

## ***Ranunculus penicillatus* (Dumort.) Bab. in Great Britain and Ireland**

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### ABSTRACT

A reinvestigation of the morphology, ecology and distribution of the varieties of *R. penicillatus* (Dumort.) Bab. in Britain and Ireland is reported and the implications for the taxonomy of the group are discussed. Evidence from field and herbarium work and cultivation experiments supports the recognition of two subspecies, subsp. *penicillatus* and subsp. *pseudofluitans* (Syme) S. Webster, **comb. nov.**, the latter comprising two varieties, var. *pseudofluitans* (Syme) S. Webster, **comb. nov.** and var. *vertumnus* C. Cook. The typification and nomenclature of the relevant taxa are outlined. A key to the taxa recognized, descriptions, and distribution maps are given.

### INTRODUCTION

*Ranunculus penicillatus* (Dumort.) Bab. comprises a group of aquatic buttercups in subgenus *Batrachium* which occur predominantly in swiftly flowing water in rivers and streams but have also been recorded from canals, ditches, lakes and pools. The *R. penicillatus* group is widespread throughout Britain and Ireland and elsewhere in Europe except in the Balkan peninsula and the extreme north (Cook 1966).

Cook (1966) suggested that *R. penicillatus* is a collection of segmental allopolyploids that have arisen from hybrids of *R. fluitans* Lam. with *R. peltatus* Schrank, *R. trichophyllus* Chaix, and possibly *R. aquatilis* L. This analysis is supported by the morphological variation exhibited by the group, which extends from plants that resemble *R. peltatus* to ones that superficially resemble *R. fluitans*, by the predominance of the hexaploid chromosome number ( $2n = 48$ ), together with sterile triploid, tetraploid and pentaploid plants (Cook 1962, 1966, 1970; Turala 1970; Turala-Szybowska 1978) and by the observed breeding behaviour of other members of subgenus *Batrachium*. Sterile hybrid plants of *R. fluitans* × *peltatus*, *R. fluitans* × *trichophyllus* and *R. aquatilis* × *trichophyllus* are known from a number of rivers in Europe where they replace their parent species, and it seems likely that plants such as these gave rise to the allopolyploids in the *R. penicillatus* group, but Cook also considered it possible that further evolution of the parent plants took place following the original hybridizations. The exact parentage of the group remains obscure.

According to the most recent monograph of the group (Cook 1966), *R. penicillatus* comprises the varieties *penicillatus*, *calcareus* (Butcher) C. Cook and *vertumnus* C. Cook. Butcher (1960) separated his *R. calcareus* from *R. pseudofluitans* (Syme) Newbould ex Baker & Foggitt on the basis of the absence of laminar leaves in *R. calcareus*. However, the type of *R. pseudofluitans* also lacks laminar leaves and is clearly the same taxon, so that *R. calcareus* is, in fact, a later name for the same species. In order to maintain a consistent nomenclature throughout the paper, this taxon is referred to as *R. penicillatus* var. *pseudofluitans* throughout. The necessary combination is made below.

Holmes (1979) considered that var. *penicillatus* and var. *pseudofluitans* merited recognition at specific rank, but that var. *vertumnus* was no more than a variant of var. *pseudofluitans* linked to

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typical material via a continuous series of intermediates. Similarly, Haslam (1978) and Haslam & Wolseley (1981) continued to recognize var. *pseudofluitans* [*R. calcareus*] at specific rank and gave no recognition to var. *vertumnus*. Haslam (pers. comm. 1980) did not consider var. *vertumnus* to be an entity with ecological relevance, whatever its genetic basis. This paper reports the results of a reinvestigation of these taxa in order to clarify their taxonomy and elucidate their ecology and distribution in Great Britain and Ireland. This investigation is based on field work, growth experiments and herbarium specimens examined in ABN, BEL, BM, CGE, DBN, DEE, E, K, LANC, LIV, LTN, LTR, NMW, OXF, RAMM, RNG and TCD. Full details of the herbarium specimens I have examined have been deposited at the Biological Records Centre, Monks Wood Experimental Station.

#### MORPHOLOGY

*R. penicillatus sensu lato* invariably possesses capillary leaves with suborbicular stipules and usually at least 100 (often over 200) segments. The flowers are normally large (petals 10–20 mm) with pyriform nectar-pits and a densely hairy receptacle.

##### VAR. *PENICILLATUS*

*R. penicillatus* var. *penicillatus* differs from vars. *pseudofluitans* and *vertumnus* in being heterophyllous (Fig. 1). In addition to the capillary leaves, which are present throughout the year, var. *penicillatus* produces laminar leaves in the summer and these leaves are normally present during the flowering period. Heterophylly in subgenus *Batrachium* has been studied experimentally in some detail (Cook 1966, 1968, 1969). The production of laminar leaves is normally controlled by an autoregulatory mechanism activated by a photoperiodic stimulus. *R. penicillatus* var. *penicillatus* is thought to show an essentially similar pattern of response to *R. aquatilis*, in which a 16-hour photoperiod under submerged conditions initiates the production of laminar leaves. However, Cook (1966, p. 66) considered it possible that some form of heteroblastic development may take place in *R. penicillatus*. That is, there might be, to some extent, a developmental sequence of the kind which is common in other heterophyllous plants. This possibility has not been investigated in the present study as it has not been possible to hold var. *penicillatus* in cultivation over long periods of time, but it is an area which requires further investigation.

The laminar leaves of var. *penicillatus* may be crenate or dentate, and frequently bear capillary appendages, the tips of the leaf-lobes being extended into fine points (Fig. 1). Var. *penicillatus* superficially resembles *R. peltatus*, which also produces laminar leaves and large flowers with pyriform nectar pits. However, in *R. penicillatus* var. *penicillatus* the capillary leaves are always flaccid and generally longer than the adjacent internodes, whereas, at least at the time of flowering, those of *R. peltatus* are normally rigid and divergent and shorter than the internodes (often less than half the length of the internodes) (Fig. 2). This character must be used with caution since the capillary leaves of *R. peltatus* show a seasonal pattern of variation, and leaves produced in mid-summer are shorter and more rigid than those produced throughout the autumn, winter and spring. Thus, although flowering shoots of *R. peltatus* bear short, rigid leaves which are shorter than the internodes, they revert after flowering to a growth form with longer, more flaccid leaves that often exceed the internodes (Fig. 3). It is also important to compare fully expanded leaves and internodes; towards the shoot apex, where the internodes are not fully elongated, the capillary leaves exceed the internodes in both species. Thus, specimens consisting only of a short terminal portion of a flowering shoot cannot be determined.

*R. penicillatus* tends to have slightly larger flowers than *R. peltatus*, with more stamens and carpels, but this character is subject to environmental modification and cannot be used as a reliable diagnostic indicator (Cook 1966). According to Dr G. Wiegleb (pers. comm. 1982) and Wiegleb & Herr (1983), *R. peltatus* and *R. penicillatus* are more difficult to separate in Germany than in the British Isles, as they show greater intergradation. There is little other published work on variation within var. *penicillatus*. Casual observations suggest that Irish plants of both *R. penicillatus* var. *penicillatus* (Fig. 1) and *R. peltatus* (Fig. 2) tend to have laminar leaves which are more truncate at the base than British plants, but this also requires further investigation.



FIGURE 1. Silhouette of *R. penicillatus* var. *penicillatus* from the River Bush at Seneirl Bridge, County Antrim, v.c. H39, in June 1986, showing capillary leaves longer than internodes, truncate laminar leaves, some lobes bearing capillary appendages (indicated by arrows), and large flowers.



FIGURE 2. Silhouette of *R. peltatus* from a mill-race in Galway City, N. E. Galway, v.c. H16, in mid-July, 1984. Late-flowering shoot showing capillary leaves shorter than internodes, truncate laminar leaves and large flowers.



FIGURE 3. Silhouette of *R. peltatus*. Vegetative shoot taken from the same plant as in Fig. 2 on the same day, showing reversion to winter growth-form with capillary leaves exceeding the internodes.



FIGURE 4. Silhouette of *R. penicillatus* var. *pseudofluitans* collected from the River Frome at East Stoke, Dorset, v. c. 9, cultivated in fast-flowing water in an artificial stream, and pressed in August 1982. Divergent morphotype, showing "untidy", divergent leaves which are shorter than the internodes.

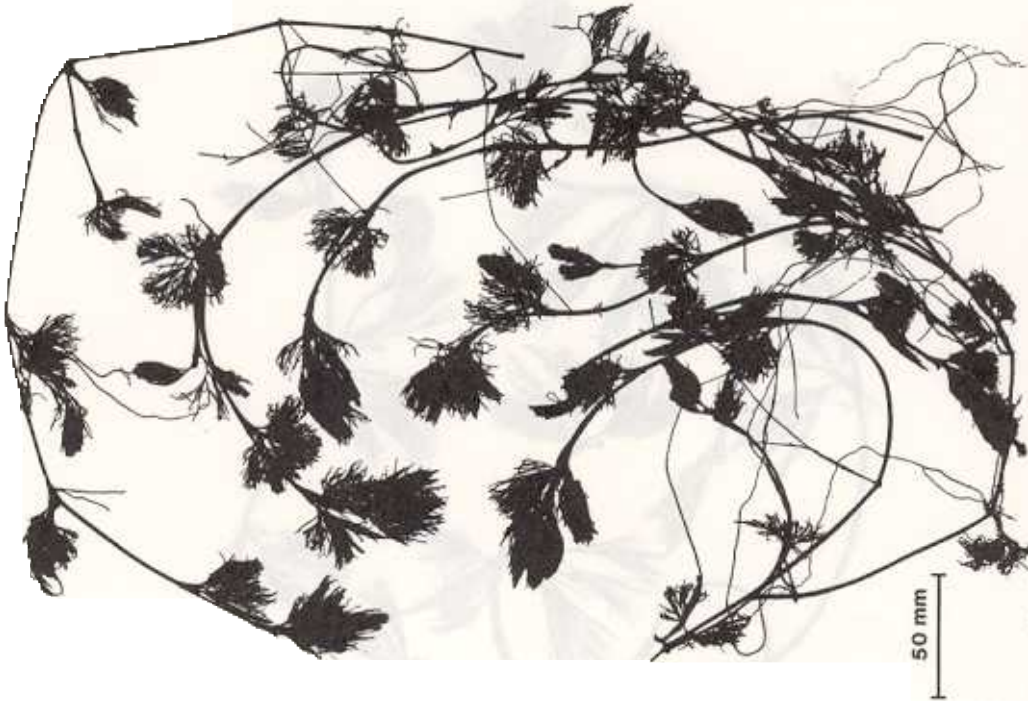


FIGURE 6. Silhouette of *R. penicillatus* var. *vertumnus* collected from the River Coin at Bibury, E. Gloucs., v.c. 33, cultivated in fast-flowing water in an artificial stream, and pressed in August, 1982. This plant shows the short, rigid globose leaves which are typical of var. *vertumnus* in the summer

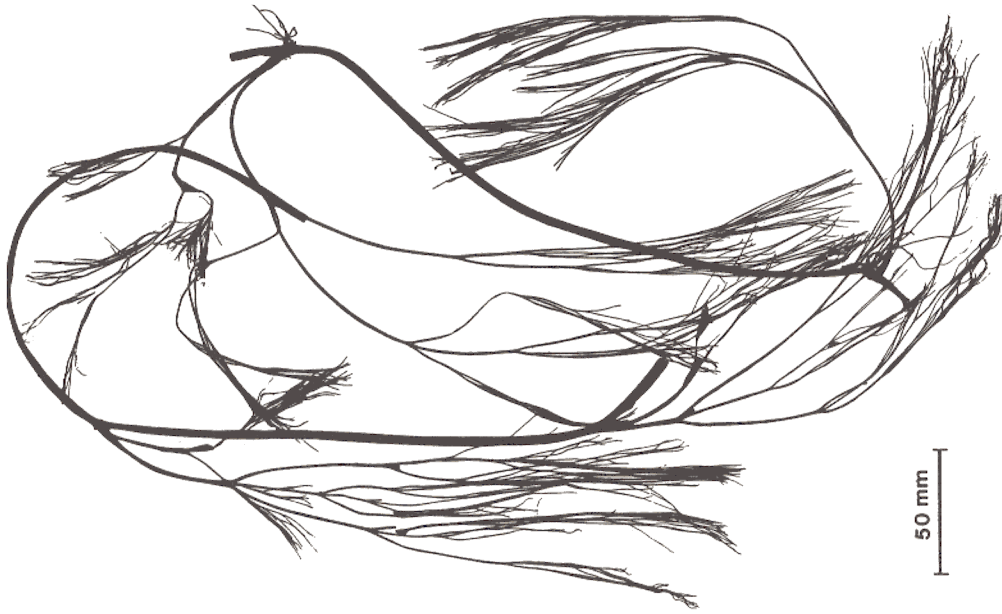


FIGURE 5. Silhouette of *R. penicillatus* var. *pseudostriatus* from the Salisbury Avon at Durrington, N. Wilts., v.c. 8. Holmes morphotype showing sparsely divided, flaccid leaves which exceed the internodes.



FIGURE 7. Silhouette of *R. penicillatus* var. *vertumnus* from the River Whitewater, Greywell, N. Hants., v.c. 12, in April 1981. This plant shows the longer, more flaccid leaves produced by var. *vertumnus* during the winter months.

**VAR. PSEUDOFUITANS AND VAR. VERTUMNUS**

Both *R. penicillatus* var. *pseudofuitans* (Figs. 4, 5) and var. *vertumnus* (Figs. 6, 7) produce only capillary leaves. Butcher (1960) included in his diagnosis of *R. calcareus* (*R. penicillatus* var. *pseudofuitans*): "only submerged leaves present, tassel-like, flaccid, ultimate segments 60–120." Cook (1966) did not refer to the negative character, the absence of laminar leaves, describing *R. penicillatus* var. *pseudofuitans* as "like var. *penicillatus* but divided leaves obconical in outline, equal to or shorter than mature internodes, segments rigid or flaccid with up to 150 ultimate segments." This description is at variance with the key (Cook 1966, p. 86) which permits the leaves to be "as long as or longer than" the internodes.

It is generally acknowledged that there is a wealth of variation within var. *pseudofuitans*. For example, Holmes (1979, 1980) has drawn attention to plants of this variety which resemble *R. fluitans* in producing very long (often up to 250 mm), sparsely divided leaves which exceed the



internodes (Fig. 5). These plants are distinguished from *R. fluitans* by their densely hairy receptacle, although this separation is difficult in some cases. In addition, the leaves in var. *pseudofluitans* normally undergo at least six levels of division, whereas in *R. fluitans* the leaves rarely undergo more than four levels of division. Other variants are described below.

The character of leaf-length compared with internode-length has caused some confusion between var. *penicillatus* and var. *pseudofluitans*. Plants of var. *pseudofluitans* have sometimes been misidentified as var. *penicillatus* on account of having leaves which are longer than the internodes. However, the presence of leaves which are longer than the internodes is only important in separating var. *penicillatus* from species such as *R. peltatus* and *R. aquatilis* and cannot be used to separate var. *penicillatus* from long-leaved plants of var. *pseudofluitans*.

There are few records of plants which are intermediate between var. *penicillatus* and var. *pseudofluitans*. This is almost certainly a result of the all-or-nothing nature of the single character which separates the two taxa. I have seen one population in the River Nanny at Duleek, Co. Meath, v.c. H22, which may be morphologically intermediate; at the time of collection, in July 1981, no fully laminar leaves were formed and only capillary and intermediate leaves were seen. Wiegleb & Herr (1983) reported plants of var. *penicillatus* growing in the rivers Lachte and Aschau in Lower Saxony, W. Germany, which only rarely form laminar leaves.

Cook (1966) reduced *R. calcareus* to the level of variety within *R. penicillatus* at the same time as describing var. *vertumnus* as a new variety. Var. *vertumnus* was described as "like *penicillatus* but lacks entire leaves; divided leaves globose to reniform, shorter than mature internodes, segments rigid, divergent, much branched with more than 200 ultimate segments" (Figs. 6, 7). However, the globose to reniform shape of the leaves of this variety is not used in his key.

Although var. *vertumnus* was described as a new variety in 1966, examination of herbarium specimens shows that this variety had been recognized more or less consistently as a distinct entity by earlier botanists. Many collections referable to this taxon have been labelled as *R. sphaerospermus* Boiss. & Blanche, but Cook (1966) considered that this name correctly applied to a smaller-carpelled species which occurs in eastern Greece, Asia Minor, Kashmir and Nepal, and from which only the diploid chromosome number ( $2n = 16$ ) has been reported. Other specimens are labelled "*R. pseudofluitans* var. *minor* Pearsall". This is a problematic name which is considered further below, but it is not an earlier synonym of var. *vertumnus*.

#### OBSERVATIONS AND MEASUREMENTS OF VAR. *PSEUDOFLUITANS* AND VAR. *VERTUMNUS*

In order to assess the reliability of different characters in separating var. *pseudofluitans* and var. *vertumnus*, and the extent to which these varieties intergrade, plants of both varieties were sampled from a large number of field sites throughout England between March and July 1981. The plants were provisionally assigned to either var. *pseudofluitans* or var. *vertumnus* using not only the key, but also the descriptions and illustrations in the monograph by Cook (1966). During this preliminary survey, both varieties were occasionally found growing side by side in a habitat, as in the River Coln at Bibury (E. Gloucs., v.c. 33). The plants at these sites were observed for three years, and remained distinct over this period, a fact which suggested that var. *vertumnus* was genetically distinct, and not merely a phenotypic state of var. *pseudofluitans*.

In addition to var. *vertumnus*, a number of distinctive variants of var. *pseudofluitans* were recorded. The term 'morphotype' was adopted for these variants since the extent to which they were genetically distinct was not known. The first of these morphotypes superficially resembled var. *vertumnus* and, according to the monograph key (Cook 1966, p. 83), conformed to this variety. These plants had leaves which were shorter than the corresponding internodes with rigid, divergent segments, often numbering more than 200, and sometimes over 300, but they differed from the description and illustration of var. *vertumnus* in having leaves which were distinctly obconical and not globose. These plants were recognized by the distinctive, untidy appearance of the leaves when the water was shaken from them, with segments that appeared to end at different lengths (Divergent morphotype; Fig. 4). Other plants had flaccid, tassel-like leaves which were longer or shorter than the internodes with from 75 to 335 ultimate segments (Flaccid morphotype). A further variant consisted of the plants described above which resemble *R. fluitans* with long, flaccid leaves and few (sometimes 70 or fewer) parallel or subparallel segments (Holmes

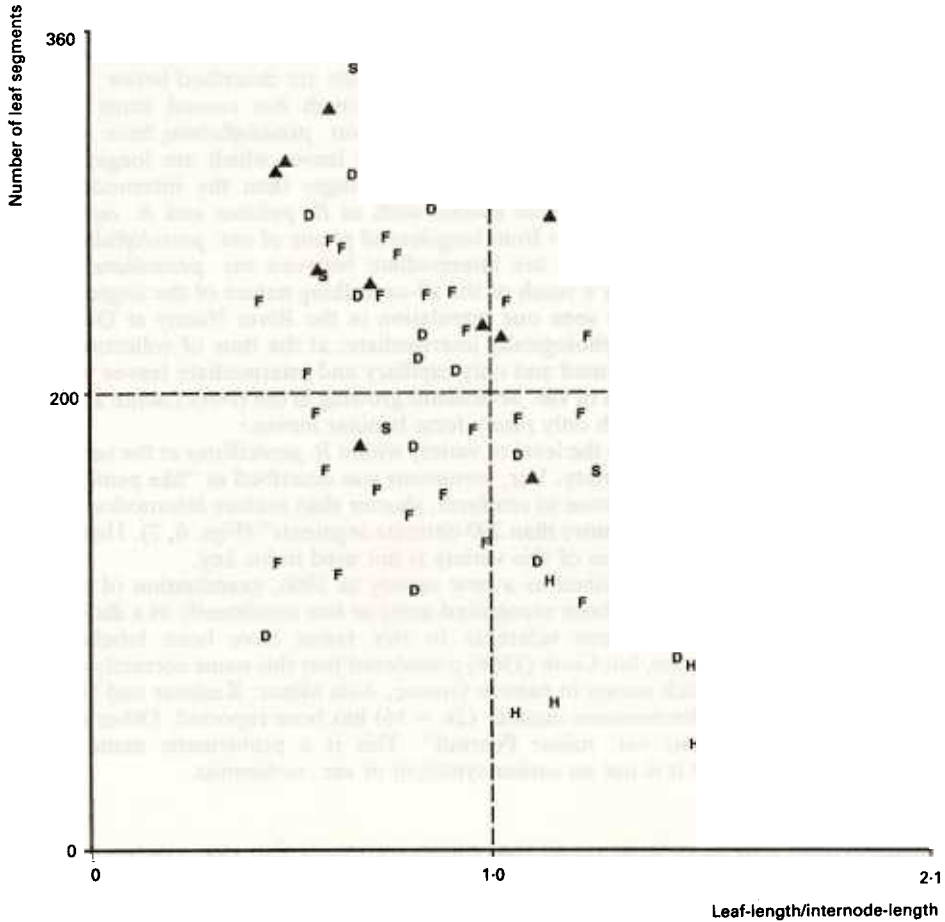


FIGURE 8. Scatter diagram of number of leaf-segments plotted against the ratio of leaf-length to internode-length in var. *vertumnus* and morphotypes of var. *pseudofluitans* (untransformed scales on both axes). ▲: var. *vertumnus*; D: var. *pseudofluitans*, Divergent morphotype; F: var. *pseudofluitans*, Flaccid morphotype; H: var. *pseudofluitans*, Holmes morphotype; S: semi-rigid plants.

morphotype). In addition, some plants had semi-rigid leaves of varying lengths with a variable number of slightly divergent segments (described as semi-rigid plants).

Leaf-length, internode-length, and number of segments per leaf were measured on four leaves on each of 63 plants comprising ten assigned to var. *vertumnus*, and 53 assigned to var. *pseudofluitans*; 13 to the Divergent morphotype of this variety, 28 to the Flaccid morphotype, eight to the Holmes morphotype and four semi-rigid plants. In order to ensure that the leaves sampled from each plant were fully expanded and comparable between plants, these measurements were made on leaves arising from the fifth to eighth internodes away from the shoot apex. The characters were plotted as scatter diagrams using three different pairs of axes. Since segment-number and the ratio of leaf-length to internode-length have been used diagnostically to separate var. *vertumnus* from var. *pseudofluitans*, the three plots used were: (i) number of segments against the ratio of leaf-length to internode-length (untransformed scale on both axes; Fig. 8), (ii) number of leaf segments against the ratio of leaf-length to internode-length (logarithmic scale on both axes; Fig. 9) and (iii) the ratio segment-number: leaf-length plotted against leaf-length (logarithmic scales on both axes; Fig. 10). The scales used were chosen to achieve the greatest degree of linearity.



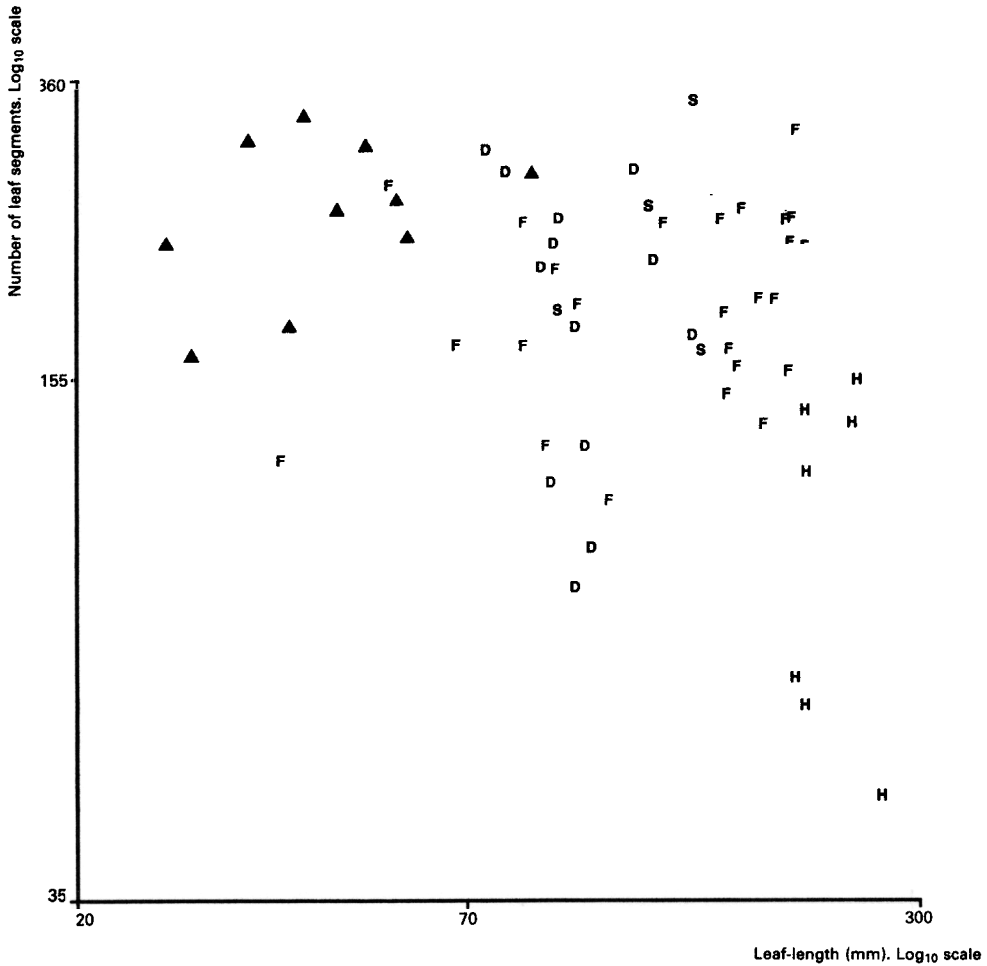


FIGURE 9. Scatter diagram of number of leaf-segments plotted against leaf-length in var. *vertumnus* and morphotypes of var. *pseudofluitans* (logarithmic scales on both axes). See Fig. 8 for explanation of symbols.

From these scatter diagrams it is clear that none of the above combinations of characters separates the two varieties or the morphotypes of var. *pseudofluitans* perfectly and there is some degree of overlap in all cases. In the first plot (Fig. 8), separation is poor mainly because of the large number of segments (up to 347) recorded in plants conforming to var. *pseudofluitans*, of both the Flaccid and Divergent morphotypes, and also because var. *vertumnus* tended to have not only shorter leaves, but also shorter internodes. It is thus not possible to make a clear separation between var. *vertumnus* and var. *pseudofluitans* using a combination of segment-number and leaf-length: internode-length ratio. In the second and third plots (Figs. 9, 10), separation of var. *vertumnus* from morphotypes of var. *pseudofluitans* is improved. In the third plot (Fig. 10), the ratio of segment-number to leaf-length provides a measure of 'frequency of branching' and when this was plotted against leaf-length, it resulted in the most linear separation of field-collected plants.

This suggests that leaf-length in itself, and the number of segments relative to leaf-length, are more important characters in separating var. *vertumnus* than the ratio of leaf-length to internode-length. In both the second and third plots, the Holmes morphotype also appears as a distinct grouping.

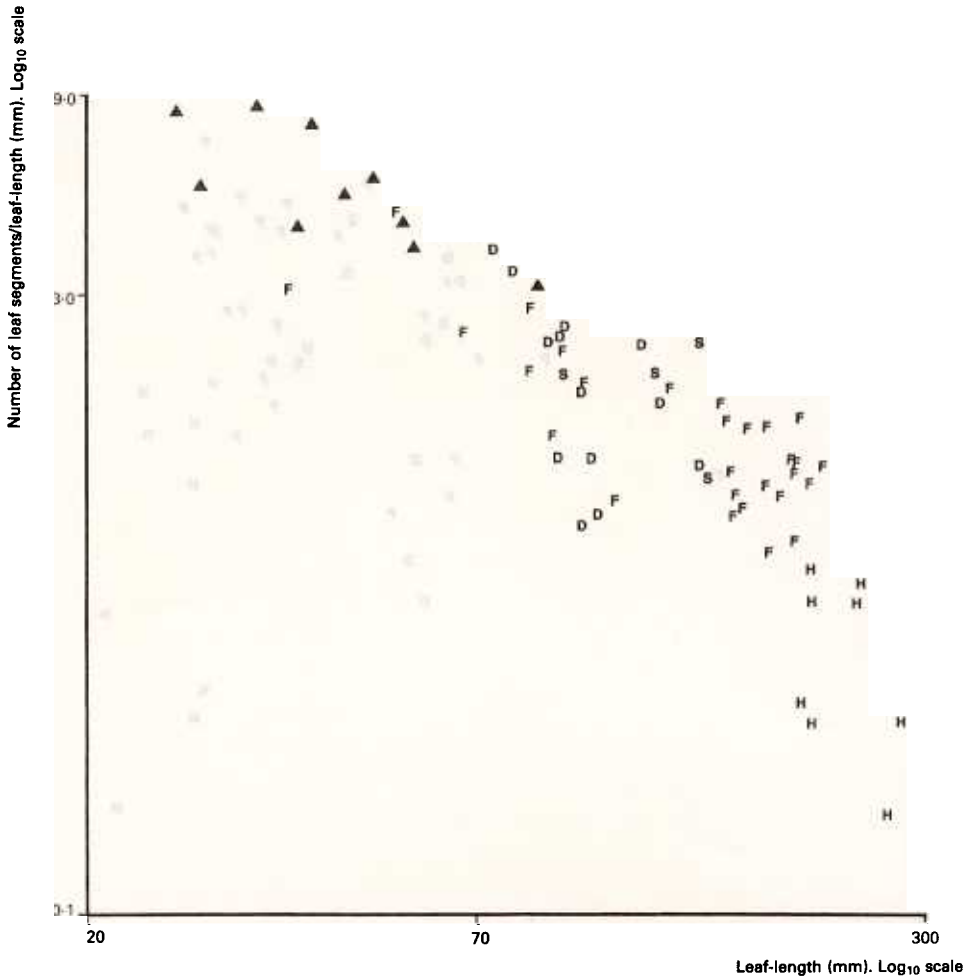


FIGURE 10. Scatter diagram of number of segments/leaf-length plotted against leaf-length (logarithmic scales on both axes). See Fig. 8 for explanation of symbols.

#### CULTIVATION EXPERIMENTS

##### METHODS

Selected plants from the preliminary survey described above were cloned and cultivated in different flow-rates and light-regimes at the Freshwater Biological Association's experimental station in Dorset, and sampled at different times of year. In this experiment the set of characters measured was extended to include petiole-length and the shape and rigidity of the leaves. Full details of the experimental design are given in Webster (1984).

##### RESULTS

The plants showed marked changes in response to different cultivation conditions and seasonal stimuli and the pattern of response was similar to that observed in the field in *R. peltatus*: shorter, more rigid leaves were produced in summer, in the absence of shade and in fast water velocities compared with those produced during the winter or in shaded or slowly flowing water. As a result

of these changes the total ranges recorded for var. *pseudofluitans* and var. *vertumnus* showed a degree of overlap in all the characters recorded. In addition, two of the cultivated clones were more or less intermediate between the two varieties and the affinities of these clones to either variety depended on their seasonal changes, which followed the same pattern of response as for the other plants.

However, because var. *pseudofluitans* and var. *vertumnus* showed the same direction of phenotypic response, there was no progressive convergence between the two varieties in cultivation, and certain statistically significant differences were maintained in spite of these changes. Thus, var. *vertumnus* retained a significantly shorter lamina, a higher ratio of leaf segments to leaf-length and a smaller ratio of leaf-length to internode-length than any morphotype of var. *pseudofluitans*, when comparing data both over different cultivation conditions and over different times of year. Var. *vertumnus* also had a significantly shorter petiole and total leaf-length (including petiole) than var. *pseudofluitans* in summer when plants grown in all cultivation conditions were compared; however, because the leaves and petioles become elongated during the winter months, these differences are not significant throughout the year. Var. *vertumnus* had the largest number of leaf-segments and the shortest internodes, when the plants were compared both over different cultivation conditions and over different times of year, but was not significantly different from the Flaccid morphotype in these characters.

Within var. *pseudofluitans*, the morphotypes described above showed greater continuity; the phenotypic changes were so great that several clones alternated between the Divergent morphotype – exhibited in swiftly flowing water in unshaded conditions during the summer months – and the Holmes morphotype – seen in shaded or slowly flowing water during the summer and in all cultivation conditions in the winter. The Flaccid morphotype had a significantly shorter lamina than the Holmes morphotype throughout different cultivation conditions and seasons, and in a constant cultivation regime it retained a shorter leaf- and petiole-length than the Holmes morphotype and a larger number of segments relative to leaf-length irrespective of seasonal changes. These were the only statistically significant differences observed between the morphotypes. The differences between the Flaccid and the Holmes morphotypes in terms of leaf- and petiole-length and the ratio of segment-number to leaf-length were over-ridden by the responses of the plants to different cultivation conditions and neither morphotype was statistically different from the Divergent morphotype. There were no significant differences between the morphotypes in terms of petiole-length, internode-length, leaf-length:internode-length ratio, or number of segments.

The relative distinctness of var. *vertumnus* compared with the morphotypes of var. *pseudofluitans* was due in part to its relative lack of phenotypic plasticity. Var. *vertumnus* showed less phenotypic plasticity in response to cultivation conditions than var. *pseudofluitans* in terms of leaf-, petiole-, lamina- and internode-length.

The globose shape of the leaves in var. *vertumnus* was retained as long as the leaves remained rigid. However, in winter and in slow water velocities and shaded conditions, the leaves became longer and flaccid, as in other plants (Fig. 7), and it became impossible to distinguish them by their shape.

When grown in shallow, still water, both var. *vertumnus* and var. *pseudofluitans* produced prostrate states, rooting at each node, which have not been reported before in these varieties. These cultivation experiments will be described in more detail in a further paper.

#### ECOLOGY AND DISTRIBUTION

##### VAR. *PENICILLATUS*

Var. *penicillatus* has a western distribution in Britain and Ireland (Fig. 11). It generally occurs in rivers over base-poor Palaeozoic and igneous rocks including granite, Tertiary basalt, Ordovician, Silurian, Devonian (Old Red Sandstone) and Upper Carboniferous series, and New Red Sandstone. In the Irish midlands, var. *penicillatus* also occurs over Carboniferous Limestone at a number of localities, including several well documented sites on the River Liffey. Var. *penicillatus* frequently forms large clones and dominates major sections of the rivers where it occurs. The rivers which this variety occupies in Great Britain are base-poor, with an alkalinity which is normally

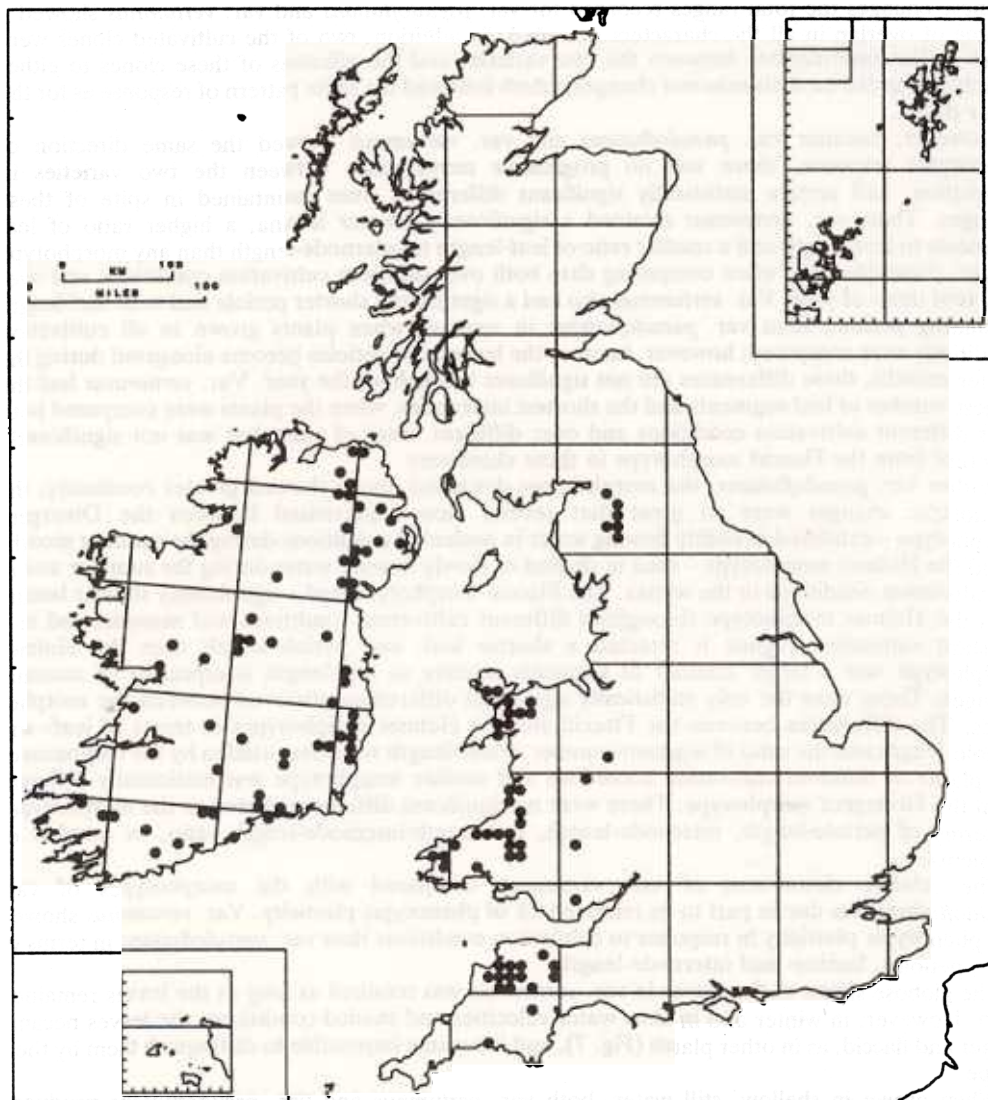


FIGURE 11. Distribution of *R. penicillatus* var. *penicillatus*. All records are based on material which has been seen by either N. T. H. Holmes or S. D. W.

within the range  $8\text{--}60\text{ mg l}^{-1}\text{ CaCO}_3$ , a pH of  $5.7\text{--}7.9$  and a low conductivity ( $30\text{--}200\ \mu\text{S cm}^{-1}$ ). It appears to be absent from base-rich rivers in Britain; reports of this variety from chalk streams in southern England (Goriup 1979) are based on misidentified var. *pseudofluitans* or *R. peltatus*. Little ecological work has been published on var. *penicillatus* in Britain, perhaps because it is rather local. Var. *penicillatus* is recorded from only 52 10-km squares in Great Britain and 57 10-km squares in Ireland. Interestingly, recent records of this variety include ones from the rivers Teign and Exe in the South West Water Authority Area, where Palmer & Newbold (1983) described var. *penicillatus* as “not recently recorded as native but may spread naturally into the area or be refound in old sites, when special protection will be necessary”, as well as in the Welsh and North West Water Authority Areas where they describe it as in need of special protection throughout the area. Newbold & Palmer (1979) considered the usual distribution of var.

*penicillatus* in relation to trophic status to be within the range oligotrophic/mesotrophic to eutrophic (0.005–0.10 mg l<sup>-1</sup> total phosphorus; 0.2–0.65 mg l<sup>-1</sup> inorganic nitrogen; alkalinity 10 to greater than 30 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH from below 6 to above 7) although it occurs only uncommonly at the more oligotrophic end of the above ranges. In his classification of British rivers according to their flora, Holmes (1983) recorded var. *penicillatus* in both his types B (meso-eutrophic plant communities associated with Sandstone and Carboniferous Limestone) and C (oligo-mesotrophic communities over resistant rocks). Var. *penicillatus* was recorded in all four groups of communities recognized within each of these types. It was absent from types A (lowland nutrient-rich communities) and D (oligotrophic upland communities).

Caffrey (1985) included var. *penicillatus* in his sensitivity grouping A (forms most sensitive to organic pollution) when considering indicators of water quality in the River Suir in Ireland. In Ireland, var. *penicillatus* appears to occur over a wider range of alkalinities than in Great Britain and is found both in extremely base-poor rivers, such as the Avonmore River (alkalinity 10–15 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 6.1–6.8) and, over Carboniferous Limestone, in more base-rich rivers such as the Liffey (120–200 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 7.8–8.2), the Deel (225–285 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 8.2–8.6), and the Inny (180–235 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 8.2–8.5).

Some 76% of field- and herbarium records of var. *penicillatus* are from rivers and 18% from streams, but it has occasionally also been recorded from loughs in Ireland, from the Grand Canal in Dublin, and from ditches in Cards., v.c. 46, and Caerns., v.c. 49, in Wales. Material from the following vice-counties has been seen by N. T. H. Holmes or S. D. W.: 2–5, 41, 42, 44, 45–47, 49, 50, 52, 69, 70, H2, H3, H5, H6, H8–13, H17, H19, H20–25, H31, H33, H34, H37–39.

#### VAR. *PSEUDOFUITANS* AND VAR. *VERTUMNUS*

Var. *pseudofluitans* is distributed throughout Great Britain, occurring over Tertiary, Mesozoic and Palaeozoic rocks (Fig. 12). Its centre of distribution is in southern England, where it occurs predominantly over Chalk, Great Oolite, London and Oxford Clays and other, mainly calcareous, deposits. Elsewhere, it occurs over Carboniferous Limestone, New and Old Red Sandstone and Silurian rocks. It becomes scarcer further north and there are rather few records from Scotland, mainly from rivers over Middle and Devonian Old Red Sandstone. Like var. *penicillatus*, var. *pseudofluitans* is frequently dominant over large stretches of river where its resistance to flow often causes backing-up and flooding, and each summer land drainage interests require the expenditure of considerable resources to remove excessive growths of this variety from rivers by biological, chemical, and mechanical means (Barrett & Murphy 1982; Dawson 1978; Dawson & Kern-Hansen 1978, 1979; Soulsby 1974; Westlake 1968; Westlake & Dawson 1982). Var. *pseudofluitans* is capable of invasion and rapid spread in rivers; this process is described by Holmes & Whitton (1977a,b) in both the River Tees and the River Wear.

Marshall & Westlake (1978) and Luther (1983) have drawn attention to the importance of macrophytes not only as weeds but as primary producers with a major role in energy input and nutrient cycling in aquatic ecosystems. On account of this dual significance, the ecology, productivity and nutrient relationships of var. *pseudofluitans* and the rivers and streams in which it occurs have received a great deal of attention (Butcher 1933; Casey & Downing 1976; Casey & Ladle 1976; Casey & Newton 1972; Casey & Westlake 1974; Dawson 1976; Edwards & Owens 1960; Holmes & Whitton 1975a, b, 1977a, b; Holmes *et al.* 1972; Ladle & Casey 1971; Owens & Edwards 1961, 1962; Raven *et al.* 1982; Westlake 1968, 1975, 1982). The large growths of this variety are capable of causing dramatic changes in the physical and chemical characteristics of rivers; Owens & Edwards (1961) described how the utilization of carbon dioxide by var. *pseudofluitans* can bring about the precipitation of calcium carbonate by raising the pH, and there have been a number of recent studies of the way in which the plants cause hydraulic roughness in waterways (Dawson & Robinson 1984; Hydraulics Research Ltd 1985). The rivers which *R. pseudofluitans* occupies are generally base-rich, with alkalinities normally within the range 100–300 mg l<sup>-1</sup> CaCO<sub>3</sub>, a pH of 7.2–8.8 and a generally high conductivity (200–1400 μS cm<sup>-1</sup>). It occasionally occurs in less base-rich rivers, notably the Tweed (alkalinity 64–145 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 7.3–8.8) and the Usk (15–96 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 7.3–8.5). Haslam & Wolseley (1981) placed *R. penicillatus* var. *pseudofluitans* in the same nutrient status band as *Veronica beccabunga*, *Apium nodiflorum*, *Berula erecta* and *Nasturtium officinale*; plants in this grouping have a preference for mesotrophic sites and, in lowland watercourses such as clay streams, they

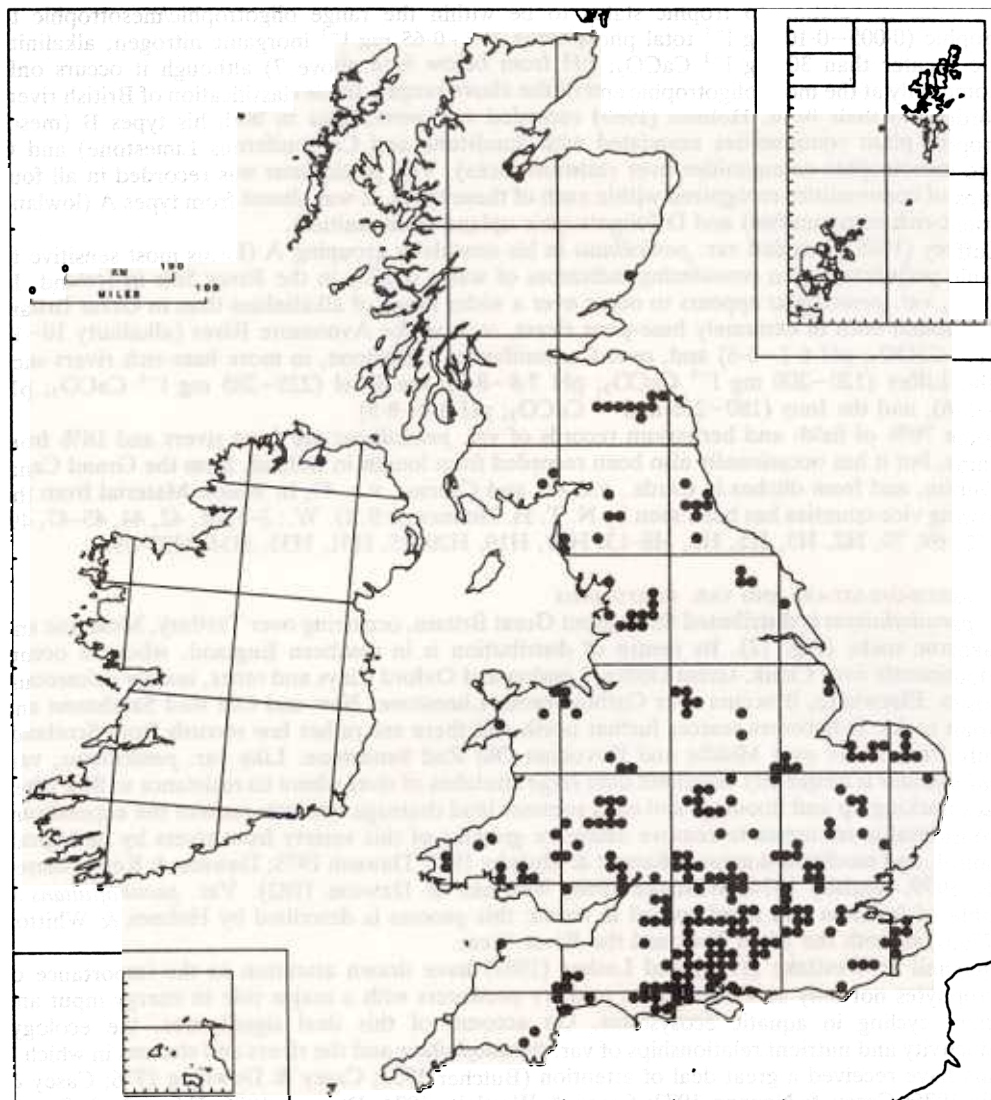


FIGURE 12. Distribution of *R. penicillatus* var. *pseudofluitans*. All records are based on material which has been seen by either N. T. H. Holmes or S.D.W.

indicate clean water, giving way to plants such as *Potamogeton perfoliatus*, *P. lucens*, *P. crispus*, *P. pectinatus*, *Myriophyllum spicatum* and *Ceratophyllum demersum* in more eutrophic stretches. Haslam (1978) considered the distribution of *Ranunculus* species in general to be correlated with the lowest nitrate (below  $1 \text{ mg l}^{-1}$ ) and phosphate (below  $0.3 \text{ mg l}^{-1}$ ) levels. Newbold & Palmer (1979) considered var. *pseudofluitans* to be distributed in waters of a trophic status from mesotrophic to eutrophic ( $0.01\text{--}0.03 \text{ mg l}^{-1}$  total phosphorus;  $0.3\text{--}0.65 \text{ mg l}^{-1}$  inorganic nitrogen; up to, or exceeding  $30 \text{ mg l}^{-1} \text{ CaCO}_3$ ; pH from  $6.0\text{--}7.0$  to above  $7.0$ ), whilst it is absent from the more oligotrophic end of the range occupied by var. *penicillatus*. This view is endorsed by Holmes (1983) who recorded var. *penicillatus* in all four groups within his types A (lowland nutrient-rich communities), from which var. *penicillatus* was absent, and B (meso-eutrophic communities associated with sandstone and Carboniferous Limestone). Var.



*RANUNCULUS PENICILLATUS* IN BRITAIN AND IRELAND

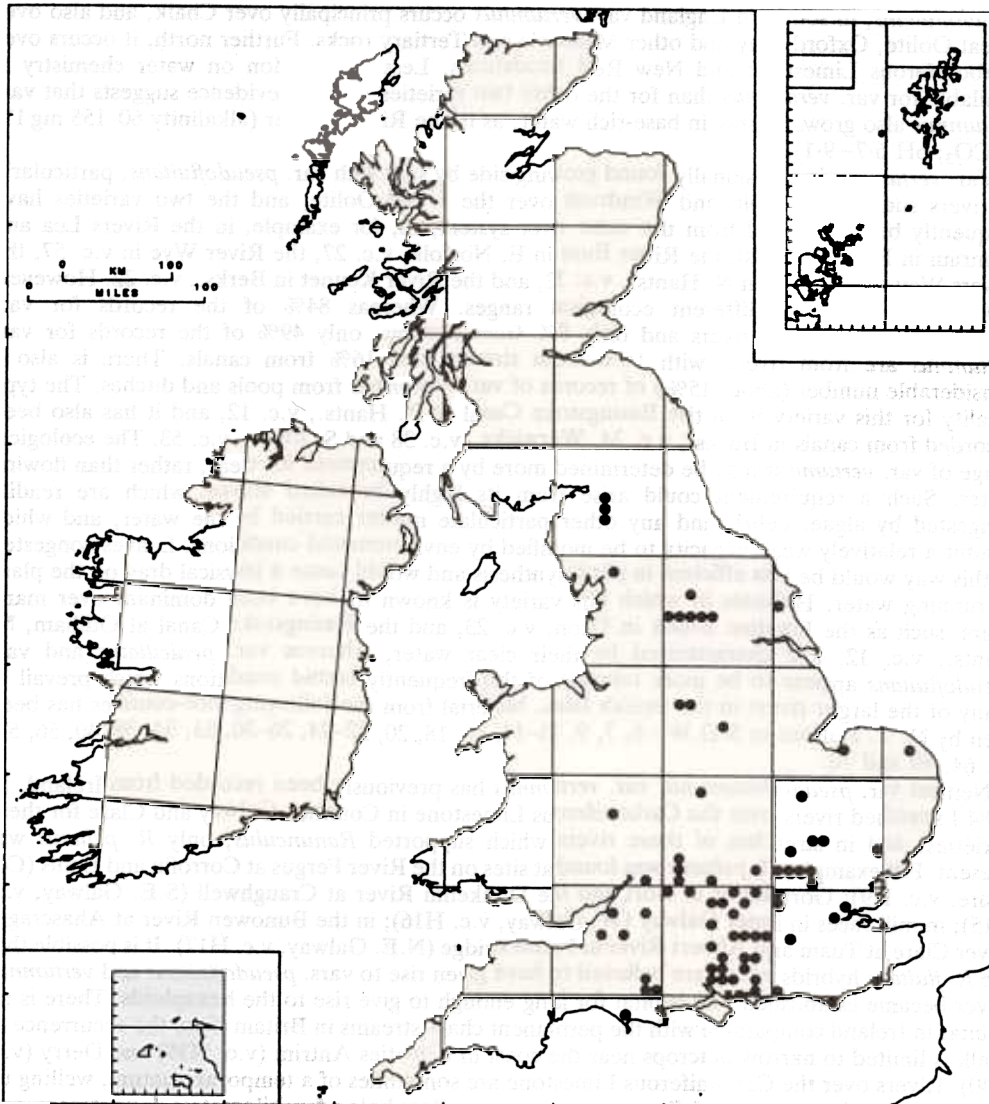


FIGURE 13. Distribution of *R. penicillatus* var. *vertumnus*. All records are based on material which has been seen by N. T. H. Holmes or S.D.W.

*pseudofluitans* was absent from both the oligo-mesotrophic communities of type C in which var. *penicillatus* occurred and type D (oligotrophic upland communities).

Var. *pseudofluitans* has been recorded from 240 10-km squares in the British Isles. Over 90% of the records used in this study were from rivers and streams. This variety has occasionally been reported from ditches, pools and lakes, and once, in 1884, from a canal. Material from the following vice-counties has been seen by N. T. H. Holmes or S.D.W.: 3, 6-9, 11, 12, 14-17, 19-30, 32-36, 38-46, 49-51, 53-57, 59-62, 64, 68, 70, 78-81, 90, 96 and 106. There is a single Irish record from H40 (see below).

Var. *vertumnus* has a similar distribution to var. *pseudofluitans*, but it is scarcer and more local throughout the distributional range and records from Scotland and Ireland are completely lacking. It has been recorded from 74 10-km squares in England and Wales (Fig. 13). Like var.

*pseudofluitans*, in southern England var. *vertumnus* occurs principally over Chalk, and also over Great Oolite, Oxford Clay and other Mesozoic and Tertiary rocks. Further north, it occurs over Carboniferous Limestone and New Red Sandstones. Less information on water chemistry is available for var. *vertumnus* than for the other two varieties, but the evidence suggests that var. *vertumnus* also grows mainly in base-rich water, as in the River Rother (alkalinity 60–155 mg l<sup>-1</sup> CaCO<sub>3</sub>; pH 6.7–9.1).

Var. *vertumnus* is occasionally found growing side by side with var. *pseudofluitans*, particularly in rivers such as the Coln and Windrush over the Great Oolite, and the two varieties have frequently been recorded from the same river system, as, for example, in the Rivers Lea and Mimram in Herts., v.c. 20, the River Bure in E. Norfolk, v.c. 27, the River Wye in v.c. 57, the Rivers Wey and Rother in N. Hants., v.c. 12, and the River Kennet in Berks., v.c. 22. However, they appear to have different ecological ranges. Whereas 84% of the records for var. *pseudofluitans* are from rivers and only 8% from streams, only 49% of the records for var. *vertumnus* are from rivers, with 16% from streams and 16% from canals. There is also a considerable number (about 15%) of records of var. *vertumnus* from pools and ditches. The type locality for this variety is on the Basingstoke Canal in N. Hants., v.c. 12, and it has also been recorded from canals in Bucks., v.c. 24, Warwicks., v.c. 38 and S. Lincs., v.c. 53. The ecological range of var. *vertumnus* may be determined more by a requirement for clear, rather than flowing water. Such a requirement could arise from its highly branched leaves, which are readily congested by algae, debris and any other particulate matter carried by the water, and which exhibit a relatively weak capacity to be modified by environmental conditions. Leaves congested in this way would be less efficient in photosynthesis and would cause a physical drag on the plant in running water. Habitats in which this variety is known to have been dominant over many years, such as the Ewelme Brook in Oxon, v.c. 23, and the Basingstoke Canal at Odiham, N. Hants., v.c. 12, are characterized by their clear water, whereas var. *penicillatus* and var. *pseudofluitans* appear to be more tolerant of the frequently turbid conditions which prevail in many of the larger rivers in the British Isles. Material from the following vice-counties has been seen by N. T. Holmes or S.D.W.: 6, 7, 9, 11–14, 16, 18, 20, 22–24, 26–30, 33, 34, 38, 40, 56, 57, 61, 64, 69 and 70.

Neither var. *pseudofluitans* nor var. *vertumnus* has previously been recorded from Ireland. In 1984 I searched rivers over the Carboniferous Limestone in Counties Galway and Clare for these varieties, and in stretches of these rivers which supported *Ranunculus*, only *R. peltatus* was present. For example, *R. peltatus* was found at sites on the River Fergus at Corrofin and Ennis (Co. Clare, v.c. H9); Gort River at Gort and the Dunkellin River at Craughwell (S.E. Galway, v.c. H15); in mill races in inner Galway (W. Galway, v.c. H16); in the Bunowen River at Ahascragh, River Clare at Tuam and Abbert River at Pallas Bridge (N.E. Galway, v.c. H17). It is possible that the *R. fluitans* hybrids which are believed to have given rise to vars. *pseudofluitans* and *vertumnus* never became established in a habitat for long enough to give rise to the hexaploids. There is no habitat in Ireland comparable with the permanent chalk streams in Britain since the occurrence of chalk is limited to narrow outcrops near the coast in Counties Antrim (v.c. H39) and Derry (v.c. H40). Rivers over the Carboniferous Limestone are sometimes of a temporary nature, welling up from the ground as springs and disappearing into a swallow-hole a few kilometres downstream, and in these habitats *R. peltatus*, which is less dependent on permanently flowing water, would be at a competitive advantage.

In June 1979 Mr P. Hackney collected specimens (BEL) from a population which apparently conforms morphologically to var. *pseudofluitans*, from the River Roe above Limavady in Co. Derry, v.c. H40. The specimens were collected when the plants were in full flower and at a time of year when var. *penicillatus* would normally be expected to form laminar leaves, but no laminar leaves were observed in the entire population. I examined this population in June 1986 and again failed to find any laminar leaves. At this point the River Roe flows over schist and gneiss and is base-poor, with an alkalinity range of 20–108 mg l<sup>-1</sup> CaCO<sub>3</sub> (average 63.1), conductivity 77–404 μS cm<sup>-1</sup> (average 190.8), and a pH range of 6.8–8.9 (average 7.64). It is a swiftly flowing river with a bouldery substrate, and the habitat is closer to that of var. *penicillatus* than to that in which var. *pseudofluitans* normally grows in Britain. The nature and origin of this population requires further investigation, but it is tempting to suggest that it has arisen as a population of var. *penicillatus* which has lost the capacity to form laminar leaves.

## DISCUSSION AND CONCLUSIONS

*R. penicillatus* var. *penicillatus* is morphologically distinct from var. *pseudofluitans* and var. *vertumnus* in producing laminar leaves in the summer. The significance of this character, which shows such dramatic phenotypic plasticity related to seasonal changes, is difficult to evaluate. The availability of this character only at certain times of year is not, I believe, a serious impediment to its use and is consistent with normal practice in flowering plant taxonomy, in which attention is often focussed on floral characters which are, in most groups, only seasonally available. The possibility that some form of heteroblastic development of laminar leaves may take place lends additional weight to this analogy.

This morphological discontinuity alone was seen by Holmes (1979) as favouring separation of var. *penicillatus* from the other two varieties at the level of species. However, there are good reasons for preferring subspecific rank. Firstly, the production of laminar leaves in var. *penicillatus* is the only morphological feature in which there is discontinuity between this variety and var. *pseudofluitans*. Although var. *penicillatus* differs from var. *pseudofluitans* and var. *vertumnus* in lacking the capacity to form short, rigid, divergent capillary leaves, var. *pseudofluitans* frequently produces capillary leaves which, in being flaccid and longer than the internodes with subparallel segments, are similar to those of var. *penicillatus*. All three varieties are similar in terms of their stipules, the size and shape of sepals and petals, nectar-pit shape, stamens, carpels and receptacle.

Secondly, evidence from *R. aquatilis*, in which the control of heterophylly has been studied in greater detail (Cook 1966, 1968, 1969), suggests that complete reliance cannot be placed on this character. Certain races of this species have apparently lost the capacity to produce laminar leaves (Cook 1968). It seems likely that *R. penicillatus* var. *penicillatus* could produce similar variants, which would be morphologically identical to var. *pseudofluitans*, and the anomalous population in the River Roe above Limavady may well have arisen in this way.

Var. *penicillatus* also has a different ecological and geographical distribution from the other two varieties, since it occurs mainly in base-poor water and has a western distribution in the British Isles, extending into Ireland, where it is widespread. There is, however, some degree of overlap between var. *penicillatus* and the other two varieties, in both ecological and geographical range; in Great Britain, var. *penicillatus* is confined to base-poor waters, but in Ireland, in the usual absence of var. *pseudofluitans* or var. *vertumnus*, it extends into more base-rich habitats. Both var. *penicillatus* and var. *pseudofluitans* have been recorded from the rivers Exe, Eden, Teifi, Afon Dwyfach and Western Cleddau, but the two varieties are rarely found growing together.

This broad ecological and geographical separation, although not complete, supports the recognition of var. *penicillatus* at subspecific rank. Plants of *R. penicillatus* are largely self-compatible and the incidence of cross-pollination is presumed to be extremely rare. Correspondingly, little weight is attached to the requirement for complete geographical isolation as a barrier to gene exchange, which has been stressed by some authors as a criterion for subspecific rank (Du Rietz 1930).

There is no clear-cut morphological, geographical or ecological discontinuity between var. *pseudofluitans* and var. *vertumnus*. Plants conforming to var. *vertumnus* exist in distinct populations which are local but widespread throughout most of southern Britain and as far north as Cumberland, v.c. 70. Cultivation experiments show that var. *vertumnus* cannot be viewed merely as representing small plants of var. *pseudofluitans* produced by growth in small streams (cf. Holmes 1979, p. 15) and it should, in my opinion, continue to be recognized as a distinct taxon. However, despite their statistical differences, the two varieties show overlapping ranges in all characters and combinations of characters investigated. This is particularly so because of the seasonal variation shown by the plants in cultivation. Some plants are intermediate between the two varieties in the field and remain so in cultivation; the affinities of these plants to either variety depend on their seasonal changes. Further, it is not always easy to distinguish the two varieties using herbarium material, since the three-dimensional nature of the plants is lost.

Var. *vertumnus* has a similar geographical distribution to var. *pseudofluitans* although it is much more local. Although the two varieties show certain ecological differences, they have frequently been recorded from the same river system, and are occasionally found growing together.

In view of the relative continuity between var. *pseudofluitans* and var. *vertumnus* in morphological, geographical and ecological characteristics, I propose to retain var. *vertumnus* at varietal rank within a second subspecies. A pragmatic advantage of this system over the current one is that plants

which are intermediate between var. *pseudofluitans* and var. *vertumnus* can at least be assigned at subspecific rank to a taxon which conveys some morphological and ecological information within *R. penicillatus*. This system also enables workers who do not wish to recognize var. *vertumnus* to assign a name at subspecific rank which is inclusive of both var. *vertumnus* and var. *pseudofluitans* without ambiguity.

Recognition of subspecies within *R. penicillatus* will also facilitate more accurate and meaningful recording of ecological, distributional and biosystematic data. The importance of critical recording below the level of species in this group is illustrated not only by the different trophic ranges of var. *penicillatus* and var. *pseudofluitans*, but also by the special nature conservation status accorded to var. *penicillatus* by Palmer & Newbold (1983), which var. *vertumnus* perhaps also deserves in Great Britain, in contrast to var. *pseudofluitans*, which is justifiably considered a weed. (To some extent this situation is reversed in Ireland, where it is var. *pseudofluitans* which is the rarity!) This applies all the more strongly since many of the current standard Floras deal only with taxa recognized at and above the level of subspecies.

#### TYPIFICATION AND NOMENCLATURE

The nomenclature of the group is beset with a number of unfortunate circumstances. *R. aquatilis* subsp. *peltatus* var. *pseudofluitans* Syme, and combinations based on this name, have previously been assumed to be synonymous with *R. penicillatus* var. *penicillatus*. This assumption is almost certainly based on Syme's description of the taxon (Syme, in Sowerby, 1863) in which he stated, ". . . floating leaves very rarely present, resembling those of var.  $\alpha$  [*vulgaris*] or  $\beta$  [*floribundus*]"'. However, I have found only three sheets in Syme's herbarium (BM) labelled "*Ranunculus peltatus, pseudofluitans*", all of which lack laminar leaves. (One sheet bears a small apical portion of a shoot with laminar leaves but this is referable to *R. aquatilis* or *R. peltatus*). I have designated one of these the lectotype, of which details are cited below. I have also examined similar material collected by Syme in CGE. *R. aquatilis* var. *pseudofluitans* is thus not synonymous with *R. penicillatus* var. *penicillatus*, but is a heterotypic synonym of Butcher's *R. calcareus*. Syme's *pseudofluitans*, in the combination *R. heterophyllus* Weber subsp. *pseudofluitans* (Syme) Moore & More, is the earliest epithet to have been applied to this taxon at subspecific rank and now applies at this rank within *R. penicillatus*.

Butcher (1960) cited the holotype of his *R. calcareus* as "Herb. Butcher, No. 21, R. Lea, Hertfordshire". The type was later cited by Cook (1966) as bearing the collection number 4, although he had not seen the specimen. I have examined material from Butcher's herbarium, which was remounted on fresh sheets after it was presented to BM, and I have been unable to find any specimen labelled by Butcher as *R. calcareus*. Only one specimen was found from the River Lea, but this did not bear the collection number 4 or the number 21. It is "*R. pseudofluitans* Baker & Foggit, type of illustration number 15 [in Butcher & Strudwick, 1930], in the River Lea, Essex Herts 6.6.1924 R. W. Butcher." In the absence of any other material, I assume that this is the holotype of *R. calcareus*. However, the specimen is inadequate and it is not possible to assign it either to var. *pseudofluitans* or to var. *vertumnus*, although it may be closer to the latter variety. *R. calcareus* (*R. penicillatus* var. *calcareus*) is therefore cited below as synonymous with subsp. *pseudofluitans*, as this is the lowest rank at which it can be determined.

As mentioned above, a large number of specimens of var. *vertumnus* are labelled "*R. pseudofluitans* var. *minor* Pearsall". These include specimens determined by W. H. Pearsall himself, and the name appears in Exchange Club Reports, e.g. Groves (1921), for specimens referable to var. *vertumnus*. The name is a problematic one, since Pearsall (1919) described *R. pseudofluitans* var. *minor* as a new combination without citing a basionym, but giving *R. pseudofluitans* Hiern *pro parte* as a synonym. In the absence of any other evidence, I have assumed that Pearsall's combination is based on Hiern's *R. hydrocharis* "form" *fluitans*\* var. *minor* (Hiern 1871, p. 104). It is not clear what Hiern meant by var. *minor* since there is no type and the only material in Hiern's herbarium in RAMM labelled var. *minor* was collected some 26 years after the

\*A. O. Chater (pers. comm., 1986) regards Hiern's "forms" as segregate species, so that this extraordinary name is not discounted as invalid on nomenclatural grounds.

publication of the name. In the absence of any material collected and annotated by Hiern before 1871, var. *minor* can only be typified by the synonym, which Hiern gives as *R. bachii* Wirtg. This is the hybrid *R. fluitans* × *trichophyllus* (Cook 1975). *R. pseudofluitans* var. *minor* is not, therefore, an earlier synonym of *R. penicillatus* var. *vertumnus*.

KEY TO SUBSPECIES AND VARIETIES OF *R. PENICILLATUS*

- 1a. Plants heterophyllous; capillary leaves produced all the year round; submerged shoots producing laminar leaves during the summer in response to long photoperiods. Capillary leaves exceeding corresponding internodes on mature stems. Leaf segments flaccid, subparallel ..... subsp. *penicillatus* var. *penicillatus*
- 1b. Plants homophyllous; only capillary leaves produced all the year round; laminar leaves never produced, even by submerged shoots in summer. Capillary leaves shorter than, equalling or exceeding corresponding internodes on mature stems. Leaf segments rigid or flaccid, divergent or subparallel ..... 2
- 2a. Leaves rigid or flaccid; segments 30–350, divergent or subparallel. Leaf-shape *obconical* whether rigid or flaccid, rigid leaves having an untidy appearance. Leaves 48–385 mm, shorter than, equalling, or exceeding corresponding internode on mature stems, and occasionally up to four times the length of the internodes. Petioles 12–148 mm long. .... subsp. *pseudofluitans* var. *pseudofluitans*
- 2b. Leaves normally rigid (semi-rigid or flaccid in winter), with divergent segments. Segments rarely less than 100, frequently exceeding 400, and occasionally over 900. Leaf-shape when rigid invariably *globose* or *reniform*, leaves becoming *obconical* only when flaccid. Leaves normally 30–70 mm, occasionally up to 132 mm in winter, usually shorter than the corresponding internodes and never exceeding twice their length. Petioles 5–15 mm, rarely exceeding 20 mm (up to 32 mm in winter) ..... subsp. *pseudofluitans* var. *vertumnus*

DESCRIPTIONS

*RANUNCULUS PENICILLATUS* (Dumort.) Bab., *Man. Br. Bot.*, 7th ed., 7 (1874).

*Batrachium penicillatum* Dumort., *Bull. Soc. Bot. Belg.*, 2: 216 (1863). *R. hydrocharis* Spenner "form" *penicillatus* (Dumort.) Hiern, *J. Bot., Lond.*, 9: 46 (1871). TYPE: specimen collected from Flandre by Scheidweiler. Without locality or date of collection, but annotated "*Batrachium penicillatum* Nob." in Dumortier's handwriting. Determined as *R. penicillatus* by C. D. K. Cook, 1968. (Holotype: BR).

Long-lived perennial, stem up to 3 m long in flowing water. Capillary leaves invariably present; laminar leaves present or absent. Stipules suborbicular to ovate, adnate to petiole for 0.75 or more of their length. Capillary leaves shorter than, equalling or exceeding corresponding internode on mature stem; petiole 5–148 mm long; lamina elongate-obconical to globose, 23–284 mm long; segments (26) 100–934, rigid or flaccid, subparallel or divergent. Peduncle in fruit 50–100 mm long. Sepals 3–7 mm long, spreading. Petals (5) 10–15 (22) mm long, broadly obovate, contiguous during anthesis; nectar-pits elongate, more or less pyriform. Stamens (8) 20–40. Carpels (15) 50–80, hairy or glabrous; style lateral to subterminal. Receptacle distinctly hairy, remaining globose in fruit.

*RANUNCULUS PENICILLATUS* subsp. *PENICILLATUS*

*R. aquatilis* subsp. *marizii* Cout., *Fl. Port.* 231 (1913).

Icones: Fig. 1 above; Cook, *Mitt. bot. StSamml., Münch.*, 6: Fig. 26, p. 157 (1966).

Laminar leaves alternate when present; petiole 50–100 mm long; lamina up to 46 mm wide and 25 mm long, reniform to suborbicular, occasionally cuneate at base, 3- or 5-lobed, lobes cuneate, sinus two thirds the length of the lamina or less. Margin of lobes entire, crenate or dentate, frequently with capillary appendages. Capillary leaves invariably flaccid, exceeding the

corresponding internode on mature stem; petiole 5–60 mm long; lamina elongate-obconical, 703–200 mm long, segments 100–150, subparallel. Peduncle in fruit usually longer than petiole of opposed laminar leaf.

*R. PENICILLATUS* subsp. *PSEUDOFLUITANS* (Syme) S. Webster, **comb. nov.**

*R. aquatilis* subsp. *peltatus* var. *pseudofluitans* Syme in Sowerby, *Engl. Bot.*, 3rd ed., 1: 20 (1863).

TYPE: "*Ranunculus peltatus, pseudofluitans*. Putney, Surrey, J. T. Syme, June 1853." (Lectotype: ex. herb. J. T. I. Boswell-Syme, **BM**, designated here.)

*R. calcareus* Butcher, *Naturalist, Hull*, 1960: 125 (1960). *R. penicillatus* var. *calcareus* (Butcher) C. Cook, *Mitt. bot. StSamml., Münch.*, 6: 158 (1966). TYPE: "In the River Lea, Essex Herts, 6.6.1924, R. W. Butcher." Labelled "*R. pseudofluitans* Baker & Foggitt, type of illus. no. 15". (Holotype: **BM**).

Laminar leaves invariably lacking.

*R. PENICILLATUS* subsp. *PSEUDOFLUITANS* var. *PSEUDOFLUITANS* (Syme) S. Webster, **comb. nov.**

*R. aquatilis* subsp. *peltatus* var. *pseudofluitans* Syme in Sowerby, *Engl. Bot.*, 3rd ed., 1: 20 (1863).

*R. pseudofluitans* Newbould ex Syme, *Engl. Bot.*, 3rd ed., 1: 20 (1863), nom. in syn. *R. pseudofluitans* (Syme) Newbould ex Baker & Foggitt, *Thirsk Nat. Hist. Soc. Bot. Exch. Club. Cur. Rep.*, 1864: 5 (1865), and *J. Bot., Lond.*, 3: 115 (1865). *R. heterophyllus* Weber subsp. *pseudofluitans* (Syme) Moore & More, *Cybele Hibernica* 5 (1866). *R. hydrocharis* Spenner "form" *pseudofluitans* (Syme) Hiern, *J. Bot., Lond.*, 9: 46 (1871). *R. aquatilis* subsp. *pseudofluitans* (Syme) Clapham in Clapham, Tutin & Warburg, *Fl. Br. Isl.* 99 (1952). *R. peltatus* subsp. *pseudofluitans* (Syme) C. Cook in Clapham, Tutin & Warburg, *Fl. Br. Isl.*, 2nd ed., 81 (1962); **comb. invalid, basion. non. cit.** TYPE: as above.

Icones: Figs. 4, 5 above; Cook, *Mitt. bot. StSamml., Münch.*, 6: Fig. 27, p. 159 (1966); Holmes, *A guide to the Batrachium Ranunculus species of Britain*. Chief Scientist's Team Notes, 14. London, Nature Conservancy Council: p. 28 (1979).

Capillary leaves shorter than, equalling or exceeding the corresponding internode on mature stem; petiole 12–148 mm long; lamina elongate-obconical, 50–284 mm long, segments occasionally as few as 26 in winter and in poor growth conditions, but normally 70–347, rigid or flaccid, subparallel or divergent.

*R. PENICILLATUS* subsp. *PSEUDOFLUITANS* var. *VERTUMNUS* C. Cook, *Mitt. bot. StSamml., Münch.*, 6: 160 (1966) (as var. of *R. penicillatus* (Dumort.) Bab.). TYPE: "In the Basingstoke Canal where it meets the River Greet, Greywell, about 8 km east of Basingstoke, Hampshire, England. C. D. K. Cook, 18 May 1958". (Holotype: **K**).

*R. sphaerospermus* auct. non Boiss. et Blanche in Boissier, *Diagn. Pl. Or. Nov.*, 3 (5): 6.

*R. pseudofluitans* var. *minor* sensu Pearsall, *Rep. bot. Soc. Exch. Club Br. Isl.*, 5: 423–441 (1919), non *R. hydrocharis* Spenner "form" *fluitans* (Lam.) Hiern var. *minor* Hiern, *J. Bot. Lond.*, 9: 104 (1871).

Icones: Figs. 6, 7 above; Cook, *Mitt. bot. StSamml., Münch.*, 6: Fig. 28, p. 161 (1966).

Capillary leaves normally shorter, and never exceeding twice the length of the corresponding internode on mature stem; petiole 5–32 mm long; lamina globose when rigid, becoming obconical when flaccid, normally 23–70 mm long, but occasionally reaching 105 mm in winter. Segments (65) 100–934, normally rigid and divergent, becoming flaccid during winter months and in shaded conditions.

#### ACKNOWLEDGMENTS

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