

## *Ranunculus bulbosus* L. in Europe

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### ABSTRACT

The variation shown by *Ranunculus bulbosus* L. within Europe has been examined, and its classification revised. The *R. bulbosus* complex had formerly been split into several specific and subspecific categories. In the classification proposed here, only the one species *R. bulbosus* L. and two subspecies are recognised: subsp. *bulbosus* and subsp. *adscendens* (Brot.) Neves.

Subsp. *bulbosus* is widespread over central Europe occurring chiefly in grasslands which are well drained. Subsp. *adscendens* is only found in the Mediterranean region, where it occurs in habitats such as marshes. Intermediate plants are found in regions with climatic conditions transitional between those under which the two subspecies grow.

### INTRODUCTION

*Ranunculus bulbosus* L. belongs to the subgenus *Ranunculus* section *Ranunculus*. Species in this section are characterised by a nectary scale which is more or less free laterally, compressed achenes with a distinct beak, and a receptacle which in fruit is not more than three times its length when in flower.

Within the section *Ranunculus*, *R. bulbosus* is characterised by the following combination of characters: Plant perennial, usually pubescent. Root-stock swollen and corm-like, or, if little swollen, roots thick and tuberous. Stems never stoloniferous. Basal leaves tripartite, entire or divided into 3 or more segments with the central segment long-stalked so that it projects beyond the lateral segments. Petiole bases leaving few, if any, persistent fibres.

Inflorescence one- to few-flowered. Pedicel sulcate. Receptacle pubescent. Buds ovoid, not subglobose. Sepals reflexed. Petals usually 10-15 mm long, broadly obovate. Nectary-scale obtriangular, more or less as broad as the claw of the petal. Achenes 2-4 mm, dark brown, keeled, with a well-defined paler border whose margin is marked by a distinct ridge; beak rarely exceeding 1 mm, hooked or straight; surface very finely punctate, or very rarely with small tubercles bearing hairs.

*R. bulbosus* is widely distributed over Europe, except in the north, where it is limited to the southern lowlands of Scandinavia and south-western Finland (Harper 1957). In the south it extends into North Africa, where it occurs in Morocco, Algeria and Tunisia. In the eastern Mediterranean it reaches as far south as Kriti and Cyprus. Eastwards it extends at least as far as north-western Iran. It has been introduced into North America and New Zealand.

*R. bulbosus* has, in previous classifications, usually been split into several specific and subspecific categories (*cf.* the treatment in *Flora Europaea* (Tutin 1964)), but from the variation pattern found within Europe, only two subspecies

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within the single species *R. bulbosus* are recognised in this present work. The two subspecies of *R. bulbosus*, subsp. *bulbosus* and subsp. *adscendens* (Brot.) Neves, may be distinguished by the following characters:

	Subsp. <i>BULBOSUS</i>	Subsp. <i>ADSCENDENS</i>
Root-stock:	A well-formed corm.	Only slightly swollen, rarely corm-like.
Roots:	Thin (rarely exceeding 3 mm in diameter)	Thick (over 4 mm in diameter), tuberous.
Basal Leaves: (produced before 1st flowering stem of the year)	Divided into 3 or more segments, middle segment usually long-stalked.	Entire, or, if divided, middle segment $\pm$ sessile.
Petiole-hairs:	Fine (rarely exceeding 0.03 mm in diameter)	Coarse (exceeding 0.03 mm in diameter)

In the northern and central parts of its European range, *R. bulbosus* is represented by subsp. *bulbosus*. This subspecies characteristically occurs in well-drained habitats, mainly in lowland grasslands where the soil has a high base-status. Although subsp. *bulbosus* often occurs in habitats where summer drought is a factor limiting the growth of the vegetation, and where its corm may remain dormant for several of the summer months, it appears to be absent from truly xerophytic communities. Subsp. *adscendens* only occurs in the Mediterranean region, where it occurs in habitats which are waterlogged for at least part of the year, such as in marshes, ditches, etc.

There is a continuous array of intermediate plants which are found in the transitional regions between the two climatically different geographical areas occupied by the two subspecies. Because of these intermediates the taxa recognised have been placed in a single species. The subspecific category would seem most appropriate for these taxa, because they are morphologically very distinct and occupy different habitats in different regions within the range of the species. Such a treatment does however leave plants which can only be designated as intermediates, but this is usually inevitable when subspecies are recognised.

The distribution of subsp. *bulbosus* is continuous across Europe. It often shows great variation in any one locality, but variation of a geographical nature is not apparent.

The distribution of subsp. *adscendens* is rather disjunct, due to the configuration of the Mediterranean lands, but the range of variation of most characters is similar throughout. The only constant difference found between plants of different regions is that plants from the Iberian peninsula have achenes with hooked beaks, whereas plants from elsewhere usually have more or less straight beaks. Such apparently trivial variation is not thought to merit taxonomic recognition.

#### MATERIAL AND METHODS

This study was largely based on herbarium material from the following herbaria: British Museum (BM), Cambridge (CGE), Coimbra (COI), Edinburgh (E), Florence (FI), Leicester (LTR), Porto (PO), Stockholm (S), Uppsala (UPS) and Vienna (W).

Plants of known wild origin were grown from as wide a range of localities as possible. They included plants of subsp. *bulbosus* from 30 localities in Britain and from 10 localities on the Continent; plants intermediate between the two subspecies from 5 localities; and plants of subsp. *adscendens* from 4 localities. Plants of this latter subspecies were also grown from seed of botanic garden origin.

Characters were investigated from as many parts of the plant as possible. The following characters were found to be of most value: form of rootstock and roots, shape of leaves, type of indumentum and form of beak of achenes. Many other characters have been used previously, but mostly it was impossible to see how such character distinctions were at all justified, as they do not show any noticeable correlation with plants of either taxon or to plants of different geographical regions.

#### DISCUSSION OF CHARACTERS

A detailed evaluation of characters and of the extent of variation found within them is given below. The chief characters separating the two subspecies have been plotted on the maps in Figs. 1 and 2. The characters plotted are: form of root-stock and roots, leaf-shape, width and type of petiole-hairs. Also marked on these maps is the limit of the Mediterranean vegetational zone, as characterised by the presence of *Olea*, *Cistus*, *Genista*, *Arbutus* and *Nerium* (taken from Thompson 1970).

#### THE ROOT-STOCK AND ROOTS

Plants of *R. bulbosus* are perennial. The root-stock is short and is vertically orientated, but 'freak' plants with a horizontal axis are found. The root-stock is always somewhat enlarged laterally and is thus corm-like. In subsp. *bulbosus* the root-stock is greatly swollen, whereas in subsp. *adscendens* relatively little expansion occurs. However in subsp. *adscendens* the roots are much thicker and are tuberous in appearance. A continuous range between these two root-stock types is to be found among plants which are intermediate between the two subspecies (examples of such root-stocks are shown in Fig. 3).

The maximum diameter of roots in cultivated plants of subsp. *adscendens* was found to be 4–6 mm, whereas in subsp. *bulbosus* it never exceeded 3 mm. The increase in the size of the roots in subsp. *adscendens* is chiefly by an increase in the number of cells in the cortex. The size of the 'corm' in either subspecies is very variable and can be greatly modified by environmental conditions, whereas root-diameter is far more constant.

The shape of the corm and the number of flowering stems produced by a corm have previously been used as diagnostic characters for taxa, chiefly within subsp. *bulbosus* as here understood; such use is not justified. Although the greatest dimension of a corm is usually its breadth, its shape is easily modified. Examples of such modifications are especially common in plants growing on sand-dunes, where they suffer continual burial by sand; these conditions can produce spindle- or carrot-shaped corms or even a beaded effect where numerous small 'corms' have been produced on the main stem.

The apical bud of an over-wintered root-stock produces a flowering stem. Lateral buds may produce other flowering stems. This is partly controlled by the environment, but corms of the same size growing together in the same con-

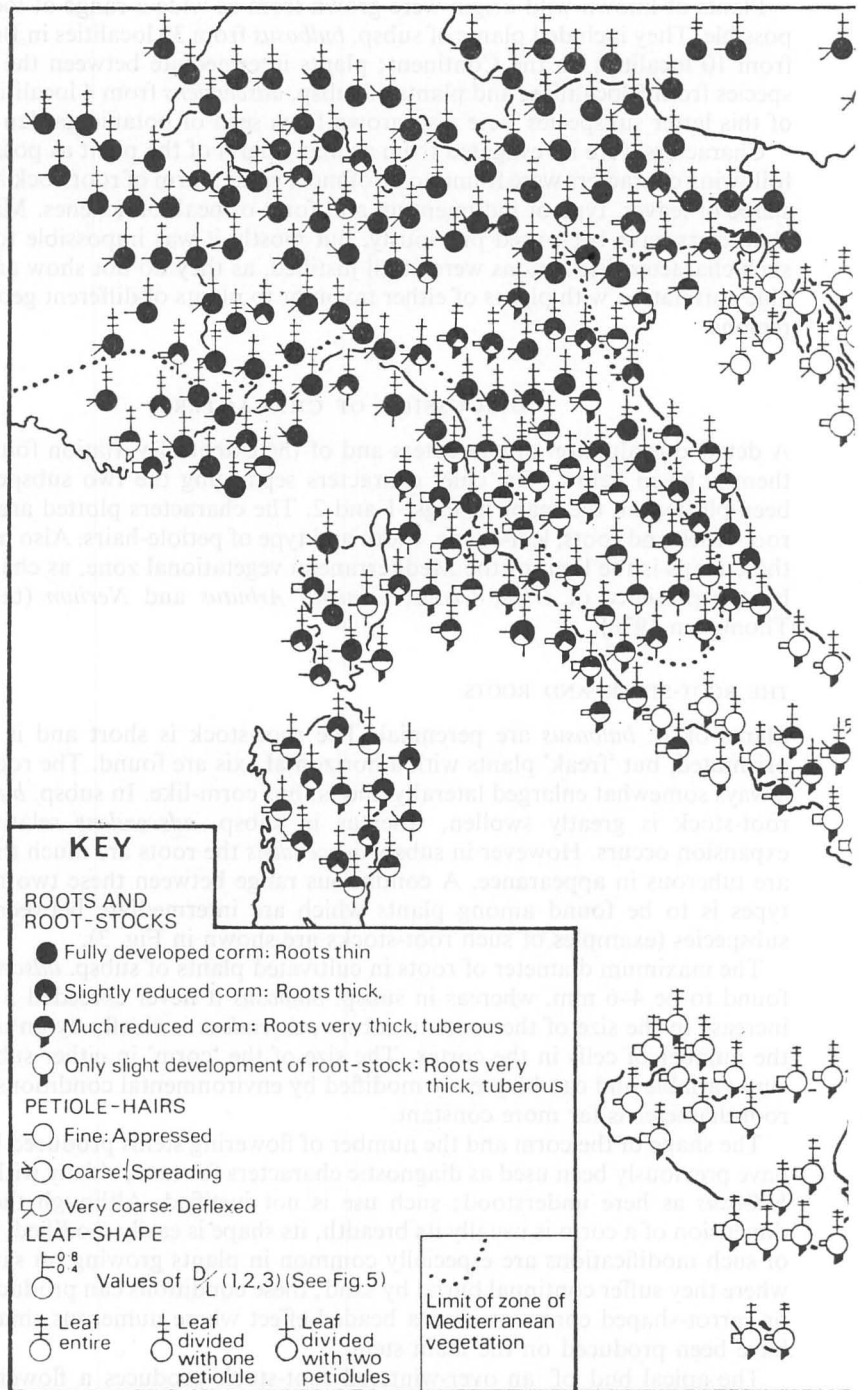
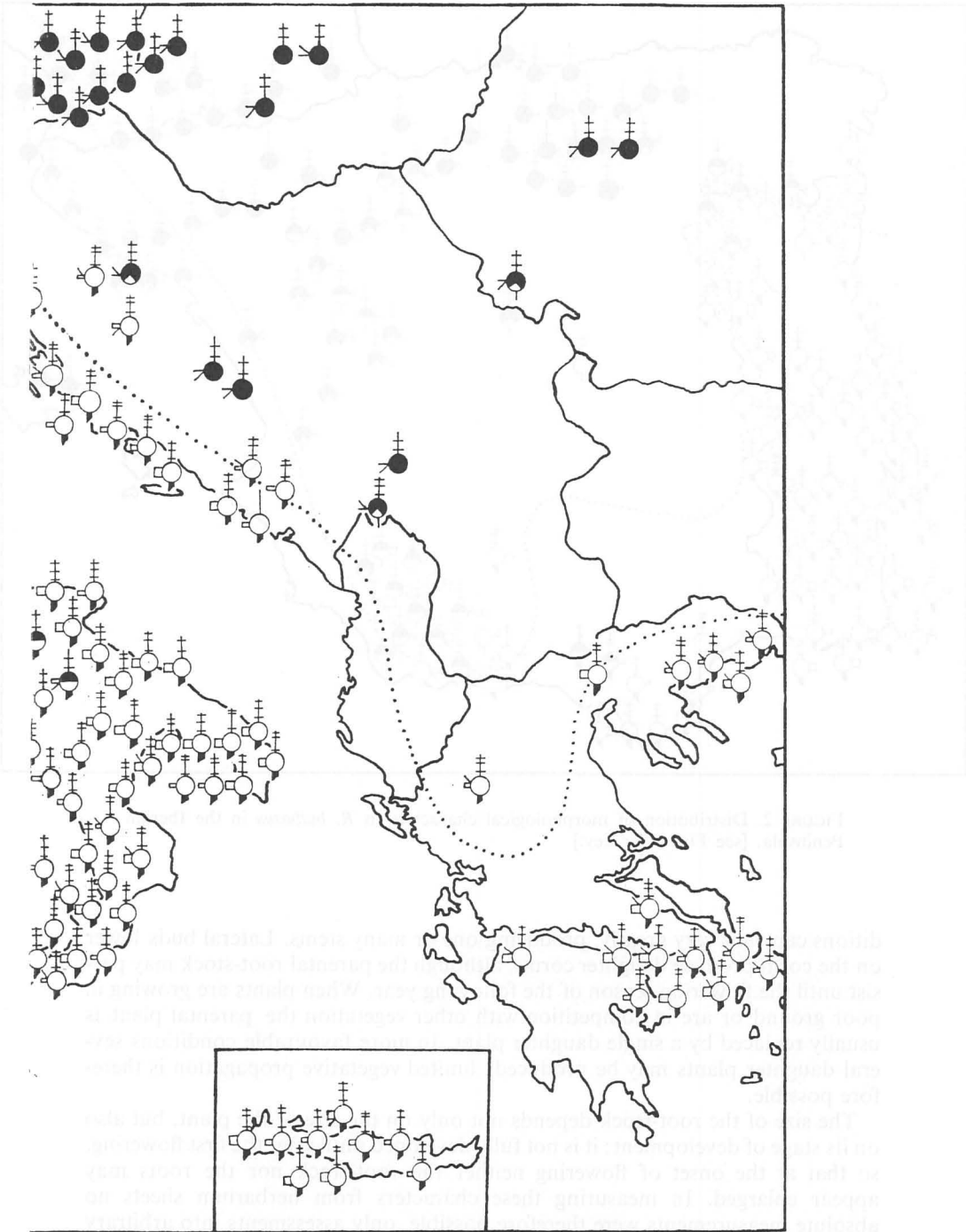


FIGURE 1. Distribution of morphological characters



in *R. bulbosus* in Italy and the Balkan Peninsula.

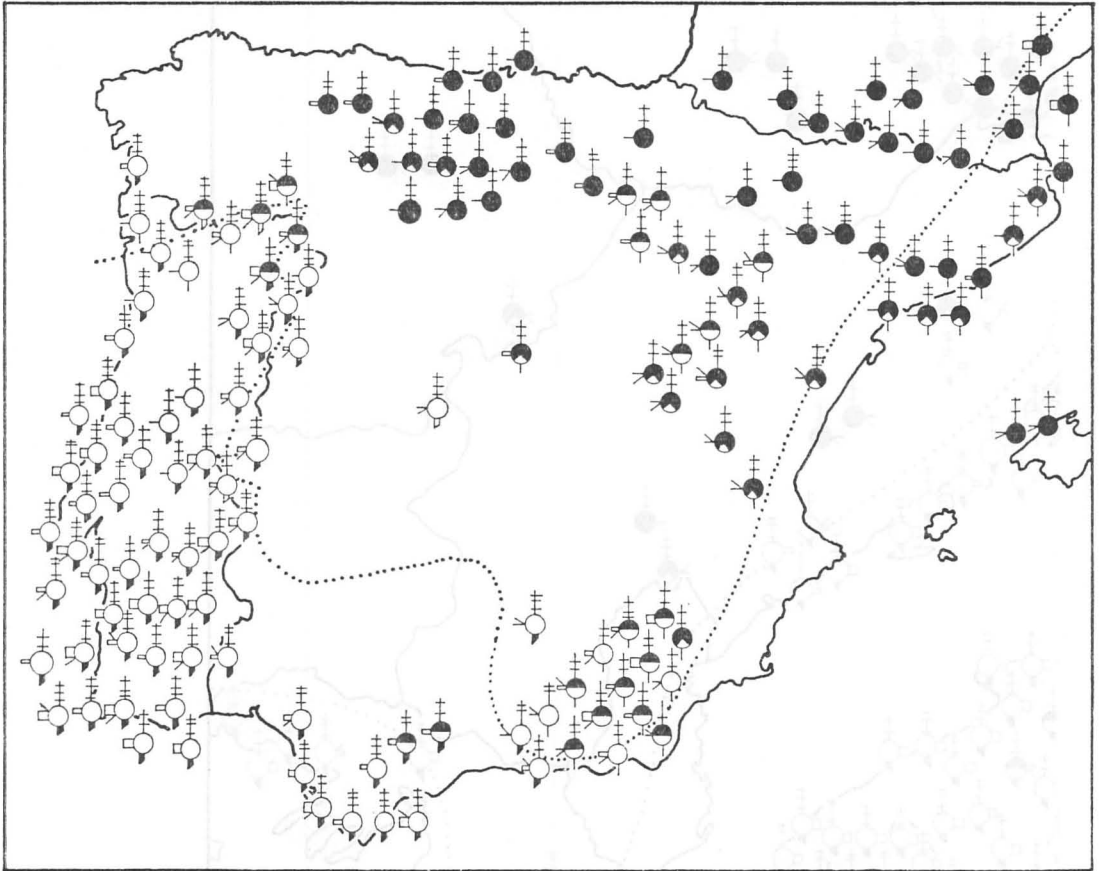


FIGURE 2. Distribution of morphological characters in *R. bulbosus* in the Iberian Peninsula. [see Fig. 1 for key.]

ditions can vary very greatly, producing one or many stems. Lateral buds lower on the corm produce daughter corms, although the parental root-stock may persist until the flowering season of the following year. When plants are growing in poor ground or are in competition with other vegetation the parental plant is usually replaced by a single daughter plant. In more favourable conditions several daughter plants may be produced; limited vegetative propagation is therefore possible.

The size of the root-stock depends not only on the size of the plant, but also on its stage of development; it is not fully developed until after the first flowering, so that at the onset of flowering neither the root-stock nor the roots may appear enlarged. In measuring these characters from herbarium sheets no absolute measurements were therefore possible, only assessments into arbitrary categories, although these were based on the expected appearance (given in parentheses) had the plant been mature.

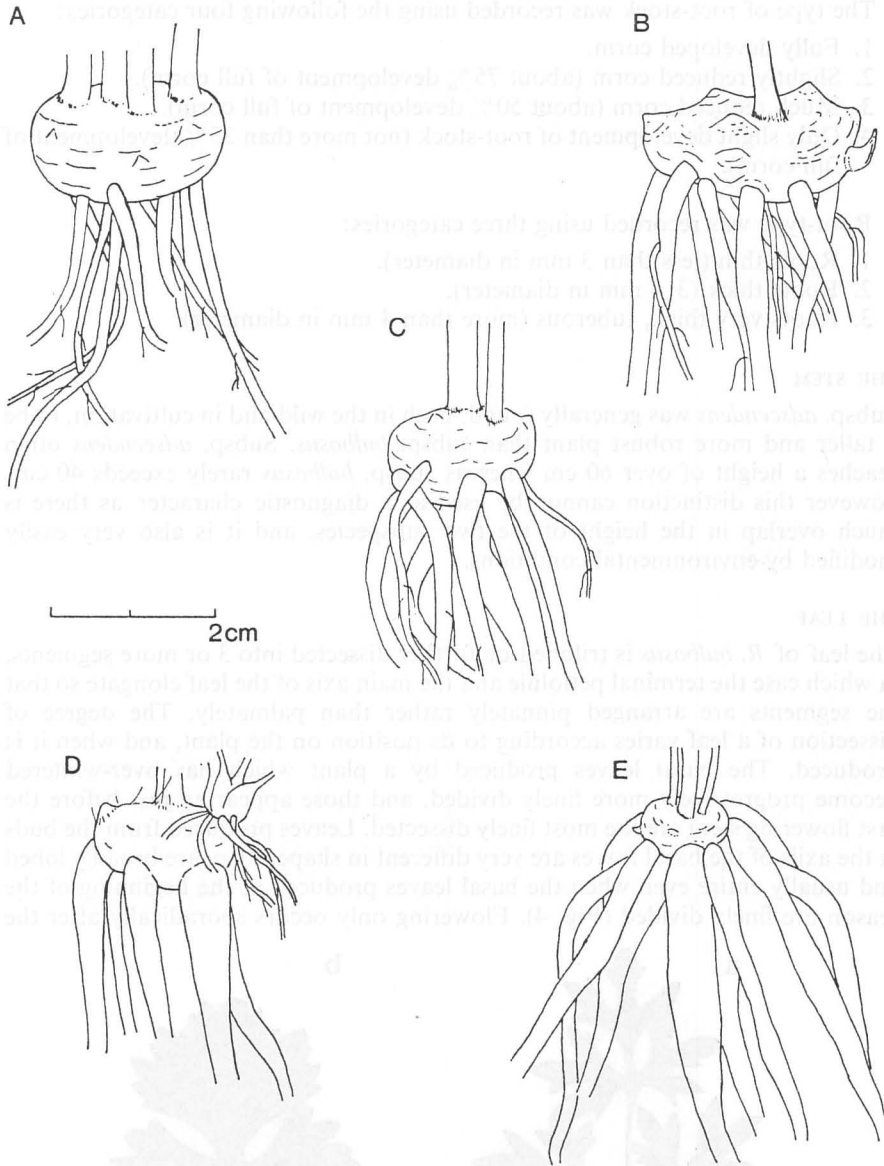


FIGURE 3. Root-stocks:

- A. subsp. *bulbosus*, Llandudno, N. Wales.
- B, C & D. Intermediate plants
- B. Genova, N. Italy
- C. Estartit, Gerona, N. Spain
- D. Ronda, S. Spain.
- E. subsp. *adscendens*, Rethimnon, Kriti.

The type of root-stock was recorded using the following four categories:

1. Fully developed corm.
2. Slightly reduced corm (about 75% development of full corm).
3. Much reduced corm (about 50% development of full corm).
4. Only slight development of root-stock (not more than 25% development of full corm).

Root-type was recorded using three categories:

1. Roots thin (less than 3 mm in diameter).
2. Roots thick (3-4 mm in diameter).
3. Roots very thick, tuberous (more than 4 mm in diameter).

#### THE STEM

Subsp. *adscendens* was generally found, both in the wild and in cultivation, to be a taller and more robust plant than subsp. *bulbosus*. Subsp. *adscendens* often reaches a height of over 60 cm whereas subsp. *bulbosus* rarely exceeds 40 cm; however this distinction cannot be used as a diagnostic character as there is much overlap in the height of the two subspecies, and it is also very easily modified by environmental conditions.

#### THE LEAF

The leaf of *R. bulbosus* is trilobed or further dissected into 3 or more segments, in which case the terminal petiolule and the main axis of the leaf elongate so that the segments are arranged pinnately rather than palmately. The degree of dissection of a leaf varies according to its position on the plant, and when it is produced. The basal leaves produced by a plant which has over-wintered become progressively more finely divided, and those appearing just before the first flowering stem are the most finely dissected. Leaves produced from the buds in the axils of the basal leaves are very different in shape. They are broadly lobed and usually entire even when the basal leaves produced at the beginning of the season are finely divided (Fig. 4). Flowering only occurs sporadically after the

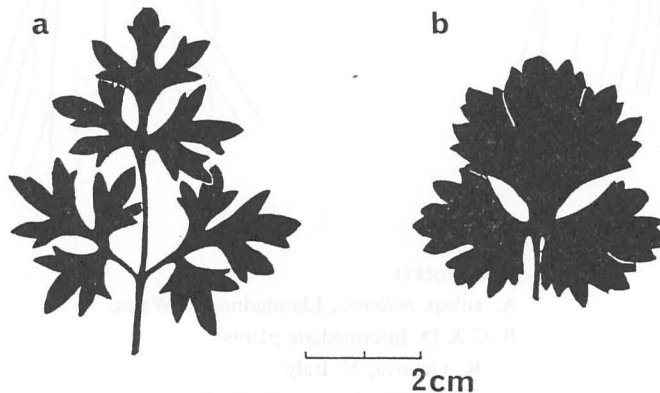


FIGURE 4. Seasonal variation in leaf-shape.  
Subsp. *bulbosus* from Keele, Staffordshire, England  
a. leaf produced before first flowering stem  
b. leaf produced later in the season.



first main peak in spring, and consequently plants with these less-divided leaves occur infrequently in herbarium collections. This perhaps explains why no such seasonal variants have been given taxonomic recognition in the past as they have in other species of *Ranunculus*.

Measurements of leaf-shapes, so that they would be comparable, were only made on the leaves produced just before the first flowering stem. Further discussion of leaf-shapes refers to these leaves only. The character which showed the most significant variation is the degree of dissection. The measurements ( $D_1$ ,  $D_2$  and  $D_3$ ) made to record this are shown in Fig. 5. The ratios of these measurements to length of lamina are plotted in Figs. 1 and 2, the length of lamina being taken as the length of the whole lamina along the main axis of the leaf.

Among the other variables of leaf-shape are the width of the lobes and the number of teeth. These do not show any close correlation with the degree of dissection of the leaf; both are very variable in any one population and do not appear to show any geographical variation.

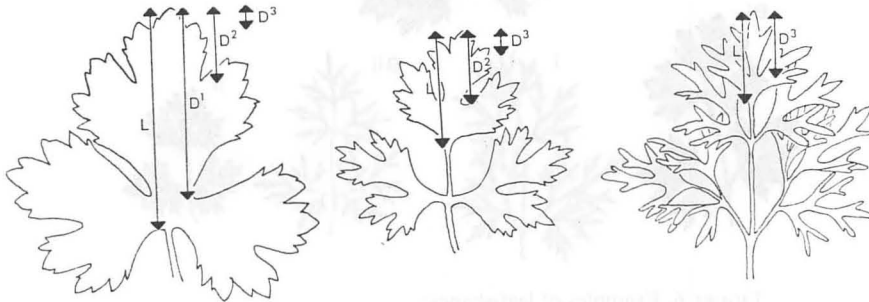


FIGURE 5. Measurements made on the leaves.

L—length of lamina

D (1,2,3)—distance from apex of leaf to the three primary divisions on the main axis of the leaf (these are ignored when at that position there is a petiolule).

Within subsp. *bulbosus* the leaves are divided into segments; only in dwarfed plants are the leaves ever simple. A wide range of leaf-shapes commonly occurs within a single population (Fig. 6). Plants with very finely dissected leaves appear to be mainly confined to lowland populations, although even here they are not the predominant kind. Little geographical variation in leaf-shape is apparent within subsp. *bulbosus* except that very finely divided leaves are rare in southern Europe. Subsp. *adscendens* has simple leaves (Fig. 6) but, if the leaf is divided into three segments, the latter are more or less sessile. Plants intermediate between the two subspecies are nearly always marked by having a divided leaf in which the central segment is stalked. Intermediate plants from the Sierra Nevada region in southern Spain are unusual, often having very finely divided leaves.

#### THE HAIRS

*R. bulbosus* is generally rather a hairy plant, except during the winter. Only very few plants of both subspecies were seen with glabrous leaves at the time of flowering; those of subsp. *bulbosus* were chiefly from montane habitats.

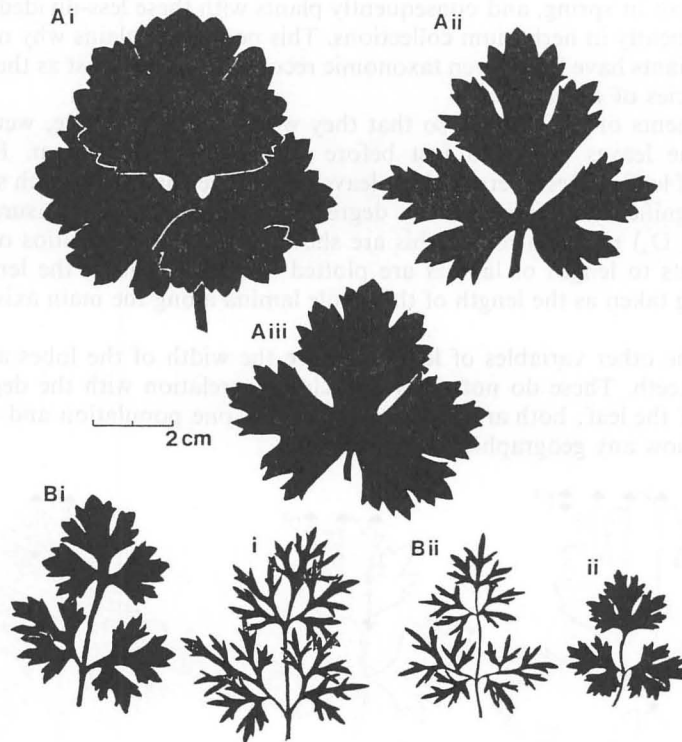


FIGURE 6. Examples of leaf-shapes:

- |                             |                                     |
|-----------------------------|-------------------------------------|
| A. subsp. <i>adscendens</i> | i. Faro, Portugal                   |
|                             | ii. Reguengos de Monsaraz, Portugal |
|                             | iii. Malaxa, Kriti.                 |
| B. subsp. <i>bulbosus</i>   | i. Copmere, Staffordshire, England  |
|                             | ii. Llandudno, N. Wales.            |

Hair-width is the only hair attribute showing any difference between the two subspecies, the width being much greater in subsp. *adscendens* than in subsp. *bulbosus*. Hair-width was measured on the longest hairs on a petiole (excluding the sheathing region). The measurements were divided into the following arbitrary categories:

1. Fine (less than 0.03 mm).
2. Coarse (0.03–0.05 mm).
3. Very coarse (more than 0.05 mm).

The results are shown in Figs. 1 and 2. The petiole-hairs of subsp. *bulbosus* fall within category 1. Those of subsp. *adscendens* are more variable (within categories 2 and 3). Also plotted in Figs. 1 and 2 are the positions of the hairs relative to the petiole. This was recorded using 3 categories: appressed, spreading and deflexed. Similar variation is found in both subspecies. The more detailed field data on subsp. *bulbosus* suggest that local variation in this character is to some extent ecotypic in nature; deflexed hairs are commoner in upland and coastal

habitats, whereas appressed hairs are typical of lowland pastures. The pubescence is very variable, but tends to be greater in plants with deflexed hairs.

#### THE FLOWER

The pedicel in *R. bulbosus* is sulcate. In subsp. *bulbosus* it is strongly sulcate for the whole length, unless it is more than half the total height of the plant. In subsp. *adscendens*, except where the pedicels are very short, the furrows fade out before the base of the pedicel. This character could only be examined on fresh material.

In the past the shape of the receptacle has been used as a diagnostic character. Although it is more or less the same within a single plant, it is very variable within populations. The commonest shapes are ellipsoid to conical, but subglobose receptacles are not uncommon. The shape and size of the sepals, petals and stamens are relatively constant throughout the species.

The size and shape of the achenes in plants from any one locality are very variable (Fig. 7). No geographical trends were found in the variation of these characters, except in the form of the beak. In subsp. *bulbosus* the beaks of the achenes are always hooked. They are also hooked in subsp. *adscendens* from the Iberian peninsula, and these achenes are indistinguishable from those of subsp. *bulbosus*. The beaks of subsp. *adscendens* elsewhere in Europe are more or less straight except for a few plants in Sicilia and southern Sardegna which have curved beaks. The achenes of these plants are also peculiar in that their beaks are longer (up to 1.2mm) than are found elsewhere in the species, and that the faces of the achenes sometimes bear hairs with tuberculate bases. These plants are discussed below (p. 225).

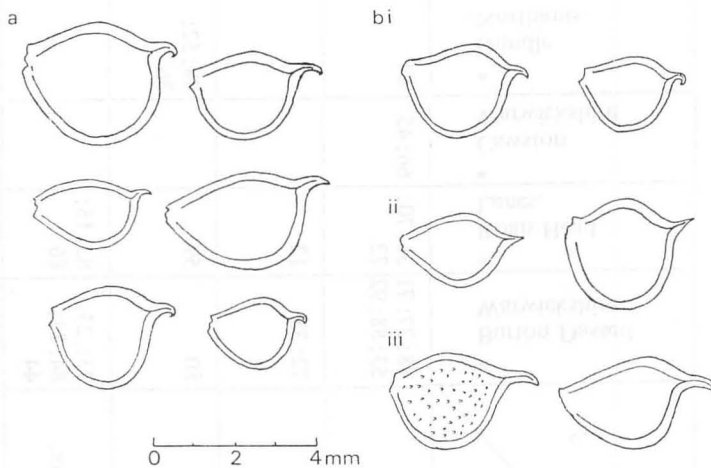


FIGURE 7. Examples of achenes:

- a. subsp. *bulbosus*, Braunston, Northamptonshire, England, showing the variation in size and shape of the achenes of plants from a single population.
- b. subsp. *adscendens*, i. Portugal  
ii. Kriti  
iii. Palermo, Sicilia.

TABLE 1. EXPERIMENTAL CROSSES BETWEEN CULTIVATED PLANTS OF WILD ORIGIN

Results expressed as percentage seed-set per flower.

+	o	* Burton Dassett Warwickshire	* Roan Head Lancs.	* Cawston Warwickshire	* Oundle Northants.	* Ilam Staffordshire	* Budapest Hungary	** Estartit N.E. Spain	** Ronda S. Spain	*** Madrid Botanic Gardens	*** Coimbra Botanic Gardens	*** Oeiras Portugal	*** Rethimnon Kriti
*Burton Dassett, Warwickshire, England		88; 27; 71 53; 88; 92	36; 70; 72	66; 45	84	30; 89; 15; 74; 50	68; 59; 67; 0	93; 23; 25; 35; 39	17; 20; 16; 28; 0	11; 16	7; 0	6; 34; 86; 0; 30; 68; 4; 24; 41	7; 79; 58; 81; 69; 47 19; 41; 25
*Roan Head, Lancashire, England		72; 33	12				81; 68	33	0; 0	46; 26	37; 41	13; 42	36; 13
*Cawston, Warwickshire, England		80	59		48; 52; 36		86; 53	80; 28	0		27	4	
*Oundle, Northamptonshire, England		33; 25; 84; 73; 44	83; 15; 86			28; 52	69	28	75; 16; 0; 34; 13; 0	61	56; 0; 30	48; 15	
*Ilam, Staffordshire, England		76; 61	57; 60	67; 76; 80	80; 64	83; 55; 92; 91; 91	96; 79; 0; 73	68; 15; 28; 88; 76	17; 12; 22; 31; 35; 26	70; 55	13; 0; 5; 14; 0	26; 0; 22; 7; 0; 9; 17	15; 5; 10; 0; 9; 35; 0

*Urçay, Cote d'Or, France	62; 64; 52			67; 46	23; 80; 71		81	5; 0	70	27; 22; 79	24; 34; 11; 7; 12	
*Bouafles, Eure, France				91; 37; 37			44; 11	65; 73; 0		26; 32; 47; 8		
**Genoa, Italy	52; 36; 37	50		55; 58; 19			91	6	56; 0; 0	70; 78; 5	5	
**Estartit, Gerona, Spain	38; 68; 79		0; 53; 50; 71; 72	66; 69	37; 52	40; 43	100; 91 92; 83	64	10; 50	54; 56; 67; 69	75; 54; 0 0; 0; 58	0; 61; 82
**Ronda, Malaga, Spain	0; 0; 41; 0	56; 19	0	0; 0; 0			0; 38			36; 0	47; 52	
***Botanic Gardens, Madrid	63; 65	48; 91; 5	76; 29; 29; 57	32; 30	63; 64	41; 60	43; 42; 37; 83; 77; 61	17	8; 36	33; 0; 71; 22; 27; 43	54; 41; 36; 56	79; 80; 0; 43; 48
***Botanic Gardens, Coimbra	35; 68; 24; 40; 38	65; 40; 33; 44	0; 35; 63; 40	32; 33; 63; 65; 60; 60	50; 38; 77; 48; 56; 29	71; 68	85; 29; 51; 29	64; 63; 0; 0; 37	0; 50; 46; 43; 48; 0	76; 39; 31; 38; 38	0; 67; 32; 43; 31; 40; 67	61; 89; 60; 35; 46; 86
***Oeiras, Portugal	88; 0; 72; 60; 76; 15	66; 79; 78; 90	89; 0; 84	85; 0; 0	90; 41; 74; 0; 23	0	80; 0; 33; 40; 63	64; 78; 83; 71	75; 0	24; 81	31; 90; 77; 97	54; 24; 91; 68; 29; 88; 83; 62
***Rethimnon, Kriti	21			0; 5	28				18	19	0; 0	9; 27

\* Subsp. *bulbosus*

\*\* Intermediate between subsp. *bulbosus* and subsp. *adscendens*

\*\*\* Subsp. *adscendens*

## CHROMOSOMES AND BREEDING EXPERIMENTS

Almost without exception the number of chromosomes recorded for members of the *R. bulbosus* complex is  $2n = 16$  (e.g. Coonen 1939, Gregson 1965, Neves 1944). Gregson found the karyotype, except for occasional abnormalities, to be constant throughout *R. bulbosus*. She says it consists of 2 pairs of chromosomes with a median centromere (2 LL), 2 pairs nearly median (2 L1), 2 pairs submedian (2Lm), 6 pairs with a much shorter arm ( $2Lp_1 + 2Lp_2 + 2Lp_3$ ) and 4 pairs with subterminal centromeres—one of these pairs with a satellite on the short arm (2L + 2L!). The karyotype given by Neves (1944) has a satellite on the long arm of the first pair of chromosomes which have subterminal centromeres, but he still found consistency in the karyotype of all the plants of *R. bulbosus* which he examined. The karyotype given by Kurita (1957) differs from that given by Gregson in the position of the satellites. An accessory chromosome was found by Gregson (1965) in material from Greece. However, not only does the karyotype appear to be the same throughout *R. bulbosus*, but it is almost identical with that of *R. sardous* Crantz, a closely related species, and of *R. ficaria* L., a species from another very different section of the genus (Gregson 1965, Larter 1932).

Some selfing and a low degree of agamospermy have been previously reported for *R. bulbosus*. These were tested for by selfing and by emasculating flowers. The plants used were grown in a greenhouse and the flowers were individually covered by cellophane bags. These tests were carried out on the following numbers of plants, several flowers per plant being tested.

	Flowers emasculated	Flowers selfed
Subsp. <i>bulbosus</i> (British)	12 plants from 7 localities	29 plants from 7 localities
Subsp. <i>bulbosus</i> (from the Continent)	3 plants from 7 localities	4 plants from 3 localities
Subsp. <i>adscendens</i>	10 plants from 3 localities	15 plants from 3 localities
Intermediate plants	—	7 plants from 3 localities

In all these tests only five seeds were set, and in each case of seed-set the tests were repeated with only negative results. It is probable that these seeds were the result of contamination and that *R. bulbosus* is totally self-incompatible and sexual.

The interfertility of plants from different regions and of different morphological types was tested by means of a series of experimental crosses. The percentages of seeds set per cross are given in Table 1. The percentage from any one cross was very variable, but usually a high seed-set was obtained at least once when a cross was repeated several times (failure to set seed could generally be attributed to the use of rather infertile pollen, or to the arrested development of the flowers, probably due to attacks of root-fly maggots). The results indicate that there are no serious barriers to crossing between different members of the species. In Fig. 8 the results are shown in the form of histograms; the data for plants of the same subspecies have been combined. The best results are shown by crosses involving subsp. *bulbosus* × subsp. *bulbosus*. Crosses within subsp. *adscendens* give lower values. Plants of this subspecies were generally less fertile than those of subsp. *bulbosus*. This point is discussed below. What is of interest, and for

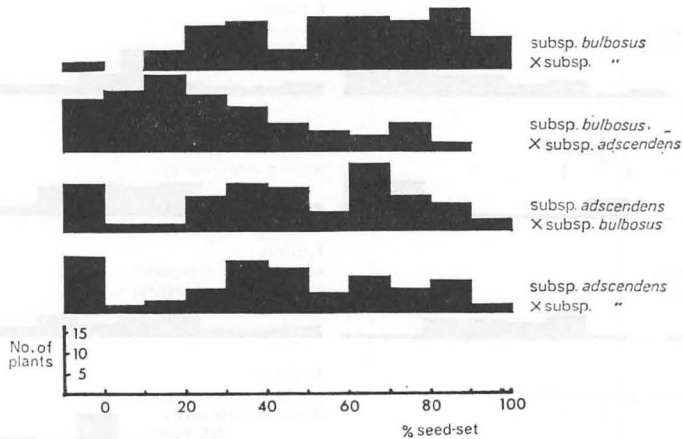


FIGURE 8. Histograms of percentages of seed-set in the experimental crosses.

which there is no apparent explanation, is that crosses of subsp. *adscendens* × subsp. *bulbosus* gave results as good as subsp. *adscendens* × subsp. *adscendens* and better than subsp. *bulbosus* × subsp. *adscendens*. Crosses between plants of the same subspecies, but from widely separated localities showed little, if any, decrease in seed-set when compared with crosses between plants from the same region.

No appreciable differences were found in the percentage germination of achenes obtained from inter-subspecific crosses compared with intra-subspecific crosses, neither were significant differences detected between the germination of achenes from intra-subspecific crosses from the same area or from widely separated areas. As in many perennial species of *Ranunculus*, the germination of *R. bulbosus* achenes is rather erratic and germination of achenes from a single head is often spread over several months.

The fertility of the  $F_1$  plants obtained from the crosses was investigated by examining their pollen fertility. A mixture of pollen grains from both inner and outer anthers of a flower was stained in cotton blue. All pollen grains with contents and of normal appearance were counted as 'good' grains. This, however, only gives an indication of true viability. Böcher (1938) showed that, under conditions in which medium-sized grains of *R. bulbosus* showed good germination, the smallest and largest grains did not germinate. Counts were only made on the first flower of a stem, as the percentage of 'good' grains decreases in subsequent flowers. Even in the first flower produced by a plant this percentage can fluctuate greatly from year to year. The measurements made, therefore, only give a rough guide to the fertility of the plant.

The percentages of 'good' pollen grains for the parental and  $F_1$  plants (maximum of 5 plants/cross) are plotted as histograms in Fig. 9. Parental plants of subsp. *adscendens* showed a generally lower percentage of 'good' grains when compared with those of subsp. *bulbosus*. This may be due to the fact that subsp. *adscendens* is from southern Europe and experiences adverse climatic conditions when grown in the British Isles. The percentages of 'good' grains in the  $F_1$  plants from the crosses between the two subspecies were slightly lower than those of the parental subsp. *adscendens*, but many plants showed a reasonably high pollen

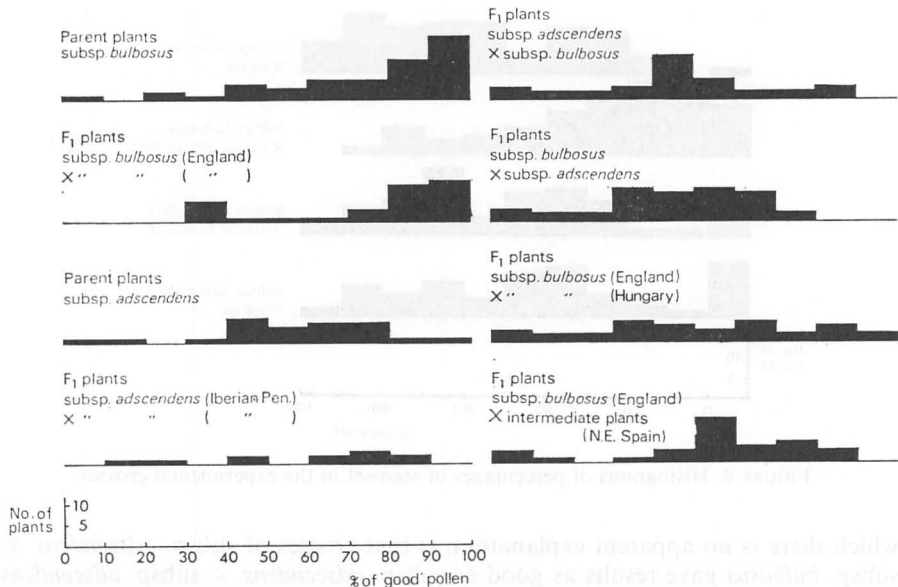


FIGURE 9. Histograms of percentages of 'good' pollen.

fertility. A general reduction in fertility was also found in F<sub>1</sub> plants from crosses of British subsp. *bulbosus* with morphologically similar plants from remote localities. F<sub>2</sub> plants showed no decrease in pollen fertility when compared with their F<sub>1</sub> parents.

Meiosis in the pollen-mother-cells of parental and F<sub>1</sub> plants was also examined. Univalents were quite common, but generally only in the plants which had a low percentage of 'good' grains.

The low percentages of 'good' grains which were found in many of the parental plants are a common feature of many *Ranunculus* species, *R. bulbosus* showing a complete range in the reduction of pollen fertility from almost '100% fertile' plants to those exhibiting complete gynodimorphism. Gynodimorphism is not as common in *R. bulbosus* as it is in *R. acris* L. (Coles 1971), and examination of pollen of British material of these two species showed *R. bulbosus* to be generally more fertile.

#### HYBRIDS WITH OTHER SPECIES

No substantiated records of hybrids between *R. bulbosus* and other species have been found, but from the results obtained in the experimental crosses described below such hybrids might well be expected to occur in the wild. Only a limited number of species was available for these tests.

*R. nemorosus* DC. and *R. polyanthemos* L. are morphologically close to *R. bulbosus* and have the same chromosome number ( $2n = 16$ ). Reciprocal crosses of *R. bulbosus* with both these species resulted in good seed being set. Seed-set of up to 72% was achieved when using plants of *R. bulbosus* and *R. nemorosus* from the same district, but in other cases the cross had to be repeated several times before any seed was set. F<sub>1</sub> plants were raised from some of the *R. bulbosus* (both subspecies) × *R. nemorosus* crosses, and these were fairly fertile; 40% of 'good' pollen was found in several plants.



*R. repens* is morphologically close to the species already discussed, but has a chromosome number of  $2n = 32$ . In crosses between *R. bulbosus* and *R. repens* no seed was ever set. Crosses between *R. repens* and *R. nemorosus* also resulted in no seed being set, but when *R. nemorosus* was used as the female parent some carpel enlargement (without any visible development of the seed) occurred. A tetraploid plant of *R. bulbosus* ( $2n = 32$ ) was produced artificially (by colchicine treatment) and when pollinated by *R. repens* some carpel enlargement also occurred. Such enlargement did not occur when these species were selfed or when they were crossed with species of *Ranunculus*, showing no close morphological relationships.

The annual *R. sardous* Crantz is morphologically very close to *R. bulbosus* and has the same chromosome number, but no seed was ever set when it was crossed with *R. bulbosus*. However, in some crosses where *R. bulbosus* was the female parent, but not in the reciprocal cross, a few carpels showed some enlargement. A much higher percentage of enlarged carpels occurred when *R. sardous* was pollinated by the closely related annual species *R. marginatus* D'Urv. ( $2n = 32$ ).

#### NOMENCLATURE

The taxonomy of *R. bulbosus* is extremely confused because of the vogue for naming minor variants and the lack of co-ordination between botanists working in different regions. *Index Kewensis* lists over forty specific names referable to this complex, and infraspecific names are equally numerous. Except for the recognition of the two subspecies, *bulbosus* and *adscendens*, the many variants which have been given taxonomic status are rejected. This is because there is complete intergradation from one form to another with no barriers to gene-exchange and there is no constancy in the form of their offspring, as could be found in inbreeding or agamosperous plants.

The synonyms given below include only the more important ones, and are those which have been most frequently applied to variants of the complex.

*R. BULBOSUS* L., Sp. Pl., 554 (1753)

Subsp. *BULBOSUS*

*R. brachiatus* Schleich., Cat. Pl. Helv., 3rd ed., 24 (1815)

*R. bulbifer* Jord., Ann. Soc. Linn. Lyon, N.S., 7: 448 (1861)

*R. sparsipilus* Jord., Ann. Soc. Linn. Lyon, N.S., 7: 448 (1861)

*R. albonaevus* Jord., Ann. Soc. Linn. Lyon, N.S., 7: 449 (1861)

*R. valdepubens* Jord., Ann. Soc. Linn. Lyon, N.S., 7: 450 (1861)

*R. castellanus* Boiss. & Reuter ex Freyn in Willk. & Lange, Prodr. Fl. Hisp., 3: 932 (1880)

*R. bulbosus* subsp. *bulbifer* (Jord.) Neves, Contrib. Portug. Ranunc., 84 (1944)

*R. bulbosus* subsp. *castellanus* (Boiss. & Reuter ex Freyn) P. W. Ball & Heywood, Reprim nov. Spec. Regni veg., 66: 151 (1962)

Many of the variants of subsp. *bulbosus* have been given taxonomic status, one of the worst offenders being Jordan. The phenotypes to which he gave specific names can occur in a single locality, but to some extent they represent ecotypes. For instance, his *R. valdepubens*, a very hairy plant, is found in upland and coastal areas rather than in lowland meadows; in this latter habitat his *R. bulbifer* is more prevalent. He describes *R. bulbifer* as the most widespread species in eastern France, and indeed his description fits one of the commonest phenotypes

found throughout Europe. This name, however, has since been applied in a much narrower sense (e.g. Neves 1944, Tutin 1964), generally to rather small plants with more or less entire leaves. Such plants, of wide geographical occurrence, are mainly of subsp. *bulbosus*, but also include some intermediates between subsp. *bulbosus* and subsp. *adscendens*; in the former case the more or less entire leaves result from environmental dwarfing. *R. castellanus* was formerly used for plants occurring in the pastures of the montane regions of northern and central Spain, but also reaching sea-level in north-western Spain. These habitats are occupied by outliers of subsp. *bulbosus* or by plants which sometimes show some intergrading with subsp. *adscendens*. The distinguishing features ascribed to *R. castellanus* are short divaricate stems and basal leaves which are small, sparsely pilose or glabrescent and which have petioles with very broad sheaths. Such characters are present in plants growing in similar habitats throughout Europe.

Subsp. *ADSCENDENS* (Brot.) Neves, Contrib. Portug. Ranunc., 170 (1944)

*R. adscendens* Brot., Fl. Lusit., 2: 370 (1804)

*R. palustris* L. ex Smith in Rees, Cyclop., 29: sp. 52 (1814)

*R. pratensis* C. Presl in J. & C. Presl, Del. Prag., 9 (1822)

*R. neapolitanus* Ten., Ind. Sem. Horti Bot. Neap., 11 (1825)

*R. heucherifolius* C. Presl, Fl. Sic., 15 (1826)

*R. tommasinii* Reichenb., Herb. Norm. Fl. Germ. Exsicc., Cent. 25: nr. 2479 (1845)

*R. eriophyllus* C. Koch, Linnaea, 19: 46 (1847)

*R. broteri* Freyn in Willk. & Lange, Prod. Fl. Hisp., 3: 930 (1880)

*R. adscendens* was described by Brotero in 1804 and again in 1827. The two descriptions, based on Iberian plants, do not completely correspond, especially with regard to the indumentum. The plants Brotero described in 1827 have often been treated as a separate species, for example Freyn named it *R. broteri*. Brotero's two descriptions merely represent plants of different appearance within the great variation shown by Iberian subsp. *adscendens*. In the material examined in this present study, no geographical trends were apparent, and no taxonomic recognition of any of the variation is considered justified.

The description of *R. palustris* L. ex Smith (in Rees) is based on a specimen in the Linnaean herbarium. However Davis (1960) found that the specimen consisted of a mixture of two elements, neither identifiable with certainty, and he therefore suggested that the name should be dropped. Davis also considered *R. eriophyllus* and *R. tommasinii* in his discussion on the synonymy of *R. neapolitanus*.

*R. neapolitanus* Ten. was based on plants of subsp. *adscendens* from Italy, and it has been widely used for plants in the eastern Mediterranean, but only rarely has it been applied to plants from the Iberian peninsula. In his original description Tenore stated that *R. neapolitanus* has a terete pedicel and achenes with longish hooked beaks. This latter feature is also shown in Table 148 of his *Flora Napolitana*, although the rest of the plant agrees well enough with subsp. *adscendens*. He later pointed out these mistakes (Tenore 1842), and material collected and determined by him in the Herbarium at Florence (In uliginosis montani, FI) is indeed of subsp. *adscendens*.

Presl's description of *R. pratensis* leaves a slight degree of doubt as to the correct application of this name. Unfortunately no type specimen has been

traced. The plant generally held to be *R. pratensis* is the variant of *R. bulbosus* which occurs in the Palermo district of Sicily, but is also to be seen in southern Sardinia. The only difference between these plants and those of typical subsp. *adscendens*, which also occurs in these regions, appears to be in the form of the achenes. In plants of '*R. pratensis*' the beak of the achene is long, 0.8–1.2 mm, and curved, whereas in plants of subsp. *adscendens* the length of the beak seldom exceeds 0.6 mm and is more or less straight. Also, in '*R. pratensis*' the faces of the achenes may bear tubercles which terminate in single-celled hairs (c 40% of plants examined). The density of such tubercles is very variable, but plants with as many as 50 tubercles on one face of the achene are not uncommon. Tubercled variants in species with usually smooth fruits are found in other closely related species, e.g. *R. nemorosus* DC. and *R. macrophyllus* Desf. (Davis 1960). The '*R. pratensis*' plants therefore appear to be merely a local variant of subsp. *adscendens* not meriting taxonomic recognition. However a more detailed study, preferably including field-work, is required before their true status is understood. The variation might possibly be due to hybridisation with another species; a possible candidate is *R. macrophyllus*. This species is not well understood, but morphologically it is close to *R. bulbosus* and is at times confused with it, as the distinguishing features are difficult to see in herbarium material. Its achenes are very similar to those of '*R. pratensis*' and, in the region where '*R. pratensis*' occurs, *R. macrophyllus* reaches the eastern limits of its distribution.

The following synonyms of *R. bulbosus* refer to plants intermediate between subsp. *bulbosus* and subsp. *adscendens*.

*R. aleae* Willk., *Linnaea*, **30**: 84 (1859)

*R. occidentalis* Freyn in Willk. & Lange, *Prod. Fl. Hisp.*, **3**: 929 (1880), non Nutt. (1838)

*R. gallecicus* Freyn in Willk., *Ill. Fl. Hisp.*, **1**: 100 (1883)

*R. bulbosus* subsp. *aleae* (Willk.) Rouy & Fouc., *Fl. Fr.*, **1**: 106 (1893)

*R. bulbosus* subsp. *gallecicus* (Freyn) P. W. Ball & Heywood, *Reprium nov. Spec. Regni veg.*, **66**: 151 (1962)

Willkomm (1883 *op. cit.*, Willkomm & Lange 1880 *op. cit.*) described *R. aleae* as very variable, and the forms which he recognised cover a wide span of the array of the intermediates which occur between subsp. *bulbosus* and subsp. *adscendens*. He separated *R. gallecicus* from others in the group mainly on leaf-shape; but it is difficult to see why he considered it distinct from his *R. aleae*.

#### DISCUSSION AND CONCLUSIONS

Only two subspecies, subsp. *bulbosus* and subsp. *adscendens*, within the single species *R. bulbosus*, are recognised within Europe and no further taxonomic divisions are considered justified. The subspecies are generally so distinct morphologically that there would be little hesitation in treating them as separate species were it not for the presence in certain areas of intermediate plants. The subspecies occupy totally different ecological habitats within different geographical regions. The fact that the species is most conveniently split into two subspecies, with intermediate types of plants occupying a relatively smaller area than the 'pure' subspecies, may be purely a result of the limited occurrence of intermediate habitats.

Little evidence of the evolution of the species is available, the chromosome number and the karyotype being uniform. Although crosses between widely separated plants, of the same or differing subspecies, were found to result in a general reduction of fertility, it is insufficient to present a significant barrier to gene-flow between all members of the species. Gene-flow and the resulting merging of the subspecies appears to be checked by the limited occurrence of the habitats required by the intermediate plants.

Further investigation is required of the variation of *R. bulbosus* to be found outside Europe. Plants with well-formed corms occur in the mountains of Morocco. These are very isolated from subsp. *bulbosus* and although similar they are not morphologically identical with it.

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#### APPENDIX

##### EXAMPLES OF HERBARIUM MATERIAL OF THE TWO RECOGNISED SUBSPECIES AND OF INTERMEDIATE PLANTS

*R. bulbosus* L. subsp. *bulbosus* (Fig. 10)

Østfold: Hvaler: . . . 1 km S. of Korsham (on the road to Bølingshamn), 10. VI. 1962, K. Lye (S)

British Isles: v.c. 97 Westernness, grass verge near the Stage House Hotel, Glenfinnan, 2. IX. 1965, M. McCallum Webster (E)



FIGURE 10.

A. subsp. *bulbosus*  
(Nieder-Österreich: Wiesen  
nächst dem roten Stadl bei Liesing,  
12.V.1927, J. Vetter (W).)

B. subsp. *adscendens* (Brot.) Neves  
(Vila Vicosa: Tapada Real: Aguas  
Férreas. 4.V.1947, A. Fernandes  
et Sousa n. 1459 (S).)

Upsalia in pratis collinis freqn., VI. 1869, F. Ahlberg (CGE)  
St Georges s. Loire, M. et L., 26. IV. 1867, G. Genevier (CGE)

*R. bulbosus* subsp. *adscendens* (Brot.) Neves (Fig. 10)

Faro, V. 1889, A. Moller (COI)

Prov. Estremadura. Sa de Arrabida in silvaticis umbrosis l. Matade Vidal,  
solo calcareo 400 m.s.m., 22. IV. 1939, W. Rothmaler & A. P. Silva (S)

Austria.\* Istria. In graminosis prope 'Pola'. 2-170m.s.m., IV & V 1897, K.  
Untchj (BM, E, W)

Crete: Rochers calcaires de Malaxa, 13. VI. 1883, E. Reverchon (E, UPS)

\* now Jugoslavia

Intermediates between subsp. *bulbosus* and subsp. *adscendens*

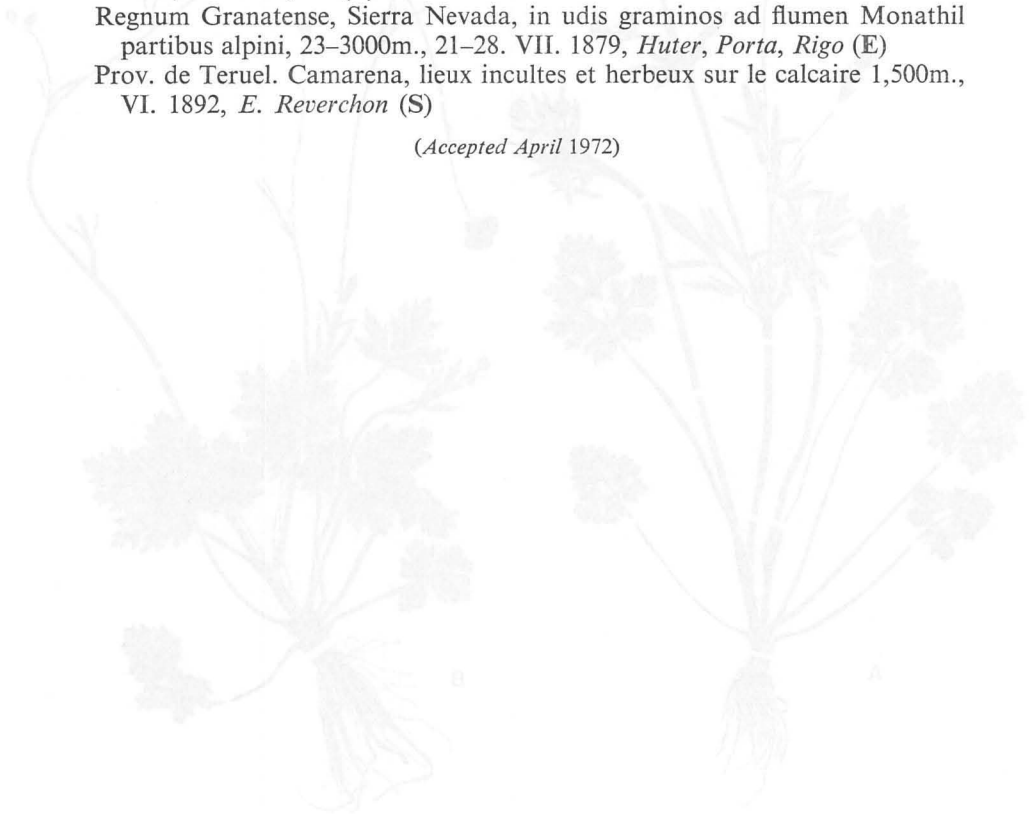
Toscana—Firenze in Gamberaia, 10. IV. 1948, *A. Contardo* (W)

Italy. Dist. Massa: Alp Apuane N.W. of Terrinca, 1000m, pasture, 26. V. 1961, *Davis* 34,315 (E)

Regnum Granatense, Sierra Nevada, in udis graminos ad flumen Monathil partibus alpini, 23–3000m., 21–28. VII. 1879, *Huter, Porta, Rigo* (E)

Prov. de Teruel. Camarena, lieux incultes et herbeux sur le calcaire 1,500m., VI. 1892, *E. Reverchon* (S)

(Accepted April 1972)



*Adiantum subsp. adscendens* (Huter) Davis  
 Firenze, Gamberaia, 10. IV. 1948, *A. Contardo* (W)  
 Dist. Massa, Alp Apuane N.W. of Terrinca, 1000m, pasture, 26. V. 1961, *Davis* 34,315 (E)  
 Sierra Nevada, in udis graminos ad flumen Monathil partibus alpini, 23–3000m., 21–28. VII. 1879, *Huter, Porta, Rigo* (E)  
 Prov. de Teruel. Camarena, lieux incultes et herbeux sur le calcaire 1,500m., VI. 1892, *E. Reverchon* (S)