

Observations on *Phyteuma tenerum* R. Schulz in England

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ABSTRACT

The taxonomic relationships of English populations of *Phyteuma tenerum* are reviewed in terms of morphological, cytological, ecological and phytogeographical criteria. Morphological differences are shown to be slight but associated with distinct ecological requirements and distribution. Chromosome counts indicate that $n = 11$ in plants from two English localities. Some preliminary comments are made on the structure of the *P. orbiculare* complex as a whole.

INTRODUCTION

In 1904, the genus *Phyteuma* L. was monographed by Schulz who proposed the name *P. tenerum* to cover a major segment of the Linnaean species *P. orbiculare*, defined by the following characters: stem densely leafy; basal leaves with prominent lateral veins; involucre bracts triangular-lanceolate, acute, much shorter than the inflorescence; ovary mostly 2-locular; widely distributed in western Europe. The new species was subdivided into two geographical subspecies: subsp. *ibericum* R. Schulz (having basal leaves elliptic, crenate, obtuse; cauline leaves \pm subbracteiform; stigmas sometimes 3; occurring in N.E. Spain), and subsp. *anglicum* R. Schulz (with basal leaves lanceolate or ovate-lanceolate, serrate, acute; cauline leaves decreasing in size but distinctly foliar; stigmas mostly 2; occupying the rest of the range of the species). Unlike some other species described by Schulz in his monograph, which have been strongly criticized and dropped into synonymy (see Kunz 1940), *P. tenerum* has always been recognized as a distinct taxonomic entity. The present study was prompted by a need for a more critical understanding of that species and by an interest in the *P. orbiculare* complex as a whole. It is also hoped that the insight gained may ultimately contribute to a better taxonomic arrangement of the entire genus. The evidence reported here was obtained through study of herbarium material from the major British herbaria and during field observations conducted in several localities in the south of England in the late summer of 1969; field studies have also been carried out on central European populations of *P. orbiculare*. Chromosome counts were made on cultivated plants of known wild origin.

MORPHOLOGY

The English populations of *P. tenerum* appear fairly homogeneous and uniform in morphology. Nonetheless, there is a certain amount of variation in some characters, even those believed to be important from the taxonomic viewpoint. These characters will be briefly discussed below.

(1) The shape of the basal leaves has been widely used in the taxonomic subdivision of the genus, and Schulz (1904) made it one of the main criteria

in delimiting both species and infraspecific taxa. It is indeed characteristic of most species, but the differences are not readily apparent unless leaves of equal maturity are compared. This is technically most difficult and, with herbarium specimens, virtually impossible since the oldest leaves, which are most important for comparison, are seldom present at flowering time when the plants are usually collected and dried. The shape of the leaves gradually changes as the plant develops, and the later leaves bear little or no resemblance to the earlier ones, those present during and after flowering being the least characteristic. Superficial observation may be quite misleading. In many local populations of *P. orbiculare* the shape of the radical leaves is of paramount importance as a taxonomic guide, and *P. tenerum* is likely to follow this pattern of differentiation. Unfortunately, Schulz does not appear to have been aware of this particular seasonal variation, and the characteristics given by him in keys and descriptions should be re-examined carefully.

(2) The prominence of the nerves of the basal leaves is difficult to assess and hardly relevant taxonomically. It may depend on the condition of the plant, time of collection, the way the plants have been dried and so forth. No specific differences could be found in the available material.

(3) The leafiness of the stem varies greatly in *P. tenerum*, as it does in *P. orbiculare*. English plants often have a densely leafy stem, as required by Schulz's diagnosis, but individuals with but four leaves do occur. Also, the cauline leaves are generally shorter than is usual in *P. orbiculare*. A statistical study might perhaps reveal a significant difference, but for diagnostic purposes these characters are almost useless.

(4) The shape of the involucre bracts proved to be a truly diagnostic character in both *P. orbiculare* and *P. tenerum*. In the first they are conspicuous, often foliar, ovate to lanceolate, always distinctly acuminate (sometime even mucronate), and generally equalling or exceeding the flowers. The bracts of *P. tenerum* differ in being tiny, triangular to narrowly lanceolate, acute (not acuminate), and invariably shorter than mature flowers. In both species the bracts vary from entire to repand, and in *P. orbiculare* they are sometimes finely serrate.

(5) The number of carpels is fairly constant in most *Phyteuma* species. It is either two (e.g. *P. nigrum* F. W. Schmidt, *P. michelii* All. and *P. charmelii* Vill.) or three (*P. hemisphaericum* L., *P. globulariifolium* Sternb. & Hoppe, *P. scheuchzeri* All.), and deviations, if any, are rare. In *P. orbiculare* this variation is considerable, and the ratio of 2- and 3-locular ovaries seems to vary from one locality to another. In the English *P. tenerum* the former clearly predominate but 3-locular ovaries are far from rare.

CHROMOSOME NUMBER

In recent years, chromosome numbers have been reported for many *Phyteuma* species (e.g. Favarger 1953, Contandriopoulos 1962, Ochlewska 1965, Gadella 1966, Polatschek 1966). These studies have clearly demonstrated the existence of a dysploid series within the genus *Phyteuma*. Contrary to the situation in other genera of Campanulaceae, polyploidy does not seem to be involved, except perhaps occasionally in *P. spicatum* L. (Ochlewska 1965). In *P. orbiculare* alone, the following numbers have been found: $2n = 22$ (Ochlewska in Skalińska *et alia* 1964, Ochlewska 1965), $2n = 22 + 0-2B$ (Polatschek 1966), $2n=24$ (Mattick in Tischler 1950, Baksay 1956, Contandriopoulos 1962, Gadella 1966),

$2n = 26$ (Sugiura 1942, Baksay 1956). As far as *P. tenerum* is concerned, the extensive chromosome study by Mlle Contandriopoulos has included one count made on a collection of this species from the vicinity of Mainz ("Mayence") in West Germany. The author reports $n = 12$ for that sample and, having found the same number in *P. orbiculare*, she concludes that the series Orbiculata as a whole is characterized by $n = 12$. No cytological work seems to have been done on English material.

Considering the striking karyological diversity encountered throughout the genus, it seemed desirable to examine material of *P. tenerum* from another part of the distribution area. The counts reported here were obtained during studies of meiosis in pollen-mother-cells, flower buds being fixed in 1:3 acetic alcohol for 24 hours and stored in 70% alcohol until examined three months later. Squashes were made in lacto-propionic orceine. For convenience, fixations were made from plants grown from seed in the University Botanic Garden at Cambridge. The localities of the collections were as follows:

Easton Hill, Bishop's Cannings, North Wiltshire (v.c. 7), leg. D. E. Coombe.
By chalk pit, Erringham Downs, north of Shoreham-on-Sea, West Sussex (v.c. 13), GR 51/212.102, leg. A. Moppett, 9/1965.

In both samples a number of meiotic divisions have been studied, and in all of them invariably 11 bivalents were found. In addition, in the Easton Hill plant $2n = 22$ could be counted in somatic mitoses in the young corolla tissue.

Thus the number ascertained for English material differs from that reported by Contandriopoulos (1962). It may well be that *P. tenerum* is represented by more than one cytotype.

It should however be pointed out that, in 6 of 13 *Phyteuma* species discussed by Mlle Contandriopoulos, the chromosome numbers given in the table (p. 265) and in the legend differ from those seen in the figures, and one cannot, therefore, be quite certain whether or not the number $n = 12$, reported for *P. tenerum*, actually belongs to this species.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

P. tenerum is an Atlantic species with a well-defined area embracing, with many gaps, most of France (except for the Mediterranean region and, oddly enough, much of the Massif Central) and extending to north-eastern Spain, south-western Germany and southern England (for distribution maps see Schulz 1904 and Contandriopoulos 1962). The distribution in England has recently been mapped by Perring & Walters (1962). Its northern limit is shown as northern Wiltshire but in the Kew Herbarium there are two interesting sheets of *P. tenerum* collected by anonymous persons in 1792 and 1833, from 'Manchester' and 'Chalky banks, Broughton, near Manchester' respectively, which suggest that it might occur farther to the north. Unfortunately, there is no additional evidence to support these records; I have failed also to find a confirmation of them in any Flora, either local or general.

Throughout its range, *P. tenerum* clearly prefers calcium-rich soils. It is not surprising, therefore, to discover that in England this species is closely associated with chalk vegetation. The species is especially characteristic of the Downs, where it is locally abundant on south-facing slopes, avoiding, however, sites

dominated by tall grasses. Unlike continental populations, which are commonly found on rocks (e.g. Liger 1952), the English *P. tenerum* seems to be restricted to grassland communities. Tansley (1949) lists it (as *P. orbiculare*) among so-called exclusive species, i.e. those either confined, or nearly confined, to chalk grasslands in England. This strong ecological specialization of *P. tenerum* is very noticeable inasmuch as *P. orbiculare*, its closest relative and immediate progenitor, is largely indifferent to soil and occurs over a wide range of habitats, from lowland peat bogs to alpine rocks.

Data concerning flowering periods indicate an interesting difference between the species. Flowering begins in lowland populations of *P. orbiculare* in late May or early June and seldom exceeds two weeks but starts a month later and continues until October in populations of *P. tenerum*.

TAXONOMY

It is obvious that the evidence presented here challenges, more than it supports, the specific status of *P. tenerum*. There is a degree of morphological differentiation combined with a fairly clear geographical separation and differences in ecological preferences and flowering time, but most of the morphological characters tend to intergrade, often making a clear-cut separation quite difficult. Forms intermediate between *P. orbiculare* and *P. tenerum* have been reported from the Vosges and adjoining parts of Germany (Schulz 1904), and Kunz (1940), in a somewhat derogatory manner, describes difficulties in identifying material from an area where the ranges of both taxa overlap.

The occurrence of 11 bivalents at meiosis casts little light on the evolutionary status and taxonomic rank of *P. tenerum*. The same chromosome number occurs also in such widely different species as *P. nigrum* (Gadella 1966, Kovanda in Löve 1970) and *P. spicatum* (Ochlewska 1965, Gadella 1966, Polatschek 1966). The earlier count, $n = 12$, has been reported for, in addition to *P. orbiculare*, *P. betonicifolium* Vill. (Favarger 1953, Contandriopoulos 1962, Gadella 1966, Polatschek 1966), *P. spicatum* (Contandriopoulos 1962), *P. zahlbruckneri* Vest (Gadella 1966, Polatschek 1966) and other species.

It has long been known that variation within the *P. orbiculare* complex is enormous, yet how much is individual and how much is of taxonomic importance remains a vexing problem. Schulz (1904) tried to cope with this variation by defining, rather vaguely, six subspecies, which, however, fail to give a true picture of the diversity encountered in natural populations. Possibly *P. orbiculare sensu lato* represents a single ecospecies with more or less well-defined geographical ecotypes ranging from Spain and southern England to the Ukraine, but it seems premature to attempt any major taxonomic realignments within that complex. It is suggested, therefore, that *P. tenerum* continues to be recognized as a distinct species until comparable data are available for a representative series of races of *P. orbiculare*.

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