation producing soil conditions more favourable to R.acris than are those soil types which naturally occur over most of the remainder of the islands. A similar restriction in localities occurs in Foula (Shetlands); evidence that these plants are indeed native is strong, as all the plants seen from this island have had a character of rootstock only rarely approached by any other plants examined throughout Britain (see chapter 3).

THE R.ACRIS s.l. COMPLEX IN ASIA

Hara (1952) gives the following taxa as occurring in Japan and the neighbouring parts of Asia: R.acris var. nipponicus Hara, R.japonicus Thunb and R.grandis Honda. Another form which from herbarium specimens appears distinct from the above taxa is R.acris var. frigidus Regel.

Hara states that the plants in Asia are as polymorphic as those in Europe. This has been amply illustrated by the few herbarium specimens that have been seen from E.Asia. All the plants appear distinct from those of Europe, but great similarity was found between juvenile forms of some of the Asian plants and those of R.acris subsp. acris.

No definite taxonomic opinions can be given on these taxa, without the examination of a great deal more material, but none of the forms seen appear to merit inclusion within R.acris L.s.s. R.acris var. frigidus Regel, is distinct from any European plants even in such

characters as form of nectary scale and stem anatomy, characters which were not found to differ between the European taxa.

Chapter 15

SUMMARY AND KEY TO THE TAXA RECOGNISED

The R.acris s.l. complex in Europe was found to consist of two distinct groups with a limited geographical range, which, it is suggested, should have specific status (R.strigulosus Schur and R.granatensis Boiss.), both of which are relatively uniform in appearance; and a third very variable group, (R.acris L.s.s.) distributed over most of Europe.

The majority of the variation within R.acris L.s.s. cannot be divided into separate infraspecific taxa. Rousi (1965) attributed the difficulties of further dividing Potentilla anserina L.ssp.anserina to its being an obligate outbreeder, combined with a vigorous vegetative reproduction as well as the frequent migrations it has undergone with man. R.acris L.s.s. was from breeding experiments similarly found to be an obligate outbreeder and it is commonly distributed as a weed seed.

The main clinal variation in R.acris L.s.s. is in a west-east direction. Deeply divided leaves are more frequent in the east and the flowers and fruits generally smaller; the hairs on the plants in the east are shorter and usually appressed rather than spreading or deflexed. The only plants within this cline which are recognised as a separate taxon^{or} are those of a type occurring in the extreme west - var.villosus (Drabble). A further cline occurs in a north-south direction in the north west of its distribution, which in the north extends along the North Coast of Russia. The majority of the plants

forming this cline are referable to var.pumilus Wahlenb., or to subsp.borealis (Trautv.) Nyman on the extreme N.E. coast of Europe.

R.acris subsp.friesanus (Jordan) Rouy & Fouc. forms no part of this clinal variation pattern, although its distribution is completely overlapped by that of subsp.acris. It appears likely that it has previously been at least ecologically isolated from subsp.acris.

The characters used in this study of variation within the complex were taken from as many parts of the plant as possible, but the number of characters which could be used was found to be limited. Most characters varied either with the age of the organ, sequence of production of the organs on the plant or with the time of year. Thus hair-density and shape of the achenes varied due to the age of the organs; bract-shape, flower-size, number of achenes and leaf-shape varied with their sequence of production; and leaf-shape and hair-density with the time of year. Consequently, so that measurements of characters would be comparable, the season in which produced and the relative position on the plant, of any organ on which measurements were made, had to be fixed. The result of this was that only a restricted number of the characters used could be measured on much of the herbarium material examined.

Distinctions in characters of flowers and fruit were found between the species recognised within the complex, but within R.acris s.s. no groups could be delimited on such characters, although certain trends were visible. Leaf-shape was found to be diagnostic for most groups,

although it was very variable even within a single locality. Hair-type was similarly found to be very variable in some localities but most groups were characterised by trends in both length and width of hairs.

Much emphasis had previously been given to the presence or absence of a rhizome among the plants of the complex. It was indeed found to be a reliable character occurring in several groups in each case correlated with characters differing from the local premorse plants. A rhizomatous rootstock appears to have arisen several times during the evolution of the complex, in each case associated with plants of limited geographical distribution centred on a mountain range. The diversity of mountain habitats is generally held to be an evolutionary impetus, and the presence of a rhizome is considered adaptive to such habitats. Davis (1960) found that the Turkish species of Ranunculus with rhizomes were to be found chiefly in woods and in stony alpine habitats, and also that in such habitats numerous unrelated genera also possessed rhizomatous rootstocks.

Chromosome number was found to be constant, except for a few individual reports, within R.acris s.s., It is suggested that there is a possibility that R.granatensis Boiss. and R.strigulosus Schur may have a tetraploid chromosome number. Chromosome counts and breeding experiments within these two species would be very valuable in clarifying their position within the complex.

Little information could be obtained from further crosses within the groups already tested, before femaleness in R.acris s.l. is further understood. Femaleness appears to be under genetical control, but fluctuates greatly, even in flowers on the same plant produced at the same time. Theoretically no advantage would appear to be obtained by an obligate outbreeder in having gynodimorphic plants. The partial femaleness, shown by the high infertility of pollen found in a large percentage of plants would seem similarly to place the plants at a disadvantage.

The main trends of geographical variation within Europe have been traced in the present work, but many gaps remain in the under-collected areas. Forms of plants which were not uncovered by this present work probably exist. This is indicated by a single plant seen from Greece which, on morphological characteristics and in chromosome number, belongs to the acris complex, but which in vegetative characters was very different from the other plants in the Iberian Peninsula, and did not exactly tally with any other plants of the complex. More intensive localised field and experimental work would be of great value in understanding the nature of local variation.

SUMMARY OF THE TAXA RECOGNISED, with the principal synonyms and examples
of herbarium material examined

R.strigulosus Schur; Enum. Pl.Transs.:17(1866)

R.acris subsp.strigulosus (Schur) Hyl.;Symb.Bot.Upsal.7:1(1943)

R.malocophyllus Schur;Enum.Pl.Transs.:16(1866)

R.csatoi Schur; in Verh.Naturf.Ver.Bruenn 17:46(1876)

(In pratis Transsilvan,D.J.Schur - determined as R.steveni Bess.

or R.strigulosus Schur (W-2 sheets);Transsilvanica,Hermannstadt,
12.VI.1906,J.Barth (W);Tilalmas prope Toroczko,Transsylvania, VII.1883,
J.de Csató,(P);Kolozsvár,comit Kolozs,14.V.1916,M.Péterfi,(C)). See
Plates 7 and 8.

R.granatensis Boiss.; Diag. Ser2(1):8(1853)

R.acris subsp.granatensis (Boiss.)Nyman;Consp:12(1878)

R.atlanticus Ball;in J.Bot.11:296(1873)

(Sierra Nevada sunny bank by the bridge over R.Genil.....,10.VI.1926,
A.J.Wilmott (EM);In Valle fluv Feint,Nevada,29.VI.1876,M.Winkler(C,W);
Sierra de Segura, above Rio Segura near La Toba, edge of water channel,
27.VI.1955,V.H.Heywood(Herb.Univ.Leicester, LIVU);Sierra Nevada lot.
humidis graminos in Dehesa de S.Gerorimo et valle fl. Monothil, 9.VII.1879,
Huter (S,E,CGE,C)). See Plates 9 and 10.

R.acris L.s.s.;Sp.Pl.:544(1753)

R.acris subsp.acris

R.boreaeus Jord.;Obs.Pl.Crit.6:19(1847)

R.tomophyllus Jord.;Diagn.:71(1864)

(Pastures about Failand and Portbury, N. Somerset, VI. 1906,
 J.W.White(CGE); Beaminster, Dorset, 2.VI.1913, I.M.Roper(CGE); Austria
 Inferior, In pratis ad,, Mauer" prope,, Wien", VI.1903, E.v.Halácsy(W);
 Tyrolen, Innsbruck, Patscherkofel, 29.VII.1931, H.Lenander(S)). See
 plate 11.

R.acris subsp.acris var.pumilus Wahlenburg; Flora Lapp. (1812)

(Lycksele Lappmark. Tärna, Norra Storfjället, Daläive, 31.VII.1944,
 H.Lenander(S); Torne Lappmark. Abisko, Nåra fallet, 23.VII.1907, M.Sondén(S);
 Torne Lappmark. Jukkasjärvi parish, Mt. Atjaktjakkko, 5.VIII.1947, H.Smith(E);
 Torne Lappmark. Karesuando parish, Mt. Peltsa, 4.VIII.1939, H.Smith(W)).

See Plate 13.

R.acris subsp.acris var.villosus (Drabble) Comb.nov.

f.villosus Drabble; Rep.B.E.C.9(3):(1930)

(Melvich, W. Sutherland, 15.IX.1897, W.A. Shoolbred(Herb. Univ. Leicester,
 CGE); Near the summit of Langa, Harris, 14.VIII.1841, (CGE); Coast near
 Rockfield, E. Ross, 19.VII.1890, E.S. Marshall(CGE)). See Plate 12.

R.acris subsp.borealis (Trautv.) Nyman; Consp.:12(1878)

R.borealis Trautv.; in Bull. Soc. Nat. Mos. 33:72(1860)

(Novaya Zemlya, Matotschin Schar, 30.VII.1908, R.Niemann(CGE);
 Novaya Zemlya, Gabina Bay, Matotschin Schar, 30.VII.1879, H.W.Fielden
 (CGE); Waigate Is. Dolga Bay, 1-10.VII.1897, H.W.Fielden(CGE); Waigatsch,
 sinus Warnek, 11.VIII.1902, O.Ekstam(S)). See Plates 14 and 15.

R.acris subsp.friesanus (Jord.) Rouy & Fouc.; Fl. Fr. 1:103(1893)

R.friesanus Jord.; Obs. Pl. Crit. 6:17(1847)

R.nemorivagus Jord.; Diagn.: 74(1864)

(Lyon à Chanelay, A. Jordan(CGE); Lyon à Villemoine, A. Jordan (CGE);

Lyon à la cité, A. Jordan(C)). See Plates 16 and 17

R.acris subsp.friesanus var.pyrenaeus nom. nov.

(Prov. Teruel. Albarracin, lieux humides et herbeux, sur le calcaire
1,300m., VI. 1894, E. Reverchon (P, S, E, BM.); Guipuzcoa. Gabo de Higuer V. 1895,
M. Gandogan(C)). See Plate 18.

Taxon of uncertain status - R.steveni Andr.; in Besser. Enum. Pl. Volh(1822).

KEY TO THE TAXA RECOGNISED WITHIN THE R.ACRIS s.l. COMPLEX IN EUROPE.

Descriptions of leaves refer to those produced before the first flowering stem of the year.

Measurements of petiole-hairs refer to the longest hairs, of lengths which occur frequently, not only sporadically on the petioles (excluding the sheath).

1. Rootstock much elongated, rhizomatous. Leaves in vegetative shoots arranged in two ranks.

2. Beaks of achenes distinctly hooked. Petiole-hairs frequently under 0.8mm., rarely over 1.2mm., often very fine (under 0.02mm. wide) but thicker hairs (up to 0.05mm.) not infrequent on some plants. Leaves thin, usually broadly lobed with many teeth.

Mainly in E.France and W.Switzerland, commonly introduced to other countries (including Sweden, Austria, Poland, Czechoslovakia).

R.ACRIS L.s.s. subsp.FRIESANUS (Jord.)Rouy & Fouc.

a) Leaves frequently narrowly lobed. Petiole-hairs always appressed, never exceeding 1.2mm. and often not exceeding 0.8mm., never very fine (0.03-0.04mm. wide).

The variety of subsp.friesanus occurring in Pyrenees, N. and E.Spain.

Var.PYRENAEUS Nom.nov.

2. Beaks of achenes straight, or only slightly curved, never hooked. Petiole-hairs long, over 0.8mm. (frequently over 1.2mm.) in length, and thick, over 0.03mm. Leaves thick, broadly lobed with relatively few teeth.

3. Beaks of achenes 0.4-0.8mm. in length. Stamens with under 20 hairs/filament. Segments of leaves rarely stalked.

E.Europe (including S.W. Ukraine, Rumania, Hungary, Yugoslavia, Bulgaria).

R.STRIGULOSUS Schur

3. Beaks of achenes over 0.8mm. Filaments of stamens often with over 30 hairs/filament. Segments of leaves often stalked.

S.Spain and Morocco.

R.GRANATENSIS Boiss.

1. Rootstock short, premorse. Leaves in vegetative shoots produced spirally. (R.acris L.s.s. excluding subsp.friesanus).

4. Central lobe of the median leaf-segment less than 40% of leaf length. Leaves rarely glabrous. Petiole-hairs deflexed, always very fine (under 0.02mm. wide), white.

N.Coast of Russia.

R.ACRIS L.s.s. subsp. BOREALIS (Trautv.)Nyman

4. Leaves variously divided, only rarely with the central lobe of the median segment less than 40% of leaf length. Leaves rarely glabrous. Petiole hairs appressed, spreading or deflexed. Petiole-hairs only rarely less than 0.02mm. wide.
- Widespread over most of Europe.

R.ACRIS L.s.s. subsp. ACRIS

- a) Leaves and petioles produced before the first flowering stem of the year glabrous, (those produced after, bearing hairs). Central lobe of the median leaf-segment 30-70% of the leaf-length. Leaves never finely divided.

Mts. and North of Scandinavia,
Central Iceland, Cairngorm Mts. (Scotland).

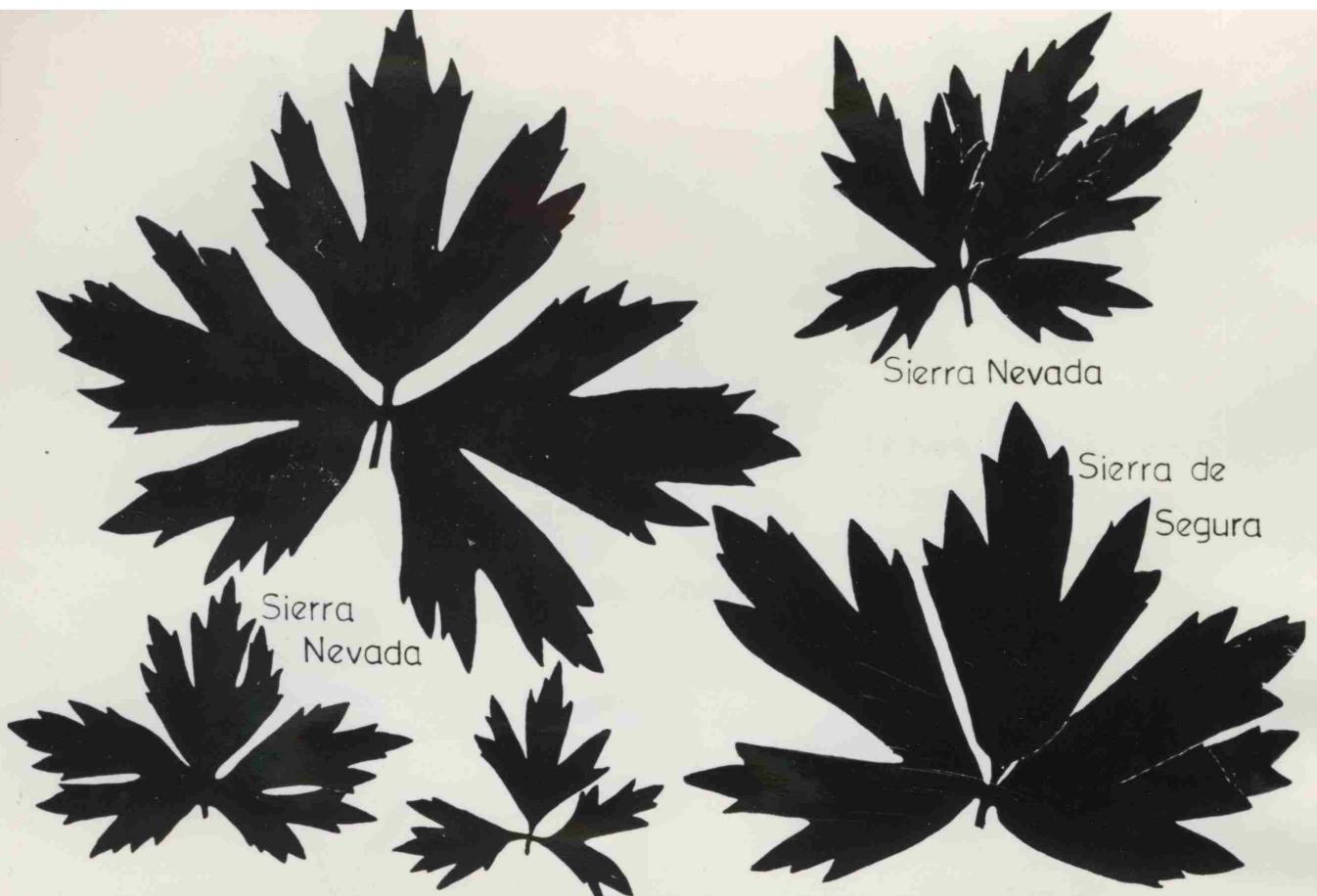
Var.PUMILUS Wahlenberg

- b) Upper surfaces of the leaves bearing numerous hairs over 1.2mm. long. Petiole-hairs deflexed, orange-brown in colour. Leaves broadly lobed.

N.Scotland, Ireland, Iceland, Faeroes.

Var.VILLOSUS (Drabble)Comb.nov.

PLATES 1-18.



Leaves from S.Spanish rhizomatous plants. R.granatensis Boiss.

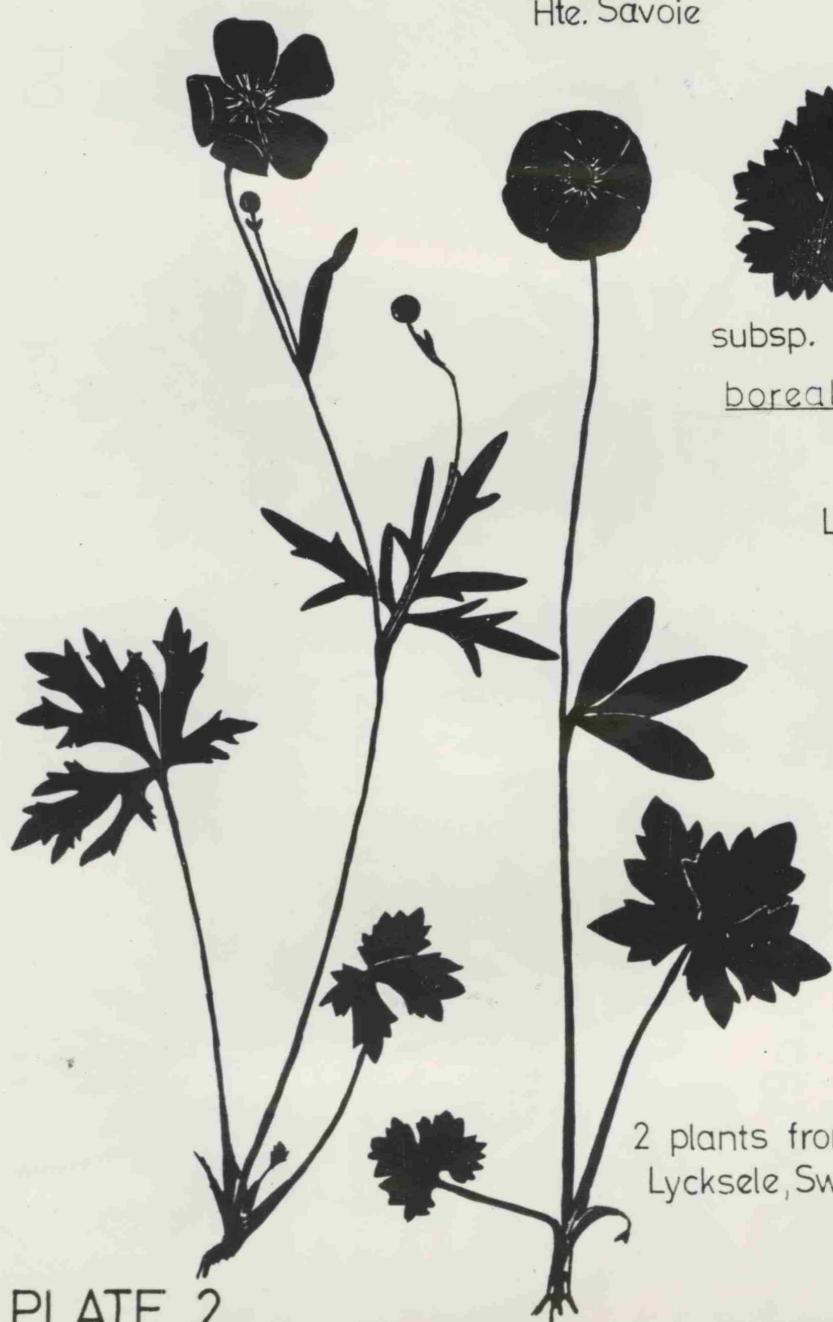


Transylvania, Rumunia

PLATE 1

Leaves from E.European rhizomatous plants.
R.strigulosus Schur

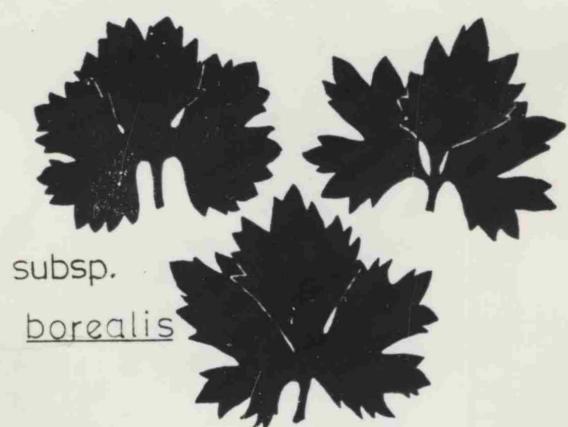
PLATE 2



2 plants from
Lycksele, Sweden

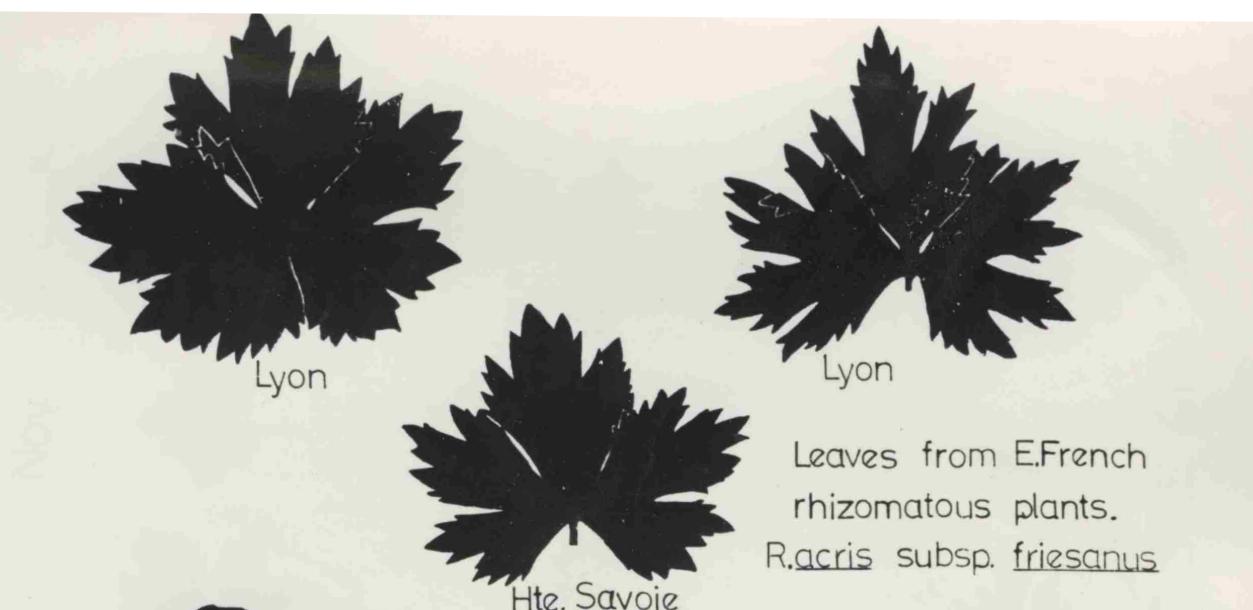
Leaves from 4 plants
Jukkasjarvi, Kiruna,
Sweden

var. pumilus



subsp.
borealis

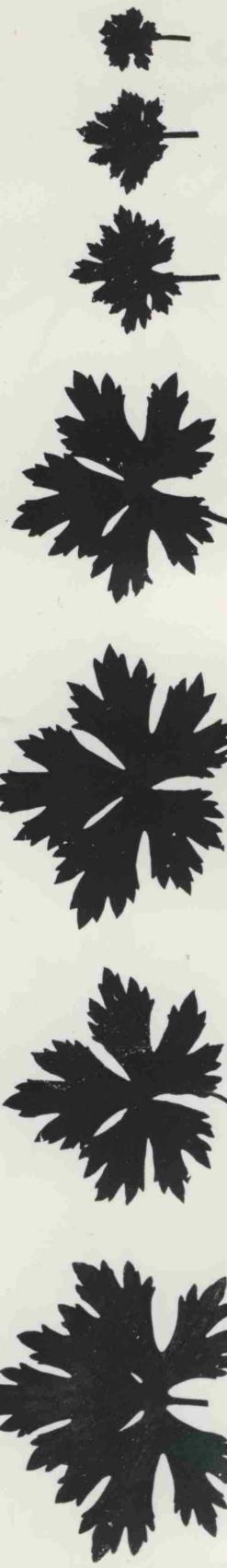
Leaves from 3 plants
Vaigach Is. N. Russia.



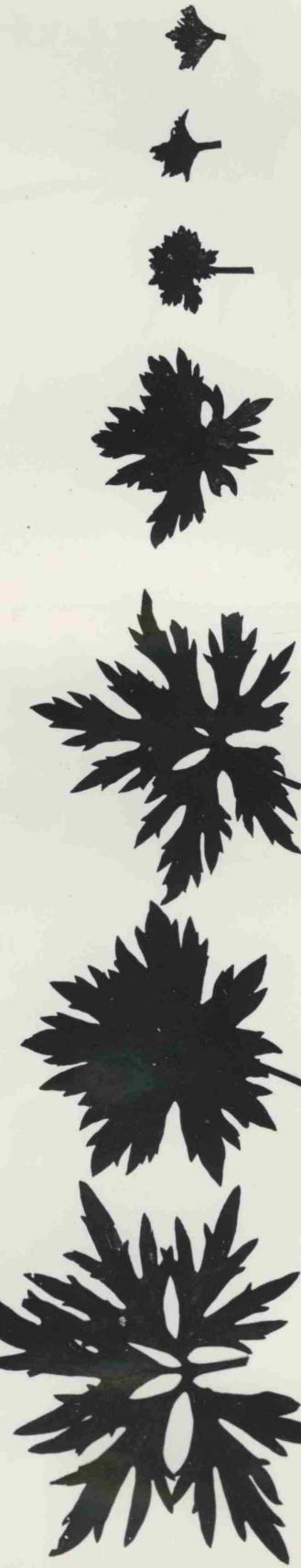
Leaves from E.French
rhizomatous plants.
R. acris subsp. friesanus

Hte. Savoie

May July Sept. Oct. Nov. Dec. Jan.



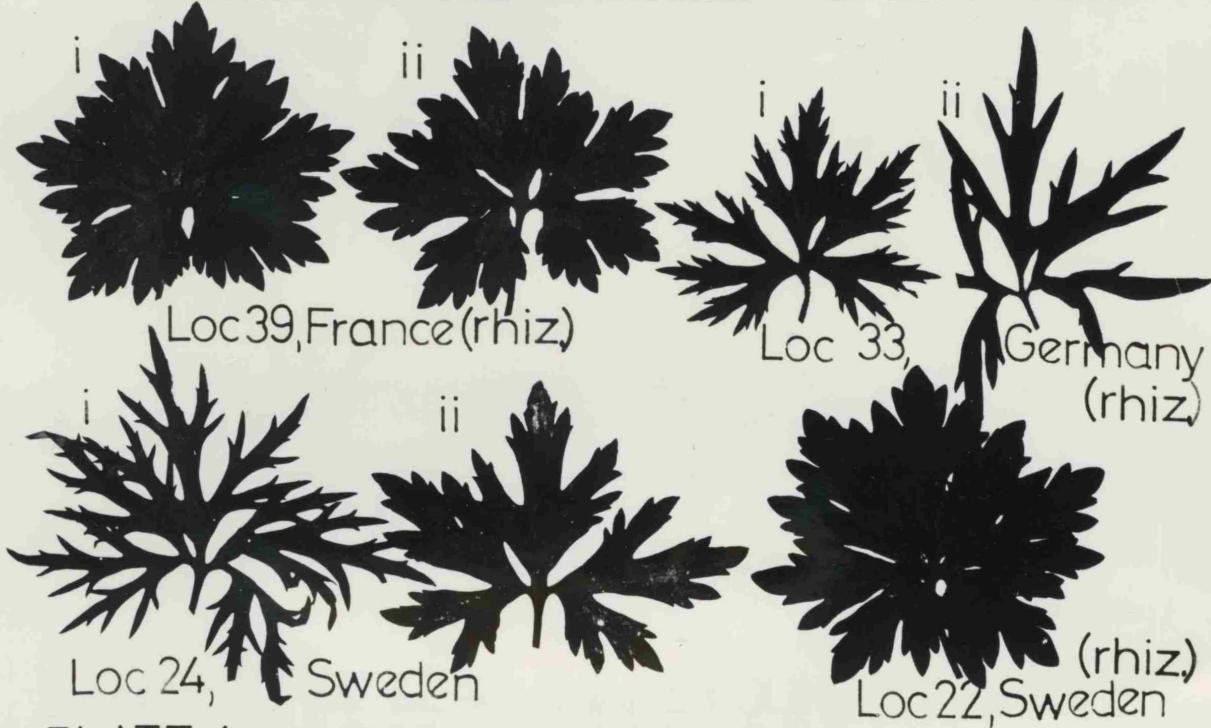
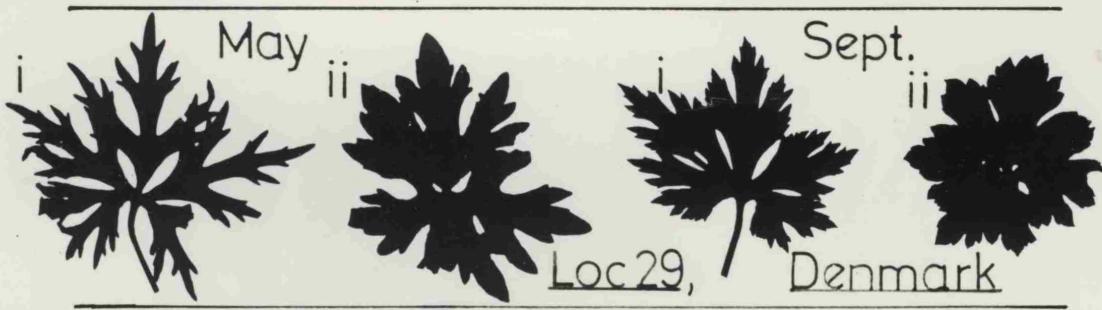
Loc 41, France (rhiz.)

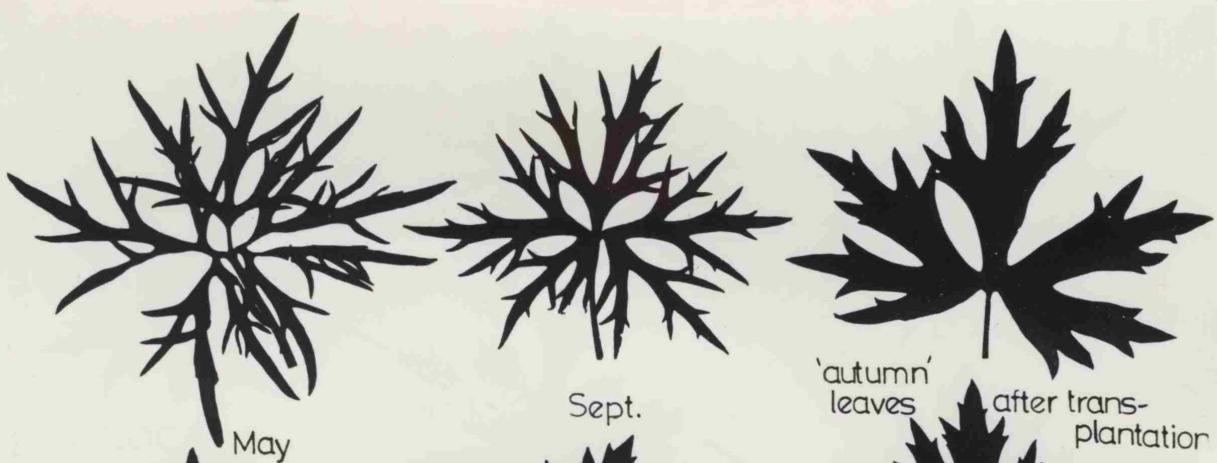


Loc 29a, Denmark



Loc 3, Finland SEASONAL VARIATION IN SHAPE AND SIZE OF LEAVES
PLATE 3



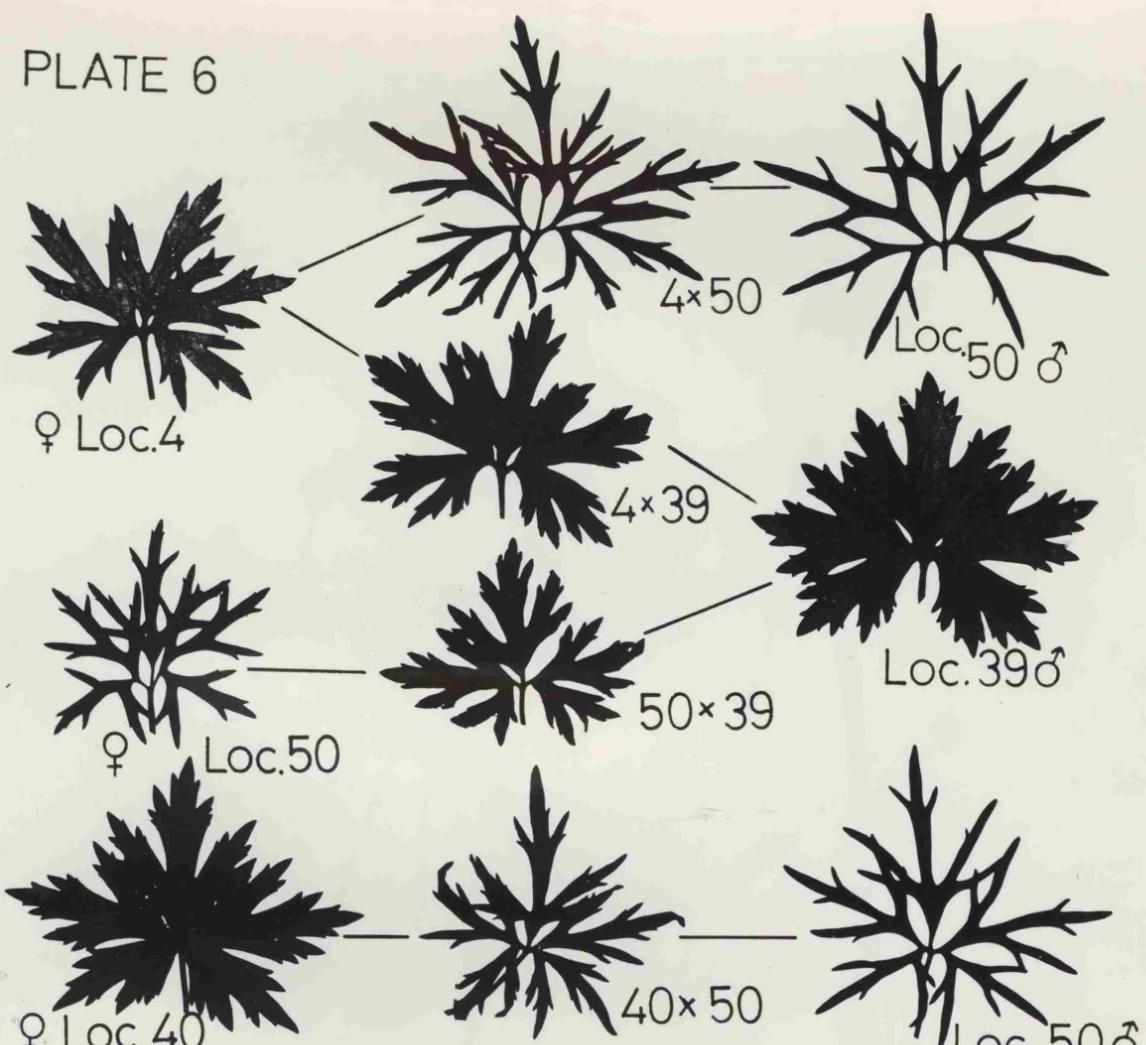


Variation in leaf shape
Loc 62a showing: from a single locality,
'Spring' v. 'autumn' leaf shape.
Effect of transplantation on leaf shape.



EXAMPLES OF LEAF SHAPE FOUND IN BRITAIN
PLATE 5

PLATE 6



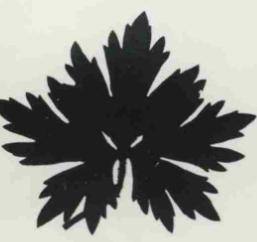
Cold
House



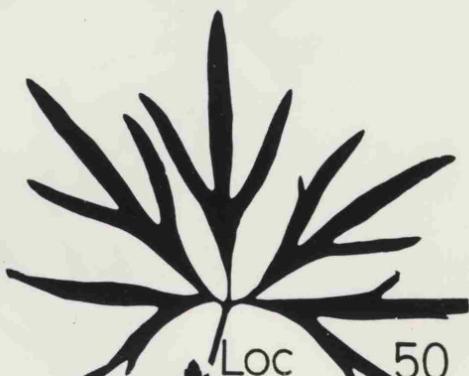
Hot
House



Loc 60



Loc 39



Loc 50

CLONAL TEST effect of environment on leaf shape

Ranunculus strigosus Schur
(R. Steveneri von Schlecht)
Proprietas fertilioris. Tm. sordidus.
Grenzg. part. p. D. Gau

Hedley
Herbarium europeum
Vienna



PLATE 7 R.strigulosus Schur



PLATE 8 R.strigulosus Schur.



PLATE 9
R.granatensis Boiss.

ELISEE REVERCHON — PLANTES D'ESPAGNE — 1903
PROVINCE DE JAEN

N° 985.

Ranunculus granatensis Boiss.

Sierra de Castril, lieux humides, sur le calcaire, 1.700 mètres.
Juillet.



MUSEUM BOTANICUM
HAUENSE

PLATE 10 R.granatensis Boiss.

No 943. Peter, Santa Fe, existente hispanico 1879.

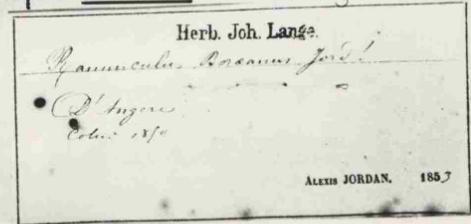
Herb. Joh. Lange.
Ranunculus hispan. Boiss.
var. granatensis. Boiss.

Saguenay Ranunculus, Sierra Nevada, loc. humilis
graminet. in Octava et Superioris et valles. Monachil.
18-2300 m. 4. Julio



R. acris L. subsp. acris

PLATE 11





Aug. No. 1024.

Deep ground, sloping to a small
valley by sea Melville
Is. Scotland. Aug 1897.

R.A.M.

R. acris, L., var. *Stevensi* (Andrz.). Sea coast, Melville, West Sutherland, 15th September 1897. W. A. SHOOTMAN. "This does not seem satisfactory for var. *Stevensi*. *R. Stevensii* was described by Andrzejewski as a species in Besser's 'Enumerat. Pl. Volhyn.' p. 22. The description begins: 'Radix subrepens, hibernaculis bulbosis, c. equibus orientis caules 2 pedales teretes' etc. The figure in Reichenbach's 'Icones' bears out this character of the root." E. G. Baker. "This plant is very similar to a *Ranunculus* which I gathered in West Rossshire, which Dr. R. von Wetstein named *R. tomophyllus*, Jord." —G. C. Drace. "This is *R. tomophyllus*, Jord., 'Annal. Lyon' (1860) et ipso in 'Diagn. Pl. Nov.', pp. 71, 72, and is a form of *R. acris*, L., as I conceive the species." J. Freyn.

(A.R.C. Report for 1897, p. 536.)

Ranunculus Stevensii, Andrz.?

PLATE 12 *R. acris* var. *villosum* (Drabble) comb. nov.



R.acris

Flora Suecica

var. pumilus Wahlenb. *Ranunculus acris* L.

Lule lappmark, Kvikkjokks kapellförs.: Högfjälldalen
mellan Jelenafj. o. Jäll, c:a 900
m.s.h.

23/7 1943

Sten Selander o. Nils Dahlbeck

PLATE 13

PLATE 14 R.acris subsp. borealis (Trautv.) Nyman



Ranunculus acris f. borealis.
Novaja Semlja.

Matotschkin Scharr. 2/3 1891. Latitud
Longitud



Racris subsp. borealis
(Trautv.) Nyman

PLATE 15

Ranunculus acris L.
forma borealis subsp.
Cape Matveeva
50' 18 July

PLATE 16

R. acris subsp. friesanus (Jordan) R&F.



RIKS MUSEUM
STOCKHOLM



PLATE 17
R.acris subsp. friesianus
(Jordan) R.&F.

HERBARIUM J. VETTER

Name: *Ranunculus acris* L. subsp.

Standort: Wien. Wiesen im Pausengang
hinter der Lanz, XII. Bez.,

3.II.1930 leg. Krennholz

APPENDIX

List of the localities of origin of the plants in cultivation

Locality Number		No. of plants in cult.	Grown from seed or plant	In cult. since
FINLAND				
L	*Espoo, Uusimaa	10	S	1965
2	*Porvoo, Uusimaa	10	S	65
3	*Tampere, Etala"-"Mame	10	S	65
4	*Punkaharju, Etala-Savo	10	S	65
5	*Kuusamo	10	S	65
6	*Oulu	10	S	65
7	Kontiolahti, Kiopio	2	S	66
RUSSIA				
8	*Leningrad	10	S	65
NORWAY				
9	Stavanger	2	P	65
10	Bergen	4	P	65
11	Ålesund	1	P	65
12	Molde	1	P	65
13	Trindheim	1	P	65
14	Rorvik, Helgeland	4	P	65
15	Brynnysund, Helgeland	3	P	65
16	Bodo, Helgeland	1	P	65

* Main localities from which plants were used in the breeding experiments and in the investigations into seasonal variation.

NORWAY contd.

17	Sortland, Lofoten Is.	2	P	65
18	Stamsund, " "	6	P	65
19	Svolvaer, " "	8	P	65
20	Finnnes, Nr.Tromso	6	P	65
21	Brønnøya, Akershus	6	S	66

SWEDEN

22	*Landskrona,Malmøhus	10	S	65
23	*Nr.Göteborg	10	S	65
24	*Nydala,Nr.Värnamo,Jököpings	10	S	65
25	*Nr.Stockholm	10	S	65
26	Mölle,Molmöhус	10	P	65

DENMARK

27	Copenhagen	10	P	65
28	Gentofte,Copenhagen	5	P	65
29	*Roskilde a)meadow	10	P	65
	b)woodland	10	P	65
30	Gilleleje,Sjaelland	3	P	65
31	Birkerød,Sjaelland	4	P	65

GERMANY

32	*Gransee,Berlin	10	S	65
33	*Karl-Marx-Stadt,Saxony	10	S	65
34	Müritz-See, Mecklenburg	1	S	66
35	Landau,Karlsruhe	4	P	66

	POLAND				
36	Wawer Koto, Warsaw	1	S	66	
	BELGIUM				
37	Namur	2	P	66	
	LUXEMBOURG				
38	Luxembourg	5	P	66	
	FRANCE				
39	*Mairon-sur-Bèze, Dijon	12	S	65	
40	Strasbourg	1	S	65	
41	*Massif de Hohneck, Vosges	10	S	65	
42	Munster, Vosges	11	P	66	
	SWITZERLAND				
43	Chiasso, nr. Como (Italy)	6	P	66	
	ITALY				
44	*Nr.Udine	10	S	65	
45	Cortina, Dolomites	3	P	66	
46	Tolmezzio, Dolomites	7	P	66	
47	Genoa	2	S	66	
48	Plain of R.Po N. of Genoa	10	S	66	
	YUGOSLAVIA				
49	Lake Bled	3	P	66	
	AUSTRIA				
50	*Graz	12	S	65	
51	Salzburg	5	S	65	
52	Villach, Carinthia	28	P	66	
53	Ossiach, Villach, Carinthia	7	P	66	

AUSTRIA contd.

54	Heiligenblut, Nr.Lienz	9	P	66
55	Villacher Alps,Carinthia	12	P	66
56	Feldkirchen,Carinthia	2	P	66
57	Hochosterwitz,Carinthia	6	P	66

HUNGARY

58	Bundapest	4	P	66
59	Dorog,Budapest	3	P	66

ENGLAND

60	*Church Stretton,Salop.	7	P	65
61	*Whitwick,Leics.	5	P	65
62	*Cawston,Warks. a) meadow b) Rd. side	10 10	P P	65 65
63	Lawford Heath, Warks.	5	P	65
64	Napton,Warks.	3	P	65
65	Chichester, Sussex	2	P	66
66	Lyndhurst,Hants.	10	P	65
67	Watlington,Oxon.	2	P	65
68	Chelmsford,Essex	2	P	66
69	Cray,Buckden,Yorks.	1	S	66
70	Adel,Leeds	1	S	66
71	Little Crosby, Liverpool	2	P	66
72	Banks,Southport,Lancs.	2	P	66
73	Middleton-in-Teesdale,Durham	9	P	66

WALES

74	Newtown,Montgomery	5	P	65
75	Aberdovey,Merioneth	5	P	65

WALES contd.

76	Tal-y-llyn, Merioneth	5	P	65
77	Cader Idris, "	5	P	65
78	Roman Steps, Nr. Harlech	5	P	65
79	Borth, Cardigan	3	P	64

SCOTLAND

80	Broadmeadows, Selkirk	3	P	66
81	*St. Mary's Loch, Selkirk	10	P	64, 66
82	Grey Mare's Tail, Dumfries	4	P	66
83	Glen Douglas, L. Lomond	5	P	66
84	Ben Lomond	2	P	66
85	Loch Tulla, Argyll	5	P	66
86	Rannoch Moor, Argyll	7	P	66
87	Loch Cluanie, Ross & Cromarty	4	P	66
88	Ratagan, L. Duich, "	2	P	66
89	Gairloch, Ross & Cromarty	3	P	66
90	Loch Maree, "	5	P	66
91	Glen Broom, "	4	P	66
92	Ullapool, "	5	P	66
93	Inverkirkaig, Lochinver, Suth.	5	P	66
94	Clachtoll, " "	10	P	66
95	Clashnessie, " "	6	P	66
96	Inchnadamff, Sutherland	6	P	66
97	Faraid Pen., Durness, Suth.	4	P	66
98	Smoo, Durness, Sutherland	10	P	66
99	Muiseal, Strathmore, Sutherland	5	P	66

SCOTLAND contd.

100	Shin Falls, Bonar Bridge, Sutherland	3	P	66
101	Bonar Bridge, Sutherland	7	P	66
102	Moy, Inverness	4	P	66
103	Braemar, Aberdeen	3	P	66
104	L.Morlich, Aviemore, Inverness	5	P	66
105	Coire an Lochain (3,700') Cairngorms, Inverness	4	P	65
106	Glen Lyon, Perthshire	8	P	65
107	Foula, Shetlands	5	P	66&65
108	*Papil Water, Fetlar, Shetlands	5	P	65

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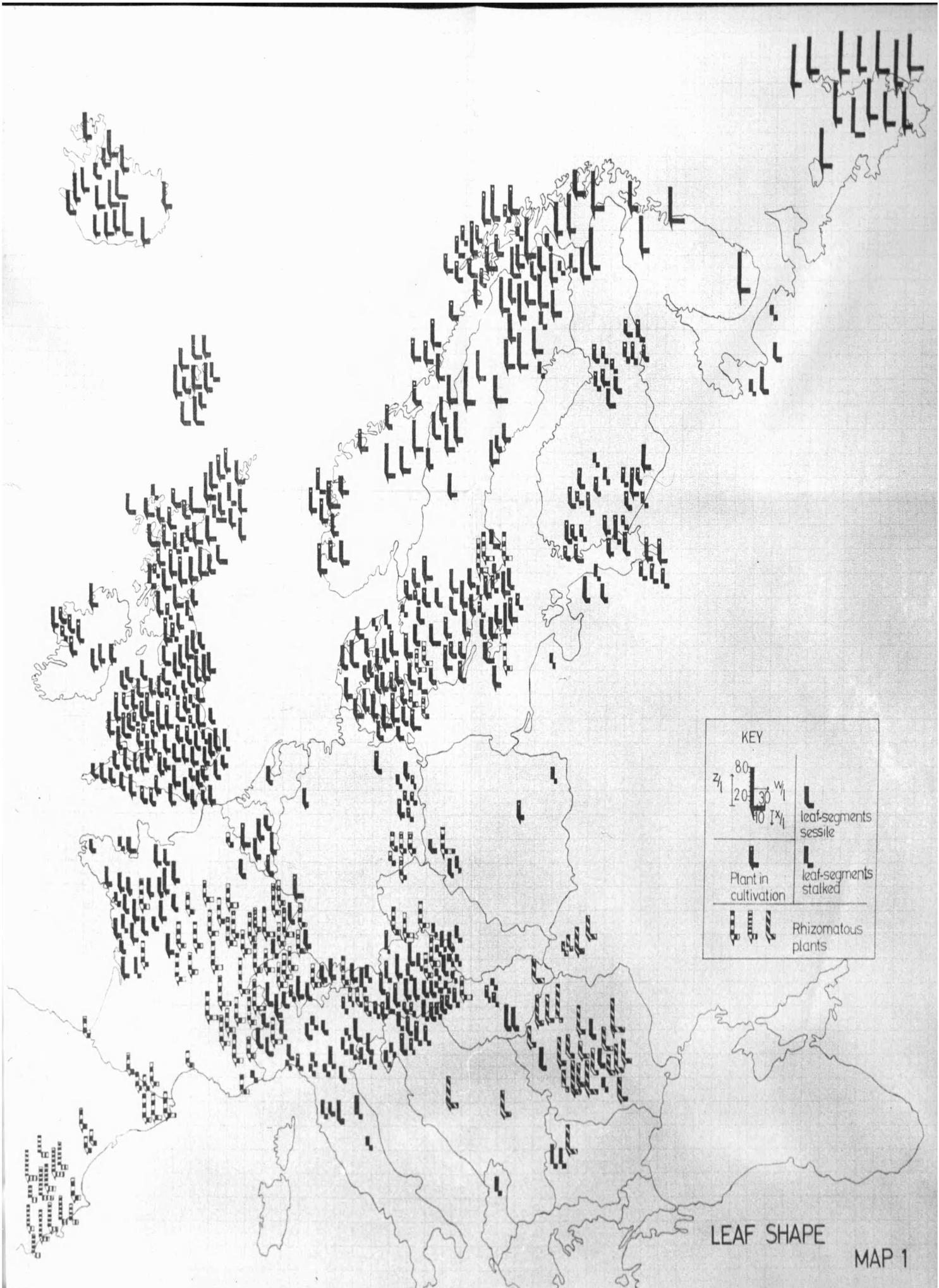
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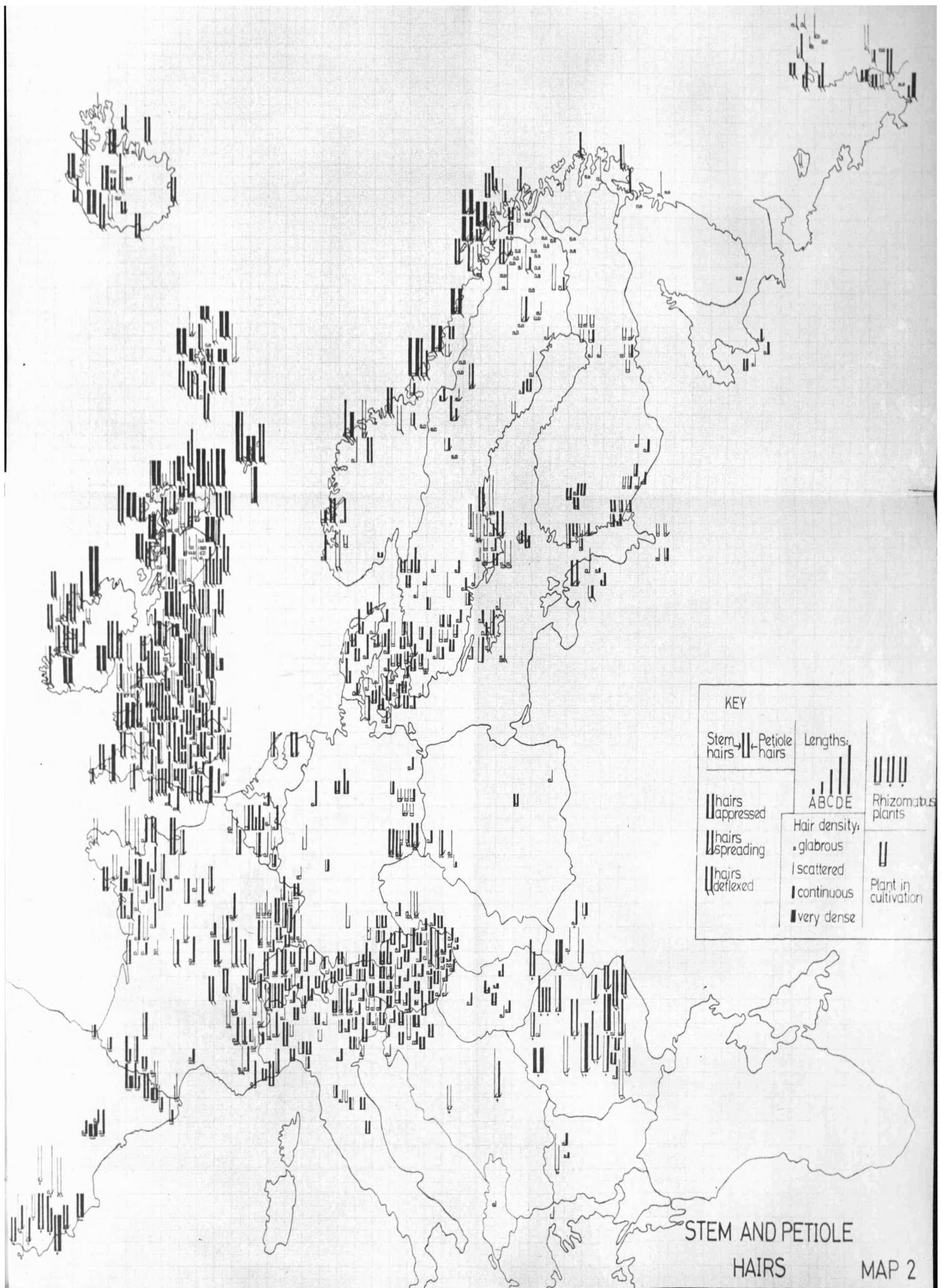
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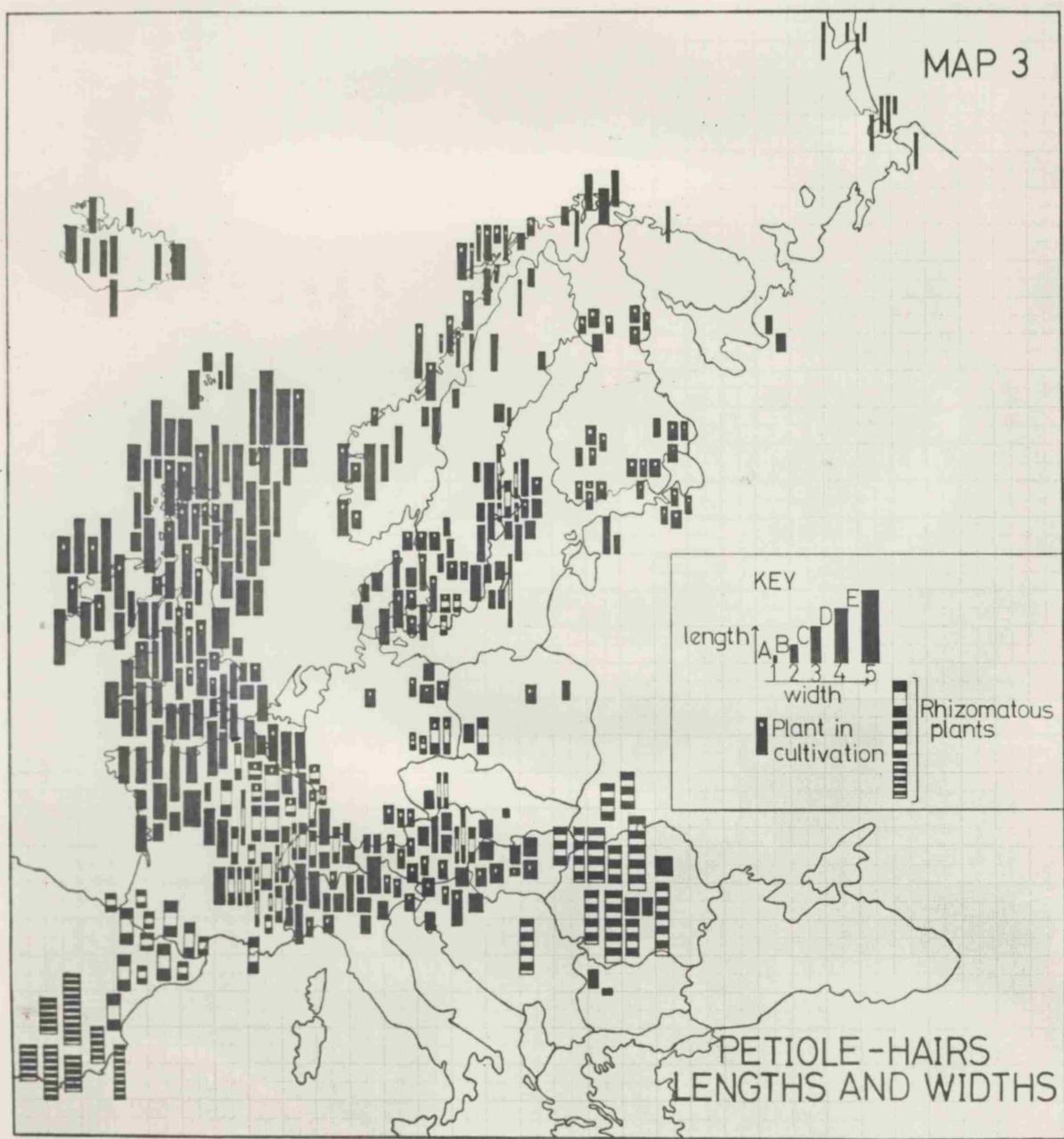
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MAPS 1-3.





MAP 3



Susan M.Coles

ABSTRACT--Systematics of the Ranunculus acris L.sens.lat. complex
in Europe.

The Ranunculus acris L.s.l. complex was examined within Europe, to investigate the geographical variation, and to see how this correlates with previous nomenclature assigned to the group.

Most of the work was carried out on herbarium specimens, but this was supplemented by cultivated material of known origin. Characters were investigated from as many parts of the plant as possible. Much variation was found to be due to the time of year or relative position of the organ on the plant. Graphical and mapping techniques were used, so that continuous variation would not be masked, but discontinuities would still show up.

Many of the numerous names previously applied to parts of the complex, were applied to parts of a continuous cline or even to seasonal variations. The following taxa are recognised in the present work.

R.granatensis Boiss.;Diag.ser.2(1):8(1853)

(syn.R.acris subsp.granatensis (Boiss.)Nyman;Consp:12(1878))

R.strigulosus Schur;Enum.Pl.Transs.:17(1866)

(syn.R.acris subsp.strigulosus (Schur)Hyl.;Symb.Bot.Upsal.
I:1(1943))

R.acris L.s.s.;Sp.Pl.:554(1753)

subsp.acris

(syn. R.boreanus Jord.;Obs.Pl.Crit.6:19(1847)

R.tomophyllus Jord.;Diag.:71(1864))

var.villosus (Drabble) comb.nov.

(syn. f.villosus Drabble; Rep.B.E.C.9(3)(1930))

var.pumilus Wahlenb.; Flora Lapp.(1812)

subsp.friesanus (Jordan) Rouy & Fouc.; Fl.Fr.1:103(1893)

(syn.R.friesanus Jordan; Obs.Pl.Crit.6:17(1847))

var.pyrenaeus nom.nov.

subsp.borealis (Trautv.) Nyman; Consp.:12(1878)

(syn.R.borealis Trautv.; in Bull.Soc.Nat.Mos.33:72(1860))

R.granatensis Boiss. and R.strigulosus Schur Have a restricted distribution and are relatively uniform in appearance. R.acris L.s.s. occurs over most of Europe and is a very variable plant.

Breeding experiments showed R.acris L.s.s. to be an obligate outbreeder, and all the plants tested, even from places as far apart as Finland, Austria and England, were found to be freely interfertile. Pollen fertility could not be used to detect any decrease in fertility of the hybrids due to the high but variable pollen infertility found in a large percentage of the parent plants. That much of the geographic variation within R.acris L.s.s. could not be split into separate infraspecific taxa could be attributed to its being an obligate outbreeder with no apparent geographical or ecological barriers within its distribution.

The main clinal variation in R.acris s.s. is in a West-East direction; a further cline occurs in a South-North direction in the North West of its distribution. R.acris subsp.friesanus (Jord.) R.& F. forms no part of this variation pattern, although its distribution is completely overlapped by that of subsp.acris. It appears likely that it has previously been at least ecologically isolated from subsp.acris.