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SPARGANIUM IN BRITAIN

By C. D. K. Cook

Institut für systematische Botanik der Universität München

The Sparganiaceae were monographed by Graebner (1900) in *Das Pflanzenreich*. About seven years later Professor Wladislaw Rothert, formerly at the University of Odessa, started to prepare a more comprehensive monograph. Unfortunately Rothert suffered the tragic fate of so many elderly Polish and Russian scientists in the Russian Revolution and his work seems to have been lost. In 1911, however, he visited the herbaria at Kew and the British Museum and wrote notes on many of the herbarium sheets. I have used these notes as a guide to the taxonomy.

Sparganium L., *Sp. Pl.*, 971 (1753).

Glabrous aquatic (occasionally semi-terrestrial) perennial herbs, reproducing vegetatively by long, thin, underground rhizomes. Stems simple or branched. Leaves linear, distichous, sheathing at the base, erect or floating. Flowers unisexual, crowded into separate globose capitula, the female capitula towards the base in each inflorescence; perianth of 3 – 6 radiate scales; male flowers of 3 – 8 stamens, the filaments sometimes partially united; female flowers of one, occasionally two, rarely three, fused carpels with a single style persisting in fruit, and as many stigmas as carpels. Fruit drupaceous with a dry, spongy exocarp, and a hard endocarp; seed albuminous, with a large embryo. Pollination mainly by wind.

There are about fifteen species in the North Temperate regions, extending from subarctic Scandinavia and North America to the Mediterranean and Mississippi Basin; the distributional belt stretches across North America, Europe, and Asia to Japan. Two species occur in South Australia and New Zealand. *S. erectum* has been collected at 12,000ft. in Tibet. The morphology and biology of the genus are dealt with by Glück (1911, 1924), Kirchner, Loew & Schröter (1908), Muenscher (1944), and Steinbauer & Neal (1948).

Most of the species have been investigated cytologically; so far, they have all been found to have the diploid chromosome number of 2n = 30. (Wulff 1938, Hagerup 1941, Lohammer 1942, Löve & Löve 1948, 1956). In view of this uniformity, the cytology was not investigated further by the writer.

The genus was widely distributed in the Northern Hemisphere in late Tertiary times. The fossil forms are very much like the plants of to-day except in the larger number of loculi. *S. multiloculare*, described by Reid from Bembridge, showed two to five loculi,while Dr. Hartz recorded an inter-glacial form of *S. erectum* with two to four loculi. Only *S. erectum* to-day frequently shows plurilocular ovaries; the highest number seen is three.

Ascherson & Graebner, *Synopsis der mitteleuropäischen Flora* **1**, 279, (1897), proposed three sections :—

I. ERECTA : Large plants with distinctly keeled or triquetrous leaves, the floating ones (when present) keeled towards the apex. Style and stigma long, filiform.

II. NATANTIA : Floating leaves rounded or flat on the back, never keeled, the midrib usually obsolete towards the apex. Erect leaves obtusely triquetrous or keeled towards the base.

III. MINIMA : Small plants. Leaves all flat, not keeled. Stigma ovoid, often sessile.

Their section Natantia is ill-defined, and floating forms of Erecta or erect forms of Minima can easily be incorporated into it.

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Holmberg (*Bot. Notis.* (1922), 203–209) suggested that the genus be subdivided into two subgenera. He based his classification on a single perianth character :—

I. MELANOSPARGANIUM : Tepala crassiora firmiora fusco-atra.

II. XANTHOSPARGANIUM : Tepala tenuia dilute colorata.

This classification is a great improvement on that of Ascherson & Graebner, as it splits the large erect forms from the smaller floating ones. In addition to the diagnostic characters cited by Holmberg, the seed of Melanosparganium (which must now be called Sparganium) has six to ten longitudinal ridges, whereas in Xanthosparganium the seed is smooth.

Hybrids between the subgenera have not been observed by the author.

Key to British Spargania

1a. Perianth segments black-tipped; inflorescence branched, male capitula on lateral branches; seed with 6–10 longitudinal ridges : subgen. SPARGANIUM. 1. *S. erectum*

2a. Fruit with distinct shoulder, upper part dark brown to black.

3a. Fruit large, (5–) 6–8 (–10) mm. long (excluding style), (3–) 4–6 (–7) mm. wide (at shoulder); upper part of fruit flattened. subsp. *erectum*

3b. Fruit smaller, 6–7 (–8) mm. long, 2·5–4·5 mm. wide; upper part of fruit domed, wrinkled below style. subsp. *microcarpum*

2b. Fruit with indistinct shoulder, spherical to ellipsoidal, upper and lower parts uniform, shiny, light brown.

4a. Fruit ellipsoid, 7–9 mm. long, 2–3·5 mm. wide. subsp. *neglectum*

4b. Fruit ± spherical, 5–8 mm. long, 4–7 mm. wide. subsp. *oocarpum*

1b. Perianth segments translucent, not black-tipped; inflorescence unbranched, all male capitula on the main axis; seeds smooth : subgen. XANTHOSPARGANIUM.

5a. Male capitula remote, usually more than three; cauline leaves keeled but not inflated at the base, triangular in cross-section. 2. *S. emersum*

5b. Male capitula approximated, usually less than three; cauline leaves not keeled at the base, flat in cross-section.

6a. Leaf-like bract subtending lowest female capitulum 10–60 cm. long, at least twice as long as the whole inflorescence; male capitula usually two, elongated. 3. *S. angustifolium*

6b. Leaf-like bract subtending lowest female capitulum 1–5 (–8) cm. long, barely exceeding the inflorescence; male capitula usually solitary. 4. *S. minimum*

Sub-genus SPARGANIUM (Melanosparganium Holmberg, 1922). Perianth segments thick, with dark brown to black tips. Seeds with 6 – 10 longitudinal ridges.

SPARGANIUM ERECTUM L., *Sp. Pl.*, 971 (1753). *S. ramosum* Huds., *Fl. Angl.*, **2**, 401 (1778).

The following description covers all the segregates discussed later :

Plant large, erect, semi-terrestrial, (30 –) 50 – 150 (– 200) cm. tall. Leaves triangular in cross-section, usually erect (may be floating in young plants or in deep water); apex broadly rounded, truncate or apiculate. Inflorescence branched (rarely simple) with male capitula borne above the female capitula on lateral branches.

On banks of ponds and slow flowing rivers, in ditches and on ungrazed marshland.

Within *S. erectum* L. there are about five forms with distinct fruit-shapes. In Europe, Asia and North America these fruit-shapes have been recognised and given taxonomic ranks varying from species to variety.

In Britain four forms have been found, but so far only *S. neglectum* Beeby has received any attention. During the past two years a critical search for characters correlated with fruit-shape has been undertaken, but with little success. The only difference found was a slight variation in geographical range. Ecological differences have been reported, but these could not be confirmed. In fact, the opposite seemed to be the case ! Along the Trent and Mersey canal south of Derby, for example, all four forms were found growing within

a quarter of a mile of each other, and all under what appeared to be similar conditions. Despite their sympatric distribution, intermediate fruit-shapes were not found.

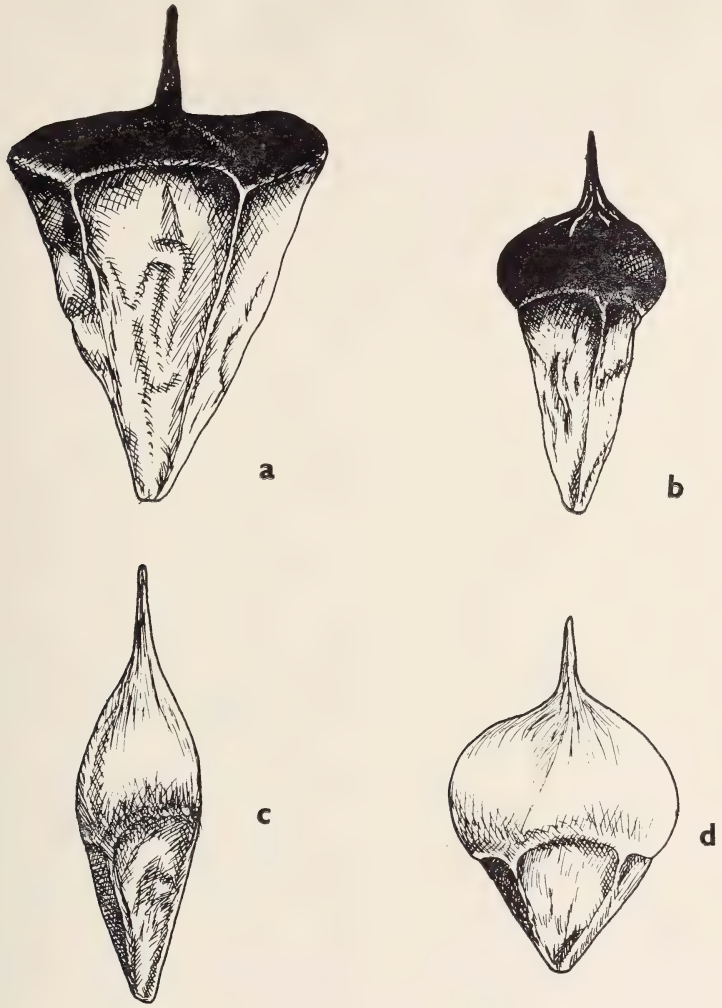


Fig. 1. Fruits of the subspecies of *Sparganium erectum* L., × c.7. (*a*) subsp. *erectum*, (*b*) subsp. *microcarpum* (Neuman) Hylander, (*c*) subsp. *neglectum* (Beeby) Schinz & Thell., (*d*) subsp. *oocarpum* (Čelak.) C. D. K. Cook.

I am adopting the classification used by Hylander (1953) in his *Nordisk Kärlväxtflora*. In this work subspecific rank is assigned to three of the forms which I have recognised as occurring in Britain; the fourth (*S. oocarpum* Čelak) is here given subspecific rank in conformity with Hylander's treatment.

S. ERECTUM L., *Sp. Pl.*, 971 (1753) subsp. ERECTUM. S. *ramosum* Huds. *emend.* Beeby, *J. Bot. Lond.*, **23**, 26, 193 (1885); *S. ramosum* subsp. *polyedrum* Asch. & Graeb., *Syn. mitteleurop. Fl.*, **1**, 283 (1897); *S. erectum* subsp. *polyedrum* Schinz & Thell., *Fl. Schweiz.* ed. 3, **2**, 14 (1914); *S. ramosum* var. *polyedrum* Holmberg, *Skan. Fl.*, **1**, 79 (1922); *S. polyedrum* Juz. in Komarov, *Fl. U.R.S.S.*, **1**, 219 (1934).

Fruit cuneate-obpyramidal, (5 –) 6 – 8 (– 10) mm. long, (3 –) 4 – 6 (– 7) mm. wide, with a distinct shoulder between upper and lower part; lower part pyramidal, (4 –) 5 – 7 (– 8) mm. long, light brown in colour; upper part flattened, dark brown to black in colour; in cross-section sharply 3 – 5-angled. Style less than 2 mm. long, persistent. Ovary usually bilocular, but occasionally uni- to trilocular (Fig. 1a).

From herbarium material and descriptions it appears that the North American *S. eurycarpum* Engelmann is the same as *S. erectum* subsp. *polyedrum* (Asch. & Graeb.) Schinz. & Thell. from Europe and Asia. If this can be established then the following should be included in the synonymy : *S. eurycarpum* Engelmann, *Gray. Man. Bot.* **5**, 48 (1864); *S. californicum* Greene, *Bull. Calif. Acad.*, **3**, 11 (1884).

South Sweden and Finland to South Mediterranean, extending eastwards to Central Siberia. In Britain occurs south of the Wash only.

S. eurycarpum in North America extends from coast to coast, the southern limit being in Florida; its northern limits are unknown.

S. ERECTUM subsp. MICROCARPUM (Neuman) Hylander, *Nordisk Kärlväxtflora*, **1**, 83 (1953). *S. ramosum* forma *microcarpum* Neuman, *Krok. Hartm. Handbk.*, **12**, 112 (1889); *S. microcarpum* Čelak., *Österr. Bot. Zeitschr.*, **66**, 281 (1896); *S. ramosum* var. *microcarpum* Asch. & Graeb., *Syn. mitteleurop. Fl.*, **1**, 281 (1897).

Type, collected from central Czechoslovakia by Neuman, ? in Prague (*n.v.*).

Fruit obpyramidal with a rounded apex, 6 – 7 (– 8) mm. long, 2·5 – 4·5 mm. wide, with a distinct shoulder between the upper and lower parts; lower part pyramidal, 4 – 6 mm. long, light brown with a slight constriction below the shoulder. The upper part domed with longitudinal ridges below the style, dark brown in colour. Below the shoulder fruit 3 – 5 angled in cross-section. Style persistent, less than 2 mm. long. Ovary usually unilocular, rarely bilocular (Fig. 1b).

Extends from the Arctic circle southwards to north Africa and east to Siberia. Occurs throughout the British Isles.

S. ERECTUM subsp. NEGLECTUM (Beeby) Schinz & Thell. *Fl. Schweiz.*, ed 3, **2**, 14 (1914). *S. neglectum* Beeby, *J. Bot. Lond.*, **23**, 26, 193 (1885); *S. ramosum* subsp. *neglectum* Neuman, *Krok. Hartm. Handbk.*, **12**, 112 (1889); *S. erectum* var. *neglectum* Fiori & Paoletti, *Fl. Anal. Ital.*, **1**, 146 (1896–98).

Type collected at Albury ponds near Guildford, Surrey; lectotype in Herb. Kew ! Isotype in Herb. Edin.!

Fruit ellipsoidal, 7–9 mm. long, 2–3·5 mm. wide, shoulder between upper and lower parts indistinct. Upper and lower parts conical, uniform light brown, shiny. Lower part 4–6 mm. long. In cross-section fruit barely angled. Style persistent, usually more than 2 mm. long. Ovary unilocular. (Fig. 1c.).

From South Sweden to North Africa, extending eastwards to the Caucasus. In Britain most common south of the Wash, but northern limit in Westmorland.

S. erectum subsp. **oocarpum** (Čelak,) *comb. nov. S. neglectum* var. *oocarpum* Čelak., *Österr. Bot. Zeitschr.*, **21**, 5 (1896); *S. oocarpum* Ostenf. & Hansen, *Bot. Tidsskr.*, **21**, 5 (1897).

Described from specimens collected from Bohemia ? now in Herb. Berlin *n.v.*,

Fruit ovoid to spherical, 5–8 mm. long, 4–7 mm. wide, uniform light brown in colour, shoulder between upper and lower parts indistinct, upper part hemispherical, lower part broadly pyramidal, 2·5–5 mm. long, almost circular in cross-section. Style persistent, usually less than 2 mm. long. Ovary unilocular, rarely bilocular (Fig. 1d).

Distribution imperfectly known in Europe; specimens have been seen from Turkey and North Africa. Not found north of the Wash in Britain.

Very poor fertility is shown in all the specimens that have been examined. This may be due to hybrid origin, although this has not been tested; on morphological grounds, the suggested parents are subsp. *erectum* and subsp. *neglectum*.

Sub-genus XANTHOSPARGANIUM Holmberg 1922. Perianth scales thin, lightly coloured. Seeds without longitudinal ridges.

SPARGANIUM EMERSUM Rehman, *Verh. Nat. Ver. Brünn*, **10**, 80 (1871). *S. erectum* L., *Sp. Pl.*, 971, *p.p.* (*saltem quoad* [*partim*?]) (1753); *emend.* Wahlenberg, *Fl. Suec.*, **2**, 582 (1826);

S. simplex Huds. *sensu* Curtis, *Fl. Lond.*, **5**, 66 (c. 1788); *S. multipedunculatum* Morong., *Bull. Torr. Bot. Club*, **15**, 79 (1888); *S. glehnii* Meinsh., *Mel. Biol. Acad. St. Petersb.*, **13**, 388–390 (1893); *S. simile* Meinsh., *loc. cit.* (1893). *S. splendens* Meinsh., *loc. cit* (1893). *S. subvaginatum* Meinsh., *loc. cit.* (1893); *S. diversifolium* var. *acaule* Fernald & Eames, *Rhodora*, **9**, 88 (1907); *S. chlorocarpum* Rydberg, *N. Amer. Fl.*, **17**, 8 (1909).

Type collected in the River Rov at Bar in the Ukraine, syntype in Herb. Kew !

Erect or floating aquatic, 20–60 cm. tall. Leaves triangular in cross-section, sheathing at the base but not inflated. Inflorescence simple, unbranched; male capitula 3–10, distinct, remote and all borne on the main axis; anthers when mature 6–8 times as long as broad; female capitula 3–6 with lower ones frequently stalked. Fruit pedunculate, ellipsoidal, frequently with a constriction around the centre; peduncle 2–3 mm. long; style persistent, 3–4 mm. long.



Fig. 2. Flowering shoots and fruiting capitula (× c. ⅔) of (*a*) ***Sparganium angustifolium*** Michx., and (*b*) *S. minimum* Wallr.

In shallow rivers and canals and by the edge of ponds and lakes, on wet mud or in water to a depth of 100 cms. Throughout North Temperate regions from the Arctic Circle south to lat. 40°N. Occurs throughout the British Isles, but not found on very high ground.

S. ANGUSTIFOLIUM Michx., *Fl. Bor. Am.*, **2**, 189 (1803). *S. natans* L., *Sp. Pl.*, 971, *p.p.* (1753); *S. simplex* Huds., *Fl. Angl.*, **2**, 401, *p.p.* (1778); *S. alpinum* D. Don ex G. Don, in Loud. *Hort. Brit.*, 375, *nomen nudum* (1830); *S. affine* Schnizlein, *Typhac.*, 27 (1845); *S. boreale* Laestadius ex Beurl, *Oefeurs. Vet. Akad. Faerhaud.*, **9**, 192 (1852); *S. vaginatum* Larsson, *Fl. Verml.*, 259 (1859); *S. borderi* Focke, *Bremen Abh.*, **5**, 409 (1877).

Described from specimens collected from Lake Mistassini in Canada. Type specimen ? at Herb. Mus. d'Hist. Nat. Paris *n.v.*

Floating (rarely erect) aquatic. Leaves flat in cross-section, sheathing and inflated at the base. Inflorescence simple, unbranched; male capitula 1–2 (–3), clustered together, appearing as an elongated capitulum on the main axis; anthers 3–4 times as long as broad; female capitula 2–4, lower capitula stalked; leaf-like bract subtending lowest female capitulum 10–60 cm. long and at least twice as long as the whole inflorescence. Fruit shortly pedunculate, ellipsoidal and light brown in colour (Fig. 2a).

In highland or northern acidic peat lochs, in water from 10 to 150 cm. deep.

An arctic-alpine species found in suitable habitats in Europe from Iceland to the Pyrenees and Alps, extending eastwards across Asia to Japan. Distribution limits for North America unknown. In Britain found in north Scotland, Pennines, north Wales and northern and western Ireland. There is also a single location near Beaulieu, Hampshire.

S. MINIMUM Wallr., *Erster Beitrag Fl. Hercyn*, **2**, 297 (1840). *S. natans* L., *Sp. Pl.*, 971, *nom. ambig.* (1753); *S. simplex* Huds., *Fl. Angl.*, **2**, 401 *nom. illegit., quoad. var.* (1778); *S. natans* var. *minimum* Hartm., *Handb. Skand. Fl.*, 43 (1820); *S. gramineum* Wallr., *loc. cit., ined. in syn.* (1840); *S. minimum* Fries, *Summa. Veg. Skand.*, **2**, 560 (1849); *Bot. Notiser*, 154 (1849); *S. rostratum* Larsson, *Fl. Verml.*, 260 (1859); *S. septentrionale* Meinsh., *Bull. Soc. Nat. Moscow, N.S.*, **3**, 174 (1889); *S. ratis* Meinsh., *loc. cit.* (1889); *S. flaccidum* Meinsh., *Mel. Biol. Acad. St. Petersb.*, **13**, 393–4 (1893); *S. perpusillum* Meinsh., *loc. cit.* (1893).

The original description was based on plants from the southern Harz Mountains in Germany. No specimens have been found in Wallroth's herbarium at Halle.

Floating (very rarely erect) aquatic. Leaves flat, usually translucent, barely inflated at the base. Inflorescence simple, unbranched; male capitula one (rarely two), if two then close together and appearing as one; female capitula (1–) 2–3, usually sessile; leaf-like bract subtending lowest female capitulum 1–5 (–8) cm. long, barely exceeding the whole inflorescence. Fruit sessile, obovoid with very short persistent style, uniform, shiny light brown in colour. (Fig. 2b).

In lochs, pools or ditches with a rich organic substratum, in 10–50 cm. of water. Temperate and arctic regions of North America, Europe and Asia. Found throughout Britain in suitable habitats.

NOMENCLATURE

The nomenclature of the British Spargania is difficult to elucidate, mainly because the earlier taxonomists chose to diagnose the species on characters that do not remain constant under all ecological conditions.

Linnaeus in his *Species Plantarum*, 971 (1753), recognised two species of *Sparganium* :

1. *S. erectum* (*foliis erectis triquetris*).
2. *S. natans* (*foliis decumbentibus planis*).

Hudson (*Flora Anglica*, ed. 2 (1778), **2**, 401) was apparently not satisfied with Linnaeus's classification, so he dropped the Linnaean species and proposed two new ones :

1. *S. ramosum* (*foliis ensiformibus triquetris, caule ramoso*).

2. *S. simplex* (*foliis ensiformibus planis, caule simplice*).

The original description of *S. erectum* L. covers the plant later described as *S. ramosum* by Hudson. *S. erectum* L. is cited by Hudson as a synonym of *S. ramosum* Huds., so that the latter is an illegitimate superfluous name.

Within his *S. simplex* Hudson described a variety β *natans* (*foliis decumbentibus planis*); as this is the same diagnosis as that of *S. natans* L., the varietal name must be based on the Linnaean species, so that the name *S. simplex* Huds. is illegitimate also.

Curtis in *Flora Londinensis* (*c.* 1788), **5**, 66, produced the earliest known full descriptions and illustrations of the two Hudson species. The Curtis description of *S. simplex* Hudson is the one accepted today; unfortunately it differs from the *S. simplex* diagnosed by Hudson. *S. simplex* Huds. was originally diagnosed as having flat leaves, while Curtis illustrated and described it with triquetrous leaves.

In the Linnaean herbarium there are three specimens of *Sparganium* : one of *S. erectum* L. and two of *S. natans* L.; of these, the specimen of *S. erectum* L. and one of the sheets of *S. natans* L. bear these names in Linnaeus' handwriting.

The specimen of *S. erectum* L. was found to be *S. simplex* Hudson *sensu* Curtis. The specimen in Clifford's herbarium based on the *Hortus Cliffortianus* (referred to in synonymy by Linnaeus) was examined in the British Museum, and was also found to be *S. simplex* Hudson *sensu* Curtis.

Linnaeus in *Species Plantarum* cited under *S. erectum* L. a variety β (*non ramosum*) with a reference to Bauhin's *Theatre*, (1620, p. 231) and *Pinax*, (1623, p. 15). Under Bauhin's list of synonyms there is a reference to *S. alternum* in L'Obel's *Historia Plantarum* (1570), 41. The illustration of *S. alternum* shows a plant that is undoubtedly *S. simplex* Hudson *sensu* Curtis.

On the other hand, under *S. erectum* (var. α), Linnaeus cites *S. ramosum* in Bauhin's *Theatre* and *Pinax*. By referring back to the illustrations in L'Obel's *Historia Plantarum*, it can be seen that var. α refers to *S. ramosum* Hudson.

It appears justifiable to assume that Linnaeus recognised the differences between the plants later described as *S. ramosum* Hudson and *S. simplex* Hudson *sensu* Curtis, but did not think them worthy of specific rank. It is quite likely that Linnaeus chose to represent only var. β in his herbarium as var. α is a large and difficult plant to mount on a small herbarium sheet.

Today it is recognised that there are two species within *S. erectum* L. From the preceding argument, *S. ramosum* Hudson should bear the name *S. erectum* L. For the plant which has been called *S. simplex* (following Curtis's misinterpretation of Hudson's name), the earliest available legitimate name must be used. This appears to be *S. emersum* Rehman, *Verh. Nat. Ver. Brünn*, **10**, 80, (1871).

The sheet of *S. natans* L. bearing this name in Linnaeus's handwriting has on it a well-preserved specimen of *S. minimum* Wallr. while the other sheet bears a poor specimen of *S. emersum* Rehman. Hylander (1945) rejected *S. natans* as a *nomen ambiguum*. This decision was fully justified and the earliest available legitimate name appears to be *S. minimum* Wallr.

In 1903 Fernald examined type material of *S. angustifolium* Michx. and declared it to be the same as *S. affine* Schnizl. Apparently this had been noticed before as Morong (1888) remarked " Engelmann has seen Michaux's specimen at Paris and it is the same as *S. affine*," but he then proceeded to drop the name *S. angustifolium* and use the later name *S. affine*. *S. angustifolium* is the earlier name and must of course be used in place of *S. affine*.

Breeding behaviour

Sparganium is strongly protogynous and in *S. erectum* the lower female capitula have frequently passed their fertile stage before the first male capitulum matures. This insures cross-fertilization for some flowers at least, but the lower capitula rarely set much seed. No self-incompatibility or agamospermous mechanisms have been found.

Many hybrids have been reported, but the only hybrids I have seen (including examination of herbarium material) are between *S. emersum* and *S. angustifolium*. These two species are fairly widely separated ecologically, the former being a species of eutrophic and the latter a species of oligotrophic waters, but they occasionally grow close together in parts of western Scotland. The hybrids appear to be fully fertile and many plants have been found that showed introgression. At Stoer in Sutherland and on the Isle of Raasay the appearance of the hybrids tends towards *S. emersum* while in Galloway introgression appears to be towards *S. angustifolium*. This allopatric introgression appears to be similar to the type found in *Typha* by Fassett & Calhoun (1952).

Evaluation of the taxonomic characters

The object of much of this study was to ascertain those characters which are of most value in separating the species. Many of the characters that have been used by previous authors have proved inconstant or readily modified by environment. The characters are annotated below and their value assessed. The key to the species is based on those characters that have proved most constant.

a. Leaf

Habit. The difference between erect and floating leaves is relative and is controlled largely by the habitat. *S. erectum* usually has erect leaves but in deep or flowing water they may be floating. *S. emersum* has erect and floating leaves, the floating leaves being found on deep-water forms and on forms exposed to wave action or water currents. *S. angustifolium* has floating leaves, but occasionally erect ones are found in very sheltered habitats. *S. minimum* is very rarely found with erect leaves.

Cross-section. *S. erectum* and *S. emersum* show a triangular cross-section. This is a good character when examining specimens in the field, but cannot easily be seen on herbarium specimens. *S. angustifolium* and *S. minimum* both have a flat cross-section. This character breaks down in *S. emersum* in the north of Scotland, possibly owing to hybridization.

Apex. In *S. erectum* the apex of the leaf has been used as a character to separate the various subspecies. Subsp. *neglectum* has been reported as having a truncate apex and subsp. *erectum* an apiculate one. These are not good characters and forms of subsp. *neglectum* have been seen with apiculate apices and forms of subsp. *erectum* with truncate apices.

Cross Veins. *S. erectum* has been described with obscure cross-veins and longitudinal veins appearing as pellucid lines without a dark border, while *S. emersum* is said to have distinct cross-veins and longitudinal veins with a dark green border. I can find no justification for these statements after examining living and dead material of both species.

Sheath. In *S. erectum* and *S. emersum* the leaf bases sheathe the stem. In *S. angustifolium* the leaf bases are inflated. This is a reliable taxonomic character for studies in the field especially when there are no flowers, but it is difficult to see in herbarium specimens. In *S. minimum* the leaf base is flat and barely sheathes the stem.

b. Stem

Colour. The base of the stem has been reported to be pink in *S. erectum* subsp. *neglectum*, but this is an unreliable character and is occasionally found in all subspecies of *S. erectum* especially when growing in stagnant water.

c. Inflorescence

Branching. The inflorescence is branched only in *S. erectum*; in all the other species it is simple.

Leaf-like bract subtending the lowest female capitulum. In *S. erectum* and *S. emersum* this bract is triangular in cross-section and about one to one-and-a-half times as long as the inflorescence. In *S. angustifolium* and *S. minimum* it is flat in cross-section. In *S.*

angustifolium it is usually between 10 and 60 cm long, the absolute length being directly proportional to the depth of water and the length of the peduncle supporting the lowest female capitulum. In *S. minimum* the bract is between 1 and 5 (–8) cm long; again, the absolute length is controlled by the habitat conditions. On this character *S. angustifolium* and *S. minimum* can easily be separated. In *S. angustifolium* the bract is usually more than twice as long as the whole inflorescence, but in *S. minimum* it barely exceeds it. The taxonomic value of this character does not appear to have been previously recognised.

d. Flower

Perianth segments. In *S. erectum* the perianth segments are thick with a black tip. In the other species they are thin with a translucent tip. This is a good character but is sometimes a little difficult to see on very old herbarium specimens. Beeby (1885) described the perianth segments of the female flowers of subspecies *neglectum* as being linear with a broad spathulate apex, while those of subspecies *erectum* were described as mostly ligulate, more membranous and scarcely or not enlarged at the apex. No distinctions can be made between these two types as intermediates appear to be more common than the extremes. In all the subspecies of *S. erectum* the perianth segments are very variable and determinations can not be made using this character.

Anther. In *S. erectum* and *S. emersum* the anthers are six to eight times as long as broad, and in *S. angustifolium* and *S. natans* they are only three to four times as long as broad. This is a good character, but it breaks down in *S. emersum* in the north of Scotland.

Carpel. In *S. erectum* the carpel is sessile and frequently plurilocular. Subsp. *erectum* usually has bilocular ovaries, whereas subspp. *microcarpum* and *oocarpum* usually have unilocular ovaries though bilocular ones are occasionally seen. *S. emersum* and *S. angustifolium* have shortly pedunculate carpels with long styles which persist in fruit. *S. minimum* has sessile carpels with short styles that do not persist in fruit; these characters are constant.

Seed. The seed has 6–10 longitudinal ridges in *S. erectum* but is smooth in the other species. This character does not appear to have been previously noted.

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GERMINATION, SEEDLINGS, AND THE FORMATION OF HAUSTORIA IN *EUPHRASIA*

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Previous Work on Germination

All the investigators quoted below on the subject of germination have found that germination is independent of the presence of roots of other plants.

Koch (1891) sowed seed of *Euphrasia officinalis* L. (an aggregate species; the species most likely to have been employed are *E. stricta* Host, and *E. rostkoviana* Hayne) in pots in the autumn, and obtained free germination the following spring. It is not stated whether the pots were in the open or not.

Wettstein (1896) described some germination experiments in his monograph on *Euphrasia*. He sowed seed in troughs in the open (in some of which seed of other plants had been sown previously, in others of which the soil was root-free) and on damp blotting paper in the windows of a room at 4–10°C. The species sown in the open were :

E. rostkoviana Mayne from three different localities
E. hirtella Jord.
E. pumila Kerner
E. salisburgensis Funck
E. minima Jacq. (two varieties).

Only *E. rostkoviana* and *E. hirtella* were sown on blotting paper. Seed of all these species, collected in 1893 and sown on 10 October 1893, germinated in March 1894, germination indoors being simultaneous with, or up to eleven days earlier than, that outdoors. Seed of *E. minima* and *E. rostkoviana*, sown under the same conditions on 25 January 1894, germinated five to twelve days later than the corresponding October sowings. Seed of *E. rostkoviana* from 1893, sown outdoors on 1 April 1894, failed to germinate; sown indoors on blotting paper on 3 April 1894, 3 seeds out of 70 germinated on 15 April 1894. Seed of *E. rostkoviana* collected in 1892 and sown on 10 October 1893 failed to germinate.

The highest percentage germination recorded by Wettstein was 70 : 42 out of 60 seeds of *E. rostkoviana* sown in October and germinating the following year (Wettstein, 1897).

Wettstein concluded that the time of germination was independent of the time of sowing; and that, if seed does not germinate during the spring following its formation, it loses its viability about the time when it would normally be germinating. He later stated, however, (1898) that the pots in which no germination had taken place were left only until the following October.

However, Heinricher (1898a) demonstrated a different state of affairs in regard to germination time. Using *E. stricta* seed of the 1895 crop sown in pots in 1896 on 27 February, 28 March, 16 April, 22 May and 23 June, he showed that the two earliest sowings gave quite good germination in March and April respectively, the next two poor germination in May and June respectively, and the last gave no germination in 1896 but good germination at the beginning of March 1897. In addition, a thick sowing of 1894 seed on 27 February 1896 gave 1 seedling in March 1896, and a sowing of 1895 seed on 24 January 1897 gave 36 seedlings by 3 March 1897. He thus demonstrated a restriction of germination to the spring, and the retention of viability into the second spring after seed-formation, if germination cannot take place in the first. It was not stated where the pots were kept.

Other results for *E. stricta* (Heinricher, 1898a) give some precise times for germination; thus, of some seed sown in a pot in a warm house on 21 January 1897, 1 seedling germinated

14 days later; sowings in pots on 27 February 1896 had started germinating 19 days later; of many seeds sown in a pot on 28 March 1896, 4 had germinated after 19 days, 20 after 35 days, and 36 after 48 days. Further results showed that seed of *E. rostkoviana* can, like that of *E. stricta*, germinate in the second spring after its formation.

E. salisburgensis and *E. minima*, sown in open ground in late October or in November, had germinated by 15 April 1897. A pot of *E. minima* seed, sown at the same time and kept in the window of the Botanical Institute, Innsbruck, had produced 2 seedlings by 21 February, and 27 by 7 April 1897 (Heinricher, 1898b).

In Heinricher's experiments the time between sowing and germination was two to four weeks, unless the sowing took place in the autumn or early winter, in which case germination was delayed until February or March; germination was confined to the period February to June.

Nichols (1934) included *E. americana* Wettst. (= *E. brevipila* Burn. & Gremli*) in an investigation of the conditions required for germination of a number of American plants. He found that seeds of this species, collected from the coast of Maine, would not germinate when kept in a greenhouse, but those exposed to winter conditions for 71 days germinated 14 to 21 days after being brought into the greenhouse.

Neidhardt (1947) sowed seed of *E. rostkoviana* (collected in the years 1934 and 1936–38) in the winter of 1938–39, and in the spring of 1939. Samples of 100 seeds were sown on damp blotting paper in petri-dishes. They were subjected to various conditions of light and temperature. Indoor temperatures up to 30°C and outdoor temperatures ranging from − 5°C to + 5°C were used. Varying alternations of high and low temperatures were employed also. Only the seed of the 1938 crop germinated, and about 20% germinated in all samples except in one that was kept at a constant temperature of 30°C, in which 10% germinated. A test using one seed per dish gave germination at the same time as the others.

Germination was said to take five to seven days; this is very quick, but germination would be visible sooner in seeds on blotting paper than in seeds in the soil; however, it seems extraordinarily quick for the sample outdoors in temperatures ranging from − 5°C to + 5°C, and may in fact have referred to germination times obtained only at the higher of the temperatures used.

Seed samples sown for cultivation in March, with 1, 2, 5, or 100 seeds per pot of soil, germinated in 15–20 days, with percentages up to 40.

It will be noted that Neidhardt failed to get seed to germinate except in the season after it was formed.

Some of my own observations on germination in *Euphrasia* now follow.

Loss of Viability in Storage

Seed removed from herbarium specimens of *Euphrasia* collected in 1951 and sown in the winter of 1951–2 showed very poor germination, and I attributed this to desiccation in storage. Ten seeds of each of eight different samples were sown on damp filter-paper on 22 November and kept in the laboratory; only one seed germinated, on 25 February 1952. Some of the seeds were attacked by mould, but a number were still unaffected on 2 April. Samples of from 50 to 150 seeds, representing several species, were sown on 1 April. About half were kept in the greenhouse, and the rest outside. No germination could be detected on 22 April or 6 May 1952. Seeds of a sample of *E. pseudokerneri* Pugsl. were sown on three separate dates and their germination gives evidence of declining viability : seed was sown in each of ten pots on 6 November and germination took place in January, February and March, 59 seedlings appearing altogether; 90 seeds were sown on 19 February in sand, and placed under fluorescent lighting in a laboratory; one seedling appeared on 20 March and no more had germinated by 22 April; a third sowing, of 81

*P. D. Sell and P. F. Yeo, unpublished.

seeds, on 1 April, had produced no seedlings by 6 May, the pot having been kept in a cold frame. All these seeds had been stored in paper envelopes in a very well heated laboratory.

All seed collected in 1952 was extracted from the plants as soon as possible and kept in a refrigerator at about 8°C in plastic bags sealed with cellulose tape, and this resulted in much better germination. In later years storage in a refrigerator was not possible, but an effort was made to keep the seeds out of very warm places in the summer and well heated rooms in winter, and at least some seeds have germinated in the majority of samples sown.

The approximate time of ripening is known for some seeds produced by artificial self- and cross-pollination; those ripening earlier spend longer in storage, and Table 1 shows a great decline in viability in storage in 1957 and a small one in 1958. The germination figures are the combined totals for the two years after seed production.

TABLE 1

Germination of seeds collected at different times

Date collected	*No. sown*	*Percentage germination*	*Proportion of samples showing germination*
1957	(sown 6 Dec. 1957)		
Late July, early August	251	1·2	2 out of 7
Mainly September	82	15·0	4 out of 4
Mainly October	208	26·9	6 out of 7
1958	(sown 16 Dec. 1958)		
Late August, September	550	9·3	9 out of 14
Mainly October	416	12·0	9 out of 9

In January 1955 two samples of 1952 seed and one of 1953 seed were sown; there was no germination in 1955.

PERIOD OF GERMINATION

The following history of the seeds of *E. pseudokerneri* already mentioned (collected at Holywell Mound, S. Lincs.) gives some indication of the germination behaviour.

Group A (2 *pots*)		*Group B* (8 *pots*)	
11 Oct. 1951 :	Seed collected	11 Oct. 1951 :	Seed collected
6 Nov. 1951 :	Seed sown in pots and placed in greenhouse	6 Nov. 1951 :	Seed sown in pots and placed in greenhouse
		26 Nov. 1951 :	Pots put out of doors
28 Jan. 1952 :	1 seedling appeared		
1–14 Feb. 1952 :	9 seedlings appeared	4–12 Feb. 1952 :	Pots brought into greenhouse
		15–29 Feb. 1952 :	32 seedlings appeared
		1–14 Mar. 1952 :	17 seedlings appeared

After three weeks in the greenhouse it appeared that the seeds were unable to germinate, and eight of the pots were therefore put outside in the expectation that frost might break the dormancy. In fact, dormancy ended in the pots in the greenhouse twelve weeks after sowing. (The seeds were probably exposed to frosts before being collected on 11 October, as there were ground frosts of 29°F, 29°F, and 26°F on 9, 10 and 11 October respectively at Cottesmore, 4 miles to the south-west). I then guessed that the seeds outside would also have become germinable and were now being retarded only by the low temperature outside; I therefore brought them into the greenhouse, and my supposition was con-

firmed, for seedlings began appearing after ten days, and the last had appeared at the end of 28 days. The same effect can be seen in the figures in Tables 2 and 4 (p. 16).

TABLE 2

Germination in 1954 of seed of *E. occidentalis* Wettst., collected at Perranporth, 1953
(25 seeds were sown in each pot on 9 November 1953)

	No. of seedlings produced	
	Pot indoors	*Pot outdoors*
21 January	1	2
11 February	2	2
15 February	6	2 (brought indoors)
18 February	14	2
22 February	19	5
25 February	20	11
1 March	20	17
4 March	20	19

A great many samples of *Euphrasia* seeds have been sown in the course of my work on the genus, the majority in the November or December after they had ripened. In these, germination in the open has taken place from January to April, the peak of germination being in March at Leicester in 1953, and in March or April according to season at Cambridge in 1954–60. In my garden at Cambridge the first seedlings of *E. pseudokerneri* have appeared at the end of January in 1959 and 1960. In nature I have found seedlings of *E. anglica* Pugsl. in Charnwood Forest, Leicestershire, on 28 February, 1953, and of *E. pseudokerneri* at Box Hill, Surrey, in March, 1953. If sowing takes place later than December, germination is likely to start late and continue until a later date. Thus, some samples sown on 17 February 1954 began to germinate in late March or early April, and continued germinating until late April or, in one case, mid-May. The latest sowing to have produced seedlings the same year was made on 14 April 1955 (*E. rostkoviana* from Friuli, Italy); two seedlings came up in the latter half of May. An exceptional case was that of a sample of seed of *E. stricta* (from Poland), sown on 15 March 1956. The beginning of germination was overlooked, and on 26 September the pot contained, in addition to a plant of *Trifolium repens* L. and three plants of *Euphrasia* with ripe seed, three apparently newly-germinated seedlings of *Euphrasia*.

On 28 May 1952, 63 seeds of *E. pseudokerneri*, collected in the greenhouse in the preceding fortnight (an unusual time of year for seed-setting), were sown and kept in the greenhouse for the rest of the summer, but there was no germination.

Exposure to Winter Cold after Sowing

Of the samples of wild-collected seed sown in December 1952, the total number sown inside was 23, of which germination occurred in 12; a total of 52 samples was sown outside and germination occurred in 47.

Some counted samples of seeds produced in 1952 by enforced self-pollination were sown in pots on 20 December 1952 and kept in the heated greenhouse. In one sample (of *E. occidentalis*) germination took place the following spring. In the rest there was no germination, but the pots were kept in the open from May 1953 until February 1954, when they were brought into a cool greenhouse, and the layer of moss on the surface of the pots was broken up. The germination is shown in Table 3. Seeds produced by artificial hybridisation in 1952 were treated in the same way; these seeds produced four seedlings in 1953 and about 68 in 1954. In one pot, two seedlings appeared in 1953 and three more in 1954.

Table 3
Germination of 1952 seed in 1954

Euphrasia *species*	*No. of seeds sown*	*No. of seeds germinating*
nemorosa	40	5
pseudokerneri	35	28
pseudokerneri	13	1
anglica	55	6

It appears from these observations that it is better, for practical purposes, to put seed out of doors in the winter for germination.

I have, however, recorded a few instances of good germination of seeds kept in a heated greenhouse from the time of sowing. Thus the sample of seed produced by self-pollination from *E. occidentalis* from Barton-on-Sea, S. Hants, v.c. 11, treated in the same way as the samples in Table 3, yielded 15 seedlings from 47 seeds in 1953 (the pot was not kept until 1954); and a large sample of seed of an atypical form of *E. nemorosa* (Pers.) H. Mart. from Roborough Down, S. Devon, v.c. 3, collected in 1952, germinated profusely, without exposure to winter cold, in February and March 1953.

Germination in second and later Springs after Sowing

In the preceding section examples were given in which germination was completely postponed until the second spring after the seed was sown; in addition one example was mentioned in which germination took place in both the first and the second spring after sowing. Both kinds of behaviour are recorded in Table 4 (p. 16). Seed pots of all the sowings made in the winter of 1957–1958 were kept and three samples showed total postponement of germination until 1959; they were sown respectively in December 1957 (only one seed germinated), February 1958, and March 1958.

Germination in both first and second springs after sowing has occurred in a number of samples sown late (January to April), but it also occurs in early-sown samples, for six of the eight samples sown on 6 December 1957 produced seedlings in 1958 and 1959, and in 1960 germination has taken place in six samples which produced seedlings in 1959 after sowing in December 1958.

I have also recorded germination in the third and fourth springs after sowing. Thus a large sample of seed of *E. nemorosa* was sown on 17 February 1954, and probably about 90 seeds germinated the same year, about 200 in 1955, and one in 1956. A sample of seed of *E. micrantha* Reichb., from a population that had been maintained in cultivation since 1953, was sown on 14 December 1956 and produced 28 seedlings in 1957, 9 in 1958, 14 in 1959 and 2 in 1960. A sample of *E. nemorosa*, sown 6 December 1957, gave 29 seedlings in 1958, 5 in 1959, and 2 in 1960, and a sample of *E. brevipila*, sown 19 March 1958, germinated first in 1959 to produce 21 seedlings, and had produced 2 more by 17 March 1960.

A Germination Trial

This trial was intended to compare the germination of seed samples sown at different dates, and of samples kept in the greenhouse from the time of sowing, or put in cold frames for varying periods before being brought into the greenhouse, or kept throughout in cold frames. Owing to a failure of heating in the greenhouse, all samples were exposed to freezing temperatures for a few days, and so no comparison was possible between samples exposed to cold and samples never chilled. Some of the pots were kept for a second year, having been kept out of doors during the second winter.

The results for *E. nemorosa* are shown in Table 4. This table shows the occurrence of high percentages of germination, an apparent decline in viability in storage, an apparent decline in viability with time spent out of doors in the first winter (for which I cannot suggest an explanation), a delay in germination in pots still out of doors when germination is beginning inside, germination in two successive years, and postponement of germination in

Table 4
Seed germination of *Euphrasia nemorosa* from Friday Street, Surrey, 26 Sept. 1953
(25 seeds per pot)

Date sown	9 *November* 1953					8 *December* 1953				13 *January* 1954				15 *February* 1954		
Pot number	1	2	3	4	5	1	2	3	4	1	2	3	4	1	2	3
Time outside (weeks)	0	4½	9	15½	All	0	5	9½	All	0	4½	All	All	0	2½	All
No. germinating																
March 1954	17	16	12	11	2	12	6	4								
April 1954				1	7				5							
April 1955	5	—	—	—	1	—	—	—	4	7	7	2	1	11	0	9
Total	22	—	—	—	10	—	—	—	9	7	7	2	1	11	0	9

the later sowings. A similar set of sowings was made with *E. occidentalis* from Perranporth on the coast of Cornwall. It was thought possible that, although *E. nemorosa* would probably require frost treatment before germinating, *E. occidentalis* from an almost frost-free locality would need little or no cold-treatment. This question could not be tested owing to the freezing of the greenhouse. The results, some of which are shown in Table 2, were similar to those given by *E. nemorosa*. The following differences were found : the three pots of the November and December sowings that were kept a second year produced only one seedling and I was in doubt whether even that was a *Euphrasia*; and the main period of germination was about three weeks earlier, both in the greenhouse and out of doors while a few seedlings came up a month earlier still, in a mild spell in mid-January.

Variation in Germination

I have sown few counted samples of seeds apart from those produced in cross-pollination or enforced self-pollination. The variation in germination seen in Table 3 seems to be typical of these and also of wild seed, although some variation may be due to different periods of storage and different times of collecting. However, there is a possibility that the testas of *Euphrasia* seeds are easily damaged and that the embryos are killed when the testas are damaged, with reduction in percentage viability as a consequence. Seeds of controlled pollination were usually collected with a curved needle after moistening, and I found that the ridges on the testa were easily broken in this process. The same needle has also been used for extracting seeds from herbarium material. A new trial of germination has now been started, using counted seeds taken from mature specimens by shaking, so as to avoid any unnatural damage to the seeds. The seed pots will be kept until the first spring when no seedlings come up.

Discussion of Germination Behaviour

My observations which indicate failure of seed to withstand dry storage conditions are consistent with the results of Wettstein and Neidhardt; Heinricher, however, obtained germination in seed that had been stored for more than a year. Loss of viability in storage was found by Vallance (1952) in *Rhinanthus*, and he overcame it by starting his germination experiments within a few weeks of the ripening of the seed.

The germination of *Euphrasia* seed is normally restricted to the spring, and the species seem to have a rigidly fixed life-cycle, which is partly governed by the restricted germination period. All the Eurasian and North American species are annuals, flowering in the summer and dying in the autumn. A seasonally fixed life-cycle is probably the rule in annuals.

It seems clear that one of the factors concerned in controlling germination is the need for exposure to winter cold. However, there must be others, because late sowing, with its reduced exposure to the winter, sometimes leads to postponed germination and sometimes

does not, while some seeds do not in any case germinate in their first spring after sowing.

Among the results quoted from previous workers on *Euphrasia*, only those of Nichols appear to provide positive evidence of better germination resulting from outdoor winter conditions, while the results of Neidhardt are complete enough to suggest positively an absence of any such effect, except for a reduction in germination at the very high temperature of 30°C. However, Heinricher (1909, p. 285) made observations on *Rhinanthus* which suggested that the duration and severity of winter cold had an effect on germination. The controlled experiments of Vallance (1952) on *Rhinanthus* showed that seeds kept moist at 20°C failed to germinate, even after a year of such treatment. Germination required a period of several weeks of chilling, after which it took place more rapidly at higher temperatures. It seems probable that *Euphrasia* has similar requirements, though if so the rather frequent germination under greenhouse conditions would have to be accounted for. However, the maximum temperature which will give effective chilling has not been determined, and the question of whether chilling can be effective if it shows a diurnal rhythm has not been examined. There is a possibility that night frosts in late summer might have provided a sufficient chilling effect in some seed samples that have been used in experiments. It is noteworthy that Vallance obtained germination throughout the year, though no seeds germinated less than two months after ripening.

It appears from my results that a spread of germination over a period of years is normal, though the proportion of second-spring germination is doubtless increased by late sowing. Previous workers who obtained germination over two or three years only did so in rather late-sown samples. However, in 1909 Heinricher (1909, p. 284) appeared to regard a spread of germination over two years as normal in *Euphrasia*, *Odontites* and *Rhinanthus*, and mentioned an occurrence of third-spring germination in *Rhinanthus*.

The spread of germination over a number of years is probably due to hereditary differences in the seeds, maintained by selection. This spread of germination is clearly of advantage in the event of an unfavourable season, such as a very dry summer in the lowlands, or an unusually cool and short one in the mountains or in the Arctic.

The Seedlings of Euphrasia and the Formation of Haustoria

Parasitism in the Rhinanthoideae was discovered by Decaisne (1847). He found that the roots of *Alectorolophus* (*Rhinanthus*), *Melampyrum* and *Odontites* had haustoria by which they were attached to the roots of "Gramineae, of shrubs and even of trees." (*Melampyrum* is a parasite of shrubs and trees). His observations were supported by those of Henslow (1847) who found *Euphrasia officinalis** and *E. odontites* (*Odontites verna* (Bell.) Dum.) bearing haustoria by which their roots were attached to the roots of Gramineae. Henslow also found isolated *Euphrasia* plants, which he supposed had destroyed their hosts.

Koch (1891) found that in *Euphrasia* growing parasitically on other species the haustoria only seized living roots, and they only parasitized the youngest or thinnest host roots. In *Melampyrum*, as opposed to *Euphrasia*, the haustoria attach themselves to dead organic matter. Saprophytism occurs in *Euphrasia* and *Rhinanthus* only after the end of the parasitic activity of the haustoria, when the affected host roots have died. Haustoria were observed also by Wettstein (1896), being numerous on plants of *E. rostkoviana* Hayne grown in troughs in the open, in which grass seed had been sown the previous year and in which they grew well and flowered. Heinricher (1898b) grew *E. salisburgensis* Funck, *E. rostkoviana* and *E. minima* Jord. out of doors, and found well-grown *Euphrasia* plants with haustorial attachments to a variety of other plants. Wettstein reported that the identification of host plants in the field was difficult because the *Euphrasia* roots are very thin and because when the Euphrasias are flowering, the host roots are dying, and nourishment continues saprophytically. However, he recorded the formation of haustoria by several species of *Euphrasia* on a variety of host-plants in the wild (1896, 1897), as also did Crosby-Browne (1950) for *E. salisburgensis*.

Parasitism of *Euphrasia* plants by others of their kind was observed by Koch (1891). *Euphrasia* seeds were germinated in pots and where they were very crowded some individuals

*Formerly all British *Euphrasiae* were referred to *E. officinalis* L., which is now treated as a *nomen ambiguum*.

grew faster than the rest and were found to be attached to their neighbours by haustoria. Wettstein (1897) also found *Euphrasia* plants attached to one another by haustoria in pots of *E. rostkoviana* which had been sown with no host-plant, although in one a weed was being parasitised by the *Euphrasia*. Heinricher (1898a) reported that thickly-sown seedlings of *Odontites odontites* (*O. verna*) with no host-plant had haustorial initials at the contact points of their root systems on 29 April, germination having started on 12 April. The genus *Odontites* is closely related to *Euphrasia*.

The anatomy of the root of *Euphrasia* has been described by Neidhardt (1947). Wettstein (1896) gave anatomical drawings of haustoria, and described the root system as consisting of extremely fine roots, with few root hairs, which occurred singly near root tips and on haustoria, and densely in a ring at the base of the hypocotyl, where they play a part in the initial anchorage of the seedling. He reported that his observations on the anatomy of the haustoria of *E. rostkoviana* agreed fully with those of Koch on "*E. officinalis*." Koch (1891) investigated in detail the anatomy of the haustorium. Characteristic of *Euphrasia* are the small size and slight growth in length of the haustoria, the simple tracheal strand (formed from one row of cells), and the clasping structures round the edge of the contact surface of the haustoria. Root hairs are more or less isolated. The attacked host root becomes internally disorganized, and the attack becomes saprophytic. About this stage, the haustorium becomes filled with food reserves and its tissue becomes loose, with intercellular spaces. The haustorium penetrates the cortex and comes into contact with the vascular tissue of the host root. Neidhardt (1947) stated that the roots of seedlings growing alone penetrate deeply into the soil, while seedlings growing with host-plants have comparatively short taproots which bear abundant branches. He also recorded that, whereas lateral roots arise endogenously, growth of haustoria begins in the outermost layer of the cortex. I have not consulted the anatomical works by Hovelacque and by Spoerri, nor the physiological work by Kostytschew, that are cited by Neidhardt.

An attempt was made by Fraysse to find out what materials were obtained from the host by the parasite (Fraysse, 1906). Fraysse (*l.c.*, p. 99) observed haustoria of *E. officinalis* in fields in Savoie in September attached to the roots of various Gramineae, Compositae and Leguminosae, and to the rhizoids of mosses, etc. He found autoparasitism (and parasitism) commonly in a relative of *Euphrasia*, *Odontites rubra* var. *serotina* (*O. verna* subsp. *serotina* (Dum.) E. F. Warb.) (Fraysse, 1906 p. 89).

Regarding penetration by haustoria, Fraysse found that in *Trifolium* and *Taraxacum* they usually penetrated the cortex but reached the host xylem only exceptionally (p. 99), the parasite in this case being *E. officinalis*. In Monocotyledons the haustoria always reached the centre of the root, and sometimes divided the entire stele.

Fraysse tested the haustoria and adjacent regions of host and parasite for starch (p. 92). In this investigation the parasite was *Odontites*. The roots were collected in August; some from plants which had not yet started to flower, and others from freely-flowering specimens. In the roots of *Ranunculus repens* and *Trifolium repens*, testing with iodine showed a disappearance of starch from the region around the haustoria. From the distribution of reducing sugar in the haustorium, as indicated by the Fehling reaction, Fraysse concluded that glucose was passing from host to parasite.

The roots of the grasses collected were poor in glucose as well as in starch, and on them the haustoria of *Odontites* contained little carbohydrate; consequently, Fraysse concluded that they obtain from grasses only water and whatever solutes it contains.

Haustoria of *Odontites* on *Leontodon autumnalis* behaved as on *Ranunculus* and *Trifolium*.

In the haustoria of *Euphrasia* Fraysse found the same physiological mechanism as in *Odontites*. He states that the haustoria were constituted only for obtaining carbohydrate, but mentions the presence of abundant protein granules in *Euphrasia* haustoria on *Trifolium* and *Taraxacum* (p. 99 seq.).

My own observations support many of those of previous workers, and slightly extend them.

The appearance of the seedlings of *Euphrasia* is shown in Fig. 1 (p.19). Photographs of

sets of seedlings of seven species, including the seedlings shown in Fig. 1 b–d, were taken on 1 or 2 April 1953. The youngest seedlings are just free of the testa, or have the cotyledons still within it; the oldest show the first pair of leaves. The degree of root-branching in plants of apparently similar age appears to vary from population to population. At the base of the hypocotyl a tuft of root-hairs develops; they give the impression of being effective in anchorage, and are probably necessary to ensure that the cotyledons come above ground.

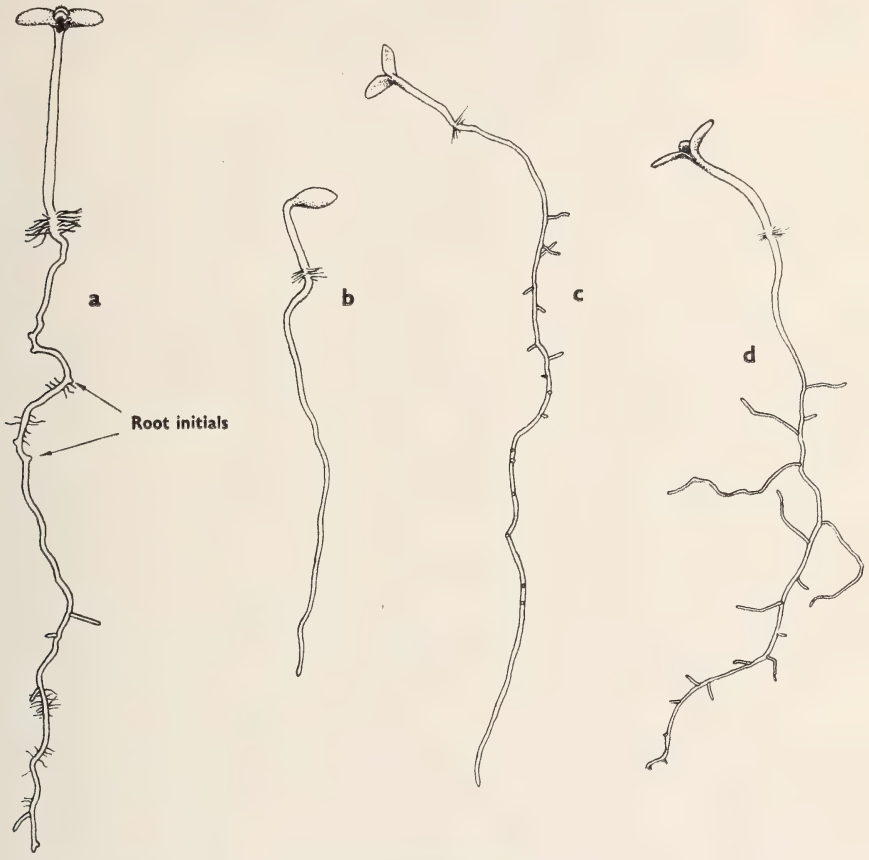


Fig. 1. (a) Seedling of *Euphrasia occidentalis*, grown in the greenhouse, drawn on 3 February 1953, four weeks after the cotyledons had appeared above ground. (b)–(d) seedlings of *E. confusa*, drawn from photograph taken at beginning of April 1953 (Root hairs not shown, except for tuft at base of hypocotyl). All approx. × 2

If they were absent the seed and cotyledons would give anchorage, and the hypocotyl would probably never appear above ground. Root-hairs are sparse elsewhere on the root system of the seedling; they are usually absent from much of it, and occur in groups here and there (Fig. 1 a). They also seem to develop around haustoria. It was noted that on five seedlings of *E. occidentalis* sand grains and organic debris were found firmly attached wherever root hairs were present. The root system often appears to branch more in pieces of peat in the potting compost than elsewhere.

Lateral branches are swollen at their base, and the initial of a lateral branch looks similar to a detached haustorium (Fig. 1). No haustoria could be seen by direct observation in any of the sets of seedlings photographed; seedlings which were left for a much longer time in the pot in which they had germinated formed haustoria, however. Two small pots, one containing seedlings of *E. micrantha* and the other *E. confusa* Pugsl., were investigated on 20 June 1953. Neither pot contained any plants other than *Euphrasia* and in both

haustorial connections between *Euphrasia* roots were seen, as well as haustoria which had become disconnected when unearthed. In the *E. micrantha* sample, roots connected by a haustorium were traced back to two different plants (Fig. 2.). In this sample a haustorium was also found connecting two branches of the same root system; another

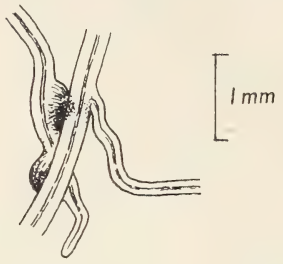


Fig. 2. Two pieces of *Euphrasia* root, each belonging to a different plant, one connected to the other by two haustoria. (*E. micrantha.* 20 June 1953).

connection of this kind was found on 13 August 1955 in the roots of an isolated plant of *E. nemorosa* growing in a pot with no host plant. Connections between *Euphrasia* roots were found in 1954 in two cultivated samples of *E. nemorosa* in which the plants also had haustorial connections with *Medicago lupulina* L., and in 1955 when the *Euphrasia* was also parasitic on *Hieracium pilosella* L.

Haustoria attached to cultivated *M. lupulina* were also seen in 1954 on *E. anglica* Pugsl., several hybrids and, in abundance, on *E. salisburgensis* (from Austria) and *E. pseudokerneri* Pugsl. Haustoria on host roots were found also on *E. micrantha.* The intended host was *M. lupulina,* but young plants of *Ranunculus* sp. and *Lamium purpureum* were also in the pot at the time of examination. Haustoria were found connecting *E. nemorosa* to *Hieracium pilosella* and *E. scottica* Wettst. to *M. lupulina* (in 1955 and 1956 respectively). These observations were made when the plants were well-grown and were about to be pressed. The soil ball was knocked out of the pot and the haustoria were seen in the mass of roots at its periphery. Two poorly-developed plants of *E. pseudokerneri* examined in May 1952 were found to have haustoria. One had flowered and fruited precociously in a pot with *Pelargonium* × *hortorum* Bailey; when dug up the *Euphrasia* had detached haustoria and one haustorium attached to a dead piece of *Pelargonium* root. The other *Euphrasia* was dug up when nearly dead; it was growing in the presence of *Plantago lanceolata* and *Prunella vulgaris* and it had a few haustoria where its root was closely applied to a dead root of one of these plants.

Very vigorous plants of *E. nemorosa* were grown in the garden in embedded ' whale-hide ' pots (which rot fairly quickly in the soil) with *Plantago lanceolata* as host. The roots of two host plants, together with their parasites, were pulled up and preserved in alcohol. The roots of each host, with its parasite, formed a dense mass in which there were numerous haustoria, but in which it was difficult to make out connections. However, each host was seen to be connected to its parasite by haustoria. In both cases haustoria were seen on large *Plantago* roots six or seven times as thick as the *Euphrasia* roots bearing the haustoria, and in one case also on relatively thin host roots.

I have not been able to trace the roots parasitised by wild *Euphrasia* plants back to their origins, except for those of a plant of *Trifolium repens* parasitised by *E. nemorosa* This was found by Mr. E. K. Horwood growing isolated in cinders which were very easily washed out of the roots. I have been able to find haustoria attached to the roots of unknown host species in young *E. occidentalis* and *E. pseudokerneri* dug up in early May and having four pairs of leaves visible. Some of the haustoria of these plants and of the plants cultivated with *Plantago lanceolata* in the garden appeared to be terminal instead of lateral as they usually are.

Euphrasia seedlings which are not established on host-plants show very slow growth

above ground, and the leaves they produce are small. However, the root system grows quite actively, and produces an appreciable length of very fine roots. For cultivation it is usually necessary to transplant the seedlings from the pots in which they germinate into pots provided with host plants. The earlier the seedlings are planted out the less they are damaged in the process, and it is therefore necessary to plant them out when they are extremely small. In practice it seems better not to plant them out as soon as they are visible above ground, but to do so two to four weeks after they appear. For example, suitable seedlings for planting out would be those shown in Fig. 1 (a), (c) and (d), while the plant in Fig. 1 (b) would have too little root to make it desirable to transplant it.

Discussion of Haustoria

Some small differences between my observations and those of previous workers may be noted. Haustorial attachments to live host roots can be found, and are in fact the rule in my experience, in *Euphrasia* plants that are well into their flowering period, whereas Wettstein stated that the host roots were dying when the *Euphrasia* plants were in flower. It seems possible that the saprophytic phase of the haustorium described by other workers exists alongside the parasitic phase, and that new haustoria continue to be formed until the *Euphrasia* plant begins to die. Kinds of haustorial attachments that have apparently not been recorded before are those between two *Euphrasia* roots formed even when a host-plant is present, and those between two roots belonging to the same *Euphrasia* plant. It seems, therefore, that *Euphrasia* roots have no immunity to attack by their own kind, and that the necessary stimulus to haustorium formation is merely contact with another root. This is consistent with the wide host range which *Euphrasia* species show (see Crosby-Browne, 1950). The occurrence of terminal haustoria does not seem to have been reported before.

Summary

1. Previous work is summarised.

2. Seed of *Euphrasia* may lose its viability in a few months in dry storage conditions, and has rarely been germinated when stored for a year and never when stored for two years or more.

3. Germination is normally confined to the months January to May.

4. Some samples give good germination without exposure to winter cold. Others fail to germinate, or germinate less well, without it.

5. Germination may be entirely or partially delayed until the second spring after seed-sowing; complete postponement is more common with late sowing (January to April). Partial postponement is probably the rule, and germination may occur in the third and even the fourth spring.

6. Germination behaviour and the percentage germination have been found to be very variable.

7. *Euphrasia* roots are very slender and are almost devoid of root-hairs except at the base of the hypocotyl. Above-ground growth is slow before establishment on the host. Young seedlings can be transplanted.

8. Haustoria sometimes appear to be terminal on the *Euphrasia* root; usually, however they are lateral.

9. Haustoria may attack roots of *Euphrasia* belonging to another plant or even to their own plant.

10. Various species of *Euphrasia* were found to have haustoria attached to the roots of a number of host-plants.

Acknowledgments

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STUDIES ON WELSH ORCHIDS

I. THE VARIATION OF *DACTYLORCHIS PURPURELLA* (T. & T. A. STEPH.) VERMEUL. IN NORTH WALES

By R. H. Roberts

Abstract

Among ten spatially isolated populations of *D. purpurella* in North Wales statistically significant differences have been found in most of the phenotypic characters. Highly significant differences exist between populations only short distances apart.

The phenotypic variation follows a reticulate pattern and, as far as these results are concerned, no useful taxonomic subdivisions appear to be possible.

Two groups of correlated characters have been found :

(*a*) among three vegetative characters : the number of sheathing leaves, the number of non-sheathing leaves and leaf width ;

(*b*) among three floral dimensions : labellum width, labellum length and spur thickness.

Introduction

The marsh orchid now known as *Dactylorchis purpurella* was first described by T. & T. A. Stephenson (1920) from plants found near Aberystwyth, Cardiganshire, v.c. 46. The variability of the species was apparent from the outset, for the Stephensons recognized two forms : dwarf plants with flowers of a vivid reddish-purple colour and a small, almost entire, irregularly diamond-shaped labellum (' form A '); and taller plants with flowers of a rich, dark purple, and a rather larger, more rounded, shallowly trilobed labellum (' form B ').

It is clear that while they felt that ' form A ' was quite distinct from other marsh orchids, they were not so confident about ' form B.'

In 1921 they visited the Isle of Arran and in several stations saw plants of ' form B ' growing with what they accepted as ' *Orchis pulchella* ' (= *O. praetermissa* var. *pulchella* Druce). The latter differed from their ' form B ' only in having unspotted leaves and being somewhat larger. Without declaring the complete identity of these forms the Stephensons (1922) nevertheless realised their very close similarity and suggested that the var. *pulchella* would be better separated from *O. praetermissa* Druce. Eight years later T. Stephenson (1930) still referred to *Orchis purpurella* ' form B ' and the var. *pulchella* as distinct forms, although he emphasized the slightness of the differences which separated them. This variety was finally transferred to *O. purpurella* by H. W. Pugsley (1935), but it was clear that even as a variety it had little to distinguish it from the " type " (Hall, 1937).

Further varieties of *O. purpurella* subsequently described by T. Stephenson (1937) are var. *maculosa*, in which the leaves are spotted all over and not merely on either the apical or basal half as normally found; and var. *crassifolia*, in which the plants are much bigger, more leafy and have much larger labella. Variations in other directions were also evident : in the population on which the description of var. *maculosa* was based some of the plants had flowers of the dark crimson-purple typical of the species, but many had rose-coloured flowers; while, in the Orkneys, populations apparently indistinguishable in other respects from *D. purpurella* were found to contain a proportion of heavily leaf-spotted plants (1930).

As Pugsley (1935) pointed out, there was little to separate these from *D. majalis* (Rchb.) Vermln. except their later flowering.

In North Wales *D. purpurella* is frequently found in suitable habitats. Even within

this restricted geographical area it shows a wide range of variation both within populations and between one population and another. The populations vary from those composed almost entirely of small, distinctive plants with short spikes of small, purple flowers (approaching Stephensons' form A), through some in which the majority of individuals are larger, leafier and with broader, more rounded, obscurely trilobed labella (presumably Stephensons' form B), to populations which, in their vegetative features, appear to approach the var. *crassifolia* Steph.

Many of the Anglesey populations are very nearly and sometimes completely lacking in leaf-marking. As these are usually composed of rather large, leafy plants, they have occasionally been recorded as *D. praetermissa* (Druce) Vermeul., a species which has not been found so far in v.c. 52.

In order to obtain some impression of the pattern of variation among these populations a biometric study of ten colonies was made in the flowering seasons in 1957, 1958 and 1959. The results are presented below.

Methods

The morphological characters studied are those which have been used in previous work on the dactylorchids (Heslop-Harrison, 1948, *et seq.*), namely : (*a*) stature; (*b*) number of leaves per plant; (*c*) leaf dimensions; (*d*) leaf marking; (*e*) labellum dimensions; (*f*) spur dimensions, and in addition, (*g*) the number of non-sheathing, bract-like leaves has been included.

To avoid the unnecessary destruction which mass collecting would entail, measurements of all the vegetative characters were made in the field; flower colour, shape of spike and leaf marking were also noted for each plant in the sample. One homologous flower was collected from each plant and kept in a stoppered jar to prevent wilting. As soon as possible afterwards labella and spurs from these flowers were mounted by pasting on thin card. They were then placed under moderate pressure to dry and measurements made within a week to avoid any errors due to shrinking.

The Populations

The localities of the populations shown in Fig. 1 are :

P1. Damp, base-rich meadow at Brithdir, near Dolgellau, Merioneth, v.c. 48.

P2. Dune slack at Mochras, Merioneth, v.c. 48.

P3. Marshy tract fringing the Artro estuary at Mochras, Merioneth. This colony is separated from P2 by over 365 yards, the intervening ground being occupied partly by a sandy ridge and partly by salt marsh. The colonies P2 and P3 have therefore been treated as distinct populations.

P4. Dune slack separated from P3 by only 95 yards of sand dunes. This colony had many plants with unusually large spikes of paler flowers, with rather larger, more trilobed labella. Because of these differences it was treated as a separate population for biometric purposes. It is not suggested that it is isolated from P3 as a breeding unit.

P5. Damp meadow land along the River Cegin, near Bangor, Caernarvonshire, v.c. 49. *Dactylorchis fuchsii* and several hybrids of this species with *D. purpurella* are the only other orchids here.

P6. Cors Erddreiniog, 3 mls. N.N.E. of Llangefni, Anglesey, v.c. 52, is an area of fen where the most abundant marsh orchid is *D. traunsteineri* (Saut.) Vermeul. (Lacey & Roberts, 1958). *D. purpurella* occurs sparsely in the small tracts of damp grassland and sedge-meadow around the main fen area.

P7. Marshy bottom of a disused limestone quarry, on the edge of Malltraeth Marsh, near Llangristiolus, Anglesey, v.c. 52. The orchids grow among grasses and sedges, with a few plants of the hybrid *D. fuchsii* × *D. purpurella*.

P8. Small coastal marsh near Llanfwrog, Anglesey. *D. purpurella* occurs mostly in the patches of grass and sedge meadow fringing the marsh. *D. fuchsii* occurs on the

rather drier parts adjacent to the marsh and here again the hybrid *D. fuchsii* × *D. purpurella* is frequent.

P9. Marshy tract along the upper edge of the salt marsh of the Cefni Estuary, Newborough Warren Nature Reserve, Anglesey. Other orchid species growing here are

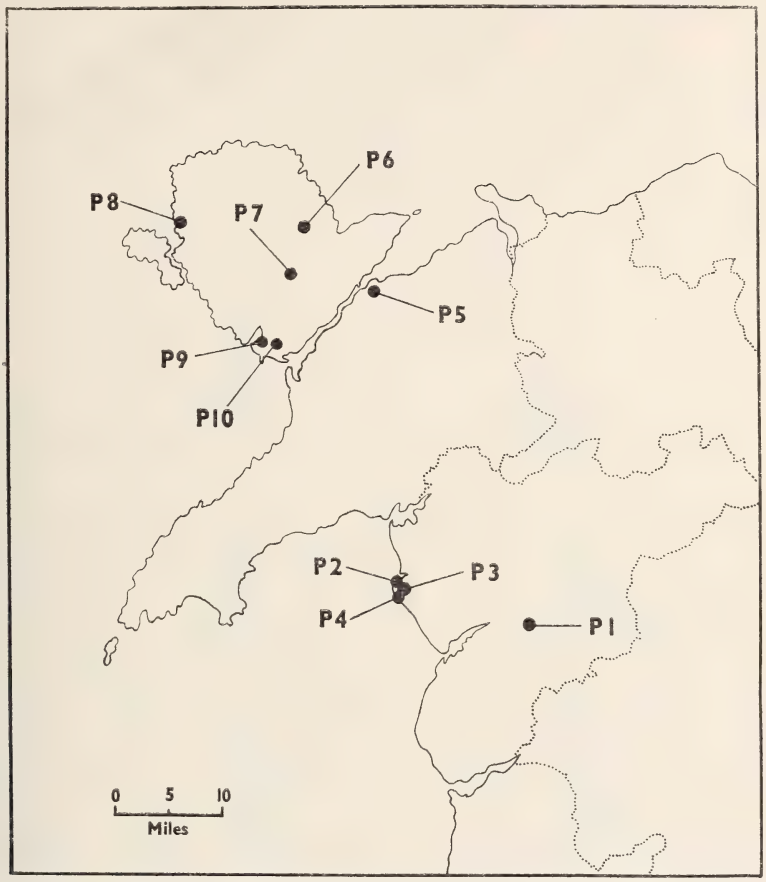


Fig. 1. Localities of the colonies of *D. purpurella* mentioned in the text.

Epipactis palustris, *D. incarnata* and *D. fuchsii*. Here also occurs a colony of heavily leaf-spotted plants whose status will be discussed in a later paper.

P10. Dune meadow near Llyn Rhos Ddu, in Newborough Warren Nature Reserve, Anglesey. This colony is over 1¼ ml. from P9, and no *D. purpurella* occurs in the intervening ground. There are no heavily leaf-spotted plants growing here, the only other marsh orchid occurring being *D. incarnata*.

Results

Stature

The dwarf habit of *D. purpurella* was emphasized by the Stephensons (1920) and the var. *pulchella* was stated by Pugsley (1935) to be, in general, taller than the "type." In the present account, therefore, stature, measured from soil level to the tip of the flower spike, has been included (Table 1), although it is realized that it is readily influenced by environmental conditions.

Leaf Number

In counting the number of leaves the non-sheathing, upper leaves were included.

For reasons given below a separate count of the latter was also made (Table 1).

TABLE 1

Population data for stature, leaf number and number of non-sheathing leaves.
N = number in sample; M = mean; S.E.M. = standard error of mean.

Populations	N	*Stature in cm.*		*Total number of leaves*		*Correlation between stature and total leaves*		*No. of non-sheathing leaves*		*No. of sheathing leaves*
		M	S.E.M.	M	S.E.M.	r	p	M	S.E.M.	M
P1	54	19·7	·48	5·1	·07	+ ·32	< ·05	·7	·06	4·4
P2	60	20·8	·31	5·3	·07	+ ·30	< ·05	·8	·07	4·5
P3	55	25·1	·55	6·0	·12	+ ·58	< ·001	1·3	·08	4·7
P4	31	23·3	·99	6·0	·22	+ ·57	< ·001	1·4	·13	4·6
P5	30	16·0	·73	6·0	·15	+ ·52	< ·01	1·1	·11	4·9
P6	50	12·2	·54	6·0	·14	+ ·41	< ·01	1·3	·08	4·7
P7	60	22·5	·40	9·2	·15	+ ·52	< ·001	2·1	·09	7·1
P8	35	22·8	1·00	8·4	·18	+ ·49	< ·01	1·9	·13	6·5
P9	32	25·8	·84	7·2	·20	+ ·56	< ·001	1·4	·09	5·8
P10	58	25·6	·58	6·9	·11	+ ·33	< ·01	1·3	·07	5·6

The mean leaf number shows a wide range of variation from 5·1 to 9·2, and is in striking contrast to the uniformity in this character shown by very widely separated colonies of *Dactylorchis traunsteineri*, in all of which the mean leaf number is around 4 (Heslop-Harrison, 1953; Lacey & Roberts, 1958). Leaf number in the individual plants varies from 4 to 12, a range considerably greater than that generally attributed to *D. purpurella* (Summerhayes, 1951).

In each of the colonies there is a positive correlation between stature and leaf number. Between the population means for these characters, however, there is no correlation. This confirms the fact, already apparent from Table 1, that the colonies of dwarf plants are not necessarily those with the least number of leaves, nor the colonies of tall plants those with the most. Similar results have been obtained in studies of *D. maculata* L. *sensu lato* (Heslop-Harrison, 1951).

Two counts of the number of leaves per plant were made in one colony (P6), the first in 1957 and the second in 1959. The same mean value of 6·0 was found on both occasions, in spite of the much drier conditions in 1959.

The number of non-sheathing, upper leaves

The number of non-sheathing, bract-like leaves is often quoted in descriptions of the dactylorchids. They have been variously described as ' transitional,' ' bract-like,' and ' non-sheathing.' As a result some confusion over their use has arisen. Compare, for example, Clapham, Tutin & Warburg (1952), and Heslop-Harrison (1956, 1957), for differing estimates.

In order to achieve greater uniformity, in the present study all those upper leaves which did not form a sheath were counted, irrespective of their size. The results, shown in Table 1 and the histograms, Fig. 2, show that the number of non-sheathing leaves varies from 0 to 4, but the latter number was only found in a very few plants in two of the colonies.

The mean values show considerable variation and statistical analysis shows that the differences between the populations in this respect are significant. The following grouping of the mean values, made on the basis of the differences between them, agrees very closely with one made as a result of a more advanced statistical treatment :

P1P2 P3 P5 P6 P10 P4 P9 P8P7

The data (Table 1) show that there is a close correlation between the number of non-sheathing leaves and the number of sheathing leaves. The correlation coefficient ($r = +\cdot 88$ with $p < \cdot 001$) indicates that an increase in the mean number of sheathing leaves is usually accompanied by an increase in the mean number of non-sheathing leaves.

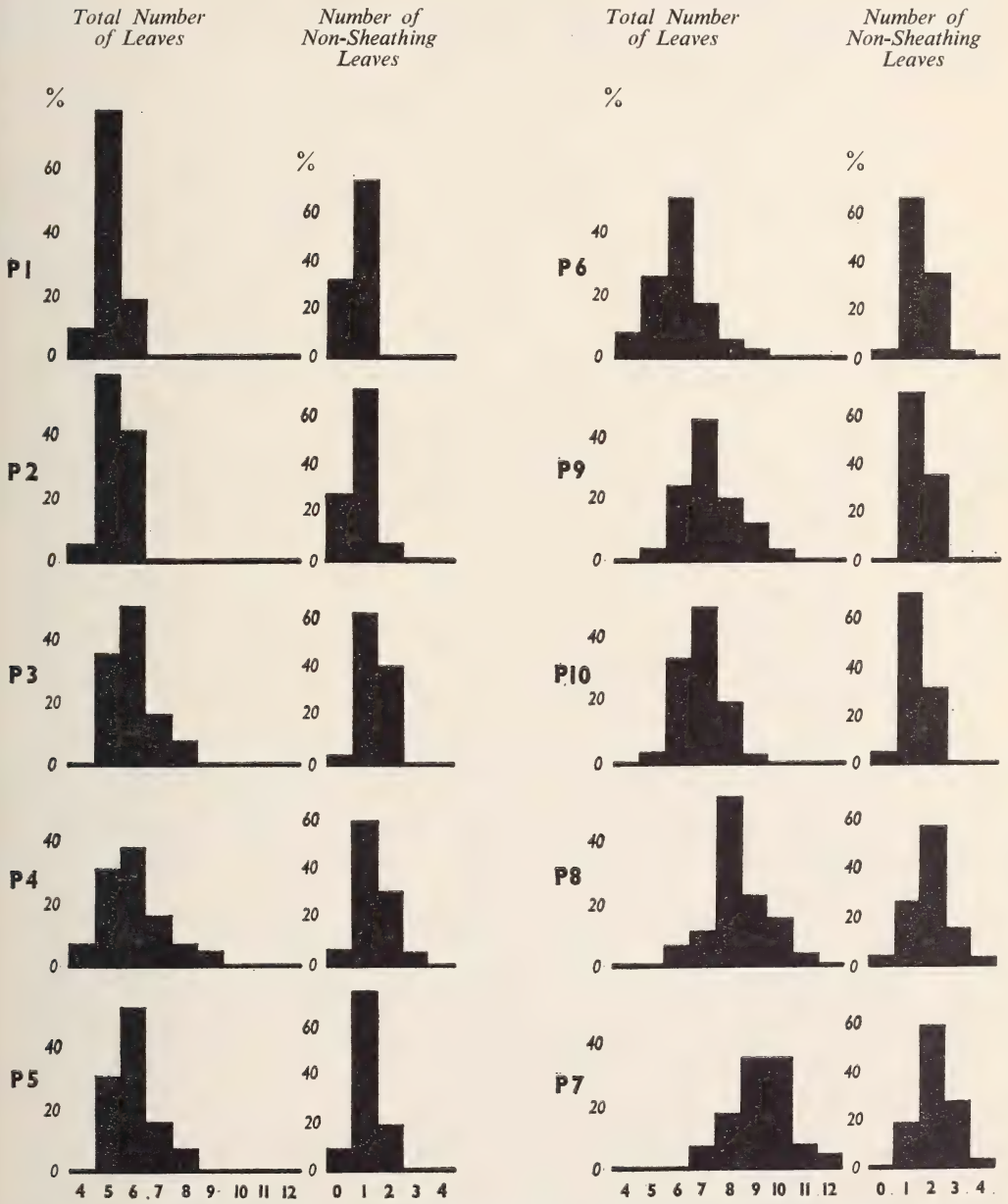


Fig. 2. Frequency distribution of the total number of leaves per plant and the number of non-sheathing leaves per plant in the ten populations.

Leaf dimensions

Both leaf measurements given in Table 2 were taken from the second fully expanded leaf from the base of the stem. Length was measured from the tip of the leaf to the opening of the sheath, and width at the widest part, which in the great majority was near or just below the middle.

The extreme variation in leaf width among the *D. purpurella* populations is shown by the fact that individual values range from 1·0 cm in the Merioneth colony, P2, to 5·0 cm in the Anglesey colony, P7. The population means for leaf width fall into four groups which are separated from one another by relatively large and statistically significant differences.

TABLE 2

Population data for leaf dimensions and leaf ratio. Symbols as in Table 1

Populations	N	*Length in cm.*		*Width in cm.*		*Ratio* $\frac{Length}{Width}$		*Correlation between total leaves and leaf width*	
		M	S.E.M.	M	S.E.M.	M	S.E.M.	r	p
P1	54	7·1	·14	1·4	·02	5·1	·13	+ ·28	< ·05
P2	60	8·5	·17	1·4	·03	6·1	·13	+ ·48	< ·001
P3	55	9·7	·25	1·8	·07	5·4	·15	+ ·66	< ·001
P4	31	10·5	·32	1·8	·09	5·8	·24	+ ·69	< ·001
P5	30	8·6	·21	1·8	·07	4·8	·24	+ ·34	·05
P6	50	9·9	·25	1·9	·06	5·2	·21	+ ·39	< ·01
P7	60	10·2	·22	3·2	·10	3·2	·15	+ ·68	< ·001
P8	35	9·9	·33	2·3	·09	4·3	·17	+ ·48	< ·01
P9	32	10·6	·24	1·8	·08	5·9	·22	+ ·76	< ·001
P10	58	11·1	·23	2·4	·08	4·6	·17	+ ·59	< ·001

The ratio mean leaf length/mean leaf width shows continuous variation in nine of the colonies, i.e., the values form a series in which the differences between adjacent pairs are very small and not significant. In the Anglesey colony, P7, however, this ratio differs by a large and highly significant amount from all of the others. This feature is very obvious in the field, and coupled with the large number of leaves, gives this population a most distinctive appearance.

The population means for leaf length and leaf width show no correlation, but, as shown in Table 2, there is a significant correlation between leaf number and leaf width within each of the populations. Between the population means for these two characters there is an even higher correlation ($r = + \cdot 91, p < \cdot 001$) : it follows that, in general, the population with fewest leaves usually has the narrowest, the one with most leaves also has the broadest.

Leaf spotting

Leaf marking in *D. purpurella* usually consists of small, solid, dark spots, approximately ·5 to 1 mm diameter. Table 3 shows the incidence of leaf spotting in the populations. It appeared to be entirely absent in only one colony (P7), although two others (P9 and P10) had a very high preponderance of unmarked plants. One colony (P1) showed leaf spotting in 100% of the individuals examined. A peculiar feature in some colonies (P5 and P8) was the occurrence of no more than two or three spots on each of the upper two or three leaves, the lower being entirely unspotted.

TABLE 3

Leaf marking. Percentage incidence in four arbitrary classes :

1. Unmarked.
2. Very few, solid spots of under 1 mm. diameter; 2 to 5 spots on each of the upper two or three leaves only.
3. More numerous, solid spots, of the same size as in Class 2, and occurring on most of the leaves.
4. Somewhat larger, solid spots, of about 1·5 to 1·8 mm. diameter; density as in Class 3.

Population	1	2	3	4
P1			100	
P2	11·7	16.7	68·3	3·3
P3	18·2	10·9	60·0	10·9
P4	19·3	6·5	67·7	6·5
P5	78·6	21·4		
P6	52·0	36·0	10·0	2·0
P7	100			
P8	61·0	39·0		
P9	93·7	6·3		
P10	98·3		1·7	

Labellum dimensions

Table 4 gives the population data for labellum dimensions. The results of *t* tests between each pair of means show that the differences between many of the populations are highly significant.

TABLE 4

Population data for labellum and spur dimensions. Symbols as in Table 1.

Populations	N	*Labellum length in cm.*		*Labellum width in cm.*		*Correlation between labellum length and labellum width*		*Spur length in cm.*		*Spur width in cm.*	
		M	S.E.M.	M	S.E.M.	r	p	M	S.E.M.	M	S.E.M.
P1	50	·63	·006	·79	·006	+ ·35	< ·01	·77	·007	·32	·004•
P2	63	·71	·006	·91	·009	+ ·41	·001	·82	·007	·33	·003
P3	77	·71	·006	·93	·009	+ ·53	< ·001	·81	·008	·33	·003
P4	34	·75	·006	·99	·012	+ ·57	< ·001	·79	·011	·38	·006
P5	35	·66	·009	·85	·013	+ ·14	> ·05	·70	·016	·31	·004
P6	35	·71	·009	·93	·014	+ ·66	< ·001	·77	·015	·33	·006
P7	60	·82	·009	·93	·008	+ ·30	·01	·84	·011	·39	·005
P8	50	·72	·006	·99	·011	+ ·27	·05	·87	·009	·33	·005
P9	58	·71	·007	·94	·011	+ ·18	> ·05	·84	·011	·32	·004
P10	95	·72	·005	·97	·005	+ ·30	< ·01	·79	·007	·37	·003

Correlation between mean labellum length and mean labellum width : r = + ·67, p < ·05;
Correlation between mean labellum length and mean spur width : r = + ·83, p = ·001

The relationships of the populations for these two dimensions are shown graphically in Fig. 3. With the exception of the colony P7 it is clear that there is a close correlation between mean labellum length and mean labellum width : for nine of the populations the correlation coefficient is + ·93 ($p < ·001$). Even when the colony P7 is included the value of *r* is + ·67 and significant with $p < ·05$.

It is worth noting that the mean labellum dimensions for the Merioneth colony, P1, agree remarkably well both with the measurements given by the Stephensons (1920) for

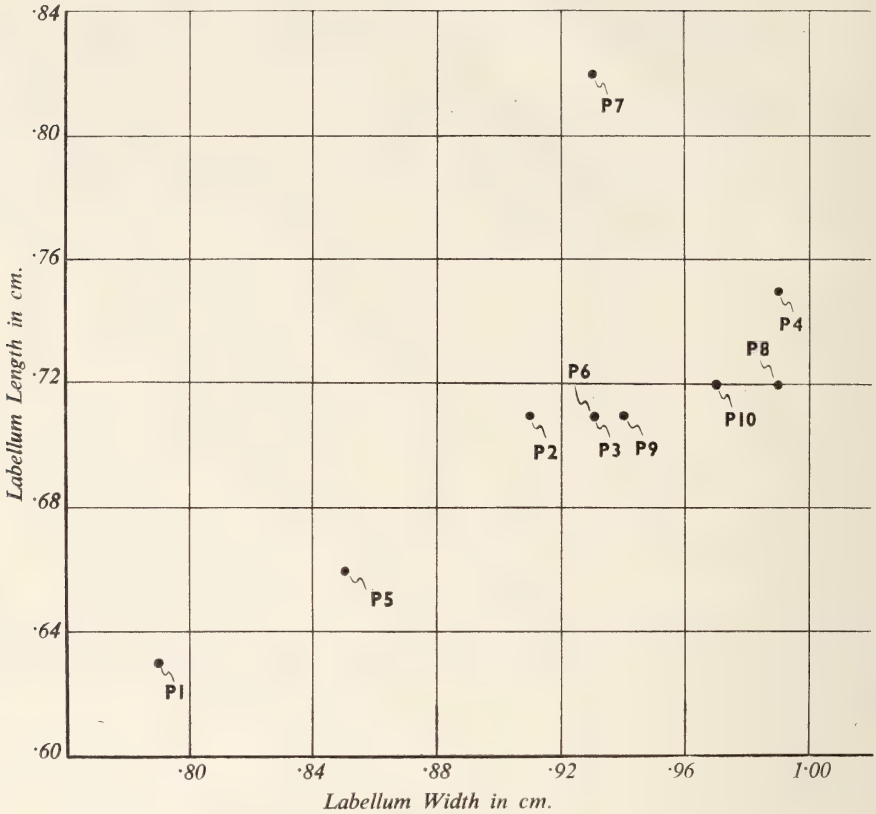


Fig. 3. Relationship of labellum width to labellum length.

their 'form A' (8 mm. × 6 mm.) and with those for an Irish colony of *D. purpurella* given by Heslop-Harrison (1953) : (·79 cm. × ·61 cm.).

Labellum shape

In order to give an impression of the variation in labellum shape in *D. purpurella* an attempt has been made to grade each colony by matching the labella to five shapes which have been taken as standards (Fig. 4), although the diversity is so great as to reduce the precision of any such grading. The results are given in Table 5.

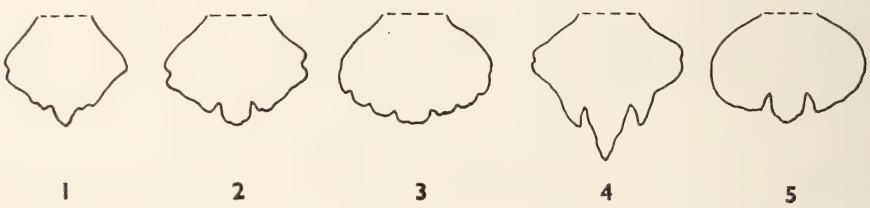


Fig. 4. Five labellum shapes used as standards for grading the *D. purpurella* colonies.

It can be seen that in the colony P1 74% of all individuals conform with grade 1, with only 4% in grade 3. In colony P2, which in vegetative features agrees closely with P1 (see Tables 1 and 2), 35% conform with grade 1 and an equal number with grade 2, while 14% conform with grade 5, a shape which is not present in P1. This colony, P2,

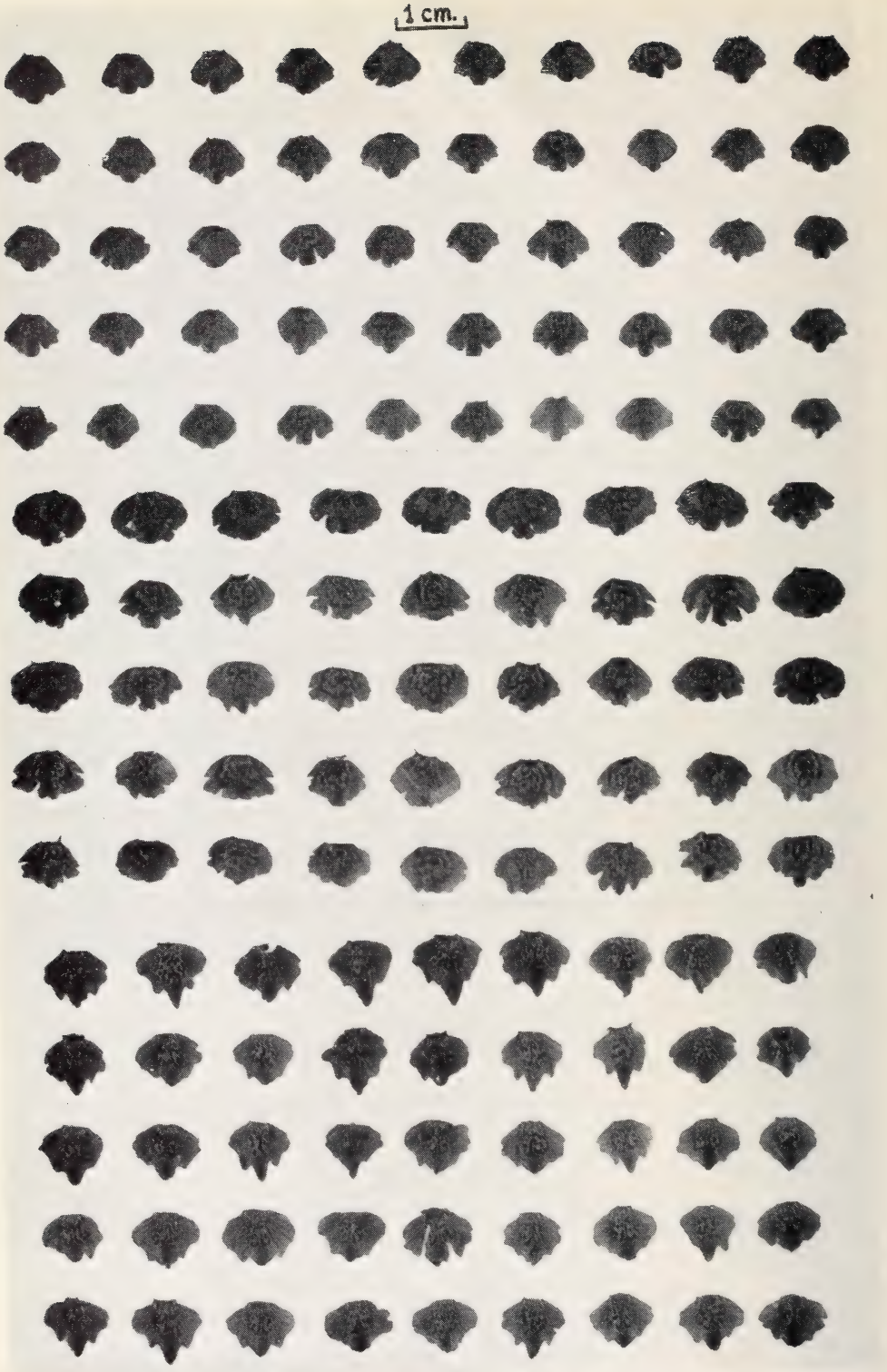


PLATE 1.

Random samples of labella from three populations of *D. purpurella* : top, 50 plants from the Merioneth colony, P1; middle, 45 plants from the Anglesey colony, P8; bottom, 45 plants from the Anglesey colony, P7. All × 1.

also differs significantly in the representation of labellum shape grades from the colony P3, which is only separated from it by 365 yards.

TABLE 5
Percentage distribution of labellum shapes in the *D. purpurella* colonies

Populations	*Labellum shape grades*				
	1	2	3	4	5
P1	74	22	4		
P2	35	35	16		14
P3	4	22	35·5		38·5
P4	3·3	23	55·7		18
P5	17	60	23		
P6		21	76	3	
P7		8·3	25	66·7	
P8		11	81	8	
P9	2	16	65	15	2
P10		20	63	6	11

The Caernarvonshire colony, P5, intermediate in labellum dimensions between P1 and most of the Anglesey colonies (P6, P8, P9 and P10), is also seen to hold an intermediate position with regard to labellum shapes, 60% of individuals here conforming to grade 2.

Of the Anglesey colonies four agree very closely in the distribution of the grades, the modal class in all of them being grade 3. The fifth, P7, which differs from all of the others by a large and highly significant amount in labellum length, also differs from all of them in the distribution of labellum shape grades : 66·7% conform with grade 4.

An impression of the variation in size and shape of labellum can be obtained from the random samples from three of the colonies, Plate 1.

Between the smallest, P1, and the largest, P7, there is a 53% difference in mean labellum area.

Flower colour and labellum pattern

Flower colour is one of the most constant and distinctive characters of *D. purpurella*, in the majority of populations being either a deep purple or red-purple. Some populations, however, contain a proportion of much paler flowers, approaching the tints found in *D. maculata* subsp. *ericetorum* : in two of the Merionethshire colonies, P2 and P4, 10% and 7% respectively had flowers of this colour.

The Aberystwyth plants from which the Stephensons described their ' form A' had flowers of a vivid red-purple, while plants of ' form B ' from Arran and Ambleside had flowers of a rich, dark purple. In the populations considered here no correlation has been discovered between labellum shape and flower colour : in the distinctive colony P1, where most labellum shapes conform with ' form A,' all flowers were of an intense, deep purple such as is almost uniformly found in the Anglesey colonies P6, P7 and P8. The two shades appear to be equally represented in the Merioneth colony, P3, where only 4% of the plants have labella of grade 1, but in the Anglesey colonies P9 and P10 the flowers are almost entirely of a red-purple colour.

Labellum pattern, which in *D. purpurella* usually consists of rather heavy, intense purple markings in the shape of broken bars, crescents and blotches, is fundamentally the same in all of the colonies, with these exceptions :

(a) in the pale-flowered plants in the colonies P2 and P4 labellum pattern was very indistinct and often lacking;

(b) in the Anglesey colony, P7, labellum pattern in most plants tended to consist of dots rather than the broken bars and crescents usually found.

Length and shape of flower spike

The Merioneth colony, P4, in addition to having a proportion of pale-flowered individuals, was also distinguished by the fact that many of them had unusually large flower spikes. Because of this, measurements of the spike length were made in the three Merioneth colonies, P2, P3 and P4. Fig. 5 shows the clear difference between the colony P4 and the other Mochras colonies in this respect.

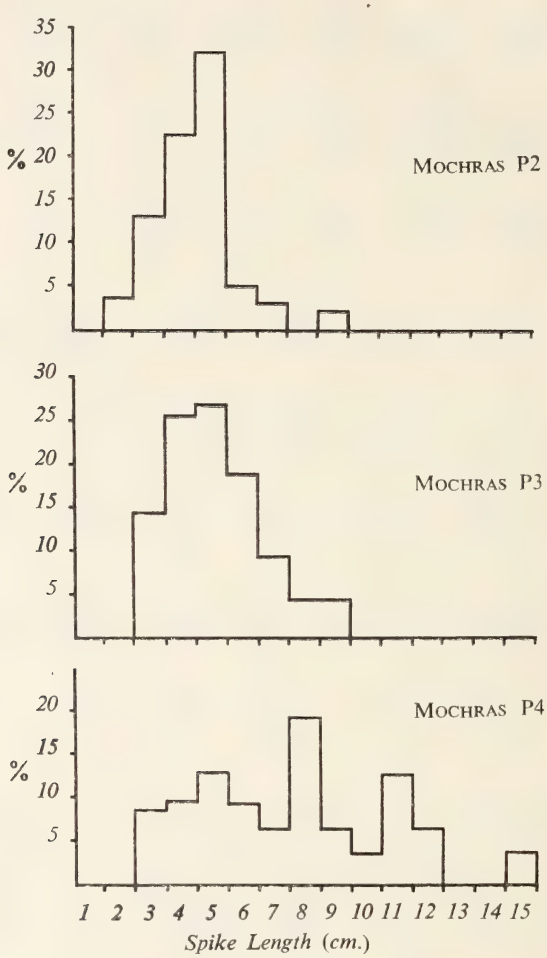


Fig. 5. Frequency distribution of spike length in the three Mochras (Merionethshire) colonies.

The shape of the flower spike deserves some comment, although this was not studied biometrically. In most populations of *D. purpurella* the spike has a more or less flat-topped appearance unique among the British marsh orchids. Two of the populations, P7 and P8, differed appreciably from the others in this character, for in both of them a very large proportion of the plants had distinctly conical spikes, very much like those of *D. praetermissa*. This was a most striking feature of these colonies in the field.

Spur size

In order that the data for spur size may be compared with those available for other species of marsh orchids the measurements have been made in the same way. Length of spur was measured from the mouth to the tip, and width about 1 mm from the mouth of the flattened spurs mounted on card (Heslop-Harrison, 1953).

The sample data (Table 4) show the wide variation in spur length that occurs among these populations : individual values vary from ·5 cm. to 1·05 cm., a range far greater than is usually given for the species.

The data for spur width show much greater regularity. These fall into two groups : those with means of ·31 to ·33 cm. and the rest with means of ·37 to ·39 cm. The difference between these two groups is relatively large and highly significant.

There is no correlation between the population means for spur length and spur width; indeed, spur length seems to vary quite independently of every other character. On the other hand there is a very high correlation between the population means for labellum length and spur width (Table 4).

Conclusions

1. For each character the difference between each pair of means was tested for significance by means of a *t*-test. The following groupings have been made as a result, and the populations placed in order of increasing means (Table 6).

Table 6

* = p < ·05, ** = p < ·01, *** = p < ·001

Character	*Grouping*
Leaf number	P1 * P2 ** P3 P4 P5 P6 ** P10 P9 *** P8 ** P7
Leaf width	P1 P2 ** P3 P4 P5 P6 P9 ** P8 P10 *** P7
Labellum width	P1 *** P5 *** P2 P3 P6 P9 P7 ** P10 P4 P8
Labellum length	P1 ** P5 *** P2 P3 P8 P6 P10 P9 ** P4 *** P7
Spur length	P5 * P1 P4 P6 P10 P3 P2 P9 P7 * P8
Spur width	P5 P1 P2 P3 P9 P6 P8 *** P10 P4 P7

In Fig. 6 the inter-relations of the populations with respect to these groups is shown. It is abundantly clear that, as far as these colonies of *D. purpurella* are concerned, none of

the populations can be completely separated from the others; rather, the pattern of variation is, to some extent, reticulate in the sense described by Turrill (1950).

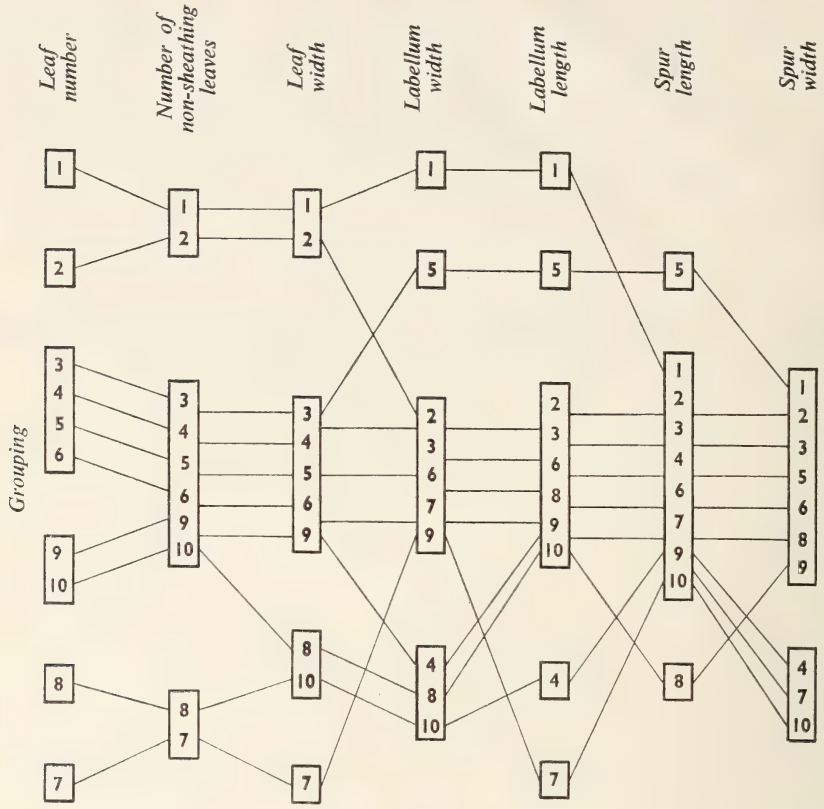


Fig. 6. A simplified representation of character variation in ten populations of *D. purpurella*. The nu mber 1, 2, 3, etc. stand for P1, P2, P3, etc. The thin lines trace the position of each colony in the network.

2. The results indicate that the degree of differentiation of the populations is not in proportion to the distances separating them. For instance, the colonies P3 and P6, separated by 35 miles from each other, agree closely in most vegetative and floral characters with the exception of stature and the incidence of labellum shape grades. On the other hand much bigger differences exist between the three Merioneth colonies, P2, P3 and P4, which are separated from each other by very short distances : P2 and P3 are effectively separated by 365 yards of salt marsh and a sandy ridge ; P3 is only separated from P4 by about 95 yards of sand dunes.

In Anglesey the two colonies, P9 and P10, separated by about $1\frac{1}{2}$ miles, differ appreciably in mean leaf width, labellum width and spur width; the other three colonies, P6, P7 and P8, differ widely from each other in several characters. P6 and P7 are about 5 miles apart and both of them over 11 miles from P8.

3. In the absence of evidence of the persistence of the character combinations found at present in these populations it may be premature to draw any conclusions about the degree of reproductive isolation prevailing among them. It is of interest, however, to note that there is some evidence in the case of the striking Anglesey colony P7 : a reference to its resemblance to var. *crassifolia* Steph. occurs in *Rep. Bot. Soc. & E. C.*, **11**, 505 (1937). A water-colour drawing of a plant gathered here by members of the B.E.C. Excursion to Anglesey in 1937 shows a plant quite typical of the colony as it is today, so it may not be unreasonable to assume that this colony, at least, has persisted more or less with its present combination of characters for over twenty years.

4. In his description of the var. *crassifolia*, T. Stephenson (1937) gives the following figures : stature 22–25 cm, number of leaves 8 or 9, second leaf from base of stem 12 cm × 4 cm (in one instance as much as 13 cm × 4·5 cm), labella mostly 11 mm wide by 8 mm long. In this colony all the plants had unspotted leaves, but the flowers, though larger, were of the same form and colour as the typical species. As far as it is possible to judge from these figures the Anglesey colony, P7, appears to be closely similar to the var. *crassifolia*, from which it seems to differ only in having narrower labella and in possessing an unusual labellum shape. Several plants in this colony were found with as many as 12 leaves, while the length and width of the second leaf were, in some cases, as much as 14·4 cm and 5·0 cm respectively.

5. It is now possible to discuss the ' form A' and ' form B ' of the Stephensons. In their original account the Stephensons gave the following figures for their ' form A' plants : stature around 12–15 cm, number of leaves 7, and width of the widest leaf 1·7 cm. A gathering of four plants of ' form A' from Aberystwyth, sent by the Stephensons to the British Museum in 1921, has labella which correspond closely in shape and size with those of the Merionethshire colony, P1, and of Irish colonies of ' form A' (Heslop-Harrison, 1953, 1954). Indeed, the mean labellum dimensions for the Merionethshire plants (·79 cm × ·63 cm) and those from Co. Donegal (·79 cm × ·61 cm) show remarkable agreement.

In other respects, however, there is no close agreement between these two colonies and the one described by the Stephensons : their mean stature is 19·7 cm and 20·2 cm; mean leaf number 5·1 and 6·56, and mean leaf width 1·4 cm and 1·99 cm respectively.

It is clear that ' form A' and ' form B ' have no significance other than in reference to the size and shape of the labellum. Where the great majority of plants in a colony have labella corresponding to ' form A' the impression gained is of a most distinctive and uniform ' type.' It was this, no doubt, which led the Stephensons to describe their two forms.

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STUDIES ON WELSH ORCHIDS

II. THE OCCURRENCE OF *DACTYLORCHIS MAJALIS* (REICHB.) VERMEUL. IN WALES

By R. H. Roberts

Abstract

Two colonies of heavily leaf-marked marsh orchids occur in Wales : one at Ynyslas, Cardiganshire, v.c. 46, and the other in Newborough Warren Nature Reserve, Anglesey, v.c. 52. The plants of both these colonies have been shown to be fully-fertile tetraploids with $2n = 80$. A biometric study has shown that these colonies are practically identical with one another.

Comparison with herbarium material has shown that they are closely allied to the continental *D. majalis* (Reichb.) Vermeul., under which they are placed as a new subspecies *D. majalis* subsp. *cambrensis*.

Some evidence is adduced that the tetraploid marsh orchid species of the subsection Majales do not always interbreed freely where they co-exist.

Introduction

At two localities in Wales there are colonies of marsh orchids which show some affinity with *Dactylorchis purpurella* and, at first sight, might be taken to be hybrids of that species with one of the *D. maculata* aggregate. Both populations consist of heavily leaf-marked plants, with flowers which are, on the whole, considerably larger and of a lighter purple than those of *D. purpurella*.

The first of these, M1, occurs at Ynyslas, Borth, Cardiganshire, v.c. 46, and was included by the Stephensons (1921) under their ' *Orchis latifolia*.' The plants grow in the very wet marshy area between the railway and the shore, with some *Phragmites communis, Agrostis stolonifera, Festuca rubra, Hydrocotyle vulgaris* and *Lotus pedunculatus*. The only other species seen in the area was *D. maculata* subsp. *ericetorum*.

The second colony, M2, was discovered by the writer, in 1956, in the marshy tract adjoining the salt marsh of the Cefni estuary, on the north side of the Newborough Warren Nature Reserve, Anglesey, v.c. 52. Associated species here are : *Equisetum palustre, Equisetum fluviatile, E. variegatum, Ranunculus flammula, Hypericum tetrapterum, Lychnis flos-cuculi, Lotus pedunculatus, Filipendula ulmaria, Parnassia palustris, Hydrocotyle vulgaris, Oenanthe lachenalii, Anagallis tenella, Prunella vulgaris, Epipactis palustris, Dactylorchis fuchsii, D. incarnata, D. purpurella, Festuca rubra* and *Agrostis stolonifera*.

The possibility that the plants of both these populations were hybrids could not be disregarded. This was especially so in the case of the Anglesey plants since *D. fuchsii* and *D. purpurella* also occur in the same area and these two species readily produce hybrids, sometimes in large numbers, wherever they occur together.

It appeared, therefore, to be a matter of some interest to determine the status of these heavily leaf-spotted plants and to ascertain their relationship with one another and with *D. purpurella* as found in Wales. Accordingly, in the seasons 1958 and 1959 the cytology and fertility of the two populations were investigated and a biometric study of them carried out.

Methods

All measurements of vegetative and floral parts, as well as the counts of the total number of leaves per plant and the number of non-sheathing leaves, have been made in the manner described in a previous study (Roberts, 1961).

Leaf measurements were taken from the second leaf from the base of the stem. In counting the number of leaves per plant, all fully developed leaves were counted, including the upper, non-sheathing ones. A separate count of the latter was also made, every leaf

which did not form a sheath being counted, regardless of its size.

The significance of the differences between means was determined on the basis of '*t*' tests. All differences significant at $p = \cdot 05$.

Cytology and Fertility

Cytological examination has shown that meiosis in plants from both localities is quite regular and a chromosome number of $n = 40$ was observed.

In several instances pollen mitosis was examined and was also found to be perfectly regular. The chromosomes were frequently sufficiently distinguishable to be counted at this stage also and the same number was again seen.

In addition, and in order to cover as large a sample as possible of the plants in these colonies, the technique of observing pollen fertility described by Heslop-Harrison (1954) was employed. Pollen from 30 plants was examined and showed very high fertility, the cells in all of the tetrads having uniformly two nuclei of slightly different sizes.

Later in the season well-swollen ovaries were gathered from marked plants and showed seed fertilities of up to 97%. The range of values obtained was similar to that found in *D. purpurella*; in samples of the latter, from two localities in Anglesey, fertilities of up to 95% and 93% respectively were observed.

It is therefore abundantly clear that these heavily leaf-marked plants from both the Cardiganshire and Anglesey colonies are fully fertile tetraploids with a chromosome number of $2n = 80$.

Vegetative Characters

The sample data for stature, leaf number, number of upper, non-sheathing leaves,

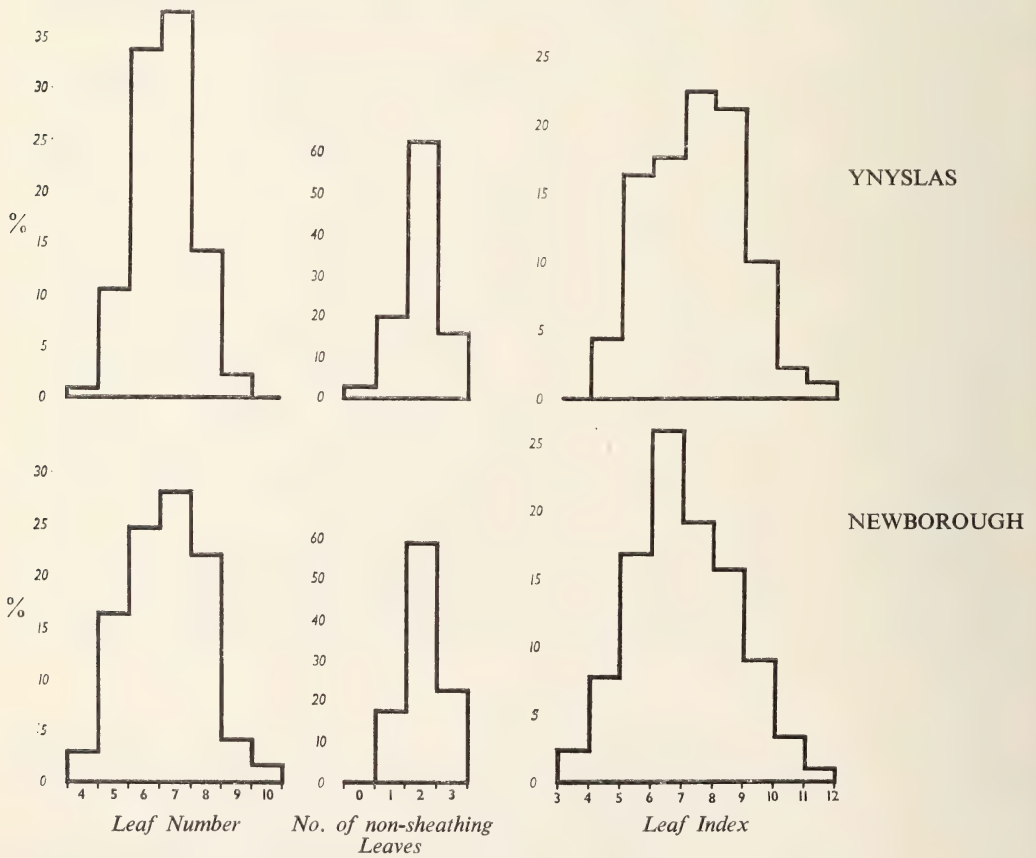


Fig. 1. Histograms of leaf number, number of non-sheathing leaves, and leaf index in the two populations.

and leaf dimensions are given in Tables 1 and 2. It will be seen that the sample means for all of these characters agree very closely in the two populations : in all except leaf ratio the very small differences between them are not statistically significant. The histograms, Fig. 1, indicate the close similarity of the two colonies in vegetative characters.

TABLE 1

Sample data for stature, leaf number, and number of non-sheathing leaves.
N = number in sample; M = mean; S.E.M. = standard error of mean.

Locality	N	*Stature (cm.)*		*Total number of leaves*		*No. of non-sheathing leaves*		*Non-sheathing leaves / Total leaves* %
		M	S.E.M.	M	S.E.M.	M	S.E.M.	
M1	85	28·0	·53	6·6	·10	1·9	·06	28·8
M2	92	27·3	·57	6·8	·13	2·0	·06	29·4

TABLE 2

Sample data for leaf dimensions and leaf index. Symbols as in Table 1

Locality	N	*Leaf length (cm.)*		*Leaf width (cm.)*		*Ratio* *Leaf length / Leaf width*	
		M	S.E.M.	M	S.E.M.	M	S.E.M.
M1	85	12·4	·24	1·7	·04	7·3	·16
M2	92	12·3	·26	1·8	·05	6·8	·17

Leaf marking in both populations consists of heavy, purple-brown, solid spots or blotches on the upper surface of the leaves and is very similar to that found in the Continental *D. majalis* and its Irish subspecies *occidentalis*. The spots are distributed over the whole of the leaf surface and not restricted to any particular part of it, as is generally the case in *D. purpurella*. There is some variation in the degree of leaf marking, from rather sparse and few spots to very many and intense, so that occasionally they tend to run together and cover most of the leaf surface. But in both of these colonies the size of the spots is fairly uniform and, in general, about 3 mm. diameter.

As in most populations of the tetraploid marsh orchids, a proportion of these plants have no leaf marking. In these colonies, however, the percentage of plants with no leaf marking is low : about 7% in the Ynyslas colony (M1) and about 18% in the Newborough colony (M2).

Leaf shape in the two colonies is also identical, the leaves being narrowly lanceolate, more or less keeled and folded, widest at or just below the middle, with a subacute, very slightly hooded apex. The ratio mean leaf-length/mean leaf-width is considerably higher than in any of the *D. purpurella* populations for which figures are available : 6·8 in the Anglesey colony, M2, and 7·3 in the Cardiganshire colony, M1. In *D. purpurella* this ratio varies from 3·2 to 6·1 (Roberts, 1961). In this respect these heavily leaf-marked colonies show a clear difference from all the *D. purpurella* populations and this feature is one which is quite noticeable in the field.

The habit of the plants on the whole resembles that of *D. purpurella*, with the exception that in a small proportion there is a greater tendency for the lower two leaves to be arcuate-recurved.

FLORAL CHARACTERS

Table 3 gives the sample data for labellum and spur dimensions in these two colonies.

The very slight difference between them in labellum width is not statistically significant. In labellum length, however, they differ by a significant amount, but this is no doubt due to the much more elongated mid-lobe of the labellum in the Cardiganshire plants. The labellum dimensions, particularly of the Anglesey colony, differ very little from those of an Irish colony of *D. majalis* subsp. *occidentalis* (Heslop-Harrison, 1953).

Flower colour and labellum pattern in the two colonies agree very closely. The colour of the flowers is on the whole a lighter red-purple than in *D. purpurella* and the heavy labellum pattern is consequently more conspicuous. In both populations labellum pattern, consisting of irregular dark lines and dots, often arranged more or less in two concentric broken loops, is more variable than in most populations of *D. purpurella* and shows the same range of variation in both of them.

TABLE 3
Sample data for labellum and spur dimensions. Symbols as in Table 1

Locality	N	*Labellum length (cm.)*		*Labellum width (cm.)*		*Spur length (cm.)*		*Spur width (cm.)*	
		M	S.E.M.	M	S.E.M.	M	S.E.M.	M	S.E.M.
M1	86	·84	·007	1·04	·010	·79	·007	·33	·003
M2	118	·79	·007	1·06	·009	·87	·008	·32	·004

The basic labellum shape in the two colonies appears to be much the same. In the Ynyslas colony (M1), however, the lateral lobes tend to be more rounded and entire than in the Newborough colony (M2), where they are angled and incised (Plate 2). In this respect the latter approach the labellum shapes found in *D. majalis* both on the Continent and in Ireland. Another feature which can only be seen in the field is that in most individuals the lateral lobes of the labellum are slightly reflexed.

Mean spur width in the two colonies differs by a small but statistically significant amount, but there is a large difference in spur length. However, there are just as large differences in mean spur length between some populations of *D. purpurella* (Roberts, 1961) and it seems that this is a normal result of population divergence. Indeed, it is clear that in spur dimensions the plants of these two colonies differ very little from the range of variation found in *D. purpurella*. The Irish subsp. *occidentalis*, on the other hand, has a much slenderer spur, which, in some plants, is curved about a third of its length from the tip (Heslop-Harrison, 1953). In the majority of herbarium specimens of Continental *D. majalis* examined at the British Museum and at Kew there was no evidence of the slenderness or of the curvature of the spur shown by the Irish plants. Where spur width in the herbarium material could be measured it was around ·30 cm in most instances. If an allowance of only 5% is made for shrinkage during drying it will be seen that this is well within the range of spur width in the two Welsh populations.

FLOWERING TIME

The Continental *D. majalis* and its Irish subspecies are both early flowering, reaching a peak in late May and early June (Pugsley, 1935; Vermeulen, 1949), though it should be noted that the flowering period of the Irish plants may extend into July (Heslop-Harrison, 1954). The plants of the Welsh populations flower with *D. purpurella* in June and July : the first plants of the Ynyslas colony (M1) were coming into flower on 7th June, 1958, and those of the Newborough colony (M2) on 3rd June, 1959. This is about a fortnight later than *D. traunsteineri*, the earliest of the marsh orchids to flower in Anglesey. In the seasons 1958 and 1959 this has been found to commence flowering around the 15th of May.

It appears, therefore, that the Welsh plants are later flowering than Continental and Irish *D. majalis*. There are, however, populations in western Scotland and the Hebrides, practically indistinguishable from some of *D. majalis* subsp. *occidentalis* in western Ireland,



a



b

Random samples of labella from homologous flowers in the two populations.
(a) 64 plants from the Cardiganshire colony, M1;
(b) 48 plants from the Anglesey colony, M2. Both × 1.

which, like the Welsh plants, also flower with *D. purpurella* in June and July (Hall, 1937; Campbell, 1937; Heslop-Harrison, 1954).

Conclusions

It is clear from the sample data that these two colonies of heavily leaf-spotted plants agree remarkably well with one another in vegetative characters; while the small differences in labellum dimensions, in the average expression of labellum shape, and in spur dimensions, are no greater than between several of the *D. purpurella* populations in North Wales (Roberts, 1961).

They also show close agreement in flower colour, labellum pattern, spur shape and in the position of the lateral sepals, which are well reflexed.

A comparison with herbarium material of Continental *D. majalis* (Reichb.) Vermeul. and of its Irish subspecies *occidentalis* (Pugsl.) H.-Harr. f., preserved in the British Museum and at Kew, justifies the inclusion of the Welsh plants under *D. majalis*. From the commonest Continental form of *D. majalis* the Welsh plants differ in possessing very much longer and narrower leaves, denser spikes of rather smaller flowers, and shorter bracts, only the lowest of which are longer than the flowers. They also differ in their habit, which more nearly resembles that of *D. purpurella*, the leaves being for the most part less spreading and more rigid. But there is some variation in this character and a small proportion of the Welsh plants, especially in the Anglesey colony, have more spreading, arcuate-recurved leaves reminiscent of some of the Irish specimens.

They differ from the Irish subsp. *occidentalis* not only in having much longer, narrower and more rigid leaves, but also in having much thicker spurs.

Among the Continental material in the British Museum and at Kew there are gatherings from the Valley of Durance, Hautes Alpes, made by M. S. Campbell in 1937, and from Thorenc, in the Alpes Maritimes, collected by D. P. Young in 1949. Two sheets of the former gathering had been labelled by H. W. Pugsley " cf. *majalis* " and " *O. majalis* (narrow leaved) " respectively; the latter gathering had been named "*O. majalis* Rchb." All of these show a very close approach to the Welsh plants, from which they seem to differ only in having longer bracts and laxer spikes of somewhat larger flowers.

Because of the clear, though minor, differences in morphological characters from *D. majalis*, both on the Continent and in Ireland, and because they occur in a separate geographical area, the most appropriate category for these Welsh plants seems to be that of a new subspecies of *D. majalis*. The name *Dactylorchis majalis* subsp. *cambrensis* is proposed for them.

Dactylorchis majalis subsp. **cambrensis** R. H. Roberts *subsp. nov.* A subsp. *majali* foliis multo longioribus (c. 12·4 × 1·7 cm.), bracteis brevioribus infimis quam flores longioribus, spicis densioribus, floribus minoribus et aetate florendi (Iunio vel Iulio) differt. Praeterea a subsp. *occidentali* (Pugsl.) H. Harr. f. foliis longioribus angustioribus erectioribus, nectariis pinguioribus et aetate florendi distinguitur. Chromosomata : $2n = 80$. Habitat : paludes udissimae prope litus Cambriae.

Holotype : marsh along the Cefni estuary, Newborough Warren Nature Reserve, Anglesey, v.c. 52, June, 1959, R. H. Roberts, in Herb. Kew.

Its present known distribution is confined to two vice-counties : 46 and 52.

Its occurrence in other localities in Wales and possibly in England is by no means improbable. There are specimens in the herbarium of the British Museum, from a Hampshire locality, which are intermediate in many respects between the Welsh plants and *D. praetermissa* var. *junialis*. Pugsley had examined these plants and said that they were not exactly his " *Orchis pardalina*," but near it. This was also appreciated by P. M. Hall and A. J. Wilmott, who, between themselves, referred to these Hampshire plants as " *pardalinoides*."

The labella in these are broader in relation to their length than they are in *D. praetermissa*, with lateral lobes which are notched and angled, and a labellum pattern consisting of broken loop markings rather than the continuous double loops characteristic of

var. *junialis*. Leaf marking, too, mostly consists of solid spots and blotches as in *D. majalis*, though in some specimens these are mixed with larger, ringed spots.

Whether or not the Welsh plants are connected by intermediates on the one hand with the Continental *D. majalis*, and on the other, through the var. *junialis*, with *D. praetermissa*, they are themselves morphologically distinct enough to merit the status given to them in this paper.

Hybridity

Within the same area as one of the colonies described here another tetraploid marsh orchid, *D. purpurella*, also occurs. This raises the question of the interfertility of the tetraploid members of the subsection Majales. Heslop-Harrison (1954) has shown that they are inter-fertile to the extent of producing a viable F1, but the fertility of the F1 generation itself has not been demonstrated.

The evidence available for this Anglesey colony (M2) suggests quite clearly that complete intergradation with *D. purpurella* does not occur here. The fact that this colony (M2) agrees so well morphologically with the Cardiganshire colony (M1), where *D. purpurella* does not occur, is, presumably, sufficient indication that it is not influenced to any great extent by introgression with *D. purpurella*.

That all the tetraploid species of marsh orchids are not capable of completely intergrading is also suggested by the co-existence at three localities in Anglesey of *D. purpurella* and *D. traunsteineri*. No plants of an intermediate character between these two species occur at any of these localities and a biometric study of the two species in these stations gives no indication that introgressive hybridisation has taken place.

It has been suggested that the tetraploid marsh orchid species interbreed freely in many areas where they meet (Heslop-Harrison, 1954), but the evidence from these Welsh localities certainly suggests that this is not always the case.

Acknowledgements

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I am also indebted to the authorities of the herbaria at the British Museum (Natural History) and at the Royal Botanic Gardens, Kew, for facilities to study herbarium material of British and Continental dactylorchids.

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GERANIUM MICROPHYLLUM HOOK. F. AS AN ADVENTIVE PLANT IN BRITAIN

By C. C. Townsend

Among a number of gatherings, principally of adventives, passed to me for determination in late 1960 by Miss M. McCallum Webster, was found good material of *Geranium microphyllum* Hook. f., a native of south-west Australia, Tasmania and New Zealand. It occurred on a railway embankment at Bordon station, N. Hants., (v.c. 12) and was apparently well established in company with *Berteroa incana* (L.) DC. In view of its very close similarity to certain native British cranesbills of the section Columbina Koch, it seems advisable to give a short account of the plant. It is a perennial, successfully ripens seed in this country, and the ejaculatory means of seed dispersal has already proved a very successful one in distributing alien plants in Britain (cf. *Impatiens* spp.). The rapidity with which *G. molle* L. and *G. dissectum* L. colonise a bare gravel pit demonstrates what may possibly be expected of *G. microphyllum* with the additional aid of the railway.

As has been observed, *G. microphyllum* might very easily be passed over in a field for some British annual cranesbills, notably *G. dissectum* L., to which it bears close resemblance in its deeply dissected leaves and hairy carpels. In view of the fact that few botanists seem to find the length of the sepal mucro a wholly convincing character, the average botanist collecting the plant and attempting to name it from Clapham, Tutin & Warburg (1952) on key characters would probably be torn between *G. dissectum* L. and *G. pusillum* L. From both of these species it may readily and constantly be distinguished by the sculpturing of the testa of the seed. In *G. pusillum* the seed is quite smooth, and in *G. dissectum* it is furnished with deep and very pronounced hexagonal areolae, giving a perfect honeycomb effect; but in *G. microphyllum* the sculpturing is very much less distinct than in the case of the latter species, needing a magnification of at least × 15 to make it out at all satisfactorily with regard to detail. The areolae are irregularly rectangular or rhomboidal, becoming most elongated towards the centre of the seed, where they strongly recall the cell shape of certain hypnoid mosses.



G. dissectum G. microphyllum G. pusillum

Fig. 1.

From the figures of the seeds (Fig. 1), for which I am indebted to my colleague Miss M. A. Grierson, it will be seen that there is also considerable difference in the sizes of the seeds of the three species, those of *G. microphyllum* falling between those of the other two in this respect.

G. microphyllum was no doubt introduced at Bordon with wool shoddy, as this material is handled in the nearby siding, where Miss Webster also found *Pelargonium inodorum* Willd., *Lupinus angustifolius* L. and *Nicotiana suaveolens* Lehm., these as casuals. It should be sought for on railway banks in the vicinity of other stations known to handle shoddy.

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A NEW VARIETY OF *VALERIANELLA LOCUSTA* (L.) BETCKE

By D. E. Allen

Valerianella locusta *var.* **dunensis,** *var. nov. A typo habitu humiliore compactiore acaulescente et foliis brevioribus differt. Holotypus in Herb. Mus. Brit.*: v.c. 71, Isle of Man; dunes (' The Ayres ') near Ballaghennie, parish of Bride, April, 1957, *M. B. Bing*; *ex hort.* Sanderstead, Surrey, July 1, 1959, *D. P. Young* no. 6724.

Differs from the type in the much dwarfer (1–3 cm), more compact, acaulescent and cushion-like habit, with leaves only up to 3·5 cm long compared with up to 7 cm in the type.

This rather striking variety of *Valerianella locusta* has been known on the dunes at Freshfield, South Lancashire, for over fifty years. It has always seemed probable that it is a distinct dune ecotype, reproducing its characteristic habit from seed, but until 1957 no attempt, as far as is known, had been made to test whether this impression was correct.

In the course of the B.S.B.I. Field Meeting in the Isle of Man in June, 1950, what was clearly the same variety (even though by then well over) was noted on the dunes on the island's north coast, and in the report on that meeting (Allen, 1954) attention was drawn to its distinctness and apparently quite wide distribution. In the spring of 1957 Miss M. B. Bing happened to send me a parcel of fresh material of various species collected on another part of these Manx dunes further to the east, and included in this were one or two specimens of the same *Valerianella*, this time in good fruit. Having no garden of my own, I took the opportunity of sending the specimens to Dr. D. P. Young and requesting him to sow the seeds in his garden in Surrey. This he very kindly did, and after two summers' observation he was able to satisfy himself that the variety fully retains its characteristics under cultivation. I can find no description of any taxon corresponding to this in the literature and accordingly now provide it with a name.

The variety is characteristic of the therophyte community of grey dunes, associated with other spring annuals such as *Erophila verna* (L.) Chevall., *Myosotis ramosissima* Rochel, *Cerastium semidecandrum* L. and *Saxifraga tridactylites* L. An interesting parallel is provided by *Spergula arvensis* var. *nana*, a similarly low-growing variety described by Linton (1907) from dry places near the shore in Jersey and Guernsey. This, according to Linton, also comes true from seed.

I have seen material of var. *dunensis* from the following localities :

V.c. 1. W. CORNWALL : Quarry, Gannel, Newquay, 1922, *E. Thurston* (K); Keen Sands, near Perranporth, 1926, *B. T. Lowne* (K).
52. ANGLESEY : Newborough Warren, 1953, *B. Welch* (BM).
59. S. LANCS.: Freshfield dunes, 1910, *W. G. Travis* (K); 1949 and since, *D. E. Allen.*
71. MAN : dunes near Rue Point, Andreas, 1950, *B.S.B.I. Field Meeting*; dunes near Ballaghennie, Bride, 1957, *M. B. Bing* (BM).
110. OUTER HEBRIDES : Clachan dunes, near Newton, North Uist, 1937, *M. S. Campbell and A. J. Wilmott* (BM).

Hart (1891, 1898) has recorded what sounds like this variety as plentiful on dunes in Co. Donegal, and a dwarf form is mentioned as occurring on dunes in Brittany by Le Gall (1852). Although the variety is to be expected in these areas, caution must be exercised in the absence of material in view of the fact that the typical plant also occurs on dunes, often in a stunted condition. I have seen material referable to the latter from dunes in Cornwall and Norfolk. Such plants are quite without the characteristic cushion-like habit of var. *dunensis*. A gathering from dunes at Bude, Cornwall, made by E. Thurston in 1925 and now in Herb. Kew, appears to consist of a mixture of the typical plant, var. *dunensis* and inter-

mediates between the two. This suggests that in some places hybrid populations may have arisen, possibly resulting in either the variety or the typical plant locally losing its distinctiveness through extensive interbreeding.

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INTERSPECIFIC RELATIONSHIPS AND INTRASPECIFIC VARIATION OF *CHENOPODIUM ALBUM* L. IN BRITAIN

I. THE TAXONOMIC DELIMITATION OF THE SPECIES

By M. J. Cole

*Botany Department, University of Southampton**

Abstract

The critical nature of *Chenopodium* in general and *C. album* in particular is discussed. Much of the confusion appears to be nomenclatural in origin. Evidence is given to show that the inclusion of *C. viride* L. (*C. suecicum* Murr) within the aggregate species *C. album* is unjustified, the resemblance being only superficial. Conversely, the status of *C. reticulatum* as a taxonomic entity distinct from *C. album* is questioned; the two are interfertile, and are separated only by the single plastic character of reticulate as against smooth seed coat, so that it seems more reasonable to account for this variation in terms of seed coat polymorphism within the one species *C. album*.

A. INTRODUCTION

The genus *Chenopodium* [Tourn.] L. comprises over 100 species, most of which are annual weeds of open habitats. Although of cosmopolitan distribution, their greatest development is in temperate regions, with 19 species either native or established in this country. The genus is characterized in general by rather mealy, simple or lobed leaves, alternately arranged, but very variable in shape. Equally variable inflorescences, either spicate, cymose or indeterminate, bear inconspicuous hermaphrodite or gynomonoecious flowers, and the seeds have characteristic testa sculpturings much used in species diagnosis.

Few workers have studied the genus exhaustively, possibly on account of its unattractive appearance. The first post-Linnean treatment of any importance is that of Moquin-Tandon (1840) in his monograph of the family. Mention must also be made of Murr (1904, 1927), who contributed extensively to the taxonomy of the group, especially to that of the *Chenopodium album* complex. By far the most important nomenclatural and taxonomic contributions, however, have been made by Aellen (1918, onwards), whose work, though exclusively orthodox, with little experimental or cytological data, has done much to pave the way for more critical analyses.

Botanists in this country have been particularly indifferent to *Chenopodium*. The only attempt at an intrageneric classification by a British worker is that of Moss (1914), whose segregation of the British species is, however, insufficiently discriminating to merit further attention. Extensive and invaluable collections in the genus were made by Druce (in Herb. Druce, Oxford University), who was particularly interested in alien forms (Hayward and Druce, 1919); but his nomenclature and taxonomy were untrustworthy, and he contributed little that was original other than recognising countless questionable hybrids.

The most extensive recent taxonomic treatment is that of Aellen and Just (1943). Of the 10 sections in the genus they recognise from American material, 4 are represented in Britain. The typical section *Chenopodium* with which we are here primarily concerned, is further subdivided into 4 subsections, on the criterion of seed-coat marking alone. Though this is the only satisfactory differentiating character, it is doubtful whether a classification based thereon does more than provide a convenient pigeon-holing system, since it frequently cuts across apparent relationships in other respects.

*Now at Dept. of Biology and Pharmacy, College of Advanced Technology, Birmingham. This series of papers represents part of the work accepted for the degree of Ph.D. in the University of Southampton.

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Indeed, the taxonomic confusion still existing in *Chenopodium* is well known, and appears mainly to result from the following difficulties :

1. The abundance of morphologically similar species, separated qualitatively mainly on characters of the seed, often absent in herbarium material.
2. The existence of polymorphism within the limits of many individual species, and of parallel variation between different species, resulting in a confusion of inter- and intraspecific variation patterns.
3. The occurrence of marked phenotypic flexibility, complicating species identification.
4. The erection – often with little foundation – of numerous putative hybrids to accommodate the complicated variation pattern.

The whole situation clearly calls for experimental work to supplement the classical approach, but a short note by Watson (1868), who attempted a few simple growing experiments, is the only example of ' experimental taxonomy ' within the group so far discovered.

The critical nature of the genus as a whole is particularly well exemplified by *C. album*, which has been considered one of the most difficult species (*cf.* Wahl, 1952). Not only is there a serious lack of clear-cut morphological criteria to distinguish it, but it shows particularly well-marked polymorphism at the biotype level and very wide phenotypic plasticity. Moreover, it is reported to hybridize extensively with related species, and the position is further complicated by the reputed existence of different intraspecific chromosome races (Maude, 1940).

The present paper attempts to delimit *C. album* more precisely, in terms of both classical description and new experimental data. Later contributions will be concerned with the cytology of *C. album* and its allies, with the degree of isolation of the species, and with its intraspecific variation pattern.

B. THE TAXONOMIC POSITION OF *CHENOPODIUM ALBUM* IN BRITAIN

The type specimen, a rather depauperate spicate form, resides in the Linnean Herbarium in London. The limits of the Linnean diagnosis have been variously interpreted in the past, and although modern botanists recognise the majority of the British species of *Chenopodium* as taxonomically distinct, there has been some confusion in the nomenclature at the species level. For a long time *C. opulifolium* Schrad. was confused with *C. viride* L. and *C. album* L. (Knuth, 1838, p. 150; but see Aellen, 1940) and, in addition, various workers have included *C. ficifolium* Sm. and/or *C. pratericola* Rydb. (*C. leptophyllum auct. non* Nutt.) within the limits of *C. album* (Bentham, 1858; Moquin-Tandon, in de Candolle, 1849; Moss, 1914).

In the most recent description of the British species (Clapham, Tutin and Warburg, 1952), *C. album* is given the status of an aggregate species, with three segregates : *C. album* L. (*sensu stricto*), *C. viride* L. (*C. suecicum* Murr), and *C. reticulatum* Aell. It is this situation which needs particular clarification here.

1. The relationship between C. album L. (sensu stricto) and C. viride L.

Much of the difficulty in discriminating correctly between these two taxa was caused by a nomenclatural error which was perpetuated for over half a century and has had far-reaching taxonomic consequences. Although the position has been discussed fully by Aellen (1940), a brief review is necessary here, since it concerns not only interspecific differences but the intraspecific nomenclature of *C. album*.

Linnaeus (1753) described the two taxa as separate species, and differentiated between them thus :

C. album : ' *Chenopodium foliis rhomboideo-triangularibus erosis postice integris : summis oblongis, racemis erectis.*'

C. viride : ' *Chenopodium foliis rhomboideis dentato-sinuatis, racemis ramosis subfoliatis.*'

Neither leaf shape nor inflorescence branching are of diagnostic importance, however, and it is impossible to separate these taxa from the Linnean descriptions alone. Later, Moquin-Tandon (1840) introduced the additional diagnostic criteria of leaf colour and seed characters :

C. album : '*pallide viridibus*' and '*semine laevi nitido margine acuto.*'
C. viride : '*glauco vel obscure viridibus*' and '*semine punctulato nitido margine sub-obtuso.*'

Despite this discrimination, many botanists have confused *C. viride* with a cymose variety of *C. album* later described by Koch (1857, p. 524) as *C. album* var. *cymigerum*. Hudson (1798, p. 106) was probably the first post-Linnean worker to make this false equation, and subsequent workers (e.g. Koch, *loc. cit.*; Babington, 1867; Syme, 1868; Murr, 1904; Moss, 1914; Hegi, 1910) largely followed Hudson; even Moquin-Tandon failed to discriminate correctly in his section on the Chenopodiaceae in de Candolle (1849), only 9 years after his earlier monograph describing *C. viride* as a separate species.

TABLE 1

Morphological differences between *C. album* L. (*sensu stricto*) and *C. viride* L. (*C. suecicum* Murr)

C. album L.	*C. viride* L.
1. Testa almost smooth with only faint irregular striae.	Testa surface regularly pitted.
2. Margin of seed sharply keeled.	Margin of seed obtusely keeled.
3. Inflorescence form variable –spicate, paniculate or cymose.	Inflorescence form invariably cymose.
4. Leaves, thick, pale green, never glaucous.	Leaves thin, often glaucous.
5. Diploid chromosome number $2n = 54$*	Diploid chromosome number $2n = 18$*
6. Anthocyanin often present.	Anthocyanin rarely present.

* See paper II of this series.

C. viride was unequivocally reinstated as a full species distinct from *C. album* by Aellen in 1933. He showed that *C. viride* was equivalent, not to *C. album* var. *cymigerum*, but to a distinct species since described as *C. suecicum* Murr. Nevertheless, there is still considerable confusion, caused not so much now by nomenclatural discrepancies as by insufficient care in determination. The discriminating characters are given in Table 1, and it is clear from this that a removal of *C. viride* from the *C. album* complex is well founded.

2. THE RELATIONSHIP BETWEEN C. ALBUM (SENSU STRICTO) AND C. RETICULATUM AELL.

Whereas the taxonomic delimination of *C. viride* from *C. album* is based on several criteria, with an evident distinction in the field, the segregation of *C. reticulatum* is by no means so clear-cut. In Aellen's original description (1928), there are only two characters concerned, namely '*folia . . . interdum manifeste triloba*' and '*semen magnum . . . in superficie reticulatum i.e. crate venularum ± regulariter quadratarum inductum, area inter venulas ± levi vel tenuiter regulariter granulato scabra.*' The first of these, i.e. the 3-lobed leaves, has since been recognized by Aellen (*in litt.*, 1955) to be inconstant. On the other hand, the impressive, raised, quadrate reticulum on the seed surface is, in its extreme expression, very pronounced and unmistakably distinct from the more or less smooth seed coat of *C. album*; and this character, moreover, was stated to breed true.

Nevertheless, since species of *Chenopodium* can usually be distinguished from one another by at least some other qualitative or quantitative criteria besides testa markings, a taxonomic segregation based on this single character must be questioned. The constancy and genetic isolation of the reticulation needs to be further assessed, the possibility of other associated morphological differences explored, and the distribution of *C. reticulatum* compared with that of *C. album*.

(a) *Seed characters*

(*i*) *Observations on the nature and degree of the reticulation*

Examination of a large number of specimens in the major herbaria and from extensive personal collections made between 1954–6 has revealed that, in any one plant of the *C. album/reticulatum* complex, a gradation may exist from markedly reticulate seeds, with granular-scabrous interfaces, to seeds which are indistinguishable from the smooth, faintly grooved seeds of typical *album* (Fig. 1). Past workers (e.g. Brenan, 1938) have desig-

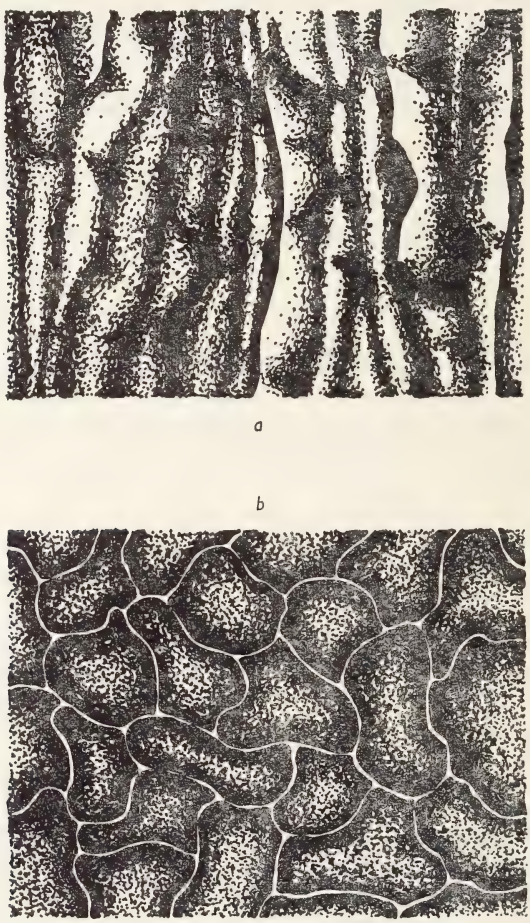


Fig. 1. Surface marking of seeds of (a) *Chenopodium album* and (b) *C. reticulatum*.

nated plants with a mixture of smooth and reticulate seeds as *C. album* × *reticulatum*, but this presupposes an initial parental segregation. For the purpose of the present investigation, therefore, *C. reticulatum* is used to embrace any plant with at least some seeds reticulate, as against *C. album* with variously sculptured seeds but with a complete absence of the

raised quadrate reticulum. This arbitrary working separation is perhaps justified by the fact that it is extremely rare to find plants of *C. reticulatum* with uniformly reticulate seeds.

There also exists a parallel series of fainter reticulate markings. These differ in showing a tram-line pattern of two parallel shallow indentations arranged in a reticulate fashion, instead of a raised reticulum. As these markings are relatively inconstant, however, occurring only sporadically in seed samples and not breeding true, they are not considered further here.

The position is further complicated by frequent heteromorphy of the seeds in size and colour. This is a relatively common phenomenon in the genus as a whole, and parallels the situation described for *Atriplex* by Salisbury (1942). In the *C. album/reticulatum* complex occasionally larger, lighter-coloured seeds (mean. wt. *c.* $16{\cdot}07 \times 10^{-4}$ g. as against *c.* $10{\cdot}80 \times 10^{-4}$ g.) may be found in a seed sample, and these rarely show reticulate markings even when the smaller seeds are extremely reticulate. In certain instances, *all* the seeds on a particular plant may be large and light brown, and this may prevent the expression of the reticulation even in what would otherwise be typically reticulate plants.

(ii) Experimental work

It was obviously necessary to invent a method of recording quantitatively the degree of ' reticulateness ' of individual plants before an experimental analysis of the variation pattern could be undertaken. Four arbitrary grades were therefore delimited, and an index ' α ' derived from these :

$$\alpha = \frac{(1 \times nA) + (2 \times nB) + (3 \times nC) + (4 \times nD)}{N}$$

where A — D = the four grades in order of increasing distinctness of reticulation
n = the total number of seeds in each class
N = the total number of seeds in the sample.

In spite of various difficulties, such as non-uniformity over different parts of the seed surface, differences in roughness of the seed, and the incidence of extraneous surface punctation, a comparison of replicates within individual samples showed sufficiently close correlation for the method to be used.

α. Experiment on the washing and drying of seed

It was frequently noticed that freshly-harvested seed from *C. reticulatum* showed considerably less reticulation than when the same seed was examined later. The ' α ' index was therefore compared on seed :

a. Freshly harvested, with the green perianth and pericarp removed between finger and thumb.
b. Freshly harvested, perianth and pericarp removed as in (a), and the seed then washed in running water.
c. Seed kept dry for > 5 days on top of a 60°C oven, and perianth and pericarp removed when dry.

The results (Table 2) show a progressive increase in the α index in relation to the three treatments. The difference between treatments (a) and (b) is attributed to a film of crushed perianth and pericarp cells obscuring the faint reticulations (subsequently checked on individual seeds) and emphasises the necessity for the seed surface to be thoroughly cleaned when observations are made on fresh material. The increase in the α index under treatment (c), however, suggests that some actual shrinkage of the testa has occurred. Not only must this be taken into consideration in any assessment of seed coat characters, but it also indicates that the degree of reticulation may be, to some extent at least, of a non-genetic nature.

TABLE 2

Changes in the degree of reticulation (α index) in seeds of *C. reticulatum* under different treatments.

Seed Sample	*Value of α index (degree of reticulation)*		
	Freshly harvested seeds	*Freshly harvested seeds 'washed'*	*'Dried' seeds*
C 1·1	2·50	—	3·73
C 1·3	1·27	3·17	3·50
C 3·2	1·55	—	2·46
C 3·3	1·77	—	2·87
C 3·4	1·63	2·53	2·93
C 5·1	1·23	—	1·50
C 6·1	1·10	1·77	2·50
C 6·4	1·60	—	1·37
A 220·1	—	1·10	3·40
A 220·2	—	1·30	3·67
O 109·1	—	1·63	3·47
O 109·2	—	2·57	3·60
O 109·3	—	1·30	3·23

β. Controlled growing experiments

Expt. I. Growth of clones under different external conditions. This experiment was set up to assess the effect of environmental factors on the degree of reticulation in genetically uniform material. Six clones were obtained by cutting individual plants of the *C. album/reticulatum* complex transversely into 5–8 ramets of 1–2 internodes each just after inflorescence initiation, root growth being stimulated by application of M. & B. No. 1 Seradix B to the lower end of each ramet. After a week's growth in sterile 'Vermiculite,' the clones thus obtained were potted out in compost in cool (c. 20°C.), warm (c. 25°C.) and hot (c. 30°C.) greenhouses. Some ramets were enclosed by cellophane-covered frames to ensure inbreeding.

The results of the experiment are given in Table 3. They show considerable variation in the α index within an individual clone, presumably due to environmental conditions, since there appeared to be no correlation between the index value and the original position of the ramet on the individual plant. The plasticity is obviously very great. For example, in Clone C 6, there is a difference in the index between C 6·4 (at 25°C.) and C 6·7 (at 20°C.) of 2·43 units, representing 81% of the total possible variation (i.e. from completely smooth to completely reticulate); even under supposedly uniform conditions (C 6·4 and C 6·3), the variation is 55%.

A comparison of the standard deviation σ of the α index of certain of these results, selected as representing a range of increasingly variable conditions, showed a direct correlation between the value of σ and the relative uniformity of the external conditions. This again suggests that differences in testa markings are at least partly a function of the environment.

Expt. II. Growth of C. reticulatum *under uniform conditions.* Plants from *C. reticulatum* seed collected from 6 different localities were grown together in a cool greenhouse (c. 20°C.), and the seed markings of these F_1 plants compared with those of their parents. The results, given in Table 4, reveal a fairly close positive correlation ($r = +0{\cdot}85$, $P = < 0{\cdot}05$) of the α index between parents and offspring, indicating a considerable measure of genetic control in the extent of seed reticulation. Moreover, the results suggest that the flexibility of expression of seed marking is not as great as might have been assumed from the previous experiment. These differences in result can be partly accounted for by the fact that the temperature in Expt. II approximated more closely to an optimum for growth; this would

TABLE 3

Variation of seed reticulation in clonal material of *C. reticulatum*.
([S] = plant covered with cellophane to ensure self pollination.)

	Ramets						
Clone	1	2	3	4	5	6	7
	Approx. prevailing temperature						
C 1	20°C	—	20°C	—	20°C [S]	20°C [S]	—
C 2	—	— [S]	— [S]	— [S]	25°C [S]	25°C [S]	—
C 3	—	25°C	25°C	25°C	25°C	25°C	—
C 4	30°C	30°C	20°C	20°C	—	—	—
C 5	20°C	—	— [S]	— [S]	—	20°C	20°C
C 6	20°C	20°C	25°C	25°C	—	20°C	20°C
	Degree of reticulation (α)						
C 1	3·73	—	3·50	—	3·03	2·73	—
C 2	—	—	—	—	1·93	1·53	—
C 3	—	2·47	3·00	2·53	2·17	2·70	—
C 4	3·07	2·40	1·60	2·63	—	—	—
C 5	1·50	—	—	—	—	1·87	1·40
C 6	1·77	3·33	2·97	1·37	—	3·47	3·80

tend to increase the heritability of a character by reducing the variance of phenotypic expression.

There is, in addition, a consistent difference between parental and F_1 scores in that the parental seed is generally much more reticulate than that of the F_1 samples. This can be explained on the hypothesis that the temperature differences prevailing during the maturation of the parent and F_1 seed respectively are responsible in such a way that the expres-

TABLE 4

Variation in reticulation (α) of seed coat of parental and F_1 *C. reticulatum*

Seed Sample	*Parental seed*	*F_1 seed*			*Average for F_1*
		Rep. 1	*Rep.* 2	*Rep.* 3	
A	1·53	1·00	1·27	—	1·14
B	1·67	1·27	1·00	1·73	1·33
C	2·23	1·83	1·80	1·67	1·77
D	3·37	1·47	1·80	1·93	1·73
E	3·47	2·47	2·40	—	2·44
F	3·80	3·60	3·07	—	3·34

sion of the reticulateness of the seeds is partly suppressed at higher temperatures; and this is supported by other general observations that material maturing in the field at low temperatures tends to be more reticulate than that grown in warm greenhouses.

The two experiments taken together thus suggest that, whereas in nature quite small

differences in the degree of seed reticulation may well have a genetic basis, the character is sufficiently plastic to be affected by abnormal environmental conditions.

γ. Breeding experiments

Since genetical differences affecting seed reticulation undoubtedly exist between *C. album* and *C. reticulatum*, further experiments were carried out to determine the nature and extent of any genetic isolation between the two.

Expt. I. Controlled reciprocal crosses. The normal emasculation techniques proved quite impracticable for the close-set inflorescences of *Chenopodium*, and the procedure finally adopted was to dust the whole of the young protogynous inflorescence of the selected female parent (previously certified as pollen-free under a binocular microscope) with pollen from the male parent before anthesis of the female parent occurred. Though such a method would obviously be invalid for any quantitative work, it was adequate for a crude indication of crossing ability.

TABLE 5

Results of controlled reciprocal crosses between *C. album* and *C. reticulatum*

Cross ♀ × ♂	*Replicates*	F_1 *seed-marking (No. plants)*		*Percentage crossing*
		At least some seeds reticulate	*Seeds all smooth*	
1. *album* × *reticulatum*	7	5	2	
2. *album* × *reticulatum*	5	—	5	50%
3.* *album* × *reticulatum*	8	5	3	
Control self	7	—	7	
1. *reticulatum* × *album*	21	18	3	
2. *reticulatum* × *album*	2	—	2	22%
Control self	8	4	4	

* Material of *C. album* from Pretoria, S. Africa.

The results of the crosses made are given in Table 5. For the crosses *album* ♀ × *reticulatum* ♂, 50% of the F_1 plants examined showed some evidence of the transfer of genes for reticulateness, in contrast to the selfed *album* control. The results of the reciprocal *reticulatum* ♀ × *album* ♂ cross, however, must be treated with caution, since, although smooth seeds appeared in the F_1 generation, some replicates of the selfed *reticulatum* control exhibited the same phenomenon. This was only to be expected from the nature of the variation of the *reticulatum* character and its possible masking by heteromorphy of the seed (p. 51) and the results as a whole are clearly indicative that at least some gene-interchange between the parental types is possible.

Expt. II. *Field experiment with uncontrolled crossing.* Equal numbers of plants of *C. album* and *C. reticulatum* were planted in four alternate rows, two feet apart, in an experimental plot, and left to set seed by natural means. Examination of the F_1 seed (Table 6) showed that reciprocal intercrossing had occurred between the parental types, while the selfed controls showed no evidence of change in seed coat markings. Even if the evidence from the presumed *reticulatum* ♀ × *album* ♂ crosses is disregarded (see above), the occurrence of c. 10% of reticulate F_1 seeds from the *album* plants not only confirms that gene-interchange may occur in the field, but also gives a minimum measure of the outbreeding potential in nature between the two variants.

TABLE 6

Results of natural cross-breeding in the field between *C. album* and *C. reticulatum*

Maternal parent seed marking	*Plants with F_1 seed marking :* *Smooth*	*reticulate*
album	9	0
album	10	2
album	4	0
album	4	1
album (control self)	10	0
reticulatum	2	7
reticulatum	0	3
reticulatum	2	14
reticulatum	0	8
reticulatum (control self)	0	5

(b) *Other morphological features*

Five possible morphological *differentiae* were examined, the characters chosen for analysis being those by which at least one other allied species may be either qualitatively or quantitatively distinguished from *C. album* : (i) Inflorescence form, i.e. presence or absence of an intraspecific cymose/spicate variation pattern; (ii) Distribution of anthocyanin, i.e. present as red or purple blotches in the axils of the leaves, restricted to the internodes, diffused through the whole plant, or absent altogether; (iii) Persistence or easy detachment of the pericarp from the seed; (iv) Seed weight; (v) Leaf thickness.

A synopsis of the position for *C. reticulatum* and for 5 other species of *Chenopodium*

TABLE 7

A qualitative comparison of *C. album* with *C. reticulatum* and five other species of *Chenopodium*

Character	*C. reticulatum*	*C. ficifolium*	*C. opulifolium*	*C. variabile*	*C. viride*	*C. berlandieri*
Seed coat marking	S	S	S	S	S	S
Inflorescence	N	S	S	N	S	S
Anthocyanin	N	S	N	S	N	S
Pericarp	N	S	N	S	N	N
Seed weight	N	S	No data	No data	No data	No data
Leaf thickness	N	No data	No data	No data	S	No data
Chromosome No.*	N	S	N	S	S	S
Potential gene* exchange with *C. album*	+	−	−	−	−	−

* Evidence given in later papers.

S = qualitatively separable from *C. album*
N = not qualitatively separable from *C. album*
\+ = potential gene exchange possible
− = potential gene exchange improbable.

is given in Table 7; data from chromosome numbers and relative potentiality for gene-exchange (for which the evidence will be given later in papers II and III of this series) have been added to complete the picture. It is clear from this that *C. reticulatum* is indistinguishable from *C. album* by any of the additional criteria here considered, and that a distinction between them is entirely dependent on the very variable reticulation of the seed.

(c) *Distribution and frequency of* C. reticulatum

Since the determination of seed characters requires microscopic examination, which is very rarely made, little is known about the relative distribution of *C. reticulatum* and *C. album* in this country. Of the 12 local floras published since the original description of *C. reticulatum* in 1928, only three (Wolley-Dod, 1937; Good, 1948; Dony, 1953) make any mention of the taxon. However, British herbaria contain much reticulate material included under *C. album*, and this has been supplemented from personal collections. A complete list of the localities and dates of collection of specimens examined showing reticulate seeds is given elsewhere (Cole, 1957), together with similar information from such published references as are available. But the records are so biased by concentration of collecting grounds and by general lack of discrimination in the literature that little reliance can be placed on them as far as general distribution is concerned; all that can be said is that *C. reticulatum* does not appear to possess a markedly different geographical or ecological range in Britain from that of *C. album*.

Nevertheless, an approximate estimate of the relative *frequency* of the *album* and *reticulatum* characters in Britain can be made from the available records if the non-random data from the literature is excluded. Of a total of 661 determinations from actual specimens, the ratio of *album* to *reticulatum* was roughly 9 : 1, showing that, for this country at least, *C. album* appears to be by far the commoner taxon.

Little can be deduced from the available records as to the origin of *C. reticulatum* in this country. Although it was not reported in the literature until 1938 (Lousley, 1938), British herbaria contain much earlier material. The oldest specimen examined, collected from Hastings in 1812, is in the Oxford University herbarium. A comparison of all the material examined in this herbarium with more recent personal collections gives the following relationship :—

	No. sheets examined	*Range of collection dates*	*Identification of specimens*	
			C. album	*C. reticulatum*
Oxford Univ. Herbarium (incl. Druce Collection)	52	1812–1938	78%	22%
Personal collections	347	1954–6	90%	10%

With the exception of one sheet, the Oxford specimens were all collected before *C. reticulatum* was described from Britain and the personal collections were likewise made independently of seed coat pattern, so these numbers may be regarded as comparatively unbiased. They suggest that the incidence of the *reticulatum* character has not changed significantly in recent years.

Extra-British records for *C. reticulatum* are very incomplete. Herbarium material and seed samples received from abroad have produced reticulate specimens from Europe, India and Australia, though similar checking through North American and Canadian material suggests that reticulate seeds are probably absent from that continent so far. Records from France are particularly interesting. From 21 specimens collected from 4 widely scattered localities by a botanist unaware of *C. reticulatum*, 14 possessed reticulate seed coats; there is therefore reason to believe that this variant may be relatively widespread in France, though it is not mentioned in any of the French floras.

C. DISCUSSION

The evidence given in the foregoing pages suggests that *Chenopodium album* L. can no longer be regarded as a critical taxonomic aggregate, and that the status of the three

segregates included by Clapham, Tutin and Warburg (1952) under the general heading of *C. album* must now be reassessed. Of these, *C. album* itself (*sensu stricto*) appears on morphological criteria to be a good and easily recognisable Linnean species, as are the other indigenous British *Chenopodia*; although in other countries its variation pattern may be complicated by hybridization, little difficulty has been experienced in determining exact species limits from British material.

The frequent inclusion of *C. viride* in the complex seems to have resulted partly from a superficial resemblance to *C. album* and partly from a persistent nomenclatural confusion in the literature. Close examination of the two, however, has shown that consistent differences can always be detected, particularly in seed coat characters and in the pattern of the inflorescence, and the recognition of *C. viride* as an independent species by Aellen in 1933 is fully supported.

The position to be accorded to *C. reticulatum*, however, is more controversial. Whereas the separation of *C. viride* from *C. album* follows from its recognition as a distinct specific entity (even to the extent of placing it in a separate sub-section of the genus by Aellen and Just in 1943), the removal of *C. reticulatum* as a component of the aggregate involves its degradation to a mere variant of the type species. Since it is indistinguishable from *C. album* in all features except the reticulation of the seed, its taxonomic status must depend on the weight to be attached to this single variable character. Admittedly the reticulation appears to have some genetic basis, and seed coat characters are generally reliable diagnostic criteria in the genus as a whole; but the character is so variable in its expression under different environmental conditions, and so unsupported by other morphological differences, that it seems only reasonable to consider those individuals with reticulate seeds as representing part of a variation pattern within the strict limits of *C. album* itself, a conclusion which is supported by the indications of gene-flow between smooth- and reticulate-seeded plants in the cross-breeding experiments.

Given, however, that the character of reticulate seeds shows quite high heritability, it is of some theoretical interest to consider the way in which intra-individual variation in reticulation may be interpreted. Although xenia (in the sense of Crane and Lawrence, 1947) has been suggested to account for similar variation in other species of *Chenopodium* (Kowal, 1953), this is considered improbable in this case in view of the results of the breeding experiments; these clearly demonstrated that the pollen had no effect upon the seed coat marking of the parental generation but only on the F_1. There is moreover little evidence of differential cytoplasmic influence, so that the only concept remaining is that of individual flexibility arising to a greater or lesser extent as a consequence of ' poor organization ' (Thoday, 1953).

It has already been indicated earlier that individual species of *Chenopodium* frequently exhibit polymorphism. This has been defined by Ford (1940, 1945) as the occurrence of two or more forms of the same species together in the same habitat, and by his definition it is also necessary to show that the existence of the rarest of the forms observed cannot be explained in terms of recurrent mutation. Since, however, even if the form appears in only a small proportion of the population it is very probable that it owes its presence to selection, it is reasonable to assume that the seed coat variation in *C. album* is a true example of polymorphism. Indeed the existence of a large breeding population in this taxon makes it even less likely that mutation pressure alone could account for the observed frequency of reticulate seeds. From the preliminary data given here it is impossible to determine whether the postulated seed-coat polymorphism in *C. album* is transient or balanced. Certainly the distributional data gives no evidence pointing to a recent rapid spread of the reticulate seed-coat genes through the *C. album* population, and this in itself suggests caution in using this character alone to indicate even incipient speciation.

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AN AUSTRALASIAN SPECIES OF *CRASSULA* INTRODUCED INTO BRITAIN

By J. R. Laundon

Abstract

A species of *Crassula* found growing in a pond at Greensted, Essex, in 1956, was identified as *Crassula recurva* (Hook. f.) Ostenf., non N.E.Br., a native of Australia. A study of the latter and related species has shown that *C. recurva* is synonymous with *Crassula helmsii* (T. Kirk) Cockayne, a plant described from New Zealand. It is suggested that *Crassula helmsii* merits recognition as an established alien in Britain.

Crassula helmsii (T. Kirk) Cockayne in Trans & Proc. New Zealand Inst. **39** : 349 (1907) – A. Berger in Engler & Prantl, Natürl. Pflanzenfam., ed. 2, **18a** : 389 (1930). *Tillaea verticillaris* sensu Hook., *Ic. Pl.* **3** : 295 (1840), *excl. descript.*; *non Tillaea verticillaris* DC. (1828). *Bulliarda recurva* Hook f. in Hook., Lond. J. Bot. **6** : 472 (2) (1847), *nom. nud. Tillaea stuartii* F. Müll. ex Hannaford, Jottings in Australia : 45 (1856), *nom. nud.* – F. Müll., Frag. Phyt. Australiae **11** : 118 (1881) *in synon. Tillaea recurva* Hook. f., Bot. Antarct. Voy. **3** (1) : 146 (1860) – Bailey, Queensland Flora : 545 (1900) – Rodway, Tasmanian Flora : 47 (1903) – W. M. Curtis, Student's Flora Tasmania **1** : 182 (1956). Type : Tasmania, *Gunn* 393 (**K**, holotype; **BM**, isotype). *Tillaea helmsii* T. Kirk, Students' Flora New Zealand : 142 (1899) – Cheeseman, Manual New Zealand Flora : 141 (1906); ed. 2 : 480 (1925). Syntypes : New Zealand, South Island, Karamea, *Spencer*; near Greymouth, *Helms. Crassula recurva* (Hook. f.) Ostenf., Dansk. Bot. Ark. **2** (8) : 47 (1918) – Black, Fl. South Australia : 259 (1924), ed. 2 : 392 (1948) – Ewart, Flora Victoria : 557 (1930) – Blackall, How to Know Western Australian Wildflowers **1** : 178 (1954) – McBarron in Contr. N.S.W. National Herb. **2** : 171 (1955); *non Crassula recurva* N.E. Br. (1890).

Succulent perennial herb; stems creeping and rooting at the nodes, simple or branched from the base with few axillary branches, usually robust and erect when in shallow water but prostrate when on damp mud or sometimes completely submerged, to 30 cm. long, terete, glabrous. Leaves opposite, sessile, connate at the base, 4–15 (– 20) mm. long and 1–2 mm. broad, linear – lanceolate to ovate – lanceolate, entire, acute, fleshy, glabrous. Flowers solitary, axillary; pedicels 2–8 mm. long, as long as or shorter than the leaves, recurved, terete, glabrous. Sepals 4, 1·4 × 0·8 mm., connate at the base, oblong, subacute, recurved, fleshy, glabrous, green. Petals 4, 1·7 × 1·2 mm., ovate, obtuse, white to pale pink. Stamens 4, 1·3 mm. long, filaments pink, anthers black. Nectar scales 4, 0·6 × 0·3 mm., obovate–spathulate, whitish. Gynoecium composed of four whitish-green carpels, the styles erect at first, later becoming recurved and beaked. Follicles each with 2–5 seeds; seeds 0·5 × 0·2–0·3 mm., ellipsoid, often apiculate, brown, the testa smooth.

AUSTRALIA : " Throughout Australia except in the extreme north," (Ewart, 1930, p. 557). In Tasmania the species is stated to be "widespread and frequent on the margins of swampy places " (Curtis, 1956, p. 182).

NEW ZEALAND : South Island, coastal areas; apparently local.

Swamps and similar wet habitats, usually growing in mud or in water. " Flowering November and December, rarely as late as February " (Ewart, 1930, p. 557).

Vernacular name in Australia : Swamp Stonecrop.

The Canterbury Museum, Christchurch, New Zealand, kindly sent a duplicate specimen of *Crassula helmsii* to the British Museum (Natural History), London, for examination. The specimen was collected by W. Townson from Westport and was from the Carse

Herbarium No. 752/1. A detailed study reveals that the plant is identical with specimens of *Crassula recurva* (Hook. f.) Ostenf., non N.E.Br., a species native to Australia. When Kirk (1899, p. 142) described *Tillaea helmsii* he wrote : " This species is closely related to the Australian *T. recurva*, Hook. f., but differs in the larger size, longer leaves and pedicels, more especially in the longer scales and in the acuminate sepals and petals.* I have only scraps of this species. Better specimens must be obtained before a satisfactory diagnosis can be drawn." The description by Cheeseman (1925, p. 480) is more detailed and some of the differences given by Kirk between *T. helmsii* and *T. recurva* are repeated ; Cheeseman states that *T. helmsii* is " Very near to the Australian *T. recurva* Hook. f., which, however, is a larger plant, with more pointed leaves, and with the calyx-lobes and petals decidedly acuminate." It is true that some specimens of *Tillaea recurva* are taller and have longer leaves than the specimen of *T. helmsii* in the British Museum, but other specimens of *T. recurva* from Australia are about the same size as the specimen of *T. helmsii*. The leaves of specimens of both *T. recurva* and *T. helmsii* are acute and identical in shape and there is no justification for describing the leaves of *T. recurva* as " more pointed." Moreover, the sepals and petals of *T. recurva* are not " decidedly acuminate," although they occasionally appear to be so in dried specimens; an examination of living material reveals that the sepals are subacute and the petals obtuse. Thus there appears to be no justification for the continued separation of *T. recurva* and *T. helmsii* as different species.

The name *Crassula recurva* (Hook. f.) Ostenf. cannot be used since it is antedated by *Crassula recurva* N. E. Br., described from South Africa in 1890 (Brown, 1890, p. 684).

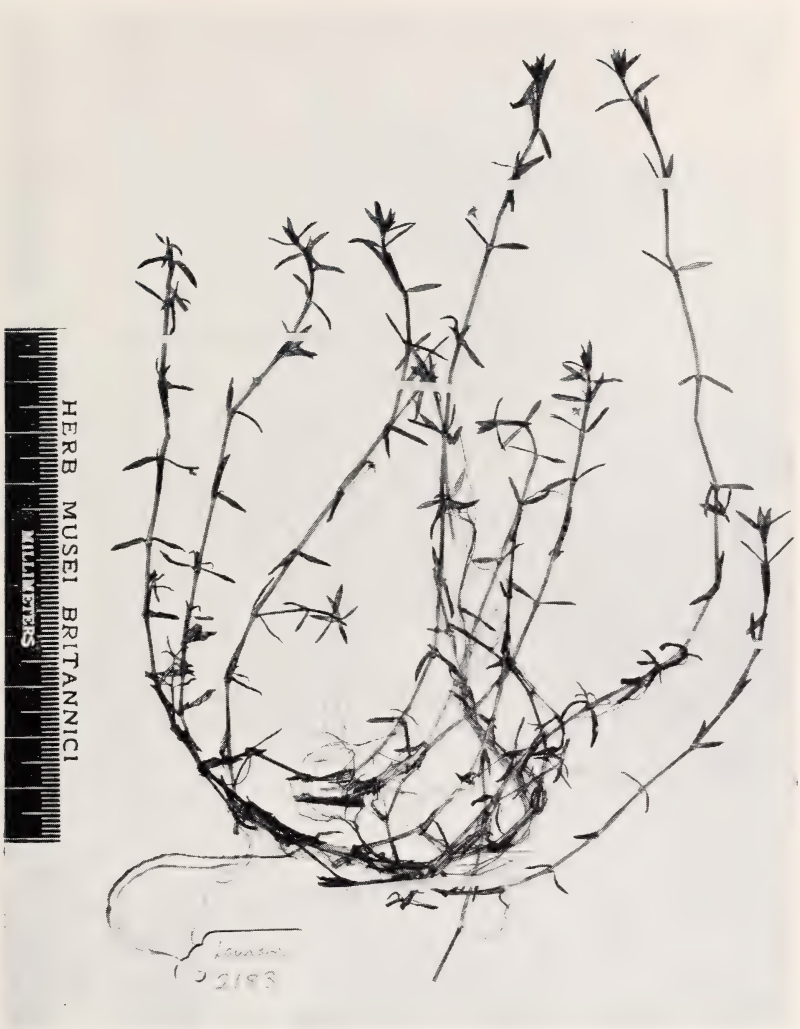
Tillaea stuartii appears to be a *nomen nudum*; the name is found on labels on a number of specimens of *Crassula helmsii* which were distributed by Müller, and in Müller (1878–1881), p. 118, "*T. stuartii*, F. v. M. First Report 11, anno 1853 " is placed as synonymous with *Tillaea recurva* Hook f. The " First Report " presumably refers to the " First General Report of the Government Botanist, Dr. F. Müller, on the Vegetation of the Colony of Victoria, in Australia; communicated by His Grace the Duke of Newcastle, Chief Secretary for the Colonies. " dated " Botanic Gardens, Melbourne, 5th September, 1853," and published in Hooker's Journal of Botany Vol. 6 p. 123 in 1854. *Tillaea stuartii* is not mentioned in the text of the report but was probably included in the catalogue which is described as follows (p. 156) : " [This Report is followed by a catalogue of all the known native plants of the Colony, systematically arranged, collected, and examined by Dr. Müller, between September, 1852, and August, 1853]." So far as can be discovered this catalogue was never published and therefore the name *Tillaea stuartii* was not published until 1856 (Hannaford, 1856, p. 45) but without any description.

Spicer (1878, p. 110), Domin (1925, p. 704) and Berger (1930, p. 389) place *Tillaea recurva* as a synonym of *Tillaea intricata* (= *Crassula intricata* (Nees) Ostenf.), whilst the *Index Kewensis* Vol. 1 (1895), Bailey (1900, p. 545) and Rodway (1903, p. 47) place *T. intricata* under *T. recurva*. Ostenfeld (1918, p. 46) shows that *Crassula intricata* is not closely related to *Tillaea recurva* but is in fact very close to *Crassula colorata* (Nees) Ostenf. (*C. acuminata* F. M. Reader). Ostenfeld bases his conclusions on a study of the type collection of *C. intricata*, namely Preiss No. 1929 in the Lund herbarium, and also on his own collection of this species in Australia. It is also evident from the original description that C. *intricata* is quite unlike *Tillaea recurva*. Nees (1844 or 1845, p. 278) describes *Tillaea intricata* as having " floribus axillaribus sessilibus oppositis pentameris distantibus " and " Flores in angulis foliorum inferiorum aggregati . . . ." Thus the flowers are very different from those of *T. recurva* which are solitary, pedicellate and 4-merous. The habitats in which the species are found are also quite different, *Crassula intricata* occurring in sandy places in the coastal area (Ostenfeld 1918, p. 47) whilst *Tillaea recurva* grows in swamps. Thus there is no justification for uniting the two species.

Crassula helmsii belongs to *Crassula* sect. *Tillaeoideae* Schönl. and to the *Crassula aquatica* (L.) Schönl. affinity. Sect. *Tillaeoideae* includes the old and ill-defined genera

*It is evident from the original description that Kirk has misworded this statement and that these characters refer to *T. recurva* and not *T. helmsii*.

PLATE 3



Crassula helmsii (T. Kirk) Cockayne from Greensted, Essex. Part of a herbarium specimen (*Laundon* 2183) in the British Museum (Natural History). 2/3 natural size.

Bulliarda DC., *Helophytum* Eckl. & Zeyh., *Tillaea* L. and several others, the merits of which are discussed by Schönland (1916, p. 41; 1929, p. 153) and Berger (1930, p. 388). There are species closely related to *Crassula helmsii* in New Zealand, South America and in Africa. *C. helmsii* closely resembles *C. granvikii* Mildbr., a species which occurs on the mountains in tropical Africa (see Hedberg, 1957, p. 100 & p. 278) but the latter has obovate petals and seeds which are minutely papillate.

In Australia *Crassula natans* Thunb. and *C. peduncularis* (Sm.) Meiger (*C. purpurata* (Hook. f.) Domin) are the only species of *Crassula*, apart from *C. helmsii*, with 4-merous, solitary, axillary flowers. *C. natans* is interesting in that it occurs also in South Africa, see Diels and Pritzel (1904, p. 210), Schönland (1916, p. 49) and Ostenfeld (1918, p. 40); it is a much smaller plant than *C. helmsii* and although some of its flowers are solitary it commonly has two flowers arising from the one axil; moreover *C. natans* has one seed in each carpel whereas *C. helmsii* has two to five. *C. peduncularis* occurs in New Zealand and South America as well as in Australia (including Tasmania); it is distinguished from *C. helmsii* and *C. natans* by the fact that many of its flowers are on long pedicels which are over twice as long as the leaves, whilst other flowers are sessile. *C. peduncularis* is often known as *C. bonariensis* Cambess. The latter name cannot be used for it is based on *Bulliarda bonariensis* DC. (1801, p. 2) which is a *nomen nudum*, whilst *Crassula bonariensis* was not described by Cambessèdes until 1829 (Cambessèdes 1829, p. 195), which was twelve years after the same species had been described by Smith (1817) as *Tillaea peduncularis* based on the same type-collection. Cambessèdes (1829, p. 195) cites *Tillaea peduncularis* Sm. in the synonymy of *Crassula bonariensis*; thus the latter is illegitimate. Some authors regard the South American and Australasian populations as distinct species, calling the latter element *Crassula purpurata* (Hook. f.) Domin. I cannot agree with this view, since the Australasian and South American plants appear to be identical in all important characters, and I am fully convinced that these plants should be united under the name *Crassula peduncularis* (Sm.) Meiger.

The introduction of Crassula helmsii into Britain

Living material of *Crassula helmsii* has been sold, under the name *Tillaea recurva*, by Perry's Hardy Plant Farm, Enfield, Middlesex, since 1927. Perry's (1960, p. 17 & p. 23) list the species under their " Submerged Oxygenating Aquatics " and under their " Collections of Plants for the Outdoor Pool. Collection 9. Six Best Oxygenating Aquatics for Outdoor Pool." The species does not appear to be sold by any other horticultural firm in England and the plant is not generally used for aquaria. It would therefore appear probable that introductions of the species in Britain have originated from plants grown by Perry's of Enfield.

The following specimens of *Crassula helmsii* have been seen from Britain :

v.c.18. SOUTH ESSEX : Greensted, pond in field next to Greensted church, Nat. Grid 52/539029, XI. 1956, *C. Bignell Pratt* s.n. (ex Herb. Lousley) (**BM**); 24. XI. 1956, *D. McClintock* s.n. (ex Herb. Lousley) (**K**); 31. VIII. 1960, *Laundon* 2183 (Plate 3) (**AK, BM, BRI, CANB, DPU, F, MEL, NSW, P, PERTH**), 2185 (**BM**), 2186 (**BM**).

21. MIDDLESEX : Enfield, cultivated at Perry's Hardy Plant Farm, 8. IX. 1960, Communicated by *Perry's* (**A, BH, BM, BP, C, G, LIL, S, TI, UPS, US, WELT**).

62. NORTH-EAST YORK : Sheriff Hutton with Cornbrough, in mud on the edge of a pool at Sheriff Hutton, VIII. 1960, *Mrs. M. Tulloh* s.n. (**BM**).

Lousley (1957, p. 14) states that *Tillaea recurva* " has also been found by Mrs. Welch near Southampton in an artificial pond." The pond referred to is at the Glen Eyre Hall, University of Southampton. In a letter to Mrs. Welch, Professor Mangham states (1957) that " our Head Gardener obtained all the plants there [at the pond] from either, 1. Perry, Enfield, Middlesex, or 2. Stewart, Ferndown, Dorset." Since *Tillaea recurva* does not appear on Stewart's lists it is probable that the plants came from Perry's. The evidence leaves no doubt that the species was planted in this locality.

Lousley (1961, p. 18) also records that *Tillaea recurva* "was reported in October [1960] by F. H. Jones from a pond at Sidcup [Kent]. Here it is known to have been introduced with *Pontederia* purchased from a well known firm of nurserymen". Mr. Lousley informs me that the nurserymen are Perry's.

There is evidence that the specimens from Sheriff Hutton with Cornbrough were also planted. Lousley (*in litt.*) states that he received specimens collected at this locality and " when I enquired I was told that it came from an ornamental pond stocked with ornamental aquatics."

The species was first collected at Greensted near Chipping Ongar, Essex, on 18th Aug., 1956, by E. B. Bangerter, and Mr. and Mrs. P. C. Hall on an outing of the London Natural History Society. The specimens were determined by Miss D. Hillcoat of the British Museum (Natural History) as referable to *Tillaea recurva* Hook. f. Later in the same year the plant was collected at the pond by C. Bignell Pratt and D. McClintock. The records were published by Lousley (1957, p. 14) and Kent & Lousley (1957, p. 347). The latter state that " this species was probably deliberately planted." From the information contained in a letter from Mr. Lousley it is evident that this is an assumption. In 1960 I made enquiries at Greensted in order to ascertain whether the species has been deliberately planted, and the evidence was found to be conflicting. A local resident said that water-lilies and other plants were introduced into the pond by its owners many years ago and had now died out. The present owners of the pond, Dr. and Mrs. Tugendhat, and the previous owner, Miss J. Price, who have between them been familiar with the pond over the past forty years, said they have introduced no plants into the pond. Thus there appears to be no direct evidence that *Crassula helmsii* was planted at Greensted. It appears likely that the plant was introduced into the pond accidentally and has since established itself. The Tugendhat family say that the *Crassula* has been in the pond for at least six years, and was very extensive before the pond was dredged a year or two ago.

In August, 1960, *Crassula helmsii* formed a dense ' mat ' covering several square yards in extent in the north-west corner of the pond, the stems arising from the shallow water. Here the species was flowering profusely. On the opposite side of the large pond, the south side, two forms of *C. helmsii* were present. One was a prostrate form, (*Laundon* 2186, **BM**), rarely flowering, and with shorter leaves than usual, which was frequent on damp mud near the edge of the water. The second form (*Laundon* 2185, **BM**) was completely submerged and sterile and had longer, narrow, less-fleshy leaves than the erect form at the other end of the pond. This submerged form was occasional and grew in company with *Ceratophyllum demersum* L. (*Laundon* 2184, **BM**) (frequent), *Callitriche* sp. (scarce), *Potamogeton crispus* L. (scarce) beneath a floating mass of *Lemna minor* L. (abundant). In view of the fact that there is no evidence that the *Crassula* was deliberately planted in the pond, the fact that no other alien aquatics or *Nymphaea* spp. appear to occur in the pond as one would expect if the pond had been stocked with plants, and the fact that the *Crassula* has spread around the whole of the pond and has flourished there for many years, it is suggested that *Crassula helmsii* merits recognition as an established alien in Britain.

Crassula helmsii is liable to be confused with *C. aquatica* (L.) Schönl. (*Tillaea aquatica* L.). The latter species was known in Britain only from a pool near Acle Dam, Yorkshire, and is now believed to be extinct. *C. aquatica* is a much smaller plant than *C. helmsii*, rarely exceeding 5 cm. in height, the leaves only 3–5 mm. in length, and the flowers are sessile in the leaf-axils, not on pedicels 2–8 mm. long as in *C. helmsii*.

Crassula helmsii flowers in August and September in Britain.

Acknowledgments

I wish to thank Miss D. Hillcoat for her work in the determination of the alien *Crassula* from Greensted and for comparing specimens of *Tillaea recurva* with *Crassula helmsii*, and Mr. J. E. Dandy for reading the manuscript. I am also grateful to Dr. W. R. Philipson of Christchurch, New Zealand, and to Perry's of Enfield for sending specimens of *Crassula helmsii*.

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NOTES ON *RUMEX ACETOSA* L. IN THE BRITISH ISLES. (BEITRAG ZUR KENNTNIS VON *RUMEX* No. XV)*

By K. H. Rechinger
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After having monographed *Rumex* for all the continents except Europe, and after having published a treatment of the central European species in the second edition of Hegi's *Flora von Mittel-Europa* (1958) and written one for "Flora Europaea" (unpublished) it became apparent that most of the major taxonomic problems have been solved more or less satisfactorily except two. One is *Rumex crispus* L., of the subgenus *Rumex* (formerly *Lapathum*), a polymorphic species evidently comprising several races characterized by slight morphological differences, some of them also ecologically different. But all these races are evidently interfertile and some of them are extremely invasive, and by their extensive spread and interbreeding they seem to have obscured the original distributional pattern of the other races. The second problem still unsolved is *Rumex acetosa* L. in a broader sense. In my treatment of *Rumex* in Hegi's *Flora von Mittel-Europa* as well as in "Flora Europaea" I had to admit that the treatment of this species and of its allies is still a tentative one and far from satisfactory.

The traditional way of distinguishing *R. acetosa* from the most closely allied European species is as follows :

1a. Branches of inflorescence not branching. Leaves 2 to 6 times as long as broad. Valves 3·0–3·5 mm. long. (Indigenous) *R. acetosa.*

1b. Branches of inflorescence (at least the lower ones) repeatedly branching. Valves smaller.

2a. Leaves 4–14 times as long as broad. Valves 2·5–3·3 mm. long. (E. Europe and Asia). *R. thyrsiflorus* Fingerh.

2b. Leaves 2–4 times as long as broad. Valves 3 (–4) mm. long. (Not known in wild state, cultivated as a vegetable and escaped from cultivation). *R. ambiguus* Gren.

R. acetosa is represented in the British Isles by at least four different taxa, which seem to be ecologically and to a certain extent also geographically differentiated.

1. A widely distributed and rather variable meadow type. Stem single or few from the short rootstock, straight upright, 30–70 (–100) cm. high. Stem leaves several to many, scattered nearly equally over the whole length of the stem; at least the inner basal leaves and the stem leaves acute and with acute lobes. Inflorescence often loose.

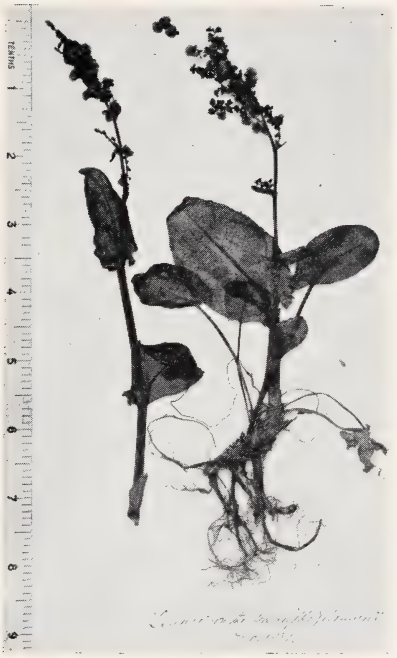
2. A coastal cliff ecotype (See plate 4) known to me so far only from sea-cliffs in Cornwall, Zennor, 20 July, 1839, *C. C. Babington* (Herb. Univ. Cantab. (CGE)), and a very similar if not identical plant also observed by myself in July 1959 in similar habitats along the north coast of Spain, Cabo Penas near Santander. Stem single from a short rootstock, stout, usually 15 (not more than 30) cm. high, with few, usually 2 to 3, stem leaves only. All leaves thickish when alive, becoming soft and membranaceous when dry, about twice as long as broad, rounded at the tip, basal lobes short, rounded. Inflorescence contracted.

3. A mountain ecotype seen from a few localities in the Scottish highlands. Stem low, 15–30 cm. high, sometimes several from the short rootstock. Leaves often rather short and rounded with short basal lobes. Stem leaves few, sometimes several from the short rootstock. Inflorescence small, ± contracted.

4. A coastal arenicolous ecotype known from the Atlantic coast of Ireland and the Outer Hebrides. Rootstock branching, with elongated straggling shoots emitting either leaf rosettes or flowering stems; the latter procumbent or ascending, often flexuous, thin,

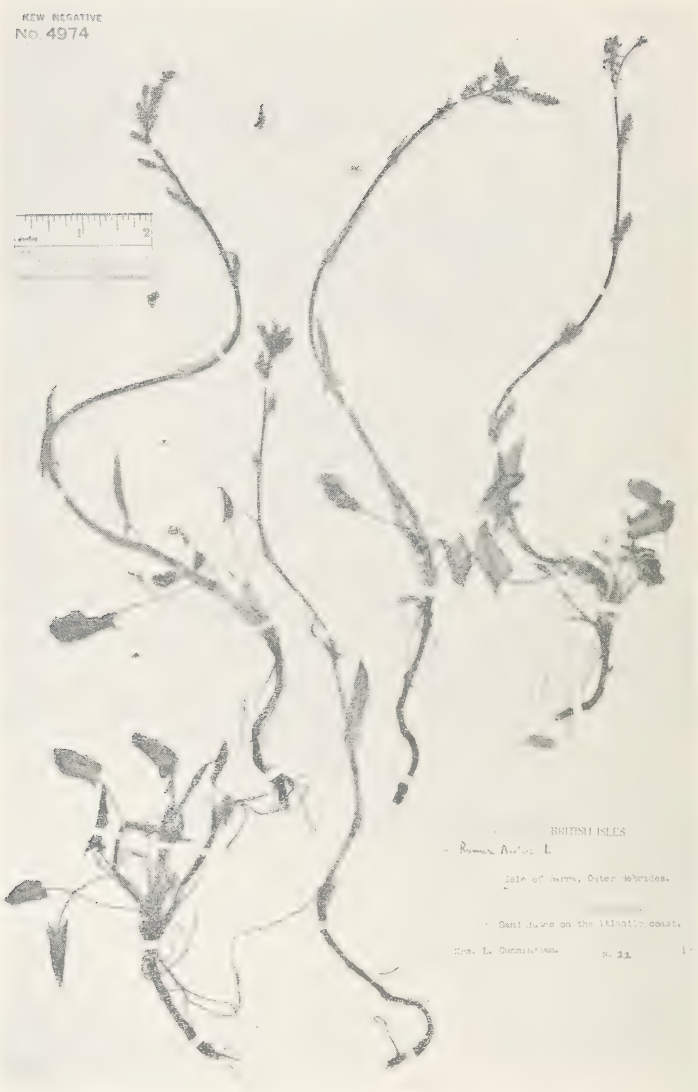
* See list of references for previous *Beiträge*

PLATE 4



Rumex acetosa L. Coastal cliff ecotype. Zennor, Cornwall, C. C. Babington, 20 July 1839.

PLATE 5



Rumex hibernicus Rech. f. Sand dunes on the Atlantic coast, Isle of Barra, Outer Hebrides, Mrs. L. Cunningham, 21 June 1946.

with either elongate short branching or abbreviated nearly simple inflorescences. Leaves very small, fleshy when alive, the basal ones 2–3, the stem leaves 3–4 (– 5) times as long as broad, mostly acute with acute deflexed basal lobes.

No. 1 corresponds to the most widely spread form which is also represented by Linnaeus's type.

No. 2 looks very distinctive, especially when alive, but I still hesitate to give it taxonomic recognition as my field experience is limited to one locality in north Spain, and as I have seen only one good fruiting herbarium specimen from Britain.

No. 3 is very imperfectly known to me from a few and incomplete herbarium specimens. It may possibly be identical with one of the taxa described from Fennoscandia as *R. acetosa* ssp. *lapponicus* Hiitonen and *R. fontano-paludosus* Kalela, the status of which is still doubtful to me.

No. 4 is the most striking of all. The first specimens I saw were those collected by Miss M. Scannell in west Ireland on sand dunes, Annagh Bay, West Mayo, 19 June 1958, in fruit, and preserved at the Irish National Herbarium. A duplicate of this specimen has been kindly presented to me by Miss Scannell and it is now in the Vienna herbarium. On 15 September, 1960, I saw the same plant growing along Dog's Bay near Roundstone, Co. Galway, on an excursion led by Prof. David Webb. Owing to the advanced season the plant had no flowers nor fruits and it looked so strange to me that I could not even recognize it as a *Rumex*. Several specimens were dug up and Prof. Webb kindly undertook to cultivate them. An excellent flowering specimen of the same taxon from sand dunes on the Atlantic coast of the Isle of Barra, Outer Hebrides, 21 June 1946, *Mrs. L. Cunningham*, is in the Kew Herbarium, and an incomplete specimen in the Cambridge herbarium, also from the Outer Hebrides, Monach Island, black sandy calcareous soil, 23 August 1949, *F. H. Perring*, evidently belongs to the same taxon. No arenicolous representative of the *R. acetosa* group was known before, as far as I know, and there is no sign of intergradation. It seems therefore advisable to give the plant specific rank in spite of the absence of distinctive fruit characters. As soon as the area of this interesting plant is better known, and, if it is indeed isolated from the other representatives of the *R. acetosa* group, as I suspect, speculation might take place whether it belongs to the coastal Atlantic element, which might have survived glaciation. The few known localities might be a hint to a similar pattern of distribution as that of *Pedicularis sylvatica* L. subsp. *hibernica* Webb (1956), which is however ecologically different from *R. hibernicus*, being a plant of blanket bogs.

Rumex hibernicus Rech. f., *n.sp.* (Plate 5) Subgen. *Acetosa* Sect. *Acetosa.* Rhizoma tenue, longe repens. Caules floriferi arcuato-flexuosi vel -ascendentes, 13–20 cm. tantum alti. Folia omnia parva, in vivo certe carnosa, in sicco crassiuscula. Folia basalia 1·5–2·5 cm. longa, 0·5–1 cm. lata, scutato-hastata, apice acuta, lobis basalibus acutis deflexis, margine interdum ± crispulis. Petiolus laminam aequans usque ea duplo longior. Folia caulina pauca sensim brevius petiolata, elongata, summa anguste linearia, margine reflexa, 20–30 mm. longa, 15–20 mm. lata, omnia lobis basalibus angustis acutis deflexis. Inflorescentia subsimplex usque breviter pauciramosa. Pedicelli filiformes quam valvae breviores. Perigonii foliola exteriora ca 1·5 mm. longa, basi connata, reflexa. Valvae (perigonii folia interiora) in statu fructifero ±3 mm. longae, ± 4 mm. latae., basi leviter cordatae, margine subintegrae vel valde indistincte sinuato-denticulatae vel subcrenulatae, tenuiter membranaceae, tenuiter reticulato-nervosae, pallide brunnescenti-virescentes interdum purpureo-suffusae, basi sub emarginatione callo minutissimo applanato reflexo provisae. Nux submatura ± 2 mm. longa, atrobruane, nitens.

Typus : West Ireland, Annagh Bay, Mullett Peninsula, West Mayo (v.c. H 27) (*M. Scannell*, **W**, **DBN**).

Geographical distribution : v.c. 110, Outer Hebrides, Isle of Barra, sand dunes on the Atlantic coast, 21 June 1946, *Mrs. L. Cunningham* No. 22 (**K**); H 12, Wexford, sand dunes, Ballyteigue Burrows, 22 May 1961, *Miss M. Scannell;* H 16, W. Galway, Dog's Bay near Roundstone, Connemara, D. A. Webb and K. H. Rechinger (no herb spec.);

H 27, W. Mayo, Annagh Bay, Mullett Peninsula, 19 June 1958, *M. Scannell* (**W, DBN**) (type locality); rocky pasture, Achill Head, Achill I., 23 June 1961, *Miss M. Scannell;* sand dunes N. of Glosh, Hullet, 12 June 1961, *Miss M. Scannell;* sand dunes S. of Annagh Head, Mollet, 12 June 1961, *Miss M. Scannell;* H 35, W. Donegal, sand dunes, Cruit Island, 24 June 1961, *Miss M. Forsyth.*

By this paper I want to draw the attention of the botanists of the British Isles to the *R. acetosa* group and to its problems. Complete fruiting herbarium material, especially from the coastal and highland districts, showing the subterranean parts would be most welcome to the author. Notes on the habitat and whether or not other representatives of the *Rumex acetosa* group were growing in the neighbourhood, and whether or not intergradation takes place, would also be most welcome. Specimens might either be sent directly to the Botany Department, Natural History Museum, Vienna, Burgring 7, Austria, or c/o the Keeper of the Kew Herbarium or the Keeper of Botany, British Museum, S. Kensington.

I wish to express my thanks to Miss M. Scannell, Dublin, for presenting duplicate specimens of the type to the Vienna Herbarium, to Prof. D. A. Webb, Dublin, for his generous hospitality and for taking me along on an excursion to the west coast of Ireland in the course of which *R. hibernicus* was observed growing, to the Keepers of the Kew and of the Cambridge herbaria for photographs of herbarium specimens, published herewith, and to Mr. J. E. Lousley for correcting the manuscript.

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NOTES ON *RUMEX ACETOSA* L.

By J. E. LOUSLEY

Dr. Rechinger very kindly invited my comments on his paper and has suggested that I add a note with a few observations.

R. acetosa is the only one of the three species with which we are concerned in Britain, since *R. thyrsiflorus* is so far unrecorded, and *R. ambiguus* occurs only in gardens. The taxonomic problems involved in *R. acetosa* in this country are very difficult indeed, and my own efforts to divide the species have been frustrated by the fact that every well marked variant transplanted to my garden has changed rapidly and the morphological characters for which it was selected have proved valueless. My experience indicates that the species is extremely plastic and that the morphological characters vary according to habitat conditions, and especially moisture. Thus, shelter or exposure to winds, and the humidity of the air, have a great influence on the variations which occur. Dr. Rechinger's paper should be a valuable stimulus to the study of these plants and it is hoped that they will encourage someone to apply to them the methods of experimental taxonomy.

Rumex acetosa is not uncommon in sandy places, and especially on dunes in the west. Salisbury lists it as an " occasional " species of late fixed dune (Salisbury, 1952, p. 254), while it is well known at Dog's Bay, West Galway (Tansley, 1939, p. 857) where Dr. Rechinger saw it. It is included in many of my lists for sandy places in the Isles of Scilly as occasional or common, while in Uig in the Hebrides, it is abundant in fixed sandy pastures of the machair (Wilmott, 1945, p. 40). Material from as many places as possible should be brought into cultivation and compared with the plant described as *R. hibernicus*.

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TRIFOLIUM OCCIDENTALE, A NEW SPECIES RELATED TO *T. REPENS* L.

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Abstract

Trifolium occidentale is described as a new species related to but morphologically, genetically, cytologically and ecologically distinct from *T. repens* L. It is known in the British Isles from relatively dry coastal habitats in W. Cornwall and the Channel Islands. It occurs on the coast of N.E. Spain, and is probably widespread in W. and N.W. France. It is believed that it is not conspecific with *T. biasolettii* Steud. & Hochst., a little-known plant from Istria and Provence which may well be conspecific with *T. repens*.

Introduction

Trifolium repens L. is one of the most widespread and variable of the clovers and many infraspecific taxa have been described from wild populations, especially in the alpine and mediterranean regions of Europe (Rouy 1899, Ascherson & Graebner 1908, Gams 1924, Hayek 1927, Vicioso 1952, Hendrych 1956). The taxonomy and nomenclature of these populations remain confused in the absence of comprehensive experimental and cytological studies, since the copious agricultural literature on this important herbage plant refers in the main only to lowland populations of doubtful natural status, or to selected ' strains ' and cultivars which are largely self-incompatible and out-breeding. In meadows, pastures and lawns there is often a range of biotypes distinct in the shape and marking of the leaflets, in flower colour, in size, and so on : these are amenable to genetic analysis but not to orthodox taxonomic treatment.

The moist, fertile man-made pastures of the schists of the Lizard peninsula (W. Cornwall) are no exception in this respect, and even the natural climax grasslands of the windswept maritime clifftops on schists, serpentine and other rocks include diverse biotypes of what may well be truly wild plants which, although often smaller in flower and leaf than the cultivated ones, and although often with petioles and peduncles remaining prostrate even when grown in a glass-house, are nevertheless clearly referable to the variable species *T. repens*.

In September 1957, I became aware that the plant recorded as *Trifolium repens* in ' Rock Heath ' (i.e. species-rich *Festuca ovina – Calluna* heath on shallow pockets of soil among serpentine rocks of the Lizard peninsula; Coombe & Frost 1956) shows a combination of characters which separates it sharply from the populations of grasslands on deeper soils. Subsequently, a systematic search with L. C. Frost in 1958 of the coast of the Lizard peninsula from Mullion to Kennack showed that not only is this distinctive *Trifolium* widespread near the sea on both schists and serpentine where the soil is sufficiently shallow (less than 15 cm.), especially on rocky knolls or south-facing slopes on the exposed west coast, but that it is, in contrast to *T. repens*, remarkable for its lack of variability. The further discovery in early 1959 of identical plants (all near the sea) at St. Ives and Mousehole (W. Cornwall), and in both Jersey and Guernsey (Channel Islands), supported the idea that this is a distinct taxon, homozygous and probably inbreeding, and not hybridizing with *T. repens* despite the juxtaposition of the two where there is an abrupt change in soil depth from place to place.

The reasons for considering this new taxon as a species distinct from any described *Trifolium* are given later; meanwhile it is convenient to refer to it as *Trifolium occidentale*.

Experimental material

Since clones of many perennial *Trifolium* species show much phenotypic variability depending on the time of year, age of the plant, and habitat (for example, dark pigmentation

is more evident in the winter and the degree of glaucousness depends on water balance and shading), ten clones of *T. occidentale* and eleven of *T. repens* for comparison were grown from comparable cuttings taken on 4 June 1959, potted up in large pans (Sankey No. 7) of John Innes compost, and kept in an unheated section (E3) of the Experimental Glasshouses at the Cambridge University Botanic Garden. During the winter and early spring the temperatures in this unheated section approximated to those in W. Cornwall. It cannot be claimed that all 21 clones grew under identical conditions because by the late spring of 1960 some of the *T. repens* clones had grown so vigorously that they were much more liable to dry out by the greater transpiration losses per pot; the plants themselves have a differential effect on their environment. In the field, of course, *T. occidentale* is the more liable to suffer drought because it grows on shallower soil than *T. repens*. Material has also been grown of both species collected from additional localities in the Channel Islands in March 1960, of *T. repens* collected from natural or semi-natural coastal habitats in Pembrokeshire and Wester Ross by H. L. K. Whitehouse in 1959 and 1960, and of *T. repens* from a number of European botanic gardens; but these plants have not been studied quantitatively.

The 21 clones studied in detail (with dates of the original collection in the field, and the underlying rock) are :

T. occidentale

O/KY Kynance, Lizard peninsula, W. Cornwall (September 1957; serpentine)*.
O/CA Caerthillian Cove, Lizard peninsula, W. Cornwall (June 1958; hornblende schist)* (Holotype); ‡ §.
O/GG Gew Graze, Lizard peninsula, W. Cornwall (June 1958; serpentine)*.
O/MU Mullion Cliff, Lizard peninsula, W. Cornwall (September 1958; serpentine)†.
O/EN Enys Head, Lizard peninsula, W. Cornwall (September 1958; serpentine)†.
O/MO Mousehole, nr. Penzance, W. Cornwall (January 1959; granite)* ‡.
O/IV The Island, St. Ives, W. Cornwall (January 1959; 'greenstone')* ‡.
O/GR Grandes Rocques, Guernsey, C.I. (April 1959; granite)† ‡.
O/PS Port Soif, Guernsey, C.I. (April 1959; blown sand over granite)† ‡.
O/JY Grosse Tête, Jersey, C.I. (April 1959; granite)† ‡.

T. repens

R/SW Canton du Pois, St. Bernard, Switzerland (Miss J. E. Tutin; June 1957).
R/LA Grassland C, Lakenheath Warren, W. Suffolk (July 1957, slightly calcareous sand).
R/GG Clifftop turf, Gew Graze, Lizard peninsula, W. Cornwall (September 1957; serpentine).
R/LU Lulworth Cove, Dorset (September 1957; Weald clay).
R/CA Caerthillian Cove, Lizard peninsula, W. Cornwall (June 1958; hornblende schist).
R/TR Tresco Flats, Scilly Islands, W. Cornwall (June 1958; acid blown sand).
R/IV The Island, St. Ives, W. Cornwall (January 1959; 'greenstone').
R/GY Cobo Bay, Guernsey, C.I. (March 1959; granite 'head' and loam).
R/GW Gweek, nr. Helston, W. Cornwall (Mrs. R. Henning, May 1959).
R/PO Poulsallagh, Burren, Co. Clare (June 1959; Carboniferous limestone).
R/YU Hajla, Yugoslavia (C. D. K. Cook, August 1959).

* Specimens pressed in June 1959 in **CGE, K, BM** and **G.**
† Specimens pressed in June 1959 in **CGE.**
‡ Specimens pressed in May 1960 in **CGE, K, BM** and **G.**
§ Specimens collected in the field at this locality in June 1958 in **CGE, K, BM** and **G.**

Diagnosis and description of Trifolium occidentale sp. nov.

The diagnosis and description are based on living plants of nine of the ten 'experimental' clones listed above (excluding clone O/PS) and therefore include clone O/CA,

from which both the specimen designated as the holotype and the isotypes were prepared, and eight other clones which I believe to be identical with O/CA. These nine clones are, I believe, identical with all but three individuals of the many thousands of plants of *T. occidentale* which I have examined in the field; the exceptions are clone O/PS from Guernsey and two further clones collected in Guernsey and Jersey in 1960, which differ in the pigmentation of the leaves.

Trifolium occidentale sp. nov. *T. repenti* ramis repentibus atque habitu generali similis; sed differt foliolis minoribus (fere 10 mm. × 10 mm.), crassioribus, subrotundis, vel obtusis vel emarginatis, glaucis, omnino immaculatis, marginibus vel cum dentibus paucioribus vel vix dentatis, nervis lateralibus in planta iam viva oculis nullo modo adjutis non translucentibus, paucioribusque, petiolis cum pilis flexuosis sparsis sed persistentibus praeditis, stipulis vini rubri colore, capitulis aliquantulum minoribus (fere 20–24 mm. latis) cum floribus lacteis paucioribus, 20 (–40) - floris, inodorisque, dentibus calycis in infima parte cum marginibus valde hyalinis, vel rectis vel convergentibus, duobus superioribus vel ovato-lanceolatis vel triangularibus et saepe in margine superiore 1–2 denticulis munitis, tribus inferioribus praedictis fere dimidio brevioribus, ovato-lanceolatis, vexillo corollae (cum ungue) 8–9 mm. longo.

Praecocius quam *T. repens* et florescit (a mens. Mart. exeunt. usque ad med. mens. Apr.) et deflorescit (a med. mens. Iun. ad med. mens. Quint.). In locis aridioribus calidioribusque habitat, in saxosis, in arenosis et in pascuis siccis, nunquam nisi in maritimis.

Holotypus in Herb. Univ. Cantab. (**CGE**) : Caerthillian Cove, near Lizard Town, W. Cornwall (v.c. 1), England; south-facing grassy slopes on shallow soil over hornblende schist, within 200 m. of the sea; altitude 20 m.; Clone O/CA, collected 23 June 1958; cultivated in Hort. Univ. Cantab.; pressed 3 June 1959. Isotypi in Herb. Bot. Reg. Kew (**K**), Herb. Mus. Brit. (Hist. Nat.) (**BM**), Herb. Cons. Bot. Genev. (**G**).

Similar to *T. repens* in general appearance, but differing in a remarkably constant combination of characters, some of which occur in populations or individuals of *T. repens*, but which together are highly characteristic of *T. occidentale*. Stems shorter than in most plants of *T. repens*, at most times green and glabrous, but sometimes reddish and sometimes very sparsely hairy, especially near the nodes. Leaflets dark green and glaucous *without light or dark markings*, *smaller* but *thicker* than in most plants of *T. repens*, rarely exceeding 10 × 10 mm., to 250 μ thick in sections of fresh material, mostly *orbicular* or very broadly cuneate at the base and slightly emarginate. Margin very narrowly hyaline, with *fewer*, less prominent teeth (becoming more prominent on drying), or sub-entire. Upper surface matt to the naked eye, minutely crystalline with a hand-lens, strongly papillose in transverse section under the microscope; lower surface very glossy. Lateral veins *fewer*, scarcely evident from above by reflected light, *not translucent* to strong diffuse light with the naked eye (in *T. repens* the lateral veins in fresh leaves appear colourless and translucent with the naked eye although they become opaque on drying). Petiole and petiolules with sparse but *persistent* flexuous, erecto-patent or patent, *colourless hairs* to 1 mm., especially at the time of flowering (less evident in the winter). Stipules deep vinous red, margins hyaline at maturity. Peduncles green, sparsely to densely clothed in colourless erecto-patent hairs ; pedicels conspicuously reddish on the upper side, sparsely hairy, about twice as long as the translucent, pinkish bracteoles at anthesis. Heads fewer-flowered than in most plants of *T. repens* : 40-flowered on well-developed heads, but often less (about 20) even on the same plant by the abortion of buds. Flowers creamy-white (never pinkish), *scentless*, after anthesis turning pale to dark brown (without any reddish tinge). Calyx green and slightly hairy at the base, the tube reddish on the upper side, the main veins red or green, the teeth green except at their red apices and at their conspicuously hyaline basal margins. The upper two calyx teeth ± parallel or convergent at anthesis, 1·5–2 mm. long, ovate-lanceolate or triangular, the base of each 1·5 mm. broad, *often with one or two prominent teeth on the upper margins*, the lower margin broadly hyaline at the base, the upper margins touching or overlapping at the base, so leaving no sinus. The lower three calyx teeth ± divergent, not much more than half the length of the others, 1·0–1·5 mm. long, ovate-

lanceolate, the hyaline margins meeting or overlapping at their widest part (0·75–1·0 mm.), slightly constricted at their bases. Standard 8–9 mm. long (including the claw), 4 mm. broad when flattened out, limb broadly elliptical, emarginate; wings exceeding the keel, notched or slightly toothed at the apex.

Nectar with ' more fructose and glucose than sucrose, whereas the type [*T. repens*] has a preponderance of sucrose ' (M. S. Percival *in litt.*, observations based on flowering material collected at Caerthillian Cove on 19 April 1959).

T. occidentale flowers earlier than *T. repens*, from late March or early April to the end of June or early July; and grows in drier, warmer places, on rocks, in dry pastures and sand dunes, always near the sea.

Variability of T. occidentale and T. repens

The greater variability of leaf size, shape and marking of *T. repens* is evident from Fig. 1. The mean length of ten terminal leaflets (each from a leaf subtending the first inflorescence on a stem) of 11 clones of *T. repens* ranges from 10·2 mm. (R/TR) to 22·2 mm. (R/CA), and the length/breadth ratio from 0·96 (R/GG) to 1·46 (R/YU; not illustrated), whereas for *T. occidentale* the corresponding ranges are 6·5 to 8·3 mm. long, and 0·90 to 0·95 length/breadth. Of course, ontogenetic drift in leaflet shape has been minimised by considering only physiologically equivalent leaves. Similarly, the maximum stem length (1 year's growth of plants in pans) varies more widely in *T. repens*, from 16 to 39 cm., but is only 6 to 12 cm. in *T. occidentale*. Also remarkable is the very great uniformity of coloration of the green* stems and dark vinous red stipules of *T. occidentale* in contrast to the

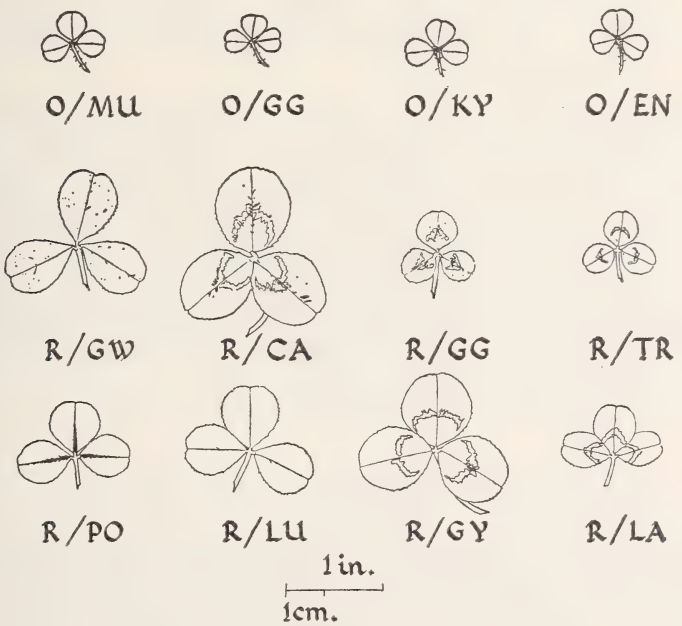


Fig. 1. Standard leaflets (see text) of four clones of *Trifolium occidentale* (top row) with neither light nor dark leaf markings, and of eight clones of *T. repens*, of which three have no light markings (R/GW, R/PO and R/LU) and two have no dark markings (R/GY and R/LA). Scale : × ½.

variation in *T. repens* in which the stems vary from green to bright or dark red, and the stipules from green to dark red veined. The length and erectness of the petioles also varies more in *T. repens* and there is clearly a selective advantage in the short, prostrate petioles of plants from extremely exposed clifftops (R/GG, 47 mm. long, R/PO, 51 mm. long)

* The stems may be reddish when the plants suffer drought.

compared with the long erect petioles (up to 129 mm.) of plants from thick *Festuca rubra – Dactylis* turf of more sheltered places. Petiole length of *T. repens* from formerly grazed grass-heath is intermediate (R/TR, 51 mm.; R/LA, 72 mm.). In *T. occidentale* petiole length varies from 37 to 59 mm. only (petiole measurements made at the same nodes as the leaflet measurements above).

Flower colour is also much more variable in *T. repens,* from pale creamy-white to the astonishingly deep, almost beetroot red of some of the plants (' var. *rubescens* DC.' of Clapham, Tutin & Warburg 1952), on Tresco Flats, Scilly Isles, where, however, the red-flowered population is clearly variable in colour and leaf-markings, R/TR being only one of a number of biotypes collected there in 1958.

So far I have found no evidence of genotypic variation in *T. occidentale* in W. Cornwall but there are two clones in Guernsey which deviate from the type. One (O/PS) forms a circular patch with marginal vigour, clearly derived from a single plant, in short sand-dune turf on the top of the 25 ft. (7·6 m.) knoll shown on the 3 in. map of Guernsey about 130 m. east of the Grandes Rocques Hotel, near Port Soif. This plant has obscure yellowish-white markings on the leaflets, but otherwise appears identical with *T. occidentale*; and as shown below, has the chromosome number, $2n = 16$, of this species. The other is a patch on the dunes about 170 m. further east-south-east and has dark markings along the lateral veins, but is otherwise typical *T. occidentale*. A hybrid origin of these two plants is unlikely in view of the chromosome numbers and breeding behaviour of *T. occidentale* and *T. repens*, and I have otherwise found no plants or populations intermediate between the two species despite their close proximity, and even intermixture, on soils of 15–20 cm. deep, in several places in Cornwall and Guernsey. A plant of *T. occidentale* from Le Pinacle, near L'Étacq, Jersey, collected in March 1960, has in cultivation scarcely glaucous, more yellow-green leaves than all the others; the 129 seedlings from an open-pollinated head of this clone all have the same coloration as the maternal parent. Otherwise it appears to be identical with other *T. occidentale*.

A consequence of the uniformity of *T. occidentale* is that each of the experimental clones, except O/PS, can be regarded as typical of the population from which it was collected, and with the exceptions mentioned, all the populations can be considered to belong to one biotype. In contrast, not only is the variation between localities very great in *T. repens*, as demonstrated, but each experimental clone is just one biotype arbitrarily selected from a genetically complex population : for example R/TR is one of a number of plants of various shades of pink and red flowers on Tresco Flats and R/GW is one of three biotypes collected by Mrs. Henning at Gweek. In some cases, however, the populations of *T. repens* appear to be more uniform in the field : R/GG, for example, seems to be the only biotype in very exposed cliff-top turf above Pigeon Ogo near Gew Graze; this may be accounted for by severe selection pressure in such extreme habitats.

Leaf anatomy

One of the most useful characters for distinguishing living *T. occidentale* is the opacity of the lateral veins of the leaflets in contrast to the nearly colourless translucence to the naked eye of those of *T. repens*. This, and the remarkable papillosity of the upper epidermis of *T. occidentale*, prompted an investigation of the leaf anatomy of the two species.

Serial sections, 16 μ thick, of the 21 clones were prepared from material collected and fixed in formalin-acetic-alcohol at the Botanic Garden on 24 October 1959. Permanent mounts stained in safranin and picric aniline blue were prepared. There was considerable shrinkage of the specimens, the mean thickness of the ten *T. occidentale* leaves being 156 μ, as opposed to about 250 μ in fresh material, but the two species showed consistent differences in structure and dimensions after preparation. O/CA and R/CA were selected for detailed study, and sections were cut at right angles to the lateral veins as well as to the main vein of the leaflets.

Fig. 2 shows the differences in structure in the region of a lateral vein between the two species. In *T. repens* the main lateral veins with their mechanical tissue (collenchyma or cellulose fibres) occupy two-thirds (or more) of the thickness of the mesophyll, and only a single layer of palisade intervenes between the vein and the upper epidermis, in which the

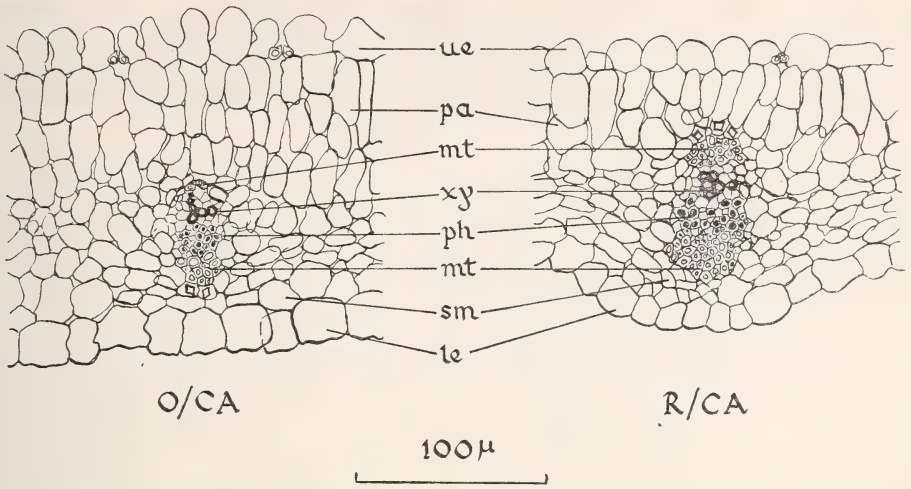


Fig. 2. Transverse sections (at right angles to the lateral veins) of leaflets of *Trifolium occidentale* (O/CA) and *T. repens* (R/CA); fixed and stained material. *ue*, upper epidermis; *pa*, palisade mesophyll; *mt*, mechanical tissue (bundle caps of collenchymatous appearance); *xy*, xylem; *ph*, phloem; *sm*, spongy mesophyll; *le*, lower epidermis. Scale : × 250.

cells are characteristically broader than high; whereas in *T. occidentale* the mechanical tissue is poorly developed on the adaxial side so that the whole vein occupies barely half the thickness of the mesophyll and three layers of palisade lie between the vein and the upper epidermis of which the cells are much higher than broad, having indeed a high conical or cylindrical form in section. The lower epidermis also tends to be thicker in *T. occidentale*.

There is, however, no absolute difference in the thickness of epidermis and mesophyll between the two species, although the total thickness of upper and lower epidermis is considerably less (mean 34 μ after preparation) in 10 out of 11 of the *T. repens* clones than it is in 9 out of 10 of the *T. occidentale* (mean 44 μ). The exceptional plants are R/PO, with a highly papillose upper epidermis, the upper and lower epidermis together totalling 44 μ, and O/PS which has the thinnest of the *T. occidentale* leaves and with a total epidermal thickness only 34 μ.

Leaf thickness and epidermal characters cannot, then, be regarded as diagnostic of *T. occidentale*, but the relation between the palisade and the lateral veins leading to the opacity of the latter appears to afford an important distinguishing character; indeed, in other sections prepared from pressed specimens of both species collected in the field the difference in development of the mechanical tissue is even more marked than in the sections of material grown in the glass-house.

Phenology

T. repens normally flowers from late May to September, but in 1959 *T. occidentale* was in full flower, both on granitic rocks and on sand dunes, in Guernsey on 2 April; and on south-facing slopes at Caerthillian Cove in W. Cornwall, where it had evidently been in flower for a few weeks already, on 18 April. By the beginning of July in 1958 and 1959 many plants of *T. occidentale* had finished flowering on the Lizard peninsula, and on 2 July 1959 some had ripe seed. In a warm glass-house at the Botanic Garden *T. occidentale*

O/CA had fully opened flowers on 15 March 1959 whereas *T. repens* R/CA had none until 27 April. The dates of flowering, however, depend very much on the age and vigour of the plants, so systematic observations were made in the spring of 1960 in the unheated glass-house on the 10 clones of *T. occidentale* and 11 of *T. repens* grown from comparable cuttings taken on 4 June 1959.

Table 1 shows that on the average the 10 clones of *T. occidentale* showed the tips of the earliest inflorescences on 14 March 1960, 46 days before *T. repens* (29 April); as the temperatures rose through April and May the differences between the two species became less. Even so, the first flowers were fully open, on the average, on *T. occidentale* 23 days before those on *T. repens* (24 April and 17 May respectively).

TABLE 1.

Mean dates of stages of flowering of 10 clones of *T. occidentale* and 11 clones of *T. repens* in a cold glass-house, 1960.

INFL = 1st inflorescence just visible beyond stipules.
TCEC = tip of corolla of most advanced flower just exceeding the calyx.
CFO = corolla fully open (anthers ripe).
CPA = corolla past anthesis (pedicel deflexed, corolla brown–*T. occidentale* – or pinkish–*T. repens*).

	INFL		TCEC		CFO		CPA
T. occidentale							
Mean date	14 March		18 April		24 April		4 May
Days from 1 March	13·6		48·6		55·0		64·8
Interval		35·0		6·4		9·8	
Standard deviation	7·6		3·3		3·2		2·3
s.e.m.	2·4		1·1		1·0		0·7
s.e.m. × ‘t’	5·4		2·4		2·3		1·6
($n = 9$, P = 0·05)							
T. repens							
Mean date	29 April		13 May		17 May		26 May
Days from 1 March	60·4		73·5		78·4		87·6
Interval		13·1		4·9		9·2	
Standard deviation	8·4		7·1		8·4		6·5
s.e.m.	2·4		2·0		2·4		1·9
s.e.m. × ‘t’	5·3		4·5		5·3		4·1
($n = 10$, P = 0·05)							
Difference (days) (*T. repens* – *T. occidentale*)	46·8		24·9		23·4		22·8

In the field in 1959 *T. occidentale* flowered earlier than in the glass-house, probably because of the higher near-surface temperatures on sunny south-facing slopes in the sunny coastal habitats than in the well-ventilated, unheated glass-house, whereas by mid-May the glass-house was much hotter by day than the normal habitats of *T. repens*, so this species flowered *later* out-of-doors.

The variability of *T. occidentale* is again rather small : all 10 clones opened their first flowers within 10 days (19–29 April), whereas the corresponding period for *T. repens* was 24 days (9 May–2 June).

None of the cuttings of the 10 plants of *T. occidentale* taken on 4 June 1959 subsequently flowered in that year, but all 11 cuttings of *T. repens* flowered before 4 October 1959. Similar observations have been made on these and other clones in 1958 and 1960.

In 1961 *T. occidentale* was flowering abundantly at Cudden Point near Perranuthnoe, W. Cornwall, on 3 April and, judging by the number of fully deflexed brown flowers, had

reached anthesis 10 days or a fortnight earlier. In a much warmer glass-house in 1961, all ten clones of *T. occidentale* flowered about 5 weeks earlier than in the cooler conditions of 1960.

Communities

Thirteen 1 m². quadrats each containing *T. occidentale* (10 from the Lizard peninsula and 3 from the west coast of Guernsey) contain 102 species of vascular plants; four additional quadrats containing *T. repens* but no *T. occidentale* include a further 8 species. The lowest value of pH recorded (air-dry soils in 1:5 suspension; glass electrode) is 5·1

Table 2.

Constancy of *Trifolium occidentale* and *T. repens* and their associates in three noda based on sixteen 1 m². quadrats from the Lizard peninsula (W. Cornwall) and Guernsey (Channel Islands). Constancy on a scale of 1 to 4 for Noda 1 and 3, 1 to 8 for Nodum 2. For details of habitats, and additional species only occurring once in the sixteen quadrats, see the text. Species marked + also occur in Nodum 4.

Nodum No.	1	2	3
No. of 1 m². *quadrats*	4	8	4
+Festuca rubra	4	8	4
+Plantago lanceolata	4	8	4
+Hypochoeris radicata	3	8	4
+Leontodon taraxacoides	3	8	4
Armeria maritima	4	7	2
+Dactylis glomerata	1	8	4
+Daucus carota [1]	4	5	4
+Plantago coronopus	4	7	2
Aira caryophyllea	2	8	2
+Lotus corniculatus	2	6	4
Sedum anglicum	4	6	2
Holcus lanatus	1	6	4
+Koeleria cristata	1	7	3
Anthyllis vulneraria	3	4	3
Festuca ovina	2	5	3
+Cerastium atrovirens	3	5	1
Jasione montana	1	7	1
+Bellis perennis	1	4	3
Cynosurus cristatus	1	2	4
Sonchus oleraceus	2	2	2
+Cochlearia danica	2	2	1
Lolium perenne	2	2	1
+Ononis repens	1	1	2
Silene maritima	1	3	1
+Trifolium occidentale	4	8	–
+Bromus ferronii	4	6	–
Trifolium scabrum	3	4	–
Anagallis arvensis	1	1	–
+Catapodium marinum	4	1	–
Herniaria ciliolata	4	1	–
Aira praecox	2	–	1
Crithmum maritimum	2	–	–
Trifolium molinerii[2]	2	–	–
Scilla autumnalis	–	5	–
Erica cinerea	–	4	–
Trifolium subterraneum	–	4	–
Geranium molle	–	3	–
Trifolium micranthum	–	3	–
T. striatum	–	3	–
Calluna vulgaris	–	2	–
Filipendula vulgaris	–	2	–
Hypericum humifusum	–	2	–
Minuartia verna	–	2	–
+Poa pratensis[3]	–	2	–
Sagina procumbens	–	2	–
S. subulata	–	2	–
+Trifolium dubium	–	2	–
Betonica officinalis	–	1	4
Trifolium pratense	–	–	4
T. repens	–	–	4
Viola riviniana	–	–	4
Carex flacca	–	–	3
Crepis capillaris	–	1	3
Prunella vulgaris	–	–	3
Scilla verna	–	1	2
Ulex europaeus	–	1	2
+Ranunculus bulbosus	–	6	4
Luzula campestris	–	5	4
Agrostis tenuis	–	4	4
Anthoxanthum odoratum	–	5	3
Galium verum	–	4	3
+Thymus drucei	–	4	3
Centaurium erythraea	–	4	2
Achillea millefolium	–	2	3
Carex caryophyllea	–	3	2
Plantago maritima	–	2	3
Rumex acetosa	–	2	3
Cerastium holosteoides	–	2	1
Cirsium vulgare	–	2	1
Polygala vulgaris	–	2	1
Chrysanthemum leucanthemum	–	1	1
Agrostis stolonifera	1	–	1

1 Mostly referable to subsp. *gummifer* Hook. f.
2 In my view better regarded as *T. incarnatum* L. subsp. *molinerii* (Balb.) Hook. f.
3 Probably includes *P. subcaerulea* Sm.

on hornblende schist; the highest values are 7·1 on ' greenstone ' and 7·4 on blown sand (with shells).

The 17 quadrats, which all lie within 800 m. of the sea and below 60 m. altitude, are closely related floristically, with *Plantago lanceolata*, *Hypochoeris radicata*, *Leontodon taraxacoides* and *Festuca rubra* occurring in 16 or 17 of them, but they can for convenience be divided into four characteristic ' noda ' (*sensu* Poore, 1955), each with a number of characteristic ' constant ' species; even so, intermediates between these noda occur in many places.

Table 2 lists the species occurring in 2 or more of the 16 quadrats comprising 3 of the noda (excluding the nodum on blown sand). In every case percentage cover was recorded, but since 7 years' observation of permanent quadrats in similar communities on the Lizard peninsula shows that the cover of most species varies within very wide limits from year to year whereas the species list for any 1 m². quadrat remains fairly stable, only constancy is given in Table 2.

The four noda distinguished are :

1. The *Trifolium occidentale – Herniaria ciliolata – Catapodium marinum* nodum.

Four quadrats from near high water mark on rocky, exposed western coasts, characterized floristically by the constancy of *Herniaria ciliolata* and *Catapodium marinum* and the occurrence of *Trifolium molinerii* and *Crithmum maritimum*. The soil is very shallow, not more than 10 cm., over granite (Guernsey) or hornblende or mica schists (Lizard). The cover of living vascular plants is never complete (25–85%) and erosion of the soil is often severe. The nodum is only developed on south- to west-facing slopes of 10 to 15°, fully exposed to wind and salt spray. The differences between Guernsey and Lizard lists are very small : *Polycarpon tetraphyllum* does not occur in this habitat at the Lizard, and *Trifolium molinerii* is not known from Guernsey. At the two Jersey stations for *T. molinerii* there is no *T. occidentale*. This nodum depends for its maintenance on severe exposure and the shallow soil; it is independent of grazing and burning. The soil pH ranges from 5·9 to 6·5.

Quadrats (the code number of a clone indicates that it was collected in the quadrat).

1 (a). South side of the Grandes Rocques peninsula, Guernsey, just above high water mark; granite; pH 6·1. Additional species ; *Cynodon dactylon*, *Polycarpon tetraphyllum*, *Sagina maritima*, *Senecio vulgaris* var. *radiatus*. (O/GR).

1 (b). South slopes of the cairn north of Caerthillian Cove, Lizard, W. Cornwall, altitude 20 m., fully exposed to the sea : hornblende schist; pH 5·9. Additional species : none.

1 (c). South-west slopes of the spur between the two valleys, Caerthillian Cove, alt. 15 m., fully exposed; hornblende schist; pH 6·5. Additional species : *Sagina ciliata*.

1 (d). West-facing cliff slope above Crane Ledges, Lizard, fully exposed, alt. 15 m.; mica schist; pH 6·3. Additional species : *Spergularia rupicola*.

2. The *Trifolium occidentale – Scilla autumnalis – Jasione montana* nodum.

Eight quadrats, less exposed than the last, extending to 800 m. from the sea and to 60 m. altitude. The soil is less shallow – up to 15 cm. deep – on south-east, south or westerly slopes of 3 to 30° over granite (Guernsey) or hornblende schist or serpentine (Lizard). The cover of vascular plants ranges from 50 to 90%. In some places cattle-grazing is heavy; rabbits were numerous until 1954. Even in the absence of grazing, periodic droughts (e.g. 1949, 1955, 1959) decimate *Calluna*, *Erica cinerea* and *Festuca ovina* and leave the community open to a large number of drought-resistant and opportunist species. On deeper soils, especially in rock crevices, *Calluna* and *Erica cinerea* survive droughts but disappear under heavy grazing. Burning is insignificant as an environmental factor. Again there are few significant differences between quadrats regardless of parent rock or location : *Isoetes histrix* and *Chamaemelum nobile* (*Anthemis nobilis*) were only found growing with *T. occidentale* in Guernsey,* although they both occur widely in spots moist in the winter on both

* *T. occidentale* has recently (April 1961) been found growing with *Isoetes* and *Chamaemelum* on serpentine at the Lizard near The Rill.

schist and serpentine on the Lizard peninsula; but *Minuartia verna* and *Filipendula vulgaris* do not occur on the schists.

This nodum lacks the extreme maritime element of Nodum 1, although *Armeria maritima* and *Daucus carota* (including subsp. *gummifer*) are still constant, but the sub-mediterranean element is augmented by therophytes such as *Trifolium subterraneum* and geophytes such as *Isoetes histrix* and *Scilla autumnalis* – this last not occurring in the other noda considered here. In addition, many pasture species come in, e.g. *Dactylis glomerata*, *Ranunculus bulbosus* and *Luzula campestris*; some of these, e.g. *Galium verum*, have often been observed to suffer severe damage from salt-laden winds in more exposed places, but this species is highly resistant to droughts which kill *Calluna* and *Festuca ovina*. The measured soil pH values range from 5·1 to 6·2.

T. occidentale occurs in similar communities, but less rich in species, on ' greenstone' (diabase) or epidiorite at Cudden Point (pH 6·9) and near Bessy's Cove (pH 5·5) in Mount's Bay, W. Cornwall.

Quadrats

2 (a). South side of the Fort Hommet peninsula, Guernsey; a relatively sheltered spot with seepage of moisture in winter, similar to *Isoetes histrix* habitats on the Lizard peninsula, alt. 10 m.; granite; pH 5·9. Additional species : *Isoetes histrix*, *Chamaemelum nobile*, *Erodium cicutarium*.

2 (b). Top of Mullion Cliff, Lizard, away from the cliff edge, alt. 60 m.; serpentine; pH 6·2; essentially ' Rock Heath ' (Coombe & Frost 1956) modified by cattle-grazing, and by rabbits in the past. Additional species : none. (O/MU).

2 (c). Enys Head, on the relatively sheltered east coast of the Lizard peninsula, alt. 45 m.; serpentine; pH 6·1. Additional species : *Senecio jacobaea*, *Trifolium arvense*. (O/EN).

2 (d). Kennack Cliff, on the east side of the Lizard peninsula, alt. about 50 m.; serpentine. Additional species : *Sieglingia decumbens*.

2 (e). Rock outcrop east of the ' British Village ' at Kynance Gate, Lizard, 800 m. from the sea, altitude 60 m.; serpentine; pH 6·2. Additional species : *Polypodium vulgare*, *Umbilicus rupestris*. (O/KY).

2 (f). Summit of Carn Caerthillian, Lizard, 220 m. from the sea, altitude 45 m.; serpentine. Additional species : *Beta vulgaris* subsp. *maritima*, *Aphanes microcarpa*, *Vulpia bromoides*, *Vicia angustifolia*.

2 (g). South-facing slope of the main valley, Caerthillian Cove, Lizard, relatively sheltered, altitude 20 m.; hornblende schist. Additional species : *Euphrasia occidentalis*. (O/CA).

2 (h). North-west facing slope of the spur, Caerthillian Cove, altitude 20 m.; hornblende schist; pH 5·1; exceptional for the occurrence of *Herniaria* on a northern aspect, and transitional to Nodum 3. Additional species : *Trifolium ornithopodioides*, *Taraxacum officinale*.

3. The *Cynosurus cristatus – Betonica officinalis* nodum.

On the hornblende schist on the Lizard peninsula both north- and south-facing slopes (10 to 27° in the four quadrats) on deep moist soils (20 cm. or more) support, under heavy cattle grazing and in situations relatively sheltered from the sea, a closed turf (95 – 100% cover) rich in mesophytic perennial herbs and grasses, with few therophytes. *T. occidentale* is absent from this nodum, but both *T. repens* and *T. pratense* are constant, and it is very similar to the pastures on non-calcareous soils described from Ireland by Braun-Blanquet & Tüxen (1952) as the *Cynosurus cristatus – Centaurea nigra* Association. The Lizard nodum, however, differs notably in the abundance and constancy of *Betonica officinalis* and the absence of *Senecio jacobaea*; the local abundance of *Plantago maritima* is also remarkable. No less than 43 species are common to this and Nodum 2, and every gradation between them can be found in the field following variations in soil depth and moisture;

indeed one quadrat listed in 1958 contained both *T. occidentale* and *T. repens*; the soil depth in this quadrat varied between 16 and 22 cm. The pH of the only soil sample collected from the four quadrats is 6·1; but generally it varies between 5·1 and 6·5 in similar closed turf, the higher values occurring in flushed soils, or nearer the sea; lower values on leached knolls, or away from the sea.

Quadrats

3 (a). North-facing slope of the spur, Caerthillian Cove, Lizard, relatively sheltered although the sea is only 40 m. away, altitude 20 m. Additional species : *Ranunculus ficaria.*

3 (b). 10 m. west of 3 (a) and 4 m. below. Additional species : none.

3 (c). South-facing slope of the main valley, Caerthillian Cove, on deep, moist soil, sheltered, altitude 20 m. Additional species : *Ranunculus acris.*

3 (d). North-facing slope of the south valley, Caerthillian Cove, relatively sheltered, altitude 20 m.; pH 6·1. Additional species : *Centaurea nigra.*

4. The *Trifolium occidentale – Bupleurum baldense* nodum.

Near Port Soif and Portinfer, just north of Grandes Rocques, Guernsey, *T. occidentale* is frequent on the south-facing slopes of the rather stable coastal sand-dunes; *T. repens* also occurs, but usually in moister hollows or on north-facing slopes. In a 1 m². quadrat at Port Soif there were 39 species of vascular plants on a southerly slope of 15° with 70% vascular plant cover; 25 species (those marked + in Table 2 and in the list below) occur in Noda 1 and 2; the other 14 include widespread dune species (e.g. *Medicago lupulina*, which frequently occurs on Cornish dunes with *T. occidentale*) and many therophytes characteristic of the Channel Islands sand dunes. The strict calcicoles which occur elsewhere in Guernsey and Jersey (e.g. *Poterium sanguisorba*) are absent, although the pH in this quadrat is 7·4 and abundant snails occur.

Additional species in Nodum 4

Agropyron junceiforme
Arenaria serpyllifolia
Bupleurum baldense
Carex arenaria
Cerastium semidecandrum
Diplotaxis tenuifolia
+Erodium cicutarium
Medicago lupulina
Mibora minima
Phleum arenarium
+Polycarpon tetraphyllum
Raphanus maritimus
Saxifraga tridactylites
Sedum acre
+Senecio vulgaris var. radiatus
Silene conica
+Taraxacum officinale
Veronica arvensis
+Vicia angustifolia

On the north-east side of Port Soif, *T. occidentale* grows in the *Ammophila* zone on less stable dunes with *Matthiola sinuata* and *Lagurus ovatus.* It has not been seen on the extensive dunes of St. Ouen's Bay, Jersey, despite its occurrence on the cliffs nearby at L'Étacq but in Cornwall it occurs abundantly on blown sand, usually with *Festuca rubra* dominant and sometimes mixed with *T. repens*, at Gunwalloe Church Cove, where it was detected by Mrs. R. Henning, at Prah Sands (pH 7·4) and in many places between the railway and the sea from Marazion to Penzance (pH of a sample near the *Cynodon* locality at Marazion 6·5).

Bryophytes and lichens

Nodum 1. Except for *Xanthoria parietina*, *Ramalina scopulorum* and other saxicoles on the rock outcrops they are not important and sometimes absent.

Nodum 2. Hypnum cupressiforme and *Cladonia rangiformis* are the most constant species, although their cover rarely exceeds a few per cent. The submediterranean element is not as pronounced as in some other of the Lizard and Channel Islands communities : *Scleropodium illecebrum*, *Scorpiurium circinatum* and *Riccia beyrichiana* occur rarely. The other species are more widespread ones : *Bryum caespiticium*, *Weissia microstoma*, *W.*

controversa, *Dicranum scoparium*, *Frullania tamarisci*, *Metzgeria furcata*, *Porella laevigata*, *Camptothecium sericeum*, *Trichostomum brachydontium*, *Cladonia pyxidata* and *Peltigera* sp.

Nodum 3. Where the vascular plant cover is 100% the lush turf contains no bryophytes or lichens, but on the more open, steep north-facing slopes, especially where there is micro-terracing, the bryophytes include *Fossombronia angulosa*, *Scapania curta*, *Saccogyna viticulosa*, *Eurhynchium striatum*, *Dicranum bonjeani*, *Mnium hornum* and *Rhynchostegiella pallidirostra*, which never occur on unshaded south-facing slopes.

Nodum 4. The only bryophyte in the one listed quadrat was *Tortula ruraliformis* (cover 25%), but *Pleurochaete squarrosa* is widespread on the Channel Islands dunes, as at Kennack Sands and elsewhere on the Lizard peninsula.

Distribution

The following list summarises the localities for *T. occidentale* given under ' Experimental material ' and ' Communities,' and includes further records. In all cases I have verified the identifications personally. I have seen the plant at undated localities in both 1959 and 1960.

Isles of Scilly : Peninnis Head, St. Mary's (granite), ' in short turf near the lighthouse,' and ' seen also on St. Agnes and Gugh in similar habitats,' Mr. and Mrs. D. L. Vercoe (per Mrs. Evelyn Almond), 1961.

W. Cornwall : Godrevy Towans, ' on clayey soil,' R. C. L. Howitt, 1959 : The Island, St. Ives, ' greenstone,' 1959; Sennen, R. C. L. Howitt, 1959; Mousehole, granite, 1959; Penzance to Long Rock, blown sand and shingle, 1961; Marazion, blown sand, R. Jefferies and L. C. Frost, 1960; Cudden Point, ' greenstone,' 1961*; Prussia Cove, Bessy's Cove and Hoe Point, shales, 1961; Prah Sands, blown sand, 1961; Halsferran Cliff, shales, 1960; Gunwalloe Church Cove, blown sand, 1960; Poldhu Cove, shales, 1960; Mullion Cliff, serpentine; Pedn Crifton, hornblende schist; Pol Cornick, Vellan Head, Gew Graze, The Rill, the British village at Kynance, Yellow Carn, Carn Caerthillian, the last seven localities all on serpentine; Caerthillian Cove, on hornblende and mica schists; Enys Head, serpentine; Eastern Cliff, Kennack, serpentine.

Guernsey : Portinfer, blown sand; Port Soif, blown sand; Grandes Rocques, granite; Fort Hommet, granite; Jerbourg Point, granite.

Jersey : Le Pinacle, near L'Étacq, granite, 1960; Grosse Tête, granite, 1959.

T. occidentale probably occurs in many more coastal localities on the Land's End peninsula and on the north coast of W. Cornwall, but I cannot find it between Eastern Cliff, Kennack, and Coverack on the east coast of the Lizard peninsula. M. J. E. Coode cannot find it at Dodman Point, W. Cornwall, and H. L. K. Whitehouse has looked without success in the extreme south of Devon, in Pembrokeshire, and in Wester Ross and Sutherland. However the plant was almost impossible to detect for nearly a year after the severe drought of 1959 even in known localities.

Dr. E. W. Davies (Mrs. E. W. Woodward) has collected a plant identical with *T. occidentale* in N.W. France, where it is probably widespread, and Mr. J. P. M. Brenan has drawn my attention to two sheets from N.E. Spain in the Herbarium at Kew which we agree are probably identical with British *T. occidentale*. These are ' *T. prostratum* Bias., *Gandoger*, *Fl. Hisp. exsicc.* 77, April 1895, Pasajes, Guipuzcoa ' and ' *T. repens* β *microphyllum*, *Gandoger*, *Fl. Hisp. exsicc.* 60, April 1895, S. Sebastian, Guipuzcoa.' (Pasajes is on the coast 4 km. east of S. Sebastian). These Spanish specimens have the very characteristic calyx, petiolar hairs and leaflet shape of *T. occidentale*; as in that species the stipules appear to have been red and the leaflets unmarked, while the adaxial mechanical tissue of the lateral veins is less well developed than in *T. repens*. The early flowering and coastal localities also correspond with *T. occidentale*. Mr. Brenan agrees that these two Spanish sheets are not the same as European specimens labelled *T. biasolettii* Steud. & Hochst. (= *T. prostratum* Bias.), an obscure taxon probably conspecific with *T. repens* (see pp. 83–86).

* Specimens pressed in April 1961 in **CGE**, **K**, **BM** and **G**.

The effects of drought and on-shore gales

Acquaintance with the vegetation of the Lizard peninsula at all seasons of the year over the last ten years makes it plain that the habitats of *T. occidentale* are much more liable to severe desiccation than those of *T. repens*. Even in normal summers this is particularly apparent at Caerthillian Cove where after a hot dry spell the shallow soil of the *T. occidentale – Herniaria – Catapodium* and *T. occidentale – Scilla autumnalis – Jasione* noda on the south-facing slopes is dry and powdery and the vegetation crisp and brown, whereas in adjacent *Cynosurus – Betonica* areas with *T. repens*, both on south- and north-facing slopes, the much deeper soil, which has a good crumb structure, remains moist and the vegetation green, or bright with flowers of *Betonica* and *Leontodon taraxacoides*. During the autumn and winter the *T. occidentale* noda become green again, *Plantago coronopus* in particular contributing largely to the sward. After the very hot dry summers of 1949, 1955 and 1959 drought effects were more severe and persistent, with the wholesale death of *Calluna* and *Festuca ovina* on the shallow ' Rock Heath ' soils, and even the *Cynosurus – Betonica* nodum suffered a temporary diminution in the more mesophytic species. The heat and drought of 1959 were exceptionally prolonged, and their effects have been very striking, particularly in contrast to the very wet summer of 1958. A certain 1 m². quadrat at Caerthillian Cove had 60% cover of *T. repens* in June 1958; in July 1960 there was none, nor could I find *T. repens* (R/GG) in the clifftop turf near Gew Graze. On the granite at Grandes Rocques in Guernsey large patches of vigorous *T. occidentale* photographed in flower in early April 1959 were reduced to a few scraps of stem and leaf by March 1960, while at Jerbourg Point I could find only a few persistent stems and one seedling. On the sand-dunes north-east of Grandes Rocques the drought effects were much less apparent, although even there *T. occidentale* was reduced in area and vigour. In Jersey in March 1960 I could find only a few plants on *north-facing* slopes near Le Pinacle, and none at all on the burnt-up south-facing slopes. In June and July 1960 I saw only one withered inflorescence on the whole of the Lizard peninsula (although every locality then known was examined carefully), in a deep rock-crevice at Caerthillian Cove, while in many of the permanent quadrats set up in 1958 the plant was invisible. However in others there were a few wilted seedlings with 2 or 3 leaves (the latter half of June 1960 was again hot and dry at the Lizard before the long wet period set in). Despite the wholesale decimation of established plants, *T. occidentale* can clearly maintain itself in much drier habitats than *T. repens*. In pans in the glass-house it wilts much less readily than *T. repens*, but this may in part be due to the less rapid loss of water from the *T. occidentale* plants, which after 10 to 12 months' growth from cuttings have a much smaller total leaf area per pan.

The recovery of *T. occidentale* on the Lizard peninsula during the wet period July to September 1960 was very striking. At Enys Head, where in a particular rock crevice there were only nine small wilted seedlings on 1 July (all the old plants having died and disappeared), there were many vigorous plants 20 cm. in diameter and numerous seedlings at all stages of growth on 28 September; these were beginning to flower on 2 April 1961. *T. repens* showed a similar recovery on deeper soils in September at Gew Graze and in the quadrat at Caerthillian Cove where in June 1960 it was invisible.

T. occidentale is much more resistant to the adverse effects of on-shore gales than most *T. repens*. In early April 1959 a spell of strong westerly winds was followed by the wholesale browning of the leaves of *T. repens* (R/GY) in coastal turf on deep soil in Cobo Bay on the west coast of Guernsey, whereas nearby *T. occidentale* on dry rocky knolls, if anything even more exposed to wind and spray, was apparently unharmed and continued to flower. R/GY is, however, a plant with conspicuously long erect petioles and large leaves; possibly the smaller-leaved *T. repens* from exposed cliffs with prostrate (R/GG) or semi-prostrate (R/PO) petioles, or with a thicker, more papillose upper epidermis like that of *T. occidentale* would suffer less damage.

T. occidentale must also tolerate high sodium chloride concentrations in the soil, especially in the *T. occidentale – Herniaria – Catapodium* nodum, where it is associated near high water mark with such plants as *Crithmum* and *Spergularia rupicola*. R. L. Jefferies

has found 11·0 m.e./100 g. air-dry soil exchangeable sodium in soil samples collected by L. C. Frost from the *Herniaria – T. occidentale* quadrat 1 (d) by the sea just south of Caerthillian Cove (exchangeable potassium 2·3, calcium 22·3, magnesium 24·0 m.e./100 g., sodium forming, as m.e., 18% of the exchangeable cations determined, magnesium 40%).

Chromosome number

Among the bracteolate clovers of *Trifolium* subgenus *Trifoliastrum* to which *T. repens* belongs the chromosome number is most commonly $2n = 14$ or 16, although 28 is reported for *T. dubium* and both 14 and 32 for *T. micranthum* (Clapham, Tutin & Warburg 1952; Darlington & Wylie 1955). The most frequently reported number in *T. repens* is $2n = 32$, more rarely 48, with 64 in spontaneous or induced autopolyploids (Atwood 1944; Darlington & Wylie 1955; Pandey 1957); $2n = 16$ has not been reported in this species.

Chromosome counts on root tips of *T. occidentale* were made by M. J. E. Coode and M. J. Swift during July and August 1960. Squashes stained with aceto-orcein gave at least one unambiguous count of $2n = 16$ in each of the experimental clones : O/AC, O/GG and O/KY from W. Cornwall; O/GR and O/PS (with light markings on the leaves) from Guernsey; and O/JY from Jersey. Another plant from Port Soif, Guernsey, collected in March 1960, also gave $2n = 16$, while in May 1960 I had seen about eight bivalents in pollen-mother-cells in a plant from Le Pinacle, Jersey.

In contrast Coode and Swift found $2n = 32$ in root tips of *T. repens* from W. Cornwall (R/CA), while in R/GG and R/GY the number appeared to lie between 26 and 36, but clear preparations were not obtained of these two clones. Nevertheless, this range is consistent with the published number of 32, and my Cornish *T. repens* plants clearly differ from *T. occidentale* from adjacent localities with its uniform 16.

Self-compatibility and homozygosity of T. occidentale

In the spring of 1959 a pan of *T. occidentale* from Caerthillian Cove, from which the clone O/CA was later grown, flowered in a *warm* section of the glass-house earlier (15 March) than the others in a cool section. The early inflorescences nevertheless produced viable seed, suggesting that the plant is self-compatible, but proof was lacking as the pan may not have contained a single clone. The seed from one early inflorescence produced 30 seedlings identical with each other and with the maternal plant in vegetative and floral characters, suggesting a considerable degree of homozygosity.

The plants grown from cuttings in 1959 were used in 1960 to test these tentative conclusions. Six clones of *T. occidentale* (O/CA, O/IV, O/MO, O/GR, O/PS, O/JY) were placed in muslin cages on 8 May after any inflorescences with corollas visible and any shoots trailing over the sides of the pans had been cut off. Unfortunately, with this treatment many of the young inflorescences aborted : their peduncles bent over at the apex and the young flower buds yellowed and died. The few inflorescences that matured were few-flowered with most of the central (distal) buds abortive. The petioles lengthened excessively and the stems reddened. In the circumstances it is surprising that any seed developed. In the caged plants some of the surviving heads were self-pollinated by hand, using wedges of stiff paper to ' trip ' the flower and rub pollen on the stigma; others were carefully left untouched to see whether they were effectively autogamous. The other four clones of *T. occidentale* and the eleven of *T. repens* were left uncovered and intermixed on the bench, but heads of some were bagged in transparent paper envelopes. Bumble-bees (*Bombus* spp.) frequently visited the unbagged, uncaged flowers, and when both *T. occidentale* and *T. repens* were in flower (late May to early July) they often pollinated each species in turn. Observations were also made on three plants collected in March 1960 in the Channel Islands: these were not grown from single shoots but it is very likely that each consists of a single clone.

Ripe seeds from one open-pollinated head of each of the plants on the open bench and from all the self-pollinated heads were sown in the glass-house, warm in winter, between 24 and 27 July 1960. Some *T. occidentale* seed germinated very rapidly : up to 50% in 2 weeks and 100% in 3 weeks in a few cases. *T. repens* in general was much slower, only R/LA approaching 25% in 3 weeks, the majority giving only 0 to 5% after six months. Some of the *T. occidentale* also produced few or no seedlings within this period.

Despite the obviously deleterious effects of the cage treatment on *T. occidentale*, and the possibility that bagging depresses seed development in both species, the data in Table 3 indicate that

(a) in two wild *T. repens* clones there is a very high degree of self-incompatibility, but much seed is set with open pollination, and

(b) in *T. occidentale* (i) there is self-compatibility to a greater or lesser degree in at least 7 clones and three other plants, (ii) self-fertilization is effective in unmanipulated

Table 3.

Numbers of seed per head (24–27 July 1960) and numbers of seedlings (31 January 1961). Unless otherwise stated, all seedlings from one head are phenotypically identical with each other and with the female parent.

T. occidentale	
O/KY	Open-pollinated : 92 seeds; 12 seedlings.
O/CA	Three heads hand-selfed in cage : 2 of these aborted, the other produced 29 plump seeds; no seedlings. One head not manipulated in cage : 31 plump seeds; 1 vigorous seedling with 5 inflorescences just visible on 31 January.
O/GG	Open-pollinated : 105 seeds; 58 seedlings.
O/MU	Open-pollinated : 90 seeds; 13 seedlings plus some just germinating.
O/EN	Open-pollinated : 92 seeds; 23 seedlings. Bagged : 59 seeds; 30 seedlings plus some just germinating.
O/MO	Three heads hand-selfed in cage : 2 aborted, the other produced 1 seed (not sown). One head not manipulated in cage : 14 seeds; 2 seedlings.
O/IV	One head hand-selfed in cage : 9 seeds; 6 seedlings.
O/GR	Three heads hand-selfed in cage : 2 aborted, the other produced 11 seeds; no seedlings. One head not manipulated in cage : 25 seeds; 2 seedlings.
O/PS	(This is the clone with yellowish-white markings on the leaves; all 17 seedlings show the parental leaf-marking). Two heads hand-selfed in cage : 5 and 6 seeds; 7 seedlings, 1 with 1 inflorescence just visible. Three heads not manipulated in cage : 5, 3 and 3 seeds; 10 seedlings, 1 with inflorescence just visible.
O/JY	Three heads hand-selfed in cage : 2 rotted, 1 no seed. One head not manipulated : 20 seeds; 1 seedling with 1 inflorescence just visible. Port Soif, Guernsey, 1960. (This plant has the dark flecks along the lateral veins of the leaflets). Open-pollinated : 70 seeds; 37 seedlings with dark flecks, 18 apparently unmarked and appearing identical with typical *T. occidentale*. Bagged : 4 seeds; 3 seedlings with dark flecks, 1 unmarked. Port Soif, Guernsey, 1960. (This is another typical *T. occidentale* from blown sand). Open-pollinated : 155 seeds; 61 seedlings. Le Pinacle, Jersey, 1960. (This is the plant with paler green leaves than the type). Open-pollinated : 152 seeds; 129 seedlings (all pale green like the female parent; some heavily infected with *Uromyces* cf. *flectens*). Bagged : 5 seeds; 5 seedlings, all like the female parent.
T. repens	
R/CA	Four bagged heads : no seed in any. Open-pollinated : 106 seeds; no seedlings.
R/GY	Three bagged heads : no seed in any. Open-pollinated : 119 seeds, no seedlings.

(Other *T. repens* clones : generally about 100 seeds per open-pollinated head, but an average of about 25 in R/TR, R/PO and R/YU and only 4 in R/SW; no germination in 6 months in most).

plants, (iii) all typical (with unmarked and dark green leaves) *T. occidentale* shows a very high degree of homozygosity for all characters obvious in the seedlings, (iv) the pale-leaved plant from Le Pinacle, Jersey, also shows a high degree of self-compatibility and homozygosity, (v) the dark-flecked plant from Port Soif, Guernsey, segregates into flecked and unflecked progeny whether bagged or open-pollinated, the unflecked F_1 being phenotypically indistinguishable from typical *T. occidentale*,* (vi) the plant with yellowish-white leaf markings shows no segregation in the 17 selfed seedlings and is probably homozygous for this character, (vii) within the limitations of the observations there is no evidence of gene-flow from *T. repens* to *T. occidentale* despite the opportunities provided for cross-pollination by bees in the open-pollinated plants, all seven open-pollinated *T. occidentale* producing progeny phenotypically similar to the maternal parent, and (viii) there is no positive evidence, at least in the F_1, of gene-flow within *T. occidentale*, since neither dark flecks nor pale leaves appeared in the open-pollinated progeny of unmarked parents; but of course we do not know whether these characters in *T. occidentale* are dominant to unmarked or ' solid ' leaves as they are in *T. repens* (Atwood 1942).

Taxonomic rank

Specific rank has been given in the past to so many European taxa which are mostly regarded as synonymous with *T. repens* L. (see, for example, Ascherson & Graebner (1908), Gams (1924), Vicioso (1952)) that convincing reasons must be found for giving a binomial to a taxon clearly closely related to this variable and wide-ranging plant. Behind all the various concepts of the species lies the idea of genetic and morphological continuity within the species and discontinuity between species, but the barriers to gene flow between populations are so diverse qualitatively and quantitatively in plants that it is largely a matter of convenience which determines whether a population should be given specific rank.

A ' good ' species should be readily identifiable in the field and preferably also in the herbarium, even although many valuable diagnostic characters may be lost in the processes of pressing and drying, particularly pigmentation, scent and taste, and habit of growth. *T. occidentale* is not easy to distinguish in dried material from all plants of *T. repens*, but the ease with which many botanists to whom I have shown the plant in the field have been able subsequently to identify it in new localities encourages me to believe that it is morphologically distinct from all British *T. repens* at least. This belief and the distinct distribution of *T. occidentale* would justify its consideration as a geographic subspecies; but the apparent absence of any hybrids in the field and the evidence that it is cytologically distinct suggest that it is best regarded as specifically distinct from *T. repens*. The case for this is quite as strong as for the specific separation of *T. dubium* Sibth. and *T. micranthum* Viv., or *T. campestre* Schreb. and *T. aureum* Poll., and certainly much stronger than for separating *T. molinerii* Balb., and *T. incarnatum* L., while among the close relatives of *T. repens*, the alpine *T. pallescens* Villars and *T. thalii* Schreb. are generally regarded as species on grounds no stronger than those for *T. occidentale*.

The problem of T. biasolettii Steud. & Hochst.

There remains the possibility that *T. occidentale* is conspecific with some extra-British *Trifolium* related to *T. repens*. *T. pallescens* and *T. thalii* are both glabrous and non-creeping, and differ widely from *T. occidentale*, although *T. thalii* has $2n = 16$ (Darlington & Wylie 1955) and it would be interesting to know if it will hybridise with *T. occidentale*. This leaves only *T. biasolettii* Steud. & Hochst., a rather obscure and local mediterranean taxon, to be considered.

The original diagnosis (in Hochstetter 1827) is :

' *Trifolium Biasolettii* Steud. et Hochst. caule parum ramoso radicante adscendente, pedunculis axillaribus petiolisque pilosis, floribus hemisphaerico-capitatis, calycis dentibus subaequalibus, stipulis membranaceis pellucidis, foliolis cuneiformi-cordatis ad medium serrulatis. Bei Pola in Istrien. Steht dem *T. patens* nahe ' (' *T. patens*' is a *lapsus calami* for *T. repens*).

* But flecks are slow to develop at the high temperatures at which the seedlings were grown, and the genetic significance of the ratio of flecked/unflecked phenotypes is uncertain.

This was amplified by Biasoletto (1829), who first noticed the plant, under the superfluous name *T. prostratum* :

' Caulis prostratus radicans, stolonem emittens quandoque abortivum, ad cujus basim pedunculus exiit longior, axillaris, ante inflorescentiam procumbens, postea vero arcuato-erectus, pilosus, pilis patentibus, sub capitulo horizontalibus. Flores hemisphaerico-capitati, amoene rosei. Calycis dentes inaequales, superiores 2 reliquis maiores, virides. Stipulae membranaceae, pellucidae, caulem involventes, arista viridi subulata terminatae. Foliola cuneiformi-cordata ad medium serrulata; petioli ut in pedunculis pilosi. Legumen trispermum. Majo floret. Habitat in graminosis, pascuis siccis'. A number of localities near Pola in Istria are given, including the island Brioni, where Biasoletto first saw it.

Steudel (1841) quotes the name as *T. Biasolettianum* Steud. et Hochst., giving as synonyms *T. repens* L. var. Koch and *T. prostratum* Biasoletto, from which it is quite clear that '*T. patens*' in the original diagnosis should be *T. repens*; all specimens from the neighbourhood of Pola confirm this.

Rouy (1899) describes *T. biasolettianum* Steud. & Hochst. (= *T. Monvernense* Shuttlew. mss.) as ' une forme,' differing from typical *T. repens* in the small size of all its parts; leaflets more deeply obcordate, broader than long and more clearly emarginate; heads almost half as small; calyx teeth more unequal, the upper lanceolate, equalling the tube, the lower triangular, only half as long, more spreading; standard only half as long again as the calyx. The specimen cited in Herb. Rouy was collected by Shuttleworth from slopes in chestnut-groves at la Chartreuse de la Verne near Collobrières, and the general distribution is given as Istria and Dalmatia. Rouy adds that Shuttleworth's specimens are identical with ones from near Pola in Istria. He makes no mention of hairiness or flower colour.

Coste (1901) ignores it, although '*T. Monvernense* Shuttl. n.sp.' was collected as early as 1869 at Collobrières (specimen in Herb. Conservatoire bot. Genève).

Ascherson & Graebner (1908) describe var. B. '*Biasoletti*' [sic], distinguished from *T. repens* var. *repens* by having stems, petioles, peduncles and pedicels pubescent or with spreading setaceous hairs. The stem is described as generally not more than 1 dm. long; leaves with long petioles, leaflets similar to those of *Oxalis acetosella*, obcordate, shortly cuneate at the base, mostly 0·5–1 cm. by 0·5–1 cm., very finely toothed near the apex, often folded up; stipules ovate-lanceolate with a subulate apex, somewhat shining; peduncles long and stiff, generally much longer than the subtending leaf; heads somewhat laxer, usually about 20-flowered; pedicels fairly equal in length; calyx with triangular-lanceolate teeth separated by *obtuse sinuses*, more or less spreading; petals a beautiful pink at first, later darker but not becoming brown, about 5 mm. long, twice as long as the calyx; pod 2–3–seeded, generally not constricted, shortly stalked; seeds oval to almost reniform, red-brown.

They go on to say that it is a very characteristic plant which has been variously assessed, sometimes only as a habitat form of warm localities, sometimes as a species. They think it should be retained as a southern race, the characters not being sufficiently sharp or constant to admit it as a species.

Gams (1924) follows Ascherson & Graebner closely in their description, but gives the name as *T. repens* var. *alpestre* Gussone. This I believe to be incorrect, Gussone's plant (1826) being described as ' glaberrimum ' : it is a dwarf *T. repens* of alpine pastures in the Abruzzi Mountains ' ad nives deliquescentes,' flowering in August and September.

Hayek (1927) gives *T. biasolettii* specific rank, but one of his specimens in Hb. Hayek (Göteborg) is actually *T. physodes* Stev., a species related to *T. fragiferum*, which also has hairy petioles.

Vicioso (1951) also follows Ascherson & Graebner, but omits all reference to hairiness; he quotes a record by Sennen from 2,200–2,300 m. in the Catalonian Pyrenees, but there is no Spanish (or Portuguese) specimen in the Madrid Herbarium.

The specimens I have seen from Provence (Collobrières, Shuttleworth; la Crau, A. Albert; Draguignan, Girod) all have at least slightly hairy petioles and are superficially similar to those from Istria, as Rouy suggested, despite his omission of this character.

Leaf-markings are not evident in any specimens from the herbaria at Kew, Cambridge, Göteborg, Geneva, Toulouse or Madrid, but like flower colour these characters are usually not preserved. Some specimens are less generally hairy than the description of Ascherson & Graebner suggests; these are usually relatively lush plants which may well have come from shaded sites under *Castanea*. Sometimes the petiolar hairs are fulvous, but this may be an artefact.

Both *T. biasolettii* and *T. occidentale* differ from *T. repens* in their hairy petioles and their relatively broader leaflets, and their habitats are generally similar – warm dry places not far from the coast. The published descriptions of *T. biasolettii* would, however, suggest a number of significant differences from *T. occidentale*.

T. biasolettii	*T. occidentale*
Leaflets deeply obcordate.	Leaflets only slightly emarginate.
Stipules membranaceous, pellucid, shining.	Stipules matt, opaque, strongly vinous red.
Calyx-teeth entire, triangular-lanceolate, separated by obtuse sinuses, the two uppermost longer than the rest, ± spreading.	Calyx-teeth ovate-lanceolate, overlapping at the base, the two upper often with one or two prominent denticulations on the upper margin and about twice as long as the two lateral teeth, ± parallel or convergent.
Corolla pink, not becoming brown.	Corolla creamy-white (never pink), becoming pale to dark brown.

In fact, examination of specimens of *T. biasolettii* from Istria and Provence shows that not only are the descriptions frequently misleading but also that other important differences distinguish *T. biasolettii* from *T. occidentale*. Specimens of *T. biasolettii* from Draguignan have most of the leaflets obtuse, and not emarginate or obcordate; the standard is generally 8–10 mm., including claw (presumably Ascherson & Graebner's ' 5 mm.' refers to the limb alone); and I fail to understand their emphasized description of ' obtuse sinuses ' between the calyx teeth.

Figure 3 shows camera lucida drawings of the two upper and two lateral calyx teeth of specimens of *T. occidentale* and typical *T. repens* from Caerthillian Cove, W. Cornwall, and of *T. biasolettii* from the *locus classicus* in Istria and from Draguignan in Provence. The calyces of herbarium material were soaked in water, with a little wetting agent added, for a day before splitting the calyx along the dorsal side, opening it out, and mounting in glycerine jelly. It is evident that the shape of the teeth, triangular-lanceolate, is very similar in *T. repens* and *T. biasolettii*; that the lateral teeth are only a little shorter than the two upper in both *T. repens* and *T. biasolettii* from Istria, but appreciably shorter (relatively) in *T. biasolettii* from Provence (as Rouy's description suggests); and shorter again in *T. occidentale*, in which the ovate-lanceolate teeth, with the two upper convergent, are very distinct from all the rest. The denticulations often present (especially in cultivated plants, or in well grown plants in the field) on the upper calyx-teeth of *T. occidentale* are absent from the calyx illustrated, which was collected in the field in June from a site on very shallow soil.

Further evidence that *T. biasolettii* is more closely related to *T. repens* than to *T. occidentale* comes from examination of leaflets of herbarium material after soaking in water (with a wetting agent) for a day. Leaflets of dried *T. repens* regain the characteristic translucence of their lateral veins with this treatment, and the two leaflets, one from Istria and one from Provence, of herbarium material of *T. biasolettii* examined in this way also show translucent veins, whereas leaflets of dried *T. occidentale* retain their opaque veins after soaking. Although the mesophyll of the leaflets of *T. biasolettii* is somewhat collapsed and decayed in the herbarium material, microtome sections of material both from Istria

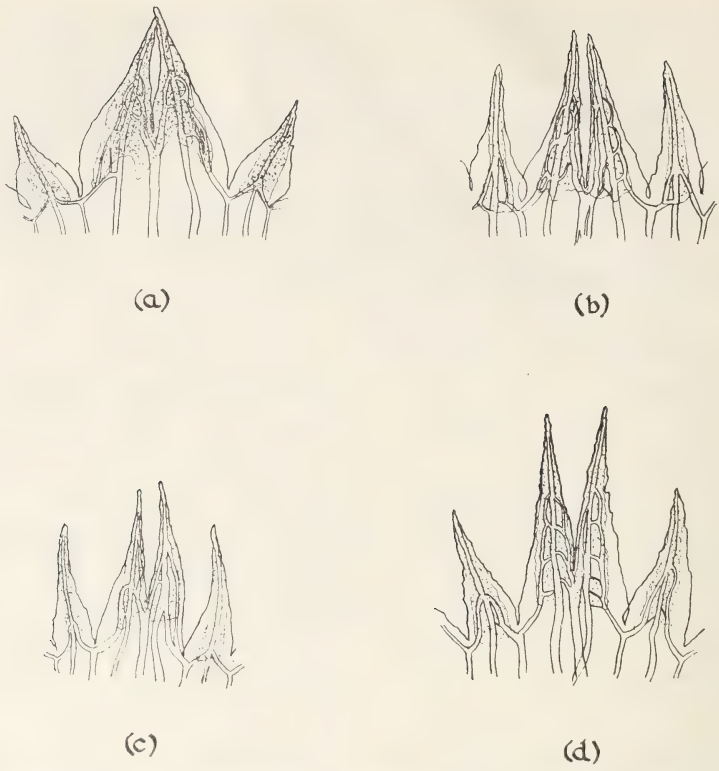


Fig. 3. The two upper (adaxial) and two lateral calyx teeth of (a) *Trifolium occidentale*, Caerthillian Cove; (b) *T. repens*, Caerthillian Cove; (c) *T. biasolettii*, Istria; and (d) *T. biasolettii*, Provence. All from herbarium material soaked in water for a day. Stippled areas : chlorenchyma. Scale : × 10.

and Provence suggest most strongly that their vascular anatomy more closely resemblee *T. repens* in that the mechanical tissue is very well developed above the lateral veins at ths expense of the palisade mesophyll (compare Figure 2). The soaked leaflets of *T. biasolettii* also suggest that the fine teeth on their margin are more numerous (15–30 on each side) than in *T. occidentale* (6–8), and again resemble *T. repens* in this respect. On the other hand, the length/breadth ratios of the soaked leaflets of *T. biasolettii* are nearer to those of *T. occidentale*, but there is clearly a wide variation and a statistical survey cannot be made on the scanty herbarium material available.

We still need more information about *T. biasolettii* from living plants – chromosome number, breeding behaviour and whether the flowers are scented or not – before coming to a firm conclusion about its status, but the morphological evidence leads me to the conclusion that *T. biasolettii* is more closely related to *T. repens*, with which it may well be conspecific, than to *T. occidentale*; and that for the time being *T. occidentale* is best regarded as a distinct species.

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SOME STUDIES IN *CALYSTEGIA*: COMPATIBILITY AND HYBRIDISATION IN *C. SEPIUM* AND *C. SILVATICA*

By Clive A. Stace

Abstract

The history of the two species, *Calystegia sepium* (L.) R. Br. and *Calystegia silvatica* (Kit.) Griseb. (= *C. sylvestris* (Willd.) Roem. et Schult.), in this country is outlined, and the merits of the characters variously employed to separate them are assessed. A numerical method, a modified Anderson Hybrid Index, is devised to enable the two species to be easily separated and any hybrids present to be recognised. Results are presented for seventy-two colonies, twelve of which were found to be intermediate between the two species. Pollination experiments were performed on various colonies of both species and the intermediates. Results given show that all colonies are totally self-incompatible, and that interspecific as well as intraspecific crosses can be successfully performed in any combination of taxa. The intermediates are thus probable hybrids between *C. sepium* and *C. silvatica*. Literature research showed that the hybrid had been previously known under several names, and that its correct name is *C.* × *lucana* (Tenore) G. Don. Both species and the hybrid were found to be commonly fertile in the field, from naturally incurred open pollination. Pollen tube and seed germination studies are described.

The significance of this system with two self-incompatible freely hybridising species producing a fully fertile F_1 generation is briefly discussed.

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1. Introduction

The presence of a related alien species of *Calystegia* (*C. silvatica*) in this country, in addition to the native *C. sepium,* has been pointed out by Lousley (1948)*. The first record of *C. sepium* is that of W. Turner for 1548 in ' The Names of Herbes ' (Clarke, 1897), and the earliest British specimen of *C. silvatica* is one from Middlesex, in 1867, in the Kew Herbarium (Lousley, 1948), although Brummitt & Heywood (1960) refer this to *C. pulchra.* The alien species is a native of south and south east Europe from south Spain eastwards to the Caspian Sea and of north Africa, being sympatric with *C. sepium* for much of its range. *C. silvatica* is widespread in Britain at present, and is commoner in the north than is *C. sepium* (Tutin, 1952). In most urban areas of south-east England it is by far the commoner species, but may be scarcer than *C. sepium* in rural habitats. It mostly occurs in waste places, hedges and shrubberies, where it may accompany *C. sepium*, but it does not seem especially common in marshy places where *C. sepium* is so typical, a fact also noted by Pospichal (1899).

The two species differ by fairly distinct characters which have been summarised with varying degrees of accuracy by several workers (Lousley (1948); Stearn (1951); Tutin (1952)).

Walters & Webb (1956) and Walters & Martin (1958) point out that intermediates occur in the neighbourhood of Cambridge, and they presume these to be hybrids. Although Dandy (1958) includes the hybrid in his ' List of British Vascular Plants,' Brummitt &

*C. *silvatica* was recorded by Praeger (1934, p. 420) from near L. Gill, Co. Sligo, Ireland.

Heywood (1960) found ' little evidence of intermediates between them there (where they are sympatric) or in this country.' Mainly on this basis they keep the two species apart, reversing the opinion of Tutin (1959) who treated *C. silvatica* as a subspecies of *C. sepium*.

Walters & Webb (1956), Baker (1957) and Walters & Martin (1958) seem agreed that both *C. sepium* and *C. silvatica* are self-incompatible, and that larger populations set seed a great deal more readily than do small populations, the former possessing some degree of genetic heterogeneity whilst the latter are usually single clones.

Work was undertaken during the summers of 1958, 1959 and 1960 on the problems outlined above, by far the most of it being conducted at Tunbridge Wells, Kent (v.c.16). Although by no means all pink-flowered plants found were considered referable to *C. pulchra* Brummit & Heywood (= *C. dahurica* sensu Walters), all were entirely omitted from this study, since opinions are by no means in agreement as to the correct status of these forms.

2. Identification of Hybrids

In order to distinguish between the two species, *C. sepium* and *C. silvatica*, and to identify any hybrids which might be found, a numerical method was devised : a modified Anderson Hybrid Index (Anderson, 1949).

The characters by which the two species differ may be summarised under the following headings :—

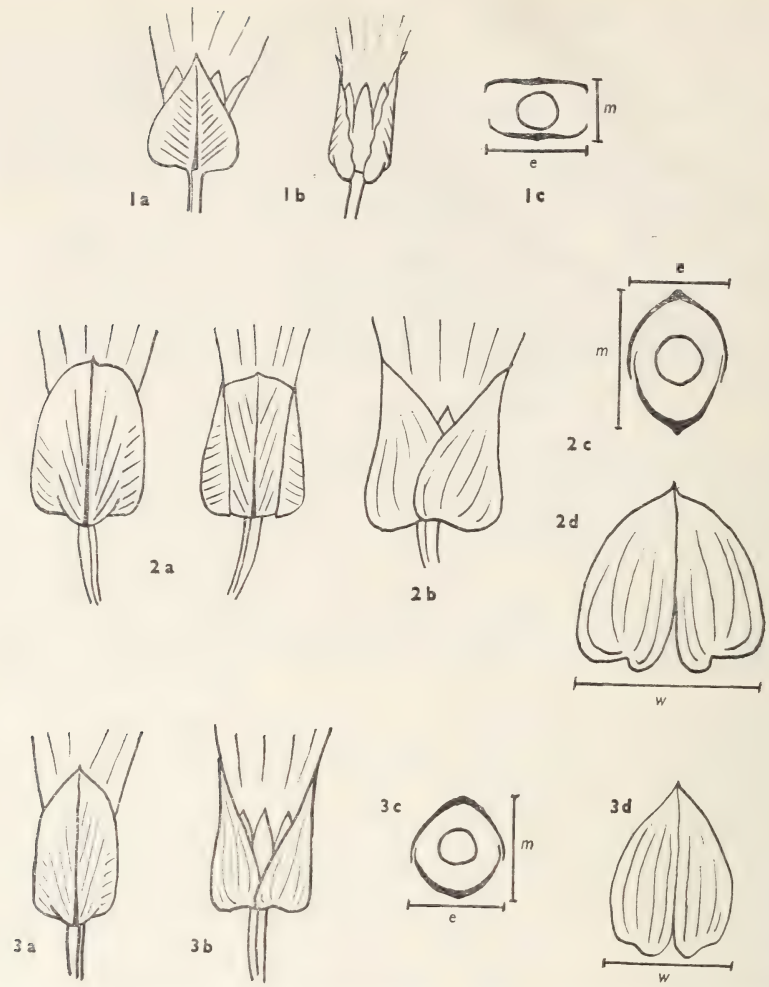
1. Size. *C. silvatica* is larger in almost all of its parts than is *C. sepium*. Stearn (1951) gives a list of the average lengths of various parts of the two species, but his figures do not indicate the ranges encountered. A list of these size differences will be found in Table 4.

2. Bracteole Shape. The bracteoles in *C. sepium* are ovate-lanceolate to ovate, acute to obtuse and rather flat. The midrib of each bracteole is not very conspicuous, being in the same plane as the rest of the bracteole. In some instances the midrib is rendered more conspicuous by becoming raised from the plane of the rest of the bracteole to give a keeled structure, especially noticeable at the base. The margins of the bracteoles are not or are very slightly wrapped around the sides of the flower, so that in side view the calyx is clearly visible usually right to the base. The margins of the bracteoles may be undulate (Fig. 1), In *C. silvatica* the bracteoles, when opened out flat, are very broadly ovate, and are obtuse or sometimes mucronate. The bracteoles are not flat but greatly inflated, and are wrapped right around the sides of the flower, rendering the calyx almost or completely invisible. In addition the midrib at the base of each bracteole is conspicuously raised so that the bracteoles are pouched or saccate. An element of asymmetry not found in *C. sepium* is present in *C. silvatica* since, where the edges of the two bracteoles meet and overlap, the same bracteole overlaps the other on each side. Thus one bracteole is larger than the other (Fig. 2).

3. Relative lengths of Stamens and Styles. The five anthers are closely adjacent to the style in *Calystegia*. In *C. silvatica* the base of the stigma lobes is always well clear of the tip of the anthers, but in *C. sepium* there is usually some and often considerable overlap, although the stigma is always clear of the stamens to some degree. Stearn (1951), however, states the opposite, since he says that the style and stamens of *C. sepium* are of the same length, but in C. *silvatica* the stamens are longer than the style.

4. Leaf Shape. Various differences are given in diverse accounts, and Scholz (1960) gives distinguishing drawings. Pospichal (1899) and Hegi (1927), however, tend to indicate that the entire range of shape is found within *C. sepium*, which is divided into two varieties partly on this feature. Although average leaf-shapes may be at variance between the two species, there is a good deal of overlap.

5. Corolla Shape. Although *C. silvatica* always has the margins of the corolla turned outwards so that there is a wheel-like brim (and the corolla is vaguely trumpet-shaped), *C. sepium* may also show this condition to varying extents. Other plants of *C. sepium* lack this character, having a straight-sided cone-shaped corolla. Pospichal (1899) and Hegi (1927) use this as a further feature for distinguishing the two varieties of *C. sepium*.



Figs. 1–3. Bracteoles of *Calystegia*. *a* & *b*. Two bracteoles from different views. *c*. Diagrammatic cross-section of bracteoles. *d*. Larger bracteole flattened out. Fig. 1. (top) *C. sepium* Fig. 2. (middle) *C. silvatica*. Fig. 3. (bottom) *C. sepium* × *C. silvatica*.

6. *Capsule Shape*. According to Tutin (1952) the smaller capsule of *C. sepium* is subglobose, whilst the capsule of *C. silvatica* is ovoid and acute.

7. *Seeds*. According to Tutin (1952) the larger seeds of *C. silvatica* are triangular-ovoid and not wrinkled, whilst those of *C. sepium* are more or less round but wrinkled. Further reference is made to fruit characters in Section 4.

Although the differences between the two species appear to be well marked, considerable confusion between them has occurred in the past. This is illustrated by the fact that *C. silvatica* was an escape in this country for at least eighty years before detection, and even in floras which recognised both species errors crept in. The diagram 3052a of Hegi (1927) appears not to be of *C. sepium* as it claims, but is according to Scholz (1960) of *C. silvatica*. It appears to the author to be closer to *C. silvatica* than to *C. sepium*, but closer still to the hybrid. In any case, the drawing is not a good one. Contrasting with this, Hutchinson's excellent drawing (1945) leaves one in no doubt that *C. silvatica* is depicted, although it is referred to *C. sepium*. This work appeared before *C. silvatica* was noticed in this country, however. Because of this confusion, considerable effort was expended in selecting the best characters for species separation.

The value of the size of various parts varies greatly from character to character, but the length of corolla and width of bracteoles were found to be the best or easiest characters to work with. Capsule shape was not used, as this would have necessitated two visits to each colony to be studied, which in many cases was not possible. In addition, capsules with less than the maximum of four seeds have a less globose shape, in extreme cases the one-seeded capsule of either species being ovoid-lanceolate. Seeds, it is thought, should be used on no account in *Calystegia*, since it is self-incompatible (see below). Seeds must be the product of two distinct clones and, although testa markings could be thought of as female alone, the shape of the seed may well be affected by the hybrid embryo inside. Since leaf and corolla shape are both too variable, and the style/stamen ratios differ but very slightly between the two species, bracteole shape was used as the only other criterion. This was measured in two ways, partly since the two methods each measured different and to some extent independent variables, and partly because size, in which two variables were measured, is considered no more important than is bracteole shape.

The precise nature of the four variables measured is as follows :—

1. *Corolla length* (*c*). Length from extreme tip of pedicel to tip of corolla.
2. *Bracteole width* (*w*). Maximum width of the bracteoles (the larger of the two if different) when flattened out. In *C. silvatica* and some *C. sepium* the midrib has to be cut longitudinally at the base to enable the bracteole to be flattened out (Figs. 2–3).
3. *Bracteole inflation* (*w*/*e*). The ratio of bracteole width (above) to *e*. This latter measurement is the width of the bracteoles in their natural state, not flattened out. Thus the lowest possible value is unity. (Figs. 2–3).
4. *Bracteole midrib conspicuousness* (*m*/*e*). The ratio of *m*, the distance between the midribs of the two bracteoles measured some 2–3 mm. from the base, to *e* (above). In *C. sepium* the value is nearly always less than unity, and in *C. silvatica* always over unity (Figs. 1–3).

It is obvious from the above that each of the four independent variables have been so arranged as to be higher in *C. silvatica* than in *C. sepium*.

These four variables were measured or calculated for six flowers randomly taken from each ' colony.' Abnormal flowers which are occasionally produced were not used. These include : flowers with abnormally small corollas (produced in the already occupied axils of some leaves late in the year); flowers with extra bracteoles (either supernumerary or modified from sepals); flowers with an extra flower in the axil of one or both bracteoles; or flowers with extra bracteoles or leaves subtending axillary flowers borne on the pedicel.

Each of the four variables was scaled to a scale of 1–10 which was constructed to embrace the entire range encountered (Table 2). This bestows equal significance to each of the four characters. The scaled figure for each variable was averaged for the six flowers, and the four averaged scaled figures were totalled. This totalled averaged scaled figure (*Ts*) was used as a character index for each colony, and is seen to run in a scale from 4 to 40. Smallest specimens of *C. sepium*, having an averaged scaled figure of one for each of the four variables, will have a *Ts* of four, whilst largest specimens of *C. silvatica* will have ten for each variable and a total of forty. The extremes actually encountered were six and thirty-five.

At first, however, two very large colonies were investigated in a slightly different manner, in order to ascertain the type of variation to be encountered. One colony (colony 72) was obviously polymorphic, appearing to the eye to consist of *C. sepium* and *C. silvatica* mixed, with no intermediates. The colony covered at least 1,000 square yards, and separation into distinct plants was not possible. Thus one flower from each branch (and there is nearly always only one in flower at a time) was treated as if a separate plant. Its *Ts* value was calculated (no averaging being here involved) and the *Ts* values of the forty-four flowers measured plotted. The results are shown in Fig. 4. Reference to this figure will show at once that two distinct taxa are present, with no intermediates. These two, *C. sepium* and *C. silvatica*, have *Ts* ranges of 7–11 and 23–29 respectively. As well as examining many known colonies in this way to make certain that the hybrid index constructed always afforded a good separation of *C. sepium* and *C. silvatica*, whether either

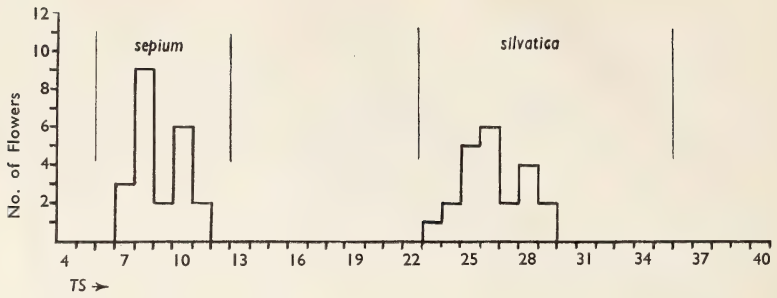


Fig. 4. Hybrid index of individual flowers of colony 72.

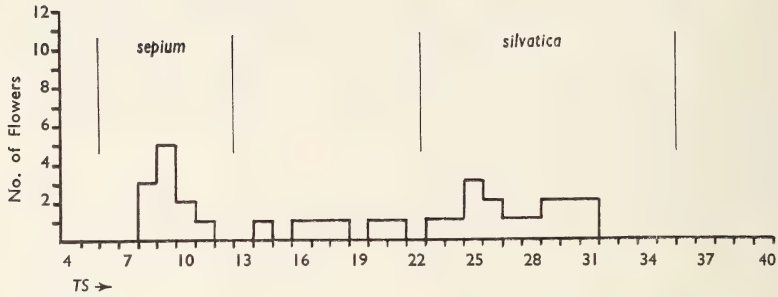


Fig. 5. Hybrid index of individual flowers of colony 71.

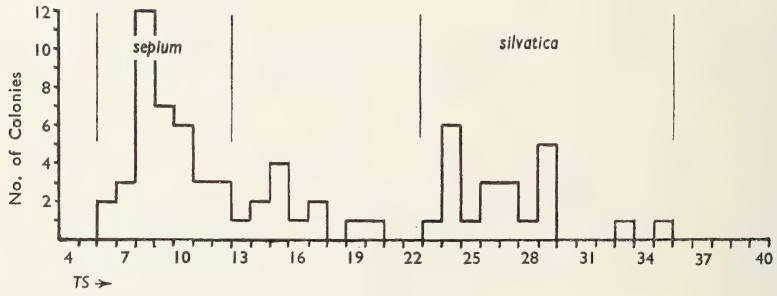


Fig. 6. Hybrid index of individual colonies of colonies 1–70.

one or both species were present in the same colonies, I searched the literature in order to gain some idea of the range of structure to be encountered throughout the whole of Europe and North Africa in the *C. sepium – silvatica* complex. It was concluded that the extreme ranges of structure described and found in the two species were quite narrow enough to fit into the present hybrid index, and still to allow the two species to be easily separated. This indicates that the four variables used are in fact suitable for species separation.

TABLE 1.

Data compiled from Colony 71.

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
45	10	2·36	7	19	23	1·21	5	72	8	30
41	10	2·41	8	17	22	1·30	5	74	8	31
38	9	2·24	7	17	21	1·24	5	72	8	29
34	8	2·12	6	16	18	1·12	4	68	7	25
39	9	2·16	6	18	22	1·22	5	73	8	28
28	6	2·00	6	14	18	1·28	5	64	6	23
53	10	2·30	7	23	27	1·18	4	80	10	31
35	8	2·33	7	15	22	1·47	6	75	9	30
32	7	2·46	8	13	20	1·54	6	71	8	29
22	4	2·20	7	10	15	1·50	6	68	7	24
30	6	2·30	7	13	17	1·31	5	70	8	26
31	7	2·07	6	15	20	1·30	5	74	8	26
18	3	1·28	2	14	8	0·57	1	50	4	10
17	3	1·31	2	13	10	0·77	2	54	4	11
16	2	1·23	2	13	8	0·62	2	48	3	9
13	2	1·30	2	10	7	0·70	2	49	3	9
15	2	1·15	1	13	9	0·69	2	49	3	8
17	3	1·31	2	13	9	0·69	2	48	3	10
14	2	1·27	2	11	7	0·64	2	45	3	9
14	2	1·27	2	11	8	0·73	2	47	3	9
15	2	1·25	2	12	7	0·58	1	46	3	8
14	2	1·27	2	11	9	0·82	3	44	2	9
18	3	1·13	1	16	6	0·38	1	48	3	8
25	5	2·27	7	11	15	1·36	5	54	4	21
22	4	1·84	5	12	13	1·08	4	51	4	17
18	3	2·00	6	9	10	1·11	4	33	1	14
20	4	1·54	3	13	13	1·00	4	56	5	16
20	4	1·82	5	11	14	1·27	5	53	4	18
24	5	2·00	6	12	14	1·17	4	56	5	20
29	6	2·42	8	12	16	1·33	5	70	8	27
24	5	2·40	8	10	15	1·50	6	64	6	25
26	5	2·36	7	11	16	1·48	6	69	7	25

Key to Letters (Lengths in mm.)

w = Bracteole Width (Flattened out).
sw = Scaled Value of *w*.
e = Bracteole Width (Natural).
m = Distance apart of Midribs.
sr_1 = Scaled Value of *w/e*.
sr_2 = Scaled Value of *m/e*.
c = Corolla Length.
sc = Scaled Value of *c*.
$Ts = sw + sr_1 + sr_2 + sc$.

The second very large colony, colony 71, differed from the last in that, to the eye, intermediates were apparently present. Otherwise the two colonies were rather similar and were treated alike. Table 1 represents the measurements and calculations for colony 71, and Fig. 5 the plotted *Ts* values. It will be seen that, as casual inspections strongly suggested, intermediates between the two species do occur in colony 71. The ranges of *C. sepium*, the intermediates and *C. silvatica* are 8–11, 14–21 and 23–31 respectively.

Colonies 1–70 were relatively isomorphic in nature and wherever pollination experiments were undertaken (see below) they proved to be uniclonal. They were always spatially isolated from other colonies, to varying degrees. Table 3 represents the measurements and calculations of just six of the seventy colonies, which are seen to be treated in the manner

TABLE 2.

Scaled equivalents of the four variables.

1 – *Corolla Length* (*c*)		2 – *Bracteole Width* (*w*)	
Scaled Number	*Measurement*	*Scaled Number*	*Measurement*
1	–39 mm.	1	–12 mm.
2	40–44 mm.	2	13–16 mm.
3	45–49 mm.	3	17–19 mm.
4	50–54 mm.	4	20–23 mm.
5	55–59 mm.	5	24–26 mm.
6	60–64 mm.	6	27–30 mm.
7	65–69 mm.	7	31–33 mm.
8	70–74 mm.	8	34–37 mm.
9	75–79 mm.	9	38–40 mm.
10	80– mm.	10	41– mm.

3 – *Bracteole Inflation* (*w*/*e*)		4 – *Bracteole Midrib Conspicuousness* (*m*/*e*)	
Scaled Number	*Ratio*	*Scaled Number*	*Ratio*
1	1·00–1·19	1	–0·59
2	1·20–1·39	2	0·60–0·79
3	1·40–1·59	3	0·80–0·99
4	1·60–1·79	4	1·00–1·19
5	1·80–1·99	5	1·20–1·39
6	2·00–2·19	6	1·40–1·59
7	2·20–2·39	7	1·60–1·79
8	2·40–2·59	8	1·80–1·99
9	2·60–2·79	9	2·00–2·19
10	2·80–	10	2·20–

TABLE 3.

Data compiled from 6 of the 70 small colonies.

Colony 3 (*C. sepium* × *C. silvatica*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
16	2	1·60	4	10	14	1·40	6	55	5	
15	2	1·50	3	10	13	1·30	5	50	4	
14	2	1·40	3	10	14	1·40	6	47	3	
17	3	1·70	4	10	15	1·50	6	48	3	
14	2	1·40	3	10	13	1·30	5	51	4	
15	2	1·67	4	9	13	1·44	6	49	3	
Mean	2		3·5				5·7		3·7	15

Colony 8 (*C. sepium*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
15	2	1·25	3	12	6	0·50	1	38	1	
14	2	1·40	3	10	5	0·50	1	38	1	
14	2	1·27	2	11	8	0·73	2	40	2	
16	2	1·23	2	13	9	0·69	2	41	2	
14	2	1·16	1	12	10	0·83	3	44	2	
15	2	1·15	1	13	8	0·61	2	45	3	
Mean	2		2				2		2	8

Colony 9 (*C. silvatica*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
28	6	2·15	6	13	20	1·54	6	68	7	
30	6	2·30	7	13	18	1·38	5	61	6	
23	4	2·10	6	11	16	1·46	6	64	6	
30	6	2·30	7	13	17	1·31	5	62	6	
28	6	2·00	6	14	20	1·43	6	66	7	
30	6	2·15	6	14	19	1·36	5	68	7	
Mean	5·7		6·3				5·5		6·5	24

Colony 11 (*C. silvatica*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
32	7	2·46	8	13	17	1·31	5	65	7	
31	7	2·58	8	12	17	1·42	6	63	6	
27	6	2·45	8	11	15	1·36	5	64	6	
31	7	2·38	7	13	19	1·46	6	64	6	
31	7	2·58	8	12	17	1·42	6	60	6	
28	6	2·80	10	10	17	1·70	7	67	7	
Mean	6·7		8				6		6·3	27

Colony 30 (*C. sepium*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
12	1	1·20	2	10	7	0·70	2	50	4	
13	2	1·30	2	10	7	0·70	2	50	4	
11	1	1·38	2	8	8	1·00	4	50	4	
15	2	1·50	3	10	8	0·80	3	53	4	
13	2	1·45	3	9	7	0·78	2	53	4	
11	1	1·38	2	8	5	0·62	2	53	4	
Mean	1·5		2·3				2·5		4	10

Colony 66 (*C. sepium* × *C. silvatica*)

w	*sw*	*w/e*	sr_1	*e*	*m*	*m/e*	sr_2	*c*	*sc*	*Ts*
22	4	1·57	3	14	14	1·00	4	54	4	
22	4	1·69	4	13	14	1·08	4	54	4	
24	5	1·85	5	13	14	1·08	4	55	5	
19	3	1·73	4	11	13	1·18	4	50	4	
23	4	1·92	5	12	13	1·08	4	49	3	
25	5	2·08	6	12	13	1·08	4	53	4	
Mean	4		4·5				4		4	17

first described. The *Ts* values are plotted in Fig. 6 : here each individual value represents a colony rather than a flower. As might well be expected, the graph in Fig. 6 shows considerable similarity to that in Fig. 5. Two main peaks, representing the two species, are present, together with numerous intermediates of varying character.

It seems likely that the intermediates shown in Figs. 5 and 6 are hybrids, *C. sepium* × *C. silvatica*, although stronger evidence for this assumption will be brought forward below.

3. Pollination and Germination Studies

Having obtained an accurate method of separating the two species and the putative hybrid, I carried out a series of pollination experiments on these three taxa. Advantage was taken of the regular flower opening sequence in *Calystegia*, a flower being in bud one day, in flower the next, and withered the next. Large buds, ready to open the following day, were enclosed in pollen-proof bags made of grease-proof paper (polythene and cellophane being rejected to alleviate condensation). Later a quicker method was employed, whereby the tip of the corolla was tied with knitting wool to prevent it from opening, the corolla itself acting as the pollen-proof bag. With intended cross-pollinations, as opposed to self-pollinations, emasculation was usually effected just prior to enclosure in the pollen-proof bag. This entailed baring the inner parts of the flower and excising the anthers, the filaments being left intact to prevent unnecessary damage. Emasculation was not always carried out, however, as *Calystegia* was known to be self-incompatible, both from the literature and from previous personal experience. However, where it was not effected, self-pollination was prevented wherever possible by supporting the flower in its bag with the apex uppermost (the stigma being distal to the anthers). Anther dehiscence occurs almost as soon as corolla opening, and is neither introrse nor extrorse, but lateral (although Warnstorf (Knuth, 1909) says it is extrorse). When the flowers had opened on the second day pollination was effected. Pollen from the chosen source was smothered on to the inside and outside of the two stigma lobes with the aid of a pencil point, after which the bag or wool was replaced. Each colony used as a pollen source was designated a colour, and a ribbon of that colour was tied on to the pedicel of all flowers pollinated from that source. Wherever possible reciprocal pollinations were effected, and pollen from as many sources as possible was used for the various flowers of each colony used as a female parent.

With three taxa, there are twelve possibilities of pollination : three selfings, three intraspecific crosses and six interspecific crosses. In addition self-pollinations were effected by pollination from one flower on to another known certainly to be on the same plant. All fifteen of these possibilities were carried out, and the results are briefly summarised below.

Selfings	*Attempts*	*Successes*
1. *sepium* flowers selfed	26	0
2. *sepium* flowers of the same plant crossed	5	0
3. Hybrid flowers selfed	9	0
4. Hybrid flowers of the same plant crossed	10	1
5. *silvatica* flowers selfed	12	0
6. *silvatica* flowers of the same plant crossed	8	0
Intraspecific Crosses		
7. *sepium* onto *sepium*	28	20
8. Hybrid onto hybrid	12	8
9. *silvatica* onto *silvatica*	14	13
Interspecific Crosses (*Hybridisations*)		
10. Hybrid onto *sepium*	10	6
11. *silvatica* onto *sepium*	12	8
12. *sepium* onto hybrid	8	4
13. *silvatica* onto hybrid	8	3
14. *sepium* onto *silvatica*	21	11
15. Hybrid onto *silvatica*	8	2

As may be seen from the above results, all three taxa are self-incompatible. Although one of the seventy self-pollinations surprisingly proved fertile, it is possible that this was the result of contamination by compatible pollen, especially as it involved transference of pollen from one flower to another rather than from the anthers to stigma of the same flower. On the other hand it could indicate that *Calystegia* is incompletely self-incompatible. All intraspecific and interspecific pollinations, in all nine of the possible combinations, proved successful to some extent, though very variously so. Although figures for interspecific pollinations are mostly the lower of the two sets, little significance should be attached to this as in many cases different colonies were involved, and the figures represent the sums of three seasons' work. The figures show that the two species are highly interfertile and that the hybrid is fertile in crosses with other hybrids and both parents, on both male and female sides. These results are considered extremely strong evidence that the intermediates between the two species, *C. sepium* and *C. silvatica*, are in fact hybrids.

The biological nature of some populations was later investigated, the results fully confirming those of Walters & Martin (1958). Small colonies, isomorphic to the eye, proved to be single clones since all combinations of pollinations proved unsuccessful. Larger colonies, nearly always polymorphic to the eye to some degree, were composed of two or more clones, since cross-pollination in certain directions produced good fertile seed. Some fairly large (isomorphic) colonies, however, proved to be single clones. Seed-set in *Calystegia* has been observed to be good in the area of study during the years 1958–60. Populations of either species and of all types of intermediates commonly bear very good quantities of seed. As Baker (1957) points out, small populations of a single clone are less likely to produce seed than are large multiclonal populations, and Baker observed that in the London area the small colonies were frequently sterile or sparsely fertile, whilst larger colonies not far distant had good seed-set. For some reason this situation appears not to exist in the present area of study, since almost all colonies produced good seed-set. In some of the larger colonies, which superficially appeared to have a better seed-set than the smaller colonies, exact counts showed that the total number of seeds produced, expressed as a percentage of the total number of seeds possible, was no larger than on many of the small uniclonal plants, which in extreme cases merely consisted of a single branch with no more than ten flowers. There are ideally and at the most four seeds per capsule in *Calystegia*. Hegi (1927) states ' seeds 4, rarely 3,' but this certainly appears to be an optimistic report. According to the number of ovules fertilized there may be any number of seeds from nil to four, capsules with one or two seeds being quite frequent, but those with nil, three or four more so. The number of seeds per capsule did not vary from species to species, nor from hybrid to species, and as far as could be ascertained the hybrid and its back-crosses appeared to be equally as fertile as the two parental species. I have found one capsule of *C. sepium* with five good seeds.

The unsuccessful self-pollinations soon made themselves quite evident as the whole flower structure, bracteoles and distal end of the pedicel had turned brown and had shrivelled by early in September. Observation on the pollen tubes of pollen on the stigma of the same flower was therefore made. Flowers were self-pollinated in the usual way, and the style and stigma removed twelve, twenty-four, thirty-six and forty-eight hours after pollination. The styles were boiled in cotton blue in lactophenol for about three minutes, when the dye stained all parts and the lactophenol entered and softened the tissues. The styles, then a tangled, limp mass, were removed and washed in lactophenol and each was squashed flat on a slide under a coverslip and ' tapped out.' Under the microscope the pollen grains and tubes appeared a dark intense blue, and the stylar and stigmatic tissue a pale blue. In all cases the pollen tubes, if present, were short and contorted, and had never penetrated more than a fractional distance into the stigma. In cases where compatible pollen had been deposited on the stigma, pollen tubes were seen to be long and straight, entering the stylar tissue. Quite obviously, assuming incompatibility to be of the normal type (Lewis, 1954), the inhibitory reaction, or lack of stimulatory reaction, (as the case may be) occurs in the stigma. Excision of the stigma did not allow self-pollination to result in fertilization, however, but the results of this experiment must be regarded as inconclusive as

yet. It is now generally considered that stigmatic inhibition indicates a sporophytic incompatibility system.

Peters (Hegi, 1927) found that the pollen of *C. sepium* is very sensitive to damp, and that in foggy conditions 50% of the grains burst. He could not get the grains to germinate away from the stigmata, glucose, sucrose and even stigma extracts not providing the essential medium. These observations were confirmed with both species on several occasions : strong glucose solutions caused plasmolysis; very weak solutions caused bursting (as did water); and intermediate solutions had no effect at all. On all plants examined the percentage of grains which appeared to be fertile (full of contents, spherical and staining black with iodine) was over 95%.

Using seeds collected from natural pollinations, attempts were made to find the best time to germinate the seeds. Three types of seed were used : white soft seeds not yet really ripe, although in brown capsules; hard, dark brown, fully ripe seeds; and similar seeds chipped with a scalpel. After about three days all the white soft seeds had germinated; the hard unchipped seeds had not yet imbibed water; and the chipped seeds provided mixed results, some germinating freely, others not, but in all cases the hard testa in some way impeding the unfolding of the cotyledons. In *Calystegia* germination is epigeal, two thin green ovate cotyledons being raised on a fairly long hypocotyl. In all seeds examined an embryo was present, and if there was no germination it was prevented either by the hard testa or by attacks from mould. Exactly similar results were obtained with seeds produced by experimental intraspecific and interspecific pollinations. Thus the presence of ripe seed may be taken to indicate a successful pollination. In artificial pollinations rather more fruits had one or two seeds than was the case in natural pollinations.

In natural conditions the seeds probably fall to the ground, taking all winter for their testa to be fully water-saturated and thus made pliable. Special adaptations for seed dispersal appear to be more or less absent, since the capsules have no explosive device, and the four sutures are not lines of dehiscence. Irregular pole-to-pole cracks appear in the capsule and many seeds drop out by reason of shaking caused by air currents. However, many seeds remain trapped in their old capsules for at least a year, and ultimately they probably rot away with the capsule wall. However, in 1946 Toole & Brown reported that after 39 years over half of the seeds of *C. sepium* were still viable (Salisbury, 1961).

4. Distribution and Description of the Hybrid

From the previous sections it seems highly probable that hybrids between *Calystegia sepium* and *C. silvatica* occur in this country, and these hybrids are fertile, forming F_2 hybrids as well as backcrosses with either parent. Twelve such colonies were found in the neighbourhood of Tunbridge Wells, Kent, v.c. 16. One British record only has apparently been published – namely ' in the vicinity of Cambridge,' v.c. 29 (Walters & Martin, 1958), but it seems probable that the hybrid does or will occur wherever the two species are in close proximity. Dr. W. T. Stearn informs me that intermediates occur with both parents by the Thames at Kew (Surrey, v.c. 17). In the Kew herbarium specimens are present from : Alderney, v.c. S (Jackson, 1932); Surrey, v.c. 17 (Clarke, 1901; Summerhayes & Milne-Redhead, 1932; Turrill, 1956); Berkshire, v.c. 22 (Elliot, 1945); Huntingdonshire, v.c. 31 (Sandwith & Gilbert, 1958); E. Gloucestershire, v.c. 33 (Riddelsdell, 1934); Glamorganshire, v.c. 41 (Wade, 1947); and Merionethshire, v.c. 48 (Milne-Redhead, 1948). Thus 1901 appears to be the first British record. The earliest material of the hybrid seen by the author (and which also pre-dates any published record) is a specimen labelled 'Anglia, Herb. Forsyth ' in the handwriting of Hooker (senior) at the Kew herbarium. It is on the same sheet as a specimen of *C. sepium* collected in France by Hooker in 1819, and it is also labelled *C. sepium*. The hybrid is most probably of the same period as the other specimen, and of garden origin.

In order to obtain an idea of the foreign distribution of the hybrid, the ranges of the two parents are clearly of some significance. *C. sepium*, in one form or another, appears

to be pan-North-Temperate, so hybrid distribution will be limited only by that of *C. silvatica*. *C. silvatica* is a native of south Europe from S. Spain and Portugal (?) eastwards to the Caspian Sea. Although neither Lousley (1948) nor Tutin (1952) mention north Africa in its area of distribution, it is obviously native there. It is mentioned in all the thorough floras of north-west Africa (Battandier, 1890; Sauvage & Vindt, 1954; Murbeck, 1905; and others), and specimens from Morocco and Algeria are present in the British Museum dating from the first half of the nineteenth century. Its range in this continent appears to be throughout most of Morocco (including Tangier), Algeria and Tunisia. It is also found in Malta (Borg, 1927), but it has not been recorded from the Balearics. These older literature records, however, should probably not be used without further confirmation. *C. silvatica* is now naturalised in various more northerly areas of Europe (Scholz, 1960), as it is in Britain. A specimen in the British Museum herbarium from Portugal (1954) may be a native or naturalised example.

In investigating the nomenclature of the *C. sepium–silvatica* complex a variety of names is encountered. Although several authors have attempted to split off species from *C. silvatica* as here understood, this does not seem to be possible. The two usual synonyms are *C. sylvestris* and *C. inflata*. Pomel (1876) described a species which he named *C. physoides* from North Africa. Pau (1924) described a variety of *C. sepium* (var. *tangerina*) which is clearly a synonym of *C. physoides*, and was treated as such by subsequent authors (e.g. Sauvage & Vindt, 1954). Moreover, examination of Pomel's description of *C. physoides* brings one to the conclusion that this taxon cannot be separated from *C. silvatica*, at least specifically. This conclusion was also reached by Battandier (1890), who gave *C. physoides* as a synonym of *C. silvatica* Griseb. The present author, then, considers that there is but one species in the *C. silvatica* group, which, as Dandy (1958) concluded, is to be referred to as *C. silvatica* (Kit.) Griseb. Even more names are to be associated with the *C. sepium* group, although most of these have been treated as varieties rather than as separate species. Pomel (1876), however, described *C. obtusa* from N.W. Africa, which should probably be included with *C. sepium*.

If all the names involved in the *C. sepium–silvatica* complex which are referable to either *C. sepium* (L.) R. Br. or to *C. silvatica* (Kit.) Griseb. are discarded, three names (involving two taxa) remain. The earliest of these is *Convolvulus lucanus*, named by Tenore (1826) from South Italy. Don (1837) transferred it to its present genus as *Calystegia lucana*, but Fiori (1926) reduced it to a variety of *Convolvulus sepium*, as he did *C. silvatica*. Choisy (1845) called it *Calystegia sepium* var. *tubata*, but it is clear that he refers to the same plant, as he gives the synonym, and the only specimen he cites is one sent to him by Tenore himself. Examination of the descriptions of *Convolvulus lucanus* given by Tenore (1826; 1824–29; and 1831, *Syll.*), and of the excellent plate given in his *Flora Napolitana*, shows clearly that his plant is *Calystegia sepium* × *silvatica*. The plate depicts a plant exactly intermediate between the two parents, and this fact is actually mentioned in his third cited work. The third name is *Calystegia barbara*, described by Pomel (1874) from North Africa, and reduced to *C. sepium* var. *barbara* by Jahandiez & Maire (1934). Pomel's description is fairly lengthy, and it appears that the plant is also a hybrid between *C. sepium* and *C. silvatica*, although perhaps closer to the former. Battandier (1890) reached the same conclusion, as he merely states under *C. barbara* 'intermediate between the two preceding.' The hybrid should thus be referred to as *Calystegia* × *lucana* (Tenore) G. Don.

Thus, although Brummitt & Heywood (1960) say that they find little evidence of hybrids where *C. silvatica* is native (or elsewhere), it is not surprising to find that hybrids are localised both in the literature and as herbarium specimens, under a great variety of names. These localities are perhaps best mentioned geographically rather than chronologically :–

NORTH AFRICA – the first record for this continent is that of Pomel (1874), who gives several localities in Algeria, which are repeated, with one addition, by Battandier (1890). A good specimen from Algeria (Gandoger, 1879) is also in the British Museum herbarium, labelled as *C. sagittata*. Sauvage & Vindt (1954) record the hybrid from Morocco, giving one locality only (Beni Mellal, Jahandiez, 1925), which was previously

recorded by Jahandiez & Maire (1934) but without a date. A specimen with these exact details of collector, date and locality is in the British Museum herbarium, named *C. sepium* var. *barbara*. The specimen may be a hybrid between *C. sepium* and *C. silvatica*, but as previously implied it is much closer to *C. sepium* than to the other parent. Nomenclaturally however, it is still a synonym of *C.* × *lucana*. Ball (1878) also recorded the hybrid from Morocco, stating ' specimina nostra intermedia sunt.' A further specimen of *C.* × *lucana* from Morocco (Trethewy, 1933) is in the Kew herbarium.

RUSSIA – A single specimen from Lenkoran on the Caspian Sea in S.W. Russia is in the Kew herbarium (Hohenacker, 1838). This is probably the specimen Lousley (1948) cited as *C. sylvestris* when he gave the distribution as ' . . . . east to the Caspian Sea at Lenkoran.'

GREECE – A specimen from Greek Macedonia is in the Kew herbarium (Russell, 1918).

ALBANIA–A specimen from Albania is in the British Museum herbarium (Baldacci, 1898).

ITALY – Tenore (1826) described the hybrid from Italy, the type localities being Auletta and Lauria in the region Lucania in south Italy. A number of other localities are given in his five cited works, all at about the same latitude as Rome or further south. A specimen is in the Kew herbarium which was sent to J. Gay by Tenore in 1830. It is labelled by Tenore, ' Macchia Matthei e Auletta.' Which of the two localities it was collected from is not clear. Auletta (one of the type localities) is in south Italy, in Lucania, whilst Macchia Matthei is close to Rome. It is possibly some (hitherto unrecognised) sort of type specimen of *Convolvulus lucanus*. An additional possibility is that it is the holotype of Choisy's *C. sepium* var. *tubata*, since Choisy (1845) said that the only specimen he had seen was one sent from Italy by Tenore. There is a second specimen at Kew sent by Tenore to Gay, which Tenore also labelled *Convolvulus lucanus*. This specimen is clearly *C. silvatica*, however, so it is possible that Tenore did not have a very clear idea of his ' *Convolvulus lucanus*'. This specimen was sent to Gay in 1827 and is labelled ' Nella Basilicata Nel Gargano etc.' by Tenore. It is most unlikely that this was the specimen referred to by Choisy (1845), as he had a good idea of *C. silvatica*. Ball (1878) recorded *C.* × *lucana* from Italy as he states ' formae intermediae praesertim in Italia occurrunt.'

SPAIN – A specimen from El Cobre, Gibraltar (Wolley-Dod, 1912) labelled *C. sepium* is in the British Museum herbarium. This is the same locality as is given in Wolley-Dod (1914) under ' *C. sepium* var. *sylvestris* (?) '.

Some of the descriptions of the hybrid taxon are fairly lengthy, and Tenore's plate is most satisfactory, but measurements have never been included. A description of the hybrid is thus given here, from British material the author has seen in the field (see also Fig. 3).

CALYSTEGIA × LUCANA (Tenore) G. Don (*pro sp.*) (= *C. sepium* (L.) R. Br. × *C. silvatica* (Kit.) Griseb.); *Convolvulus lucanus* Tenore, *Fl. Neap. Prod. App.*, **5**, 9, (1826); *Convolvulus sepium* var. *lucanus* Fiori, *Nuov. Fl. Anal. It.*, **2**, 296 (1926); *Calystegia lucana* G. Don, *Gen. Syst.*, **4**, 296, (1837); *Calystegia sepium* var. *tubata* Choisy in DC., *Prod. Syst. Nat.* **9**, 433, (1845); *Calystegia barbara* Pomel, *Nouv. Mat. Fl. Atlant.*, **1**, 83, (1874); *Calystegia sepium* var. *barbara* Jahandiez & Maire, *Cat. Pl. Maroc*, **3**, 591 (1934).

A fertile hybrid between *C. sepium* and *C. silvatica*, capable of crossing with other similar plants and with either parent. It is intermediate between its two parents in all characters, and may be distinguished from them by : pedicels 30–100 mm. long; corolla white (always?), 41–62 mm. long; stamens 20–21 mm. long; style and stigma 20–23 mm. long; bracteoles broadly ovate, 14–25 mm. wide when flattened out, acute, obtuse or mucronate at apex, weakly cordate at base, slightly to strongly inflated, midrib very prominent especially at base, edges overlapping at each side and partially obscuring the calyx. Ratio of midrib-to-midrib (*m*) to edge-to-edge (*e*) measurement of bracteoles in natural condition 0·85–1·45.

Known from Britain, Morocco, Algeria, S.W. Russia, Greece, Albania, Italy and S. Spain.

Since not all the previous literature giving details of measurements of *C. sepium* and *C. silvatica* flowers is satisfactory, this opportunity is taken of compiling a list of the most useful taxonomic measurements of the three taxa (Table 4). The figures given in this table represent the normal ranges found in the 72 colonies studied, only very abnormal measurements being omitted, and they have been found to hold good for all the British herbarium material seen. Great caution should be exercised in applying these figures to foreign material, however.

With regard to some characters, the literature proves somewhat controversial, due probably in part to vastly different areas and times of observation. For example, Stearn (1951) gives the stamen length of *C. sepium* as 15 mm., and of *C. silvatica* 25 mm. In addition to the information given in Table 4, pollen grain sizes were also investigated. Hegi (1927) gives the diameter of *C. sepium* pollen as 76–84 μ, and Erdtman (1952) as 75–80 μ. Diameters of grains were first measured in colony 71, when it was seen that they afforded good separation of the three taxa : the diameters encountered were 67–77 μ, 77–86 μ and 82–91 μ for *C. sepium*, *C.* × *lucana* and *C. silvatica* respectively. However, it was later found that this distinction is not constant, for one colony of *C. sepium* possessed grains of 83–88 μ.

Literature regarding seed and capsule shape and size is especially diverse. The accounts of Pospichal (1899) and Hegi (1927) are very similar, the latter probably adapted from the former. Neither account refers to any substantial difference in either capsule or seed shape, and the only measurement given is ' about 5 mm.' for the seed length in *C. sepium*

TABLE 4.

Characteristic measurements of the 3 taxa.

	C. sepium	*C.* × *lucana*	*C. silvatica*
Length of corolla	36–55 mm.	41–62 mm.	58–82 mm.
Length of pedicel	24–80 mm.	30–100 mm.	70–140 (–200) mm.
Length of stamens	17–18 mm.	20–21 mm.	23–26 mm.
Length of style + stigma	16–19 mm.	20–23 mm.	24–28 mm.
Width of bracteoles	10–18 mm.	14–25 mm.	21–45 mm.
Bracteole ratio, *w/e*	1·00–1·50 (–1·75)	1·40–2·40	(1·75–) 2·00–3·25
Bracteole ratio, *m/e*	0·40–1·10	0·85–1·45	1·15–2·20
Length of capsule	9–10 mm. (mean = 9·15 mm.)	—	8·5–10 mm. (mean = 9·60 mm.)
Width of capsule	8·5–10 mm. (mean = 9·40 mm.)	—	9–11 mm. (mean = 9·85 mm.)
Length of capsule beak	1·5–2·0 mm.	—	2·5–4·0 mm.
Length of seeds	4·5–5·0 mm.	—	4·5–6·0 mm.

(Hegi). Although a number of authors give minor differences between the fruits of the two species, none give the striking differences described by Tutin (1952). With regard to the capsule Tutin states that in *C. sepium* it is subglobose and 7–8 mm. long, whilst in *C. silvatica* it is ovoid, acute, and about 12 mm. long. Furthermore Tutin states that in *C. sepium* the seeds are 4–5 mm. long and more or less round but wrinkled, whilst in *C. silvatica* they are 6–7 mm. long, triangular-ovoid and not wrinkled. In neither case do the data coincide with those collected by the present author (Table 4). Examination of many colonies produced no constant differences in the seeds of the two species, either in shape, size or texture. With regard to the capsule, no constant size difference was found. The capsules of the two species showed a rather minor difference in most cases, the beak being larger and stouter in *C. silvatica*, and less abruptly delimited from the rest of the capsule. The overall shapes are the same in both species, however, never approaching a condition which

could be described as acute, but being broadly ovoid to subglobose, and very obtuse to truncate at the apex.

As pointed out in Section 2, it is important to use only four-seeded capsules for these considerations. Apart from the fact that a capsule with fewer than four seeds is less rounded, the seeds are quite different in shape, since the two flat faces of the seeds, which are present where the seed adjoins its two neighbours in the capsule, are absent when there are no neighbouring seeds. In extreme cases the solitary seed is quite round in section. Seeds of *C. silvatica*, however, do tend to have more conspicuously flattened faces than those of *C. sepium*, and the hilum tends to be more sunken. An additional precaution is that only absolutely ripe seeds should be used, as the apparently mature yet soft and still hydrated seeds of both species often found in brown capsules are considerably larger than in the truly mature (hard, dry) state. Although Pospichal (1899) and Hegi (1927) give the seed colour as black, Tutin (1952) gives it as dark brown. Observation showed that seed colour varies from light brown to black, sometimes on the same plant.

Professor Tutin has kindly informed me that his original observations on fruit characters were carried out with small samples, and that subsequent sampling showed the characters, as described above, to be inconstant.

All the known colonies of *C.* × *lucana* were separated by shorter distances from pure colonies of the parent species than from other hybrid colonies, and were thus relatively unlikely to be pollinated by the same taxon (although eight such pollinations were successfully performed artificially). Fruit found on hybrid colonies varied in form from and between that of the two species, and measurements are thus omitted from Table 4, being of little or no significance.

5. Discussion

Since the hybrid is highly fertile and capable of forming backcrosses with either parent, as well as forming F_2 hybrid generations, intermediates of every possible degree may be expected to occur. Fig. 6 shows that the hybrid characters in the area investigated already overlap those of *C. sepium*, but not those of *C. silvatica*. If individual flowers are included it is found that the only *Ts* values possible (4–40) that are not occupied by at least one flower are 37, 39 and 40.

Because of this overlap it is difficult to designate a range of structure in terms of *Ts* values to the hybrid, but the author considers this range to be 13–21, whilst those of *C. sepium* and *C. silvatica* are 6–12 and 23–31 (–35) respectively. In colony 71 (Fig. 5) it is interesting to note that the average *Ts* value for the hybrid element (17·5) is extremely close to the halfway point (18) between the mean *Ts* values for *C. sepium* (9) and *C. silvatica* (27). The mean *Ts* values for *C. sepium* and *C. silvatica* colonies in colonies 1–70 (Fig. 6) are exactly the same as in colony 71, namely 9 and 27 respectively. The mean value for the hybrid colonies is lower, however, being 16. This indicates that the majority of hybrid colonies encountered resulted from crosses involving smaller than average parents, since from the data in Fig. 5 it seems that hybrids are almost exactly intermediate between their two parents.

The hybrid colonies in the area of study (12 out of 70 colonies) represent some 17% of the total. The name of the hybrid, *C.* × *lucana*, should theoretically be applied to all plants possessing a genotype derived from two species, whether or not these plants are morphologically distinguishable from either parent.

Undoubtedly, from this situation, originally hybrid populations may merge into either parent by continued backcrossing to that parent. The results of this, hybrid swarms, provide interesting genetical investigations into introgression and its effects. Anderson (1949) quite correctly criticises workers who, having proved that hybrids exist in the wild, do not continue their investigations further along the lines indicated above. Unfortunately, due to lack of time and facilities, genetical investigations could not be pursued in the present situation. Introgression may well have a bearing on pink-flowered forms of *C. sepium*

and *C. silvatica*, since Brummitt & Heywood (1960) state that the former species may have pink corollas, but that *C. silvatica* is never predominantly pink-flowered. If hybridisation occurs, and back-crossing to *C. silvatica* follows, pink-flower genes will undoubtedly leak into the latter species. Brummitt & Heywood (1960) refer all predominantly pink-flowered plants with inflated bracteoles to their *C. pulchra* (which Scholz (1960) reduces to a variety of *C. sylvestris*). I have so far reached no personal conclusions as to the taxonomic status of pink-flowered Calystegiae.

The present work may at first seem in part open to the same criticism that Pritchard (1960) describes for *Gentianella*. This is that we have (possibly in error) assigned equal importance to each of the four characters used in the hybrid index, since each was transferred to a scale of 1–10. Pritchard, however, was attempting to separate a series of populations, previously recognised as a single group, into two subspecies. The present author suggests that in the present situation this criticism (if it existed) would assume far less importance, since here we are attempting to find a numerical method of expressing the difference between two well-defined taxa, a difference at once obvious to the eye. When we find that method, and have proved it to be successful with a large number of colonies (only plants appearing intermediate to the eye actually falling between the two species ranges), it is relatively much less important than in the case of *Gentianella* that some of the characters may be given slightly too much or too little significance. In the case of *Gentianella* there is no good yardstick informing the worker that he is on the right lines. In addition, the fact that many workers have used the hybrid index with great success (cf. Anderson, 1949) would suggest that its method can be safely applied here.

As has been found with many other self-incompatible plants, the majority of outcrossings prove successful. Assuming the genetical basis of incompatibility in *Calystegia* to be of the normal S-allele type, results would tend to suggest that there are a very large number of S-alleles involved in this system, since the chances of finding a similar S-allele even in fairly close proximity (outside the same clone) are apparently small. It seems likely, therefore, that *C. silvatica* has been introduced into this country on numerous occasions.

As far as the experimental taxonomist is concerned, there is little doubt as to the category that the *C. sepium–silvatica* complex falls into. Using the nomenclature of Turesson, as modified by Clausen, Keck and Hiesey (Heslop-Harrison, 1953), this complex would comprise a single ecospecies if we assume that hybridisation involves no loss of fertility. The number of results so far obtained, however, are not sufficient to be certain of this, and it may be that some slight loss in fertility is incurred, especially after several generations. In this case the complex would fall within a single coenospecies.

Not until Tutin (1959) relegated *C. silvatica* to *C. sepium* subsp. *silvatica* (Kit.) Tutin* had the two taxa been regarded as anything but ' good ' species by modern British taxonomists. Brummitt & Heywood (1960) keep the two species apart, mainly on the evidence that they do not hybridise. Although, in fact, they do readily hybridise, and natural hybrids are very widespread, many pairs or more of taxa are known which hybridise freely and yet are retained as species nomenclaturally. One of the best examples is the genus *Geum*, where whole groups of species comprise a single coenospecies, and several pairs a single ecospecies (Gajewski, 1957). As Gajewski points out, the evolution of an interspecific sterility barrier may not occur apace with morphological differentiation and there is no reason to assume that the two are directly related. A quick glance through the species of *Calystegia* in the British Museum herbarium shows that several of them are quite close to *C. sepium* and *C. silvatica* in appearance, and from the diverse remarks made on the sheets it appears that considerable difficulty has been encountered in the past in naming many specimens. At least two or three species are closer to *C. sepium* than is *C. silvatica*. It is thus clear that only after a detailed cytotaxonomic investigation, on the lines of Gajewski's work on *Geum*, will it be possible to state with any certainty the relation of *C. sepium* and *C. silvatica* to the other species and to each other. Until this is done it is not possible to assess the importance of interfertility between *C. sepium* and *C. silvatica* as

*I have since found that this combination was first made by Braun-Blanquet & Maire, Fl. Maroc, 217 (1924).

taxonomic evidence. If several other groups of species in the genus are found to be capable of hybridisation amongst themselves and/or with the *C. sepium/silvatica* group, then all the species are best treated as taxonomically distinct, since introduction of the sub-species concept here would result in very few species with numerous subspecies – a structure which Gajewski rejects. It might equally be found, on the other hand, that the only two species hybridising in the genus are *C. sepium* and *C. silvatica*, when introduction of the subspecies concept (cf. Tutin, 1959) would be advantageous, especially since *C. silvatica* is severely limited geographically when compared to *C. sepium*. The author suggests, however, that until any such monographic work is undertaken the two taxa, *C. sepium* and *C. silvatica*, are best maintained as distinct species, producing the fertile hybrid *C.* × *lucana*.

I do not suggest that conclusive proof of the hybrid origin of the numerous intermediates found in the wild has been produced, but I consider that the circumstantial evidence outlined above is sufficient to assume this. The results are published as they stand, as there seems to be little chance that I shall be able to pursue the subject further for some time.

6. Summary

1. Of the several characters which have been used in the past to separate *C. sepium* and *C. silvatica*, some are considered inconstant, their use being limited to extreme or 'typical' plants. It would seem that the best diagnostic characters are the sizes of some parts and the shape of the bracteoles, so that plants without flowers may not be referable to their correct taxon in all cases.

2. By means of a hybrid index of four variables *C. sepium* and *C. silvatica* may be easily separated, and any intermediates (hybrids) which might exist recognised. Of seventy small colonies examined twelve (or 17%) proved to be of hybrid derivation. Two polymorphic colonies were also investigated, one being solely a mixture of the two species, the other a mixture of the two species with the hybrid between them.

3. In the wild, all three taxa are found to be commonly fertile from natural pollination, and pollen from them is seen to be full and spherical, although germination in glucose solution did not occur.

4. Pollination experiments showed that all three taxa are (probably 100%) self-incompatible. Pollen tube studies showed that the contorted tubes resulting from germination on incompatible styles entered the stigma for a short distance, but that they failed to reach anywhere near the style.

5. Further pollination experiments showed that the three taxa are freely interfertile in all six possible combinations, and that small populations are usually single clones, whilst large (polymorphic) ones are multiclonal.

6. All seeds obtained (either from natural pollinations or from artificial intraspecific or interspecific crosses) proved easy to germinate when in the sub-mature stage. After the seeds become completely mature and desiccated germination may be effected by chipping followed by a long period of soaking, but naturally the seeds appear to enter a dormant stage. Thus the presence of full seeds always indicates fertility.

7. Literature research showed that the hybrid has been long known in North Africa and in Italy, as *C. lucana* and *C. barbara*. The hybrid should be called *C.* × *lucana* (Tenore) G. Don. A list of the most important diagnostic measurements separating the three taxa is given. *C.* × *lucana* is known from several areas of England and Wales and also from the Channel Isles, Spain, Italy, Albania, Greece, S.W. Russia and N.W. Africa.

8. Difficulties in assigning limits to a fertile hybrid are pointed out, and the possibilities of introgression and its possible effects on pink-flower characters are commented upon.

9. The present situation is compared to that in *Geum*, and reasons put forward for maintaining the two species distinct, at least for the present.

A specimen of the hybrid from Colony 71 (*Ts* = 16), on which many of the pollination experiments were performed, has been deposited in the British Museum herbarium (**BM**).

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TAXONOMY AND NOMENCLATURE IN SOME SPECIES OF THE GENUS *ARUM* L.

By C. T. Prime

1. The relative status of Arum italicum and Arum neglectum

Recent studies of the distribution of *Arum neglectum* (Townsend) Ridley and *Arum italicum* Miller (Prime, Buckle and Lovis, 1955, 1960) have made it difficult to sustain the two as separate species. The differences between the two have been discussed by Ridley (1938) but plants intermediate in every respect can be found in large populations on the Continent, and in the extreme west of England. There is a ratio cline, the *italicum* form being commoner in the Mediterranean area, and the *neglectum* form in south Britain. Particularly attractive forms of *Arum italicum* with dark green leaves, diverging basal lobes and a well-marbled white venation have been cultivated in this country and are occasionally found as escapes. This fact complicates the interpretation of the distribution in the British Isles, but the main facts of the cline are clear enough, and it seems best to treat the two as subspecies.

The first real attempt to classify the common Aroids was made by Tournefort (1719). He describes three genera, *Arum*, *Dracunculus* and *Arisarum*. Linnaeus's copy of this book, now in possession of the Linnean Society, contains his names against the species listed, and he included them all as belonging to the single genus *Arum*. Tournefort gives the synonymy for *Arum maculatum* and amongst the names may be noted '*Arum venis albis* C. B. Pinax' and '*Arum venis albis, Italicum, maximum*, H. R. Par.' (See Bauhin, C. (1623) and Joncquet, D. (1665)). Against all the synonyms, including the two above, Linnaeus has written only one name, *Arum maculatum,* so it is clear that he considered all these to refer to the one species.

Miller (1759) describes *Arum maculatum* and *Arum italicum* separately. The description of *Arum italicum* reads:

" *Arum acaule foliis hastatis acutis petiolis longissimis spatha erecta.* Arum without Stalk, pointed Spear-shaped leaves, with very long Petals, and a large upright Spathe. This is the *Arum venis albis, Italicum, maximum. H. R. Par.* Largest *Italian Arum* with white Veins."

Again, Linnaeus in his own annotated copy of the *Dictionary* ignores this species, so he evidently regarded its description by Miller as unwarranted splitting. Miller goes on to say that the plant " grows naturally in Italy, Spain and Portugal from whence I have received the Seeds. The Leaves of this Sort rise a foot and half high, are very large, running out to a Point; these are finely veined with white, interspersed with black Spots, which together with the fine shining green of their Surface, make a pretty Variety. The Flowers grow near a Foot high, and have very long upright Spathas, which are of a pale green, inclining to white; these appear at the End of April, or Beginning of May, and the Seeds are ripe in August."

It seems therefore quite clear that Miller intended his description to apply to the more common Mediterranean plant with marked white veins and not to the plant found in this country. Townsend (1883) first described the latter as *A. italicum* var. *neglectum.* He makes the following observation " The Isle of Wight plant more frequently has dark coloured spots on the leaves, which are rarely seen on the continental *A. italicum.* The basal lobes are less triangular in outline, and are less spreading than those of the usual continental plant; the apex of the leaf is more rounded. The Isle of Wight form is in my experience rare on the Continent, but I have it from Cannes, together with the usual form from

Bordighera, and both retain their own characters. *A. italicum* appears earlier but flowers later than *A. maculatum*." He cites a specimen in the British Museum Herbarium collected by Trimen. Ridley (1938) gave a fuller description, and raised the variety to specific rank.

Though Townsend's diagnosis is rather slight, and not quite characteristic of *A. neglectum* as understood today, the name is validly published. As a subspecies of *A. italicum* it becomes **Arum italicum** Mill. subsp. **neglectum** (Townsend) Prime, *comb. nov.* (*A. italicum* var. *neglectum* Townsend, *Fl. Hants.*, (1883); *A. neglectum* Ridley, *J. Bot., Lond.*, **78** : 144 (1938). Holotype : Ventnor, October 1866, *Trimen* (**BM**)).

The principal differences between the two subspecies are :

Subsp. *italicum*	Subsp. *neglectum*
1. Leaf-shape relatively narrow. Length/ width 1·7.	Leaf-shape relatively broad. Length/ width 1·5.
2. Leaf-apex pointed, almost acuminate.	Leaf-apex rounded at side, acute.
3. Basal lobes of leaf relatively narrow, diverging, not overlapping. Angle between mid-line of lobe and petiole about 60°.	Basal lobes relatively broad, less divergent, sometimes overlapping. Angle between mid-line of lobe and petrole about 45°.
4. White venation very marked.	White venation absent or inconspicuous.
5. Leaves dark green.	Leaves lighter green.
6. No. of seeds per fruit 2–4.	No. of seeds per fruit 1–2.
7. Fruits rather more turgid.	Fruits less turgid, slightly more oblong in shape.

The last difference is a reflection of the different number of seeds in the fruit.

The Distinction between Arum italicum *and* Arum maculatum.

Arum maculatum, it may be emphasised, is a very different plant from *Arum italicum*. *A. italicum* is larger in all its parts; it is winter-green, the leaves being fully expanded by early November. The petioles are longer in proportion to the blade length and the laminae stand more erect. The spathes are relatively larger than the spadix when compared with *A. maculatum*. The spathes droop earlier, and the reproductive organs occupy a relatively greater space, for the ring of ovaries is about twice as long as broad. In *A. maculatum* this ring is about one and a half times as long as broad. The rudimentary male flowers do not taper very directly into the filaments, and the spadix is yellow with a fairly sharply contracted base. The fruits are larger and contain two to five seeds, which are also larger than those of *A. maculatum*. The fruits of *A. italicum* are also slower to turn to the bright red colour of autumn, and are usually hardly as bright in colour.

2. The Subspecies of Arum maculatum

The Danish plant with 28 chromosomes, an account of which has already been given (Prime, 1955) is a distinct form of *Arum maculatum* and should be treated as a separate subspecies. This raises the problem of the correct typification of *A. maculatum* L. It would of course be convenient if it could be demonstrated that the name *A. maculatum* subsp. *maculatum* should be applied to the more widely distributed and commoner plant with $2n = 56$ chromosomes. As Linnaeus himself said (*Critica botanica*, p. 246 in W. T. Stearn, 1957), "If an accepted genus has to be split up into several, according to the Law of Nature and of Science, then the name which formerly belonged to the whole should be kept to denote the best known and officinal plant."

It seems most likely that the name *A. maculatum* was first given to this plant, but although at the moment plants with 28 chromosomes are known only with certainty from Denmark, they may occur elsewhere. Schmucker (1925) gives $2n$ = c.32 for some German plants, probably in error for $2n = 28$, and it seems not unreasonable to believe that plants

with $2n = 28$ may occur in Germany and even further afield. In Denmark, *Arum maculatum* ($2n = 56$) has been widely planted, but the plant with 28 chromosomes is confined to the southern part of the country. It is common on the islands of Lolland and Falster; frequent on Bornholm, Møn, and the south and west part of Zeeland. In east Jutland, where it is only found in rich soils and woods towards the sea, its existence is probably due to the fact that the summer is relatively warm and long.

The name *A. maculatum* was first used for the species by Tabernaemontanus (1590) and Bauhin (1623), and this name was retained by Linnaeus in *Species Plantarum* (1753). The specimen in the Linnean herbarium (No. 1079·8) is most likely of the subspecies with $2n = 56$, but the nature and condition of the specimen make it impossible to decide with certainty. Another early reference to a specimen is in the *Hortus Cliffortianus* (1737). The phrase name here is the same as in the *Species Plantarum*, i.e. "*Arum acaule, foliis hastatis integerrimus, spadice clavato,*" Habit and distribution are given as " *Crescit ad sepes in umbrosis per Germanium, Hollandiam, Angliam, Galliam, Italiam.*" The species described in the *Hortus Cliffortianus* are essentially those growing at that time in Clifford's garden, which was at Hartekamp in Holland, and they are also the plants represented in his herbarium. This herbarium is in the British Museum, and has been consulted, but the specimen labelled in a later unknown hand is not *Arum maculatum* at all but a quite different unidentified Aroid.

The only illustrated work cited by Linnaeus is by l'Obel (1591), but the illustration is inadequate for a definite identification to be made. It is thus not possible at the present time to select a satisfactory nomenclatural type for *Arum maculatum*. However, in the absence of conclusive evidence demonstrating which of the two subspecies is in fact the type subspecies of *A. maculatum*, it nevertheless remains more probable that Linnaeus originally described the plant with $2n = 56$ chromosomes, and therefore the name *A. maculatum* subsp. *maculatum* should be applied to this plant. Accordingly, the plant with $2n = 28$ chromosomes is described below as a new subspecies.

Arum maculatum subsp. **danicum** Prime, subsp. nov. Surculus maximus cormi in medio situs; folia immaculata et pro longitudine latiora quam in subsp. *maculato*, minus hastata; spatha ad imam partem collata, brevior quam in subsp. *maculato*; spadix cylindrica, non latior basim versus. Chromosomata $2n = 28$.

Holotypus : Grönnese Skov, nr. Frederiksvoerk, North Zeeland, T. W. Böcher, 11 May 1961, in Herb. København (**C**).

Isotypus in Herb. Mus. Brit. (**BM**).

Distributio. Solum in Dania meridionali-orientali.

Main shoot of corm centrally situated; leaves unspotted, relatively broader than in subsp. *maculatum*, less hastate; ratio of spathe length to the basal part less than in subsp. *maculatum*; spadix uniformly cylindrical, not tapering from the base. Chromosome number $2n = 28$.

Distribution (so far as is known) confined to Denmark, mainly in woods on the islands and in south-east Jutland (Køie, 1939).

I should like to acknowledge with many thanks the very great help I have received in preparing this paper from Mr. J. F. M. Cannon and Dr. W. T. Stearn of the British Museum (Natural History), and from Dr. J. D. Lovis of Leeds University.

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New Records for Illinois Vascular Plants. Winterringer, G. S. and Evers, R. A. (Eds.). Pp. 135. Illinois State Museum, Scientific Papers Series, Vol. XI. 1960.

The State of Illinois is comparable in area with England and Wales, being about 400 miles long and 200 miles wide. It is divided into 102 counties and these, the basic unit of plant recording, are thus almost equivalent in area to the British vice-county.

This work is essentially a topographical botany and first supplement rolled into one, and is the sort of work H. C. Watson would have liked to have produced if the printing processes of today had been available 100 years ago. Instead of a printed list of counties, there is a map for each species (sometimes two rare species share one map) showing by a symbol, conventionally placed in the centre, those counties from which a species has been reliably recorded. In all there are 1,375 maps dealing with over 1,500 species; the number of vascular plants in Illinois is of the same order as the number found in England and Wales.

Vascular Plants of Illinois by G. N. Jones and G. D. Fuller was published in 1954, and the present work is proof of the stimulus which it gave to the study of the Illinois Flora. Within 6 years 70 species have been added, an increase of about 5%, and details of these finds are listed. Many of them are European species, introduced into the United States, which are still spreading, and a British botanist visiting Illinois will feel more at home in the future now that he can expect to find *Butomus umbellatus*, *Calamagrostis epigejos*, *Puccinellia distans*, *Epipactis helleborine*, *Cerastium atrovirens*, *Rosa micrantha*, *Trifolium fragiferum*, *Myosotis sylvatica*, *Verbascum virgatum*, *Carduus acanthoides*, *Hypochaeris radicata* and *Senecio viscosus*. All of these have been recently recorded for the first time in the State.

The number of new county records made in the same period is phenomenal. In some cases the number of county records has doubled in 6 years and this suggests that botanical recording in this part of the United States has now reached the position in which we found ourselves in Britain over 100 years ago. Further evidence for this is obtained from an assessment of the number of species which are known from every county in Illinois – the total is only about 20, whereas in England and Wales with a similar area and number of counties the total is at least ten times as great. It seems that, if new county records are your special pleasure, you stand a better change of success in Montgomery and Cumberland, Illinois, than in v.cs 47 and 70, Great Britain.

Considering the level of knowledge of the flora which has been achieved, then the use of maps to show species distribution on a county basis is understandable. However, the value of the work is less great than it might be for a foreign botanist whose main interest in the flora is likely to be the distribution of species he knows elsewhere in relation to climate, geology, and topography, for no maps of these features are included. It would have increased the cost of production very little for such maps, on the same scale, to have been added. Then we might have understood why *Geum rivale* is confined to the north-east of the State and *Arabidopsis thaliana* to the south and what combination of factors determines that in distribution *Silene vulgaris* and *Myosurus minimus* are almost mutually exclusive. The omission is particularly frustrating for the British botanist for Illinois is in the part of North America which has a climate most similar to our own to judge from maps of Thornthwaite's climatic regions.

The greatest difficulty which presents itself to a British plant geographer is status. One assumes that the same difficulty applies in the United States : yet no attempt is made in the work to distinguish between native and non-native distributions : another hazard which confronts the would-be interpreter and somewhat reduces the reliance which can be placed upon the maps.

F. H. Perring.

A California Flora. Philip A. Munz (in collaboration with David D. Keck). Pp. 1681, with 2 maps, 134 text figures and colour frontispiece. California University Press, Berkeley and Los Angeles; and Cambridge University Press, 1959. Price 86s. 6d.

It is tempting for a European botanist to consider California in relation to Spain, which is of similar size, lies nearly in the same latitude, and has a similar huge total (nearly 6,000 species) of vascular plants, but the physical features and geological history of the two countries are so different that, in the end, it is perhaps best for him to confine any comparison to the plants of the drier, desert areas in California and the more arid Spanish provinces. Some British botanists will be interested in California from a different motive : many of our aliens or garden plants, for instance in the *Compositae*, *Polemoniaceae*, *Boraginaceae* and *Rhamnaceae* (*Ceanothus*), are natives of this State while, in reverse, several hundreds of European and North African species are completely naturalised there. Others, plant geographers, will perhaps concentrate on the extension south (or the failure to extend south) from the Rocky Mountains into the Californian

sierras of familiar genera and even species of northern, sometimes alpine or subalpine, distribution; while tree-lovers will be most interested in the great Redwood and Douglas Fir forests of the moist coastal region.

Professor Munz's excellent new flora of California, with its brief but lucid introductory sections, can be warmly recommended to European taxonomists, ecologists and plant geographers. It discards the 6 Merriam Life Zones recognized by the late W. L. Jepson, whose large-scale *Flora of California*, begun in 1909, is due to be completed. Instead, the author has 5 Biotic Provinces, 11 major Vegetation Types, and 29 Plant Communities, which are fully classified, and throughout the text the native species are assigned to one or more of these, with a description of habitat, altitudinal range and distribution within the State. The body of the work follows customary lines, with indented keys, and text figures illustrating characters of orders, families or subdivisions of families, not of lower ranks. Chromosome numbers (with author citations) are given when known, and references to revisions follow generic descriptions. The order of the families is unconventional and was prepared by Professor Munz's collaborator, Dr. David D. Keck. There are two small maps, for counties and main topographical features; European readers could have wished for a larger, coloured, folding map with place-names. Thin paper, like that of Fernald's edition of Gray's ' Manual', was inevitable or the book would have needed two volumes.

The author does not give a summary of the composition of the flora, but a statistical report on his book was published in *Leaflets of Western Botany*, vol. ix, No. 8, pp. 117–123 (November 1960), by Gladys L. Smith and Anita M. Noldeke, and this was followed by a summary of the endemism prepared by A. M. Noldeke and J. T. Howell (l.c., pp. 124–127). These writers provide a total of 5,675 native species, with 1,414 (or 29·02%) endemic species and 29 endemic genera. Some idea of the extent of evolution within Californian genera may be gathered from the large representation of *Carex* (144 species), *Astragalus* (93), *Phacelia* (87), *Lupinus* (82), *Mimulus* (77), *Eriogonum* (76), *Cryptantha* (59), *Trifolium* (49) and *Arctostaphylos* (43). The high endemism is explained, as Professor Munz points out, partly by the nature of the region, so broken up into separate mountain ranges and low-lying valleys, and partly by changes in climate and migrations both north and south and from altitude to altitude. With such a field of exploration before them, and such a nice book to work with, British botanists might soon give up their exhausting climbs in the Scottish Highlands, and even skip the more rewarding limestone cliffs of Asiatic Turkey.

N. Y. Sandwith.

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THE TAXONOMIC SEPARATION OF THE CYTOLOGICAL RACES OF *KOHLRAUSCHIA PROLIFERA* (L.) KUNTH *SENSU LATO*

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Introduction

It has been realised for some considerable time that *Kohlrauschia prolifera* (L.) Kunth contains both diploid and tetraploid plants (Blackburn, 1933, Böcher *et al.*, 1953, 1955). The cytotypes appear to have different distributions, the more widespread diploid being replaced in W.S.W. Europe by the tetraploid. Because of the close morphological similarity between the cytotypes, and the difficulty of separating them, *K. prolifera* has come to be widely referred to in the literature as an example of the phenomenon of semi-cryptic polyploidy (cf. Heywood, 1958, Larsen, 1960). In the course of a revision of the whole genus, we have had occasion to make a detailed study of the *K. prolifera* group, as a result of which it has become apparent that not only can the diploid and tetraploid races be separated fairly satisfactorily on the basis of their seed-coat morphology, but the differences had been recognised precisely many years previously.

Although it has usually been assumed that the tetraploids have arisen from the diploids by autoploidy, the morphological evidence suggests that another diploid species, *K. velutina* (Guss.) Reichb., is involved and that the tetraploid has been formed as a result of allopolyploidy between it and diploid *K. prolifera*.

Typification of K. prolifera

This species was based on *Dianthus prolifer* L., *Sp. Pl.*, 410 (1753). Typification has proved difficult since there is no positive evidence that the specimen of *Dianthus prolifer* in the Linnean Herbarium has a claim to being selected as a lectotype. The sheet does not bear the *Species Plantarum* number normally found on those of species described in the first edition. If, however, the specimen is accepted as authentic there is no reason to suppose that it is other than diploid *Kohlrauschia prolifera*, although in the absence of seeds it cannot be identified with certainty. The synonyms and distribution given by Linnaeus could apply to either the diploid or tetraploid species. This kind of situation arises occasionally with the typification of species in polyploid groups where the various species may be separated from one another by micro-characters which are not available for examination in the type material. In such cases the wisest course is to accept a typification which does not upset the traditional interpretation of the species, unless there is strong evidence to the contrary. Accordingly the name *K. prolifera* (L.) Kunth is accepted here for the diploid species which occurs in most countries of Europe and to a small extent in N.W. Africa and Anatolia.

The Identity of Dianthus nanteuilii Burnat

During the investigation of the genus it was necessary to account for *Dianthus nanteuilii* Burnat which was published in *Flore des Alpes Maritimes*, **1**: 221-222 (1892) with a full description based on 38 specimens from various localities at Cannes and Agay. The leaf sheaths are described by Burnat as ' aussi larges que longues ' and the seeds are described in considerable detail : ' absolutely intermediate between the two preceding species [*D. prolifer* and *D. velutinus*] in dimensions and shape : more convex dorsally than in

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D. velutinus, and less hollow-concave than in the latter, the outer surface striate-tuberculous, with tubercles similar to those of *D. velutinus*, but much closer together and less projecting.'

Burnat considered the species (apart from the rare presence of glandular hairs) intermediate between *D. prolifer* and *D. velutinus*, but Nanteuil thought that a hybrid origin was unlikely in view of the commonness of the new form in the vicinity of Cannes while only one specimen of *D. velutinus* was seen. *D. prolifer* did not on the other hand appear to be less abundant although it flowered later. He gave the following times of maturity of the first seeds :

velutinus	20th May
intermediate	1st June
prolifer	25th June

Time of flowering needs further investigation both in the field and in cultivation, but *D. velutinus* does appear in the light of later observations to be the earliest of the three to flower (cf. Böcher *et al.*, 1953).

Further examination of large numbers of individuals by Nanteuil failed to reveal any transitional forms. This is confirmed by our own comparative studies on a wide range of material from diverse provenances.

It is interesting to note that, although Burnat appears to have been the first to publish a description of this species, there are two older sheets in the Kew Herbarium from the Pyrenees which have manuscript names and extensive and accurate descriptions appended.

Kohlrauschia velutina (Guss.) Reichb.

The third taxon involved in this complex, *K. velutina*, is characterized by its long leaf sheaths (at least twice as long as broad) and by its strongly tuberculate seeds. The epithet *velutina* refers to the dense glandular-tomentose indumentum which is usually found on some of the internodes in the middle part of the stem. This character is not, however, constant and forms with glabrous stems occur which have in the past been confused with *K. prolifera*, especially in Italy, Sicily and Sardinia.

K. velutina is diploid (Böcher *et al.* 1953, 1955) and is regarded by some writers, such as Briquet (1910), as only subspecifically distinct from *K. prolifera*. It is widely distributed in the Mediterranean region from Portugal and Spain to Turkey and Palestine. The karyotype has, however, been shown to be quite distinctive (Böcher *et al.*, *loc. cit.*) as discussed below.

Taxonomic comparisons

The accompanying table sets out the differences between the three units. From this it will be seen that several characters can be employed to separate them, with *K. nanteuilii* occupying an intermediate position. Of these characters, however, the only constant and reliable ones are those of the seed testa.

Table 1

	K. prolifera	*K. nanteuilii*	*K. velutina*
Internodes (middle part of stem)	Glabrous	Glabrous to tomentose	Densely glandular-tomentose, rarely glabrous
Leaf sheaths	Broader than long to about as long as broad	1–2 times as long as broad	At least twice as long as broad
Width of Petal limb	2–3·5 mm	2–3 mm	1·2–2·5 (– 3) mm
Inner bracts	Obtuse	Obtuse or mucronate	Mucronate
Seed size	1·3–1·9 mm	1·2–1·9 mm	1–1·3 (– 1·4) mm
Testa pattern	Reticulate (Plate 6a)	Tuberculate (Plate 6b)	Tuberculate to papillose (Plate 6c)



a. (top) *K. prolifera* (København 3325), b. (middle) *K. nanteuilii* (København 3248)
c. (bottom) *K. velutina* (København 3303)

The details of the seed testa are shown in Plate 5. The characteristic pattern of each species is easily appreciated by using a low-power dissecting microscope, although with a little practice an ordinary × 10 hand-lens is adequate. Through the courtesy of Professor T. W. Böcher and Dr. Kai Larsen we have been able to examine specimens and seeds from spontaneous plants grown in Copenhagen whose chromosomes have been counted by them. This material is listed below :

Origin	*Culture No.* (København)
nanteuilii $2n = 60$	
CHANNEL ISLANDS	
Jersey, St. Ouens Bay	3248
Jersey, Quenvais	3249
FRANCE	
Béziers	1733
Port Vendres	1715
MADEIRA	3111
SPAIN	
Soria	3321
PORTUGAL	
Coimbra	2483
CANARY ISLANDS	
Gran Canaria	37, 38
Tenerife	36
prolifera $2n = 30$	
HUNGARY	
Budapest	3325
SPAIN	
Lloret de Mar, Barcelona	3323
POLAND	
Tomice, distr. Poznan	3324
Poznan	3365
SWEDEN	
Øland	2963
Gotland	2878
DENMARK	
Kregme	2282
FRANCE	
Mt. Louis above La Cassagne	1696
Luchon	1627
Bouleternère	1700
SWITZERLAND	
Hort. Bot. Lausaniensis	663
velutina $2n = 30$	
PORTUGAL	
Sacavem	3303
BELGIUM	
Hort. Bot. Antverpen	913

In all cases the correlation between chromosome number and seed testa type has been confirmed in the *prolifera-nanteuilii* pair. Similarly, the cultivated material of *K. velutina* has its characteristic testa configuration and the expected chromosome number of $2n = 30$.

In view of the fallibility of the other characters used to separate the units, the seed testa pattern alone appears to be constantly correlated with level of polyploidy in the diploid-tetraploid *prolifera* pair. In cases such as these it is important that the constancy of the polyploid markers be checked over a wide range of material (Heywood, 1960, Heywood and Walker, 1961). We feel that the correlation is now well established in this group; moreover, examination of testas has been made of seed from extensive collections of herbarium material which on other characters and distributional grounds agree with determinations as *K. prolifera*, *K. nanteuilii* and *K. velutina*. Again the correlation has been satisfactory and no breakdown between the testa pattern differences has been noted. It is proposed therefore that the tetraploid form of *K. prolifera* be recognised as a separate species and the appropriate combination is made below :

Kohlrauschia nanteuilii (Burnat) P. W. Ball & Heywood, *comb. nov. Dianthus nanteuilii* Burnat, Fl. Alpes Marit., **1** : 221 (1892); *Tunica prolifera* proles *T. nanteuilii* Rouy & Fouc., Fl. Fr. **3** : 160 (1896); *Tunica nanteuilii* Gürke, Pl. Eur. **2** : 338 (1903); *Tunica prolifera* var. *nanteuilii* Briquet, Prodr. Fl. Corse **1** : 569 (1910).

Distribution : *British Isles.* V.c. 10, Isle of Wight; 11, S. Hants; 13, W. Sussex; 15, E. Kent (introduced); 28, W. Norfolk (introduced); Channel Islands, France, Corsica, Sardinia, Spain, Portugal, Morocco, Madeira, Canary Islands.

Kohlrauschia prolifera (L.) Kunth occurs as a rare alien in the British Isles. Specimens have been seen from v.c. 14, E. Sussex, and v.c. 28, W. Norfolk, and it may also be found elsewhere.

The Origin of K. nanteuilii

It is suggested by Böcher *et al.* (1953) that the tetraploid race probably arose by autoploidy from diploid *K. prolifera*. As pointed out above, the morphological evidence does not lend support to this view since *K. nanteuilii* is intermediate in most characters between diploid *K. prolifera* and *K. velutina*. It seems possible therefore that *K. nanteuilii* may be an allotetraploid derived from the other two species. The strains of *K. velutina* examined cytologically by Böcher *et al.* were distinct from diploid *K. prolifera* in possessing a pair of very short chromosomes. If our theory is correct, an examination of the karyotype of *K. nanteuilii* may provide confirmation, since it should possess the short chromosome pair. Plants are being cultivated for this purpose.

Discussion

The taxonomic recognition of polyploid races showing slight morphological divergence is a subject which has provoked considerable controversy (*cf.* Heywood, 1960; Löve, 1960). When no single morphological character can be detected which allows a constant separation to be made between polyploid races, it is doubtful if nomenclatural recognition serves any useful purpose. Similarly, when the characters proposed to distinguish the polyplotypes can be appreciated only by a specialist, it is of little value to recognise them as separate species knowing that the possibilities of correct identification by a non-specialist are slender (*cf.* Heywood, 1960, p. 183).

In this case, however, one morphological character, seed testa-pattern, which can be easily appreciated, appears to be constantly correlated with level of ploidy; other characters (as noted in Table 1) are satisfactory in a fair percentage of cases; and the geographical distribution of the diploid and tetraploid races is clearly distinct. There are, in addition, a number of physiological differences, although these need further investigation. These factors, as well as the probable alloploid origin of the tetraploid, seem to us to favour specific recognition. The close taxonomic similarity of the three species *K. prolifera*, *K. nanteuilii* and *K. velutina* could then be indicated in practice by grouping them in a species aggregate.

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INTERSPECIFIC RELATIONSHIPS AND INTRASPECIFIC VARIATION OF *CHENOPODIUM ALBUM* L. IN BRITAIN

II. THE CHROMOSOME NUMBERS OF *C. ALBUM* L. AND OTHER SPECIES

By M. J. Cole

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Abstract

A survey of the chromosome number of *Chenopodium album* L. in Britain and abroad has, contrary to the previous reports, shown that intraspecific polyploidy is probably absent, all determinations giving only the hexaploid, $2n = 54$. Counts from *C. reticulatum* ($2n = 54$) and *C. viride* ($2n = 18$) confirm respectively the integration into and separation from the *C. album* complex of these two taxa. Ten additional species have also been counted, seven of these being first records for this country and three, new determinations for the genus.

1. Introduction

In the first paper of this series (Cole, 1961) reference was made to the possible part played by intraspecific chromosome races in determining the variation pattern of *C. album*. The survey presented below is based primarily upon counts of *C. album* and aims to assess how significant this putative variable may be. Counts on the additional species are included so that an overall picture of the chromosome numbers of the genus from British material is available, data which are invaluable in an investigation into the hybridisation-potential of *C. album* to be presented in a later paper in this series.

Three chromosome races have been reported in the literature from material identified as *C. album* L. : a diploid $2n = 18$ (Winge, 1917; Löve & Löve, 1944; Maude, 1940) : a tetraploid, $2n = 36$ (Cooper, 1935; Bhargava, 1936; Witte, 1947) : and a hexaploid, $2n = 54$ (Kjellmark, 1934). In addition Kawatani & Ohno (1950) reported a tetraploid with a basic number of $x = 8$, i.e. $2n = 32$. Since this is the only report of a basic number of $x = 8$ from the species it should be accepted with reserve.

This paper aims to reconcile these various reports in the literature which are summarised, together with counts of additional species of *Chenopodium*, in Cole (1957).

2. Methods

Satisfactory counts were made either from actively growing root meristems or from P.M.C. preparations. Root tip squashes were prepared either from primary radicles or, often with better results, from the more vigorous secondary roots from larger plants growing in pots, in soil or sand, in a greenhouse. Excised roots were pretreated in a saturated solution of α-bromo-napthalene for 2-4 hours at room temperature (c. 20°C) and then fixed overnight in acetic-alcohol (1 : 3). The material was then softened in N/1 HCl at 60°C for 4 minutes and the apices severed and teased in 1–2% acetic orcein in 45% acetic acid (Omara, 1948). This method gave deeply staining chromosomes against a clear cytoplasm. The preparations were dehydrated using the freeze-dry method of Conger and Fairchild (1953) and finally were made permanent in 'Deepex' through xylol. Alternatively, by sectioning at 10 μ young inflorescences, which were fixed in acetic alcohol, embedded in paraffin wax, and stained in either Feulgen or Heidenhain's haematoxylin, most stages of microsporogenesis were found.

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Herbarium specimens of all material used for cytological preparations have been sent to either Dr. Paul Aellen, Basle, Switzerland, or Mr. J. P. M. Brenan, Royal Botanic Gardens, Kew, for confirmation of identification. These specimens have now been deposited in the Herbarium of the University of Southampton.

3. Results

(*a*) Chenopodium album

(*i*) *British material.*

During 1954 and 1955 seed was collected from over 100 widespread localities in Great Britain. From this collection 27 chromosome determinations were made representing 18 vice-counties. Table 1 shows that without exception only the hexaploid ($2n = 54$) (Fig. 1) was found, suggesting that in this country at least intraspecific polyploidy appears to be absent in *C. album* L. It is also pertinent to note that identical counts were obtained for *C. reticulatum* Aell. and *C. album* throughout. This evidence was cited in the first paper of this series (Cole, 1961) where it was suggested that *C. reticulatum* does not deserve separate taxonomic recognition from *C. album*.

Table 1

Chromosome counts of *C. album* L. (incl. *C. reticulatum* Aell.) and the localities of the British material

v.c.	*Locality*	*Seed marking**	*Root tip or Pollen mother cell preparation*	*Diploid Chromosome No. 2n*
1	Penzance, Cornwall	A	R.T.	54
11	Romsey, Hants.	A	R.T.	54
11	Southampton, Hants.	A	R.T.	54
11	Southampton, Hants.	A	R.T.	54
11	Southampton, Hants.	A	P.M.C.	54
15	Sandwich, Kent	A	R.T.	54
20	Bayfordbury, Herts.	A	R.T.	54
30	Luton, Beds.	A	R.T.	54
31	St. Neots, Hunts.	A	R.T.	54
35	Newport, Mon.	A	R.T.	54
36	Hereford	A	R.T.	54
36	Hereford	A	R.T.	54
45	Dale Fort, Pembs.	A	R.T.	54
60	St. Annes on Sea, Lancs.	A	R.T.	54
67	Newcastle, Northumberland	A	R.T.	54
70	Penrith, Cumberland	A	R.T.	54
72	Gretna, Dumfries.	A	R.T.	54
72	Dumfries, Dumfries.	A	R.T.	54
92	Inverurie, Aberdeenshire	A	R.T.	54
95	Elgin, Moray	A	R.T.	54
11	Southampton, Hants.	R	R.T.	54
11	Southampton, Hants.	R	R.T. & P.M.C.	54
11	Southampton, Hants.	R	P.M.C.	54
12	Winchester, Hants.	R	R.T.	54
15	Sholden, Kent	R	R.T.	54
17	Merton Park, Surrey	R	R.T.	54
25	R. Deben, Suffolk	R	R.T.	54

*A = *C. album* R = *C. reticulatum*

27 counts from 18 vice-counties (no counts from Ireland available); all hexaploid, $2n = 54$.



Fig. 1. Chromosomes from the genus *Chenopodium*.

a. *C. viride* L. ($2n = 18$) Oslo, Norway; b. *C. ficifolium* Sm. ($2n = 18$) Southampton; c. *C. murale* L. ($2n = 18$) Southampton; d. *C. album* L. ($2n = 54$) Southampton; e. *C. reticulatum* Aell. ($2n = 54$) Southampton; f. *C. urbicum* L. ($2n = 36$) Holbury, Hants; g. *C. bonus-henricus* L. ($2n = 36$) Southampton; h. *C. berlandieri* Moq. subsp. *zschackei*, (J. Murr) Zob. ($2n = 36$) Southampton; i. *C. polyspermum* L. ($2n = 18$) Southampton; j. *C. opulifolium* Schrad. ex Koch & Ziz ($n = 27$) Southampton; k. *C. variabile* Aell. ($n = 18$) Romsey, Hants; l. *C. album* L. ($n = 27$) Saskatchewan, Canada; m. *C. reticulatum* Aell. ($n = 27$) Southampton. a–i, root tip mitoses × *c.* 1000. j–m, PMC metaphases × *c.* 1350. All drawings are either by camera lucida or are tracings from photographs.

TABLE 2

Chromosome counts of *C. album* L. (incl. *C. reticulatum* Aell.) and the localities of the foreign material

Locality	*Seed marking*	*R.T./P.M.C.*	2*n*
Saskatchewan, Canada	A	P.M.C.	54
Ottawa, Canada	A	R.T.	54
Minnesota, U.S.A.	A	R.T.	54
Carenac, France	A	R.T.	54
Neuchâtel, Switzerland	A	R.T.	54
Coburg, Germany	A	R.T.	54
Bremen, Germany	A	R.T.	54
Copenhagen, Denmark	A	R.T.	54
Pavia, Italy	A	R.T.	54
Christchurch, New Zealand	A	R.T.	54
Rouen, France	R	R.T.	54
Vienne, France	R	R.T.	54
Dandenong, Australia	R	R.T.	54

13 Counts from America, Europe and Australasia; all hexaploid, $2n = 54$.

TABLE 3

Chromosome counts of *Chenopodium* spp. excl. *C. album* L. Localities of British material

Species	*Locality*	*v.c.*	*R.T/P.M.C.*	2*n*
C. ficifolium Sm.	Southampton, Hants.	11	R.T.	18
C. murale L.	Southampton, Hants.	11	R.T.	18
C. polyspermum L.	Romsey, Hants.	11	R.T.	18
C. viride L. (*C. suecicum* J. Murr)	Enfield, Middx.	21	R.T.	18
C. viride L. (*C. suecicum* J. Murr)	Newark, Notts.	56	R.T.	18
C. viride L. (*C. suecicum* J. Murr)	Dumfries, Dumfries.	72	P.M.C.	18
C. bonus-henricus L.	Southampton, Hants.	11	R.T.	36
C. rubrum. L.	Southampton, Hants.	11	R.T.	36
†*C. opulifolium* Schrad.	Southampton, Hants.	11	P.M.C. & R.T.	54
**C. berlandieri* Moq. ssp. *zschackei* (J. Murr) Zob.	Southampton, Hants.	11	R.T.	36
**C. urbicum* L.	Holbury, Hants.	11	R.T.	36
**C. variabile* Aell.	Romsey, Hants.	11	P.M.C. & R.T.	36

*New determinations.

†First count on British material contradicting a previous Continental record (see text).

Other numbers are first counts on British material confirming previous Continental records.

(*ii*) *Foreign material.*

Seed sent from colleagues abroad enabled counts to be made from other continents. The results (see Table 2) are in agreement with those from Britain : only the hexaploid count was recorded and this from plants with both smooth and reticulate seed coats.

(*b*) *Species of* Chenopodium *other than* C. album

Seed was available from ten additional species and their chromosome numbers were determined (Table 3 and Fig. 1). Of these six are first records for this country and confirm previous counts from abroad, three (*C. urbicum* L., *C. variabile* Aell., and *C. berlandieri* Moq. subsp. *zschackei* (J. Murr) Zob.) are new determinations and one (*C. opulifolium* Schrad. ex Koch & Ziz $2n = 54$) differs from the previous record from Germany (Wulff, 1936) of $2n = 36$.

4. Discussion

The results of this investigation suggest with reasonable certainty that *C. album* L. (incl. *C. reticulatum* Aell.) exists, at least in this country, and probably elsewhere, only as a hexaploid ($2n = 54$). Attempts however should be made to reconcile this result with the previous contradictory reports in the literature, since it was Kjellmark (1934) who alone obtained the hexaploid count.

One possible explanation put forward by Aellen & Just (1943) to account for these divergent counts was that of polysomaty. This phenomenon has been reported extensively from the *Chenopodiaceae* and in particular from *Chenopodium*, (Wulff, 1936; Lorz, 1937; Maude, 1940; Witte, 1947). However, hexaploid cells are unlikely to have arisen as a consequence of simple polysomaty (only tetraploid and octoploid cells would be expected) and it can be assumed that any hexaploid counts reported are probably indicative of a true diploid number and are not of polysomatic origin.

A much more feasible explanation is that these discrepancies are errors arising from the taxonomic misidentification of the original material used, mistakes which are easily made in this critical genus. For example, out of five samples of seed sent as *C. album* L. from four independent sources in Scandinavia, four were suspected on seed characters to be *C. viride* L. Two chromosome numbers were recorded, a diploid ($2n = 18$) from the material suspected to be *C. viride* and a hexaploid ($2n = 54$) from the single specimen of *C. album*.

It is suggested that similar confusion between these two species might easily explain the previously recorded reports of $2n = 18$ for *C. album* of Winge (1917) and Löve & Löve (1944) from Denmark and Sweden respectively : their material was probably *C. viride* L. (*C. suecicum* J. Murr) which is notably abundant in Scandinavia.

From this country also Maude (1940) reports a diploid number of $2n = 18$ for *C. album* which may similarly refer to *C. viride*, known to occur in Merton Park. Certainly material of *C. album* from that locality collected personally in 1954 gave the hexaploid count (see Table 1).

The record of $2n = 36$ from the U.S.A. attributed to *C. album* (Cooper, 1935; Witte, 1947) may also be a consequence of misidentification, this time with *C. berlandieri* Moq. subsp. *zschackei* (J. Murr) Zob. ($2n = 36$). There is ample evidence to show that this last species has been long confused with *C. album* in the U.S.A. (cf. Wahl, 1952) and data from the Kew herbarium, for example, show that, out of 23 specimens from North America initially determined as *C. album*, Aellen redetermines 18 of them as *C. berlandieri* subsp. *zschackei*.

On the basis of these observations it is suggested that taxonomic misidentification is largely responsible for the previous reports of varying chromosome numbers for *C. album*, and whilst this conclusion must remain tentative until further counts have been made, the evidence is sufficiently strong to suggest that in Britain, at least, *C. album* L. (incl. *C. reticulatum* Aell.) exists only as the hexaploid $2n = 54$.

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STUDIES ON *RANUNCULUS* L. SUBGENUS *BATRACHIUM* (DC.) A. GRAY
I. CHROMOSOME NUMBERS

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It has been thought worth while to publish a list of chromosome numbers even though work is still in progress. It is hoped to publish a taxonomic account later but in order to avoid undue confusion the references to the original descriptions are cited. A complete set of herbarium specimens of all the plants counted is deposited in the herbarium of the Botany School, Cambridge, England. An incomplete set is in the Botanische Staatssammlung, München, Germany. The specimens in München are suffixed by **M**. The collection of microscopical preparations will, for the time being, be kept by myself. All counts are cited as somatic numbers. When localities alone are cited it means that these are the origins of material that I have counted.

R. HEDERACEUS L., Sp. Pl., 556 (1753).

2n = 16. Langlet (1927), Böcher (1938). The Lizard, Cornwall, **M;** Sellings, Kent; an unknown locality in Portugal; Eifel, Wirftal, Prüm, Germany, **M.** An artificial autotetraploid ($2n = 32$) has been induced from the Lizard population using colchicine treatments. There is no evidence that this tetraploid occurs in nature.

R. OMIOPHYLLUS Ten., Fl. Nap., **4**: 338 (? 1830). (*R. lenormandii* F. W. Schultz).

2n = 16. 6 km N. of Polizzi Generosa, Madonie Mts., Sicily, **M.**

2n = 32. Larter (1932). Two Bridges, Dartmoor, Devon, **M.**

R. TRIPARTITUS DC., Icon. Pl. Gall. Rar. **1,** 15, tab. 49 (1808). (*R. lutarius* (Revel) Bouvet).

2n = 48. (Fig. 1a). The Lizard, Cornwall, **M;** Arne, Dorset. The count $2n = 32$, Cook (1959), was an error.

R. OLOLEUCOS Lloyd, Fl. Loire-Inf., 3 (1844).

2n = 16. (Fig. 1b). Maarne, 20 km S.E. of Utrecht, Netherlands, **M.**

R. BAUDOTII Godr., Mem. Soc. Roy. Nancy 1839, 21, fig. 4 (1840).

2n = 32. Böcher (1938), Christiansen in Sørensen (1955). Brading, Isle of Wight, **M;** Zicksee, St. Andrat-Frauenkirchen, S. E. Austria, **M.**

R. PELTATUS Schrank, Baier. Fl., **2** : 103 (1789).

2n = 32. Between Erlangen and Dechsendorf, Nürnberg, Germany, **M.** Herbarium specimens of plants collected in Denmark and counted by K. Larsen have been seen in the herbarium of the Universitetets Botaniske Museum, Copenhagen, Denmark. The Danish localities are : Hestehaven (18.V.1952); Bastrup (13.V.1953); Plejelt, N. of Fredensborg (17.V.1953); Vejenbrød (25.V.1953); Baesbakke, Fyns Hoved (7.VI.1953).

R. AQUATILIS L., Sp. Pl. 556 (1753).

2n = 48. Christiansen in Sørensen (1955). Castle Donington, Leicestershire, **M;** Stretham, Cambridgeshire, **M;** Tuddenham, Suffolk; Pöcking, Starnberg, S. Germany, **M;** Erling, Herrsching, S. Germany, **M.**

R. aquatilis and *R. peltatus* are frequently confused. The following counts of **2n = 32** could refer to either. Larter (1932), Böcher (1938), Svälov in Ehrenberg (1945), Delay (1947), Turala in Skalińska (1959).

R. TRICHOPHYLLUS Chaix in Vill., Hist. Pl. Dauph. **1,** 335 (1786).

2n = 16. Langlet (1927).

2n = 32. Reese (1957). Wicken Fen, Cambridgeshire, **M;** Woodwalton Fen, Huntingdonshire; Bretby, Derbyshire; the river Würm, Obermenzing, München, S. Germany, **M;** Aschholding, S. Germany, **M;** Oberstdorf, S. Germany, **M.**

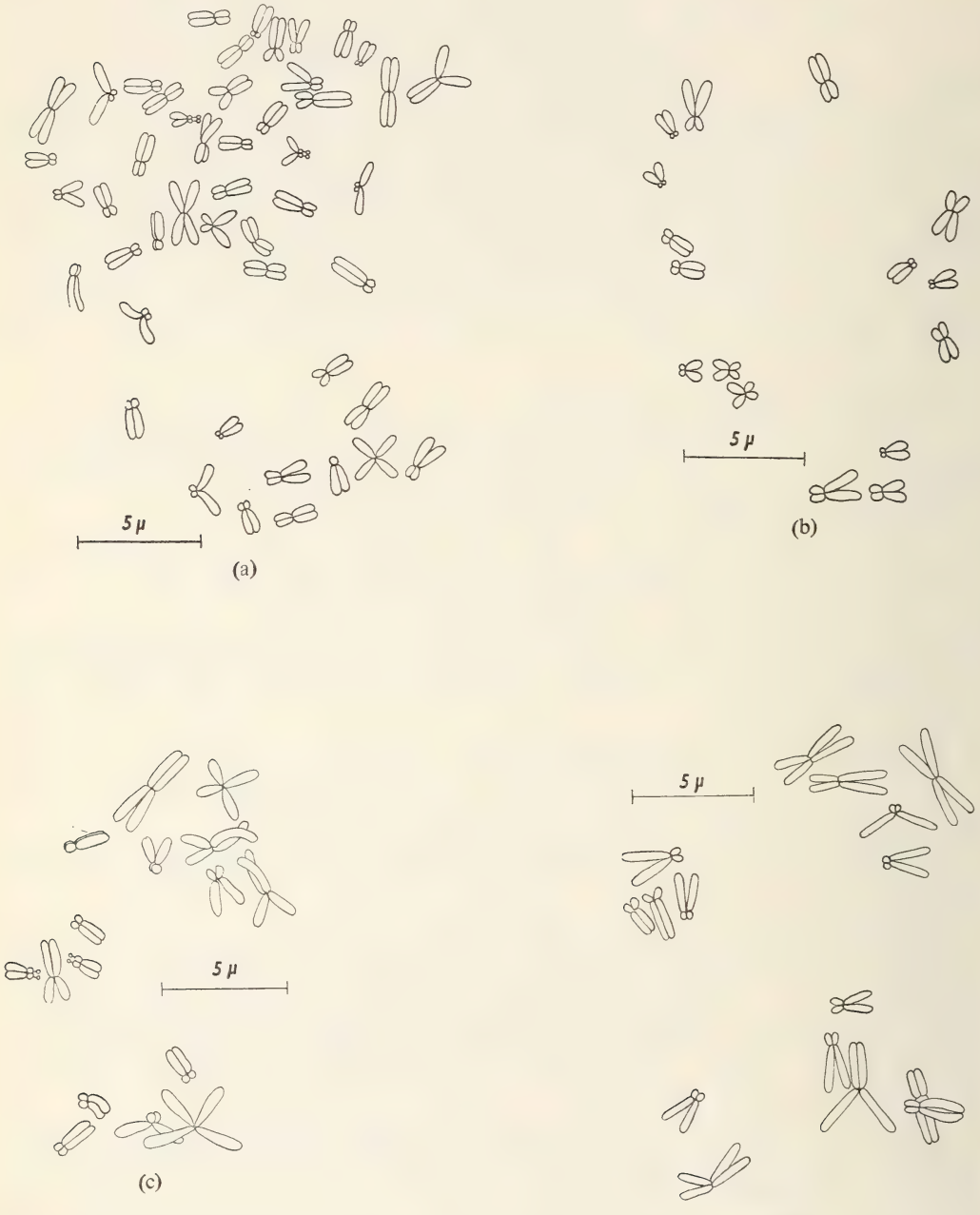


Fig. 1. Root-tip mitoses in *Ranunculus* spp., × *c.*3500. (a) *R. tripartitus*, Lizard, Cornwall, $2n = 48$. (b) *R. ololeucos*, Maarne, Holland, $2n = 16$. (c) *R. rionii*, Prater, Wien, Austria, $2n = 16$. (d) *R. sphaerospermus*, between Qurna and Madina, Iraq, $2n = 16$.

R. TRICHOPHYLLUS subsp. LUTULENTUS (Perrier & Songeon) Vierhapper, Abh. Zool.-Bot. Ges. Wien, **16** : 109 (1935); including *R. confervoides* Fr.

2n = 32. Mattick in Tischler (1950), A. & D. Löve (1956), Jørgensen, Sørensen & Westergaard (1958). Funtensee, Berchtesgadener Alpen, S. Germany, **M;** Geissalpsee, Allgäuer Alpen, S. Germany, **M.**

R. RIONII Lagger, Flora, **31** : 49 (1848).

2n = 16. (Fig. 1c). Pond near the ' Lusthaus ', Prater, Wien, Austria, **M** (*Dupla-Exsiccata ex hb. Mus. Wien, Ch. Cook & A. Patzak*, 24.VI.1960); Himberg, S.E. Austria, **M;** Maqil, Basra, Iraq. The original material of the Iraq collection is in the Naturhistorisches Museum, Wien, Austria, (*K. H. Rechinger fil., No.* 15808, 16.III.1957).

R. SPHAEROSPERMUS Boiss. & Blanche in Boiss., Diag. ser. 2, **3** (5) : 6 (1856); not *R. aquatilis* subsp. *sphaerospermus* sensu Clapham in Clapham, Tutin & Warburg (1952) which belongs in the "*pseudofluitans*" group.

2n = 16. (Fig. 1d). Between Qurna and Madina, Iraq; the original material of this collection is in the Naturhistorisches Museum, Wien, Austria, (*K. H. Rechinger fil., No.* 8477, 17.III.1957).

R. CIRCINATUS Sibth., Fl. Oxon., 175 (1794).

2n = 16. Scheerer (1939), Turala in Skalińska (1959). Cheddar, Somerset; Hemington, Leicestershire; Wicken Fen, Cambridgeshire; Oberlaus, Glonn, S. Germany; Nymphenburg, München, S. Germany, **M.**

R. FLUITANS Lam., Fl. Fr., **3** : 184 (1778).

2n = 16. Quorndon, Derbyshire; Donaueschingen, Württemberg, Germany, **M;**.

2n = 24. Schleissheimer Kanal, Dachau, S. Germany, **M,** (sterile).

2n = 32. Temple Bridge, Suffolk, **M;** Wicken Fen, Cambridgeshire; Whatstandwell, Derbyshire.

THE ' PSEUDOFLUITANS ' COMPLEX.

This complex contains many topo- and ecodemes some of which are genetically distinct. They are more or less confined to flowing water and range from types that look like *R. fluitans* to types that look like *R. peltatus.* As the whole group is imperfectly known no attempt has been made to name the various genodemes. Some are simple hybrids involving *R. fluitans* and *R. trichophyllus, R. peltatus, R. aquatilis* and, perhaps, *R. circinatus.* There is evidence that some are allopolyploids from these hybrids and some morphologically similar types have almost certainly arisen in different localities.

2n = 24. The River Würm, Obermenzing, München, Germany, **M,** (sterile).

2n = 32. River Elz, Prechtal, Pfalz, Germany, **M,** (sterile); Sigmaringen, Württemberg, Germany, **M,** (fertile).

2n = 40. Peakirk, Northamptonshire; Monsal Dale, Derbyshire, (both sterile).

2n = 48. Greywell, Hampshire; Puddletown, Dorset; Foulmere, Cambridgeshire; Oberlaus, Glonn, S. Germany, **M,** (all fertile).

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STUDIES IN THE BRITISH *EPIPACTIS*
V. *EPIPACTIS LEPTOCHILA*; WITH SOME NOTES ON *E. DUNENSIS* AND *E. MUELLERI*

By Donald P. Young

Abstract

Records for *Epipactis leptochila* (*Godf.*) Godf., *sensu stricto*, are enumerated. In England it is confined to calcareous areas in the south, where it is frequent on the Chilterns and Cotswolds. It also occurs in France, Germany, Denmark and Switzerland. The plant is strongly calcicolous, and its usual habitat is in beech-woods with an open ground-flora and in heavy shade. Some variation in floral morphology occurs in this species. Godfery's type, in particular, has the column and lip much more elongated than in the bulk of specimens. A freak plant from Germany had a column like that of *E. muelleri*, implying that such a column-form can arise by mutation. An achlorophyllose plant has also been seen. The equation of *E media sensu* Bab. non Fr. with *E. leptochila* was based on false premises.

E. cleistogama C. Thomas may be a form or state of the last species.

E. dunensis (T. & T. A. Steph.) Godf. is only known from five British vice-counties; Continental records cannot be substantiated.

E. muelleri Godf. is known from France, Switzerland, the Benelux countries and Germany. It is a plant of lightly shaded habitats, and is closely related to *E. dunensis*.

As originally conceived (Godfery 1921b; Stephenson & Stephenson 1921b), *Epipactis leptochila* (Godf.) Godf. included all the then known self-fertilised forms except *E. muelleri* Godf., which was distinguished by a different fertilisation mechanism. The separation from it of *E. dunensis* (Godfery 1926) and later of *E. vectensis* (Brooke & Rose 1940; now called *E. phyllanthes* G.E.Sm.) has left the residual *E. leptochila* as a much better-defined entity. Now that the somewhat confused records for these species have been sorted out, it is possible to reappraise the distribution, ecology, and morphological variation of *E. leptochila, sensu stricto*.

Distribution

In Britain, *E. leptochila* is frequent on the escarpments of the Chilterns and Cotswolds. Elsewhere it is uncommon, in scattered localities along the chalk range from Wiltshire to Kent; on the Carboniferous Limestone of the Wye Valley and Cheddar; and in one or two localities in Devon. On the Continent, it is in rather widely separated localities from Denmark to the Swiss Jura; its distribution is very incompletely known, and its eastern limit is uncertain (Fig. 1). I have seen the colonies marked ! *in situ*.

British Records

V.c. 3. S. DEVON : Dunsford and Cornwood (Martin & Fraser 1939) (**TOR**; the specimen from the first locality is now too worm-eaten to confirm, but the second is correct).

6. N. SOMERSET : ash-whitebeam scrub, Cheddar Gorge, 1957, *J. T. H. Knight* (**K**).

8. S. WILTS.: beech-wood on chalk, Winterslow, 1957, *A. Roseweir*! (**K**).

11. S. HANTS.: beech-woods on chalk, Hursley, 1954 (**K**, herb. Young), and W. Tytherley, 1956, *A. Roseweir*! (**K**). These are the first two authentic records for Hants; all previous ones are referable to *E. phyllanthes*.



Fig. 1. Known distribution of *Epipactis leptochila.*

13. W. SUSSEX: wood on chalk, Treyford, 1960 *Miss D. W. Fawdry*, conf. *V. S. Summerhayes* who had found a doubtful specimen at the same spot 12 years previously. Earlier records refer to *E. phyllanthes.*
15. E. KENT : ash-hazel coppices on chalk, Kingston! (Brooke & Rose 1940) and Womenswold, 1955, *B. J. Brooke, R. Gorer & F. Rose.*
17. SURREY : beech-woods, W. Horsley (type locality), and E. Horsley, *F. Rose*; beech-yew wood, Woldingham, long known and still extant; Kingswood Valley, 1924 (Salmon 1931), not seen recently. All are on chalk.
20. HERTS.: beech-wood on chalk, Tring, 1943, *H. W. Pugsley* (**BM**), 1953! (**K**, herb. Young).
22. BERKS.: frequent on chalk between Streatley and Pangbourne. Bisham, 1925, *C. B. Tahourdin* (**SLBI**).
23. OXFORD : frequent on the chalk.
24. BUCKS.: frequent on chalk above the Thames between Hambleden and Marlow, and for about 5 miles northwards; thence in scattered localities as far as Chequers.
33. E. GLOS.: frequent on the Cotswold escarpment and valleys from Stroud to Cheltenham, thence apparently less frequent as far as the Worcs. border, and eastwards as far as Guiting (cf. Riddelsdell, Hedley, & Price 1948).

34. W. GLOS.: frequent on the Cotswolds from Stroud to Wotton-under-Edge. Madgett (Wye Valley), 1933, *J. E. Lousley* (herb. Lousley).
35. MONMOUTH : between Tintern and Wyndcliff, 1920, *C. E. Salmon* (BM).

Records for the following vice-counties are either erroneous or based on insufficient evidence, or else refer to segregates now made separate species:

V.c. 9. Three records are given in the *Dorset Flora* (Good 1948). Of these, one (Badbury) is not supported by specimens, and the other two prove to be of *E. helleborine* (specimens in herb. Good).

V.c. 10, 12 : Published records all refer to *E. phyllanthes.*

V.c. 14 : Wolley-Dod's tentative record from Saxonbury Hill (cf. Wolley-Dod 1937) has never been confirmed, and it appears that *E. purpurata* was mistaken for it. The locality is an oak-wood on sandstone, and seems now to be an unlikely habitat for *E. leptochila.*

V.c. 30 : An erroneous record has been withdrawn (Dony 1953).

V.c. 40 : The record by Godfery (1919) from Bomere Pool was based on a single admittedly poor specimen, said to be of 'the only *Epipactis* in sight' there. This specimen is not now extant, nor has the record ever been confirmed. Independent searches of the woods around Bomere Pool by Miss E. P. A. Jones and myself brought to light only *E. helleborine*, in a somewhat small-leaved form that might simulate *E. leptochila* if in poor condition. A specimen of *E. helleborine* collected there by Leighton in 1835 is in herb. BM. These woods are on sandstone, and vary from very dry to marshy, but seem unlikely to support *E. leptochila.*

V.c. 51 : The record refers to *E. phyllanthes.*

V.c. 52, 59, and 60 : The records refer to *E. dunensis.*

V.c. 66 in the *Comital Flora* was a misprint for 60, but has been repeated by copyists.

European Records

FRANCE

Seine-Mme.: beech-forests on chalk in two places, Forêt d'Eu, 1959, *B.S.B.I. field meeting*! (herb. Young).

GERMANY

Lr. Saxony : on calcareous soils in the neighbourhood of Stadtoldendorf and Hildesheim (Krösche 1929); beech-forests on Jurassic Limestone, S.E. of Hildesheim and Osterwald W. of Elze! on chalk, Sieben Berge E. of Alfeld! on Muschelkalk, Holzberg S. of Stadtoldendorf! (herb. Young).

Württemberg : beech-forests on Jurassic Limestone around Urach, 1953, F. Rose! (Herb. Young).

Sachsen-Anhalt : " in sylvis mont. calc. umbrosis," Alte Stolberg, 1885, Vocke (UPS).

DENMARK

On chalk, Møns Klint and near Hesnæs (Falster) (Young 1953).

SWITZERLAND

Berne : fir-beech forests on Jurassic Limestone near Tavannes (Young & Renz 1958) (herb. Young, herb. Renz)

AUSTRIA

Ost-Tirol : mixed woods on limestone, Matrei, 1961, *C. D. Sayers* (K).

The record from Bomere Pool raises a point of synonymy. Bomere Pool is the *locus classicus* for *Epipactis media, sensu* Babington, and on this basis Godfery (1919; 1933, p. 75) regarded *E. media* Bab. non Fr. as a synonym of *E. leptochila*, at least in part. Since *E. leptochila* does not in fact grow there, and *E. helleborine* certainly does, this synonymy cannot be upheld. The question of what Babington intended by *E. media* has been discussed by Stephenson and Stephenson (1921a), and there is little to add to their remarks, except to note Babington's revealing statement (1852), ' The true *E. latifolia* is a much less frequent plant in this country than my *E. media*, which is often mistaken for it by British botanists.'

ECOLOGY

The most striking feature that emerges is that the plant is strongly calcicolous – much more strictly so than any other European *Epipactis.* Every station for which geological

data is available is on calcareous rock, and this comprises the great bulk of records. It is also noticeable that it occurs particularly on steep slopes where the calcareous rock is free from overlying drift. Conversely, no station has been recorded as on neutral or acid soils (the Devonshire records ought to be reinvestigated with this in mind).

Tree cover is usually beech, occasionally admixed with yew or fir. At Cheddar it is under heavily-shading scrub, and in Kent it is in ash-hazel coppices. The species usually affects heavy shade, and soon disappears if the trees are cleared. It is normally associated with a low and very open ground-flora. In a typical locality on the Cotswolds, the principal associated species were *Fragaria vesca*, *Sanicula*, *Viola riviniana*, *Bromus ramosus*, *Hedera*, *Hieracium* sp., *Epipactis helleborine*, *Cephalanthera damasonium*, *Neottia nidus-avis*, and *Pyrola minor*.

In this country, *E. leptochila* can be found in good quantity in most stations, and hundreds of plants may occur in a square km. of woodland. The reverse seems to be the case in Germany, where it is very unusual to find more than half-a-dozen plants together. This seems to be the consequence of the rather different nature of central European beech forests, where beech regenerates freely. They are subjected to regular attention of foresters engaged in trimming, thinning, and felling. This leads to a cycle of disturbance of the shade cover, alternating with the growth of a shrub layer of beech (and ash) seedlings, *Rubus idaeus*, etc. The places most productive of *Epipactis* spp. are forests of young trees which have not reached the reproductive stage, and which shelter a ground flora which is quite open or almost absent. In suitable places in the Schwäbische Alb around Urach, *E. leptochila* is associated with *E. helleborine*, *E. atrorubens*, *Cardamine bulbifera*, *Lathyrus vernus*, *Cephalanthera damasonium*, *C. rubra*, and *Epipogium aphyllum*. At the other end of its range, at Møns Klint in Denmark, *E. leptochila* is again associated with *E. atrorubens*, but in Britain their ecological requirements have diverged and the two are confined to quite different areas. *Cephalanthera rubra* is, in all its known stations in this country, in areas where *E. leptochila* is frequent. *Epipogium* is also associated with *E. leptochila* in the Chilterns, and *Cardamine bulbifera* is frequent in the same area, but the association is not invariable because neither of these is strictly calcicole.

E. leptochila is one of the earliest species in the genus to flower. In a normal English summer it starts in mid-July and continues for 3-4 weeks, thus being about 3 weeks ahead of *E. helleborine*. On the Continent it is later, commencing in early August, still ahead of *E. helleborine* but later than *E. atrorubens*.

Variation

Like other species of the genus, *E. leptochila* shows considerable and sometimes puzzling variability. Variation in size and number of flowers is dependent on the age and state of nourishment of the plant, and has no other significance. There is a moderate range of leaf-size, from 6·0 × 2·5 to 10·0 × 4·5 cm. for the largest leaf of mature plants; the length/breadth ratio is fairly constant, but narrower leaves (to 8·5 × 1·5 cm.) do occur

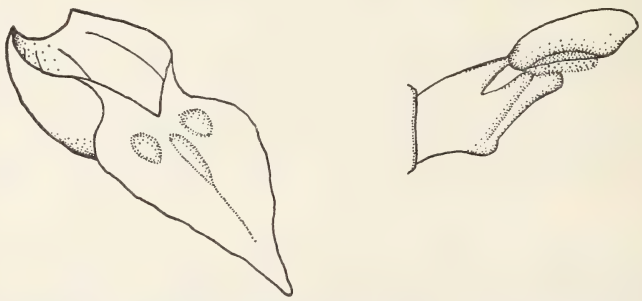


Fig. 2. Labellum and column of *Epipactis leptochila* (v.c. 33 : Cranham Woods). × 5.

occasionally. The floral architecture shows some variability, mainly in the breadth of the labellum and the shape of the column. Perhaps the only definable characters of the species (apart from absence of rostellum) are that the epichile is acute and at least as long as broad, and that the column has a well-marked clinandrium. Characteristic, but not invariable, features are that the epichile is usually very noticeably longer than broad, acuminate, and prolonged at the base into broad wings decurrent on the hypochile, giving the epichile a sagittate shape; and that the prominence on the column that bears the anther is prolonged forward, sometimes so much so as to form a short broad filament (Fig. 2). It is unfortunate that Godfery's type, represented by a population at West Horsley, is an unusual and extreme variant having a long narrow epichile and a longly stipitate anther, well shown in his illustrations (Godfery 1920, pl. 553 fig. 1, and 1933, pl. K fig. 1). *E. leptochila* var. *cordata* Brooke (1950), which perhaps represents the other extreme, is described as having a cordate and broadly acuminate epichile. Unfortunately the colony on which this was based has disappeared, and no specimens or illustrations survive. An elaborate catalogue of variations has been given by Krösche (1930, 1932, 1936). The value of this compilation is more than doubtful, since it includes, uncritically, both normal and teratological variants, and is overshadowed by attempts to force them into a taxonomic framework. The West Horsley population is the only one known to me where the distinct characters of the population are obvious, but genotypic differentiation between populations is to be expected and could probably be demonstrated biometrically.

Two abnormal plants seen in recent years deserve mention. The first was from a scattered population in the Sieben Berge (Germany) showing rather considerable variation in floral architecture. In one plant the column, in every flower, had no clinandrium, so that the pollinia overhung the stigma exactly as in *E. muelleri*. This variant does not appear anywhere in Krösche's papers, but on his arrangement it would fall within *E. muelleri* – where, from the shape of the labellum, tepal size, and other characters, it certainly did not belong. Assuming that the absence of clinandrium was genotypic – and there is no reason for supposing otherwise – then the occurrence of this form amongst an otherwise normal population implies that it had arisen by mutation. Hence the similar column-shape of *E. muelleri* could conceivably have arisen from a single mutation, rather than by gradual evolution.

The other noteworthy freak was a single achlorophyllose plant found in Hampshire (v.c. 11) by Mr. A. Roseweir in 1954, amongst a large and otherwise normal population. This plant reappeared yearly up to 1957. Despite its deficiency in chlorophyll, and also despite being picked (by persons unknown) on two occasions before reaching anthesis, it kept all the vigour of a normal plant. Its cells were probably not completely without chlorophyll, since the stems and flowers were lemon-yellow and the leaves a pale greenish-yellow. [Coloured photographs of this were taken by Mr. D. E. Kimmins, and a copy has been deposited in the British Museum (Natural History)]. Achlorophyllose plants have been reported in other species of *Epipactis* and in *Cephalanthera*. The phenomenon has recently been discussed by Burgeff (1959), who regards it as demonstrating that the plants can live entirely saprophytically with the aid of the symbiotic fungus. No other explanation appears possible, although objections have been raised in the past to this idea; not the least of these is that the roots are often well below the humus layer which supplies saprophytic nourishment. Burgeff suggests that nourishment can be transmitted for some distance through the fungal hyphae; it would be desirable to have more direct evidence on this.

The hypochile of *E. leptochila* usually contains nectar, which is sweetish to the taste but does not seem to attract insects. In other autogamous species the hypochile is always quite dry inside.

E. CLEISTOGAMA C. THOMAS

This taxon has been distinguished from *E. leptochila* by the different fertilisation mechanism : instead of the pollinia falling bodily on to the stigma in the opened flower,

in *E. cleistogama* the flowers do not open, and friable pollen is scattered in the bud stage (Thomas 1948). On gross morphology there seems to be no significant difference between the two; the distinctive features ascribed to *E. cleistogama*, such as robust habit, are within the range of *E. leptochila*. The plant has, moreover, apparently vanished from its former stations (where *E. leptochila* still occurs). If it reappears, it would be desirable to watch marked plants for several seasons to see whether they are constantly cleistogamous. For the present, it seems best to regard it as a form or state of *E. leptochila*. According to Krösche (1929, 1932, 1936), all German forms of *E. leptochila* shed friable pollen in the bud, but complete cleistogamy has not been noted in German examples.

E. DUNENSIS (T. & T. A. STEPH.) GODF.

The known distribution of *E. dunensis* in Britain is as follows :

V.C. 52. ANGLESEY : Newborough Warren, well-known.
59. S. LANCS.: Hall Rd. to Southport, well-known.
60. W. LANCS.: Lytham, 1873, *E. F. Linton* (**CGE**)—probably other records exist, but plant not seen recently.
68. CHEVIOTLAND : Holy I., 1958, *A. J. Smith*! (**E**).
69b. N. LANCS.: Roanhead-Sandscale dunes, 1952, *G. Wilson* (**K**).

The following records for *E. dunensis* on the Continent have been published, but in no case do any specimens exist :

FRANCE : Coutainville (Manche) (Meslin 1928).
BELGIUM : Nieuport-Bains and (?) le Coq-sur-Mer (Godfery 1933, p. 78).
GERMANY : coast opposite Usedom (Pomerania) (Godfery 1933, p. 78).

I have visited the alleged localities in France and Belgium, and have found no *E. dunensis* nor ground apparently suitable for it. At Coutainville and also a few miles north of it, there is a little of a dwarf dunal form of *E. helleborine*. Meslin's description and figure could well refer to this. The plant he depicts has internodes shorter than the leaves, and a very flexuous stem, which point to *E. helleborine* rather than to *E. dunensis*. He speaks of the rostellum being evanescent in the freshly-opened flower; in exposed situations this does in fact occur with *E. helleborine*. In *E. dunensis* the rostellum disappears in the early bud stage. (A further diagnostic difference is the usual dull purple suffusion of the flowers of *E. helleborine*, whereas *E. dunensis* has pale green tepals and the lip marked with

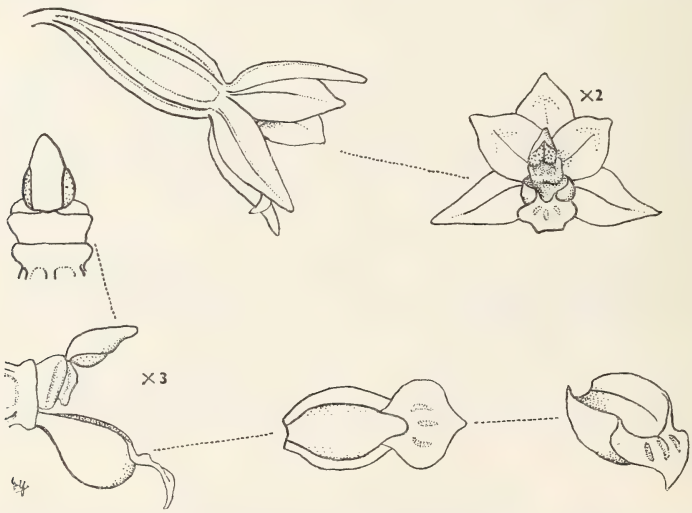


Fig. 3. Dissections of flower of *Epipactis muelleri* (France : Thorenc). The items are from different flowers, and show minor differences of shape and size.

rose-pink). Several specimens from coastal localities in Belgium in the herbarium of the Brussels botanic garden (**BR**), labelled *E. dunensis*, are either *E. helleborine* or *E. palustris*. The Belgian coastal dunes have suffered much in recent years from building and desiccation. Nannfeldt (1946, p. 5 footnote) similarly doubts the Pomeranian record, after examination of much herbarium material from that area.

The evidence for the occurrence of *E. dunensis* on the Continent is thus unsatisfactory, and we may claim it as a British endemic. However, suitable habitats for it do exist on the French and Dutch coasts, and it would be worth searching for there. It is curious that the common dunal species of the Channel and North Sea coasts of the Continent is *E. helleborine*, whereas in Britain this is extremely rare in dunes – Kenfig is the only such station certainly known to me.

E. MUELLERI GODF.

This species is not British, but it is appropriate to summarise present knowledge of it in relation to our own species. Detailed descriptions have been given by Godfery (1921a), Zimmermann (1922, as *Parapactis epipactoides*), and Krösche (1934), and recently an excellent one, illustrated, by Reichling (1955). Some diagrams of the dissected flower are given here (Fig. 3). Throughout its range it varies but little. Characteristic recognition features are the slender habit and narrow undulate leaves. The column is constantly as described by Godfery and other authors, with virtually no clinandrium, i.e. the anther is attached almost directly above the stigma and the pollinia overhang the latter. The anther has, usually, a hooked empty tip which may be clearly visible in soaked-out herbarium specimens. The labellum only varies to the extent that it may be cordate or rhomboid, but it is always short, broader than long, and obtuse. The flowers are smaller than those of *E. leptochila*.

E. muelleri is very closely related to *E. dunensis*, which it resembles in vegetative parts and in flower size, structure (except the column), and colour. The roots are thicker ($2{\cdot}24 \pm 0{\cdot}54$ mm., against $1{\cdot}48 \pm 0{\cdot}28$), but this could be the result of different habit



Fig. 4. Known distribution of *Epipactis muelleri* (black circles and shading) and of *E. dunensis* (open circles)

(see Part VII, p. 140). The ecological requirements of the two species are somewhat similar, except that *E. dunensis* is entirely maritime and *E. muelleri* entirely inland.

The autecology of *E. muelleri* has been discussed by Reichling (1955). It is a thermophile, affecting open woods and forest borders and clearings, often amongst grass. It is calcicole, but not so strongly so as *E. leptochila*. The ecology of the latter, which favours cool, heavily shaded situations, is in strong contrast.

The authenticated distribution of *E. muelleri* is as follows, although it must be very incompletely known (see also Fig. 4).

FRANCE

Pas-de-Calais : Desvres, 1959, *B.S.B.I. field meeting*!
Somme : Cambron, 1959, *idem*!
Seine-Mme.: near Hodeng, 1959, *idem*! (L, herb. Young); near Bazinval, 1960, *M. de Blangermont & J. Liger* (Herb. Young).
Hte. Saône : N. of Champlitte, 1959, *B. J. Brooke & R. Gorer* (Herb. Young).
Alpes-Mme.: Thorenc! (K, herb. Young; *locus typicus*).
Pyr. Or.: Bourgmadame, 1926, *Sennen* (Pl. d'Esp., 5883) (LD).

SWITZERLAND

Valais : near Vallorbe, 1955, *C. Sipkes* (L, herb. Young).

BELGIUM

District Calcaire Moisan, in several places (Young 1958).

LUXEMBURG

Frequent! (Reichling 1955).

HOLLAND

Limburg : near Maastricht, 1945, *H. W. E. Croockewit* (herb. Vermeulen).

GERMANY

Rheinland : Driburg (Müller 1868, p. 7; the classical description) : Echternachterbrück, 1908, *J. Groves* (BM); near Münstereifel, 1927–8, *H. Höppner* (Orchid. exsicc. VI, 137 & 76) (LD).
Lr. Saxony : Hildesheim region and near Stadtoldenorf (Krösche 1934).
Württemberg : Tuttlingen, Würmlingen (Zimmermann 1922).
Thüringen : near Sondershausen, 1885, *F. Heinmann* (UPS).

Other records are given by Godfery, Zimmermann, Soó, etc., but without seeing specimens or precise descriptions I defer acceptance of them. Further search is needed to determine its distribution more precisely.

ACKNOWLEDGMENTS

My thanks are offered to Messrs. B. J. Brooke, E. P. Bury, A. J. Smith and especially to Prof. L. Reichling, Mr. A. Roseweir, and Mr. C. Sipkes for their kindness in taking me to see *Epipactis* colonies; to Dr. F. Rose and Mr. V. S. Summerhayes for helpful discussions; and to several herbarium authorities for allowing me facilities to examine specimens.

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STUDIES IN THE BRITISH *EPIPACTIS*
VI. SOME FURTHER NOTES ON *E. PHYLLANTHES*

By Donald P. Young

Abstract

Self-fertilisation of *E. phyllanthes* occurs by germination of pollen in the clinandrium. The somatic chromosome number is 36. Plants answering to var. *pendula* have now been found in several places in the south of England, and there is no material dividing-line between this form and var. *vectensis*. A list of new records is given. The species also occurs in Ireland, and in France and Denmark, and its distribution appears to be Atlantic in pattern. One natural habitat for it is in wet willow-holts on the alluvium of chalk streams.

The following notes are supplementary to Part IV of this series (Young 1952).

Fertilisation

In Part IV the speculation was advanced that *E. phyllanthes* might be apomictic, as the process of fertilisation was not visible. Emasculation experiments showed that, if the pollinia were removed before their membrane had ruptured, no seed was set. If, however, the pollinia had become friable (which occurred long before the perianth had opened), it was not possible to remove them completely, and eventually a limited number of seeds matured in the capsule. Later, Dr. O. Hagerup kindly made sections of the column of an unexpanded flower, and demonstrated that the pollen was germinating in the clinandrium, on the upper edge of the stigma. From there pollen-tubes were passing down the stylar canal into the ovary, and embryos were already formed. Although union of gametes was not actually observed, he had no doubts that self-fertilisation was occurring in this case (Fig. 1).



Fig. 1. Longitudinal section of column from unopened flower of *Epipactis phyllanthes* (v.c. 24 : Dorney), showing germination of pollen; x 35. (Preparation and drawing by O. Hagerup).

Dr. Hagerup also made a chromosome count on Danish *E. phyllanthes*, and found $2n = 36$*. Most other European species normally have $2n = 40$.

*This was first reported by Hagerup (1947) under the name *E. leptochila*, which has been quoted by other authors. To the best of my knowledge, the chromosomes of *E. leptochila sensu stricto* have not yet been counted.

Variation

Plants which would come under var. *pendula*, i.e. with hypochile equalling the epichile, have now been found at E. Tisted (v.c. 12), Thakeham (v.c. 13), Wilstone (v.c. 20), and Harpsden (v.c. 23). These are within the area in which var. *vectensis* (hypochile shorter than epichile) and varieties with a degenerate lip are general. Other plants, e.g. from Thriplow (v.c. 29), possess a broad cordate epichile like var. *pendula*, but a smaller hypochile. There is thus no material dividing-line, either geographical or morphological, between var. *pendula* and var. *vectensis*. The names are retained here for convenience of description.

Lip variation in colonies recently discovered has been on the same lines as previously described. As observed in Part IV, a few colonies contain more than one lip-form, but in the majority the lip-shape is constant throughout the population. On the other hand, variation between colonies is very great. The distribution of forms with a degenerate lip-shape is centred on the southern counties, but within this area the different forms seem to be distributed quite at random. In parts of Hampshire and Wiltshire, particularly, colonies are thickly scattered within a few miles of one another, yet scarcely two are identical in flower-form. Their evident isolation suggests that very little long-distance dispersal by seed takes place. Probably most of these small populations have been reduced to a single biotype. They may be the relics of a very variable population extending over the southern counties when they were mainly forest-covered.

Unfortunately, the lip-shape in colonies outside Britain has not been studied very fully, on account of scanty and poor material. However, in all specimens where it could be discerned, the lip was perfectly differentiated.

Distribution

E. phyllanthes has been found on the Continent and also in Ireland. Its distribution appears to be Atlantic in character, running from the Pyrenees up the west coast of France, through England and Ireland, and reappearing in Denmark (Fig. 2). It should be looked



Fig. 2. Known distribution of *Epipactis phyllanthes*.

for in northern France, where it is unrecorded but likely to occur.

In Parts II and IV, reference was made to an allied Scandinavian plant tentatively included under *E. persica* (Soó) Hausskn. ex Nannf. Further investigations by the writer (Young 1953) showed that this was best regarded as a separate species, *E. confusa* D. P. Young. This is a more slender plant, with narrower leaves, smaller and less pendent ovaries, smaller seeds, thinner and less copious roots, and 40 somatic chromosomes. It is related to *E. persica* (*sensu stricto*), which is an Asiatic species extending from Turkey to Afghanistan. The ranges of *E. phyllanthes* and *E. confusa* just overlap in Denmark.

European Records for E. phyllanthes

FRANCE

Maine-et-Loire : recorded by Jovet (1957); I have not seen the specimen.

Vendée : pine forest on sand-dunes, Forêt d'Olonne, 1880, *C. Pontarlier* (**LD, UPS**), 1953! (herb. Young) (lip small, perfect; var. *pendula*).

Charente-Mme.: pine forest, Forêt de Foulerot near St. Georges d'Oléron, 1891, *N. Reau* (**P**); Forêt d'Arvert, 1889, *A. Guillon* (**P**).

Basses-Pyr.: Bayonne, 1836, *Grenier* (**P**); pine plantations on banks of R. Adour, Boucau and Anglet, 1883, *Blanchet* (**MANCH, P**) (lip perfect, rather narrow).

Hte.-Garonne : wood at mouth of the Ariège, Toulouse, 1850, *Timbal-Lagrave* (**P**).

Pyr. Or.: Olette, 1853, *Loret* (**P**).

DENMARK

Jutland, Falster (var. *pendula*; Young 1953).

New British Records

The following are supplementary to the list given in Part IV. Some have already been published in " Plant Records," but references are only given to where substantial further information can be found. Records are recent unless a date is quoted.

The lip-form is indicated as follows : (*a*) var. *phyllanthes*, (*b*) var. *degenera*, (*c*) var. *vectensis*, (*d*) var. *pendula*. I have seen the colonies marked ! *in situ*.

V.c. 5. S. SOM.: roadside near Taunton, 1891, *C. Bailey* (**MANCH**).

8. S. WILTS.: beech plantations, Boyton (*c*; epichile broad, reflexed), *B. M. Stratton* (**K**, herb. Young); edge of beech-wood, Erlestoke (*c*), *W.O. Cobbett*!; under beeches, Harnham (*b*), *D.E. Coombe*!; beech-belts, Berwick St. James (*c*), Steeple Langford (*a*), and Durnford (*c*), *A. Roseweir*; beech-belt, Winterbourne (*c*, epichile only just longer than hypochile), *J. Hemsley* & *A. Roseweir*; plantation, Stapleford, 1876, *E. S. Marshall* (**K**); beech-yew belt, Stapleford (*c*), A. *Roseweir*; beech-belt, Coombe Bissett, *Miss H. Lamb* (**K**).

11. S. HANTS.: willow-holts, Nursling (*c*) (several hundred plants over a wide area; **K**, herb. Young), near Swaythling (*b*) (**K**), and Bossington (*b*) (**K**), and plantation on river mud, Eling (*c*) (Herb. Young), *P. Bowman*!; plantation on alluvium of Itchen, Twyford (*b*, differentiation almost perfect), *A. Roseweir*!; canal bank amongst *Petasites*, Otterbourne (*b*), *Mrs. J. Goater*!; beech-wood, Bishop's Waltham (*b*) (**K**), and beech-belts, Little Somborne (*b*), W. Tytherley (*b*), and Broughton (*b*) (**K**), *A. Roseweir*.

12. N. HANTS.: beech-yew belt, Crawley (*c*) (**K**), *A. Roseweir*!; some miles from the previously-known Crawley locality, where *P. Bowman* found var. *vectensis* occurs as well as var. *degenera*!; beech-woods, E. Tisted (*d*) and Cranbourne, beech-clump, Hurstbourne Priors, and beech-belt, Overton (*b*), *A. Roseweir*; in adjoining beech-belts, Nether Wallop and Abbott's Ann (*a*) (**K**), *Miss D. Stevens*!; hedgebank, Conford (*a*), *Mrs. E. Briggs* & *Mrs. Missen*!.

13. W. SUSSEX : copse beside lake, Arundel (*b*), *Miss B. M. C. Morgan* & *Miss D. Powell* (herb. Young); under oaks on sandy soil, W. Chiltington (*a*), *Miss D. A. P. Long* & *Mrs. Thatcher*; shady roadside, on chalky grit (over sand), Thakeham (*d*), *J. T. H. Knight*.

16. W. KENT : plantation belt, Eynsford (*b*), *Mrs. Denton*! (**K, S, UPS**, herb. Young).

17. SURREY : Mr. Spicer's park near the railroad, Esher, n.d., *H. C. Watson* (**K**); this would be on the bank of the R. Mole.

20. HERTS.: amongst grass in orchard, Chorley Wood, *R. F. Turney*! (**K**); edge of wood on bank of stream, Wilstone (*d*), *R. I. Sworder* (herb. Young).

23. OXON.: plantation beside tributary of Thames, Crowmarsh (*c*), 1925, *R. R. Hutchinson* (**CYN**), 1956! (**K**); beech-wood, Harpsden (*d*), *G. J. Munday*! (**BR**, **K**, herb. Young); beech-wood, Bix, *D. J. Tennant*; beech-wood, Rotherfield Greys (*b*), *V. S. Summerhayes* (**K**).
24. BUCKS.: beech-wood, Chalfont St. Giles, *R. F. Turney*! (**K**); beech-wood, Great Marlow, *F. Rose*.
29. CAMBS.: mixed wood on bank of stream, Thriplow (*c*; epichile broad, cordate), *Mrs. G. Crompton* (**CGE**, herb. Young).
48. MERION.: sand-dunes, amongst *Salix repens*, Morfa Dyffryn (*d*) (Benoit 1959; **K**, herb. Young).
51. FLINT.: now known to be in a number of places around Rhyd-y-Mwyn and Pant-y-Mwyn in Mold R.D., under willows, beech, and ash (*d*).
55. LEICS.: 'Leicestershire,' n.d., *R. M. Norman* in herb. Syme (**BM**).
60. W. LANCS.: sandhills between St. Anne's-on-Sea and Fairhaven (*d*), 1890 and 1902, and waste ground, St. Anne's, 1901, *C. Bailey* (**MANCH**).
61. S. E. YORK : S. Cave (*c*) (Young 1955; **K**).

H20. WICKLOW : dunes, Brittas Bay (?*c*) (Webb 1953, Sipkes 1954; **TCD**, herb. Young).

H33. FERMANAGH : damp mossy woods on limestone, Lurgan River glen, 1948, *R. D. Meikle & J. McK. Moon* (**K**).

H40. DERRY : beech-wood on sandy soil, Castledawson (*d*), *D. McClintock & J. McK. Moon* (herb. Young).

Ecology

It has become clear that one natural habitat for *E. phyllanthes* is in willow-holts on the calcareous alluvium of chalk streams. There are numerous such habitats along the rivers Test and Itchen, even on the tidal reaches. The plant also grows in equivalent habitats such as plantations on stream and river banks. It seems to have been overlooked in such places until recently; their herbaceous flora is usually coarse and botanically uninviting, but *E. helleborine* sometimes accompanies *E. phyllanthes* in them. These orchids are quite amenable to periodical inundation, but they avoid hollows where the ground is permanently waterlogged, keeping to ridges and banks where the drainage is better.

Most of the recently reported woodland stations have again been in small copses, tree-belts and the like. When the plant has been found in extensive woods it has usually been near the margins. This behaviour has already been remarked in Part IV. *E. phyllanthes* clearly prefers comparatively light shading, in contrast to *E. leptochila* and *E. purpurata* which seek heavy shade in the interior of woods. *E. helleborine* is intermediate in this respect, and the Continental *E. muelleri* (see Part V) requires only very light shade.

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STUDIES IN THE BRITISH *EPIPACTIS*
VII. SEED DIMENSIONS AND ROOT DIAMETERS

By Donald P. Young

Abstract

Seed-dimensions and root-diameters are characters of some taxonomic significance in *Epipactis* species. Preliminary data on these measurements is given in the tables.

Epipactis are notoriously variable plants, and it is not surprising that their quantitative characters show a wide amplitude and much overlapping between species. The data which follows indicates that the dimensions of the roots and seeds are more absolute characters and of taxonomic significance. It is not the result of a serious biometric study, but simply arose from examination of material that happened to be available. It is presented as an indication of where properly designed studies might be profitable.

Seed dimensions

The size of seeds is well known to be almost independent of the size and vigour of the parent plant. Dymes (1921, 1923) has shown that seed morphology is sometimes a useful taxonomic character in the Orchidaceae. Table 1 gives the dimensions of the seeds of all species of *Epipactis*, Section *Epipactis*, of Europe and the Mediterranean region, including five non-British species. Samples were mounted in Canada balsam, and measurements were made by means of a micrometer eyepiece on ten seeds taken at random (but rejecting twisted or undeveloped ones).

On the basis of size and shape of the seeds, the species fall mainly into two groups : (i) *E. purpurata*, *E. microphylla*, *E. leptochila*, and the three glabrous-stemmed species *E. phyllanthes*, *E. confusa*, and *E. persica*, with large seeds 1·15–1·3 mm. long, and about 4·5 times as long as broad (5·2 in the first species); (ii) *E. helleborine*, *E. atrorubens*, *E. muelleri*, and *E. dunensis*, with smaller seeds, 0·9–1·0 mm. long, length/breadth ratio about

Table 1
Seed dimensions of *Epipactis* species.

Species	*Number of collections*	*No. of seeds measured*	*Length, mm.*		*Breadth, mm.*		*Length/breadth*
			Mean	*s.d.*†	*Mean*	*s.d.*†	
E. purpurata	3	30	1·29	0·14	0·25	0·035	5·2
*persica	3	27	1·29	0·18	0·29	0·04	4·5
phyllanthes	17	170	1·28	0·12	0·28	0·045	4·5
*microphylla	1	10	1·16	0·06	0·26	0·04	4·5
*confusa	3	30	1·15	0·15	0·27	0·035	4·3
leptochila	2	20	1·15	0·04	0·27	0·03	4·3
*condensata	2	18	1·19	0·12	0·31	0·04	3·9
atrorubens	3	30	1·04	0·17	0·30	0·035	3·5
helleborine	4	40	0·97	0·09	0·27	0·025	3·4
dunensis	5	44	0·95	0·17	0·29	0·04	3·3
*muelleri	1	10	0·91	0·12	0·27	0·025	3·4

* Non-British † Standard deviation

3·4. The shorter seeds tend to a bluntly clavate shape, whereas the longer ones are more fusiform, with the areolation of the testa elongated. *E. condensata* Boiss. (*E. troodi* Lindb. f.) is somewhat anomalous, with very large seeds 1·2 mm. long but with a length/breadth ratio only 3·9. This species, from the Levant, is quite different in appearance from any of the other species mentioned, and need not be further discussed here.

The standard deviation of the pooled length measurements for each species was in most cases less than $\pm$ 10%, emphasising the absolute nature of the character. However, marked differences were sometimes found between different colonies of the same species, particularly with *E. atrorubens*. At present, too little data is available to say whether this is significant. Some influence of habitat and also of season is to be expected.

The almost identical dimensions of the seeds from *E. dunensis* and *E. muelleri* should be noted. This reinforces the suggestion (see Part V) that these two are very closely related.

Root diameter

The roots of *Epipactis* plants are emitted from the rhizome and the base of the stem and are, strictly speaking, all adventitious. They are cylindrical with no taper except at the extreme tip, and they are of practically uniform thickness regardless of their length or position, or of the age or size of the plant. The thickness is characteristic of the species : the thin wiry roots of *E. dunensis*, for instance, can be distinguished at a glance from the thick fleshy ones of *E. phyllanthes*.

Some data on the root diameters of all the European species (except *E. palustris*) is given in Table 2. Two or three pieces of root about 1 cm. long were cross-sectioned, and a random selection of sections was mounted in Canada balsam. The diameter of each section was measured in two perpendicular directions.

The standard deviations, as can be seen from the table, are mostly around $\pm$ 20%. The average diameters range from 1·5 to 3·1 mm. over the various species, so that the root diameter may provide a character of useful significance.

There is one apparent ecological effect here, that plants (*E. helleborine* and *E. phyllanthes*)

Table 2
Root diameters in *Epipactis* spp.

Species	*Number of*			*Root diameter, mm.*	
	Stations	*Plants*	*Measurements*	*Mean*	*s.d.*
E. purpurata	2	3	42	3·09	0·59
phyllanthes (inland)	7	7	84	2·94	0·37
phyllanthes (dunal)	2	3	32	2·26	0·30
*microphylla	1	1	12	2·61	0·42
*confusa	4	4	48	2·54	0·40
*muelleri	5	6	74	2·24	0·54
helleborine (inland)	3	3	50	2·19	0·48
helleborine (dunal)	4	4	48	1·88	0·29
leptochila	6	6	39	2·07	0·34
atrorubens	3	3	48	1·91	0·28
dunensis	2	4	74	1·48	0·28

* Non-British.

growing in dune sand have roots noticeably thinner than those from woodland habitats. These are separated in Table 2. Measurements from more stations will be needed before a satisfactory test of statistical significance can be applied (for *E. phyllanthes* the available data gave $P < 0{\cdot}05$ as between dune and inland colonies), but the existence of such a

difference would not be surprising. If granted, it brings an interesting corollary : the difference in root-diameters between *E. dunensis* and *E. muelleri*, which at first sight seems to separate them widely, might be explained (at least in part) as the result of their different habitats.

The specific root-sizes do not fall naturally into groups. Neglecting dune plants, they might be arbitrarily classified as (i) species with thick roots (2·5–3·1 mm.), *E. confusa*, *E. microphylla*, *E. phyllanthes*, *E. purpurata*; (ii) those with thinner roots (1·9–2·2 mm.), *E. atrorubens*, *E. leptochila*, *E. helleborine*, *E. muelleri*. Perhaps *E. dunensis* could be regarded as a third class, with very thin roots.

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SOME NOTES ON *GALEOPSIS LADANUM* L. AND *G. ANGUSTIFOLIA* EHRH. EX HOFFM.

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Abstract

Galeopsis angustifolia Ehrh. ex Hoffm. is formally typified. The characters normally used to separate the two species are reviewed, and that of leaf shape is shown to have only limited application. Attention is drawn to the structure of the hairs of the calyx in these two plants, which seems to be diagnostic as far as tested. The status of the varieties listed in the second edition of Druce's *British Plant List* is investigated; only one is believed to be worthy of recognition. There appears to be no reliable evidence of the hybridisation of the two species.

Preamble

My interest in the British forms of *Galeopsis ladanum* and *G. angustifolia* arose when, as an amateur botanist, I found myself unable satisfactorily to place many gatherings on the basis of the account given by Warburg (1952). In conversation with other botanists, I found that I was not alone in this, and have found subsequently in some of the larger herbaria sheets annotated with such remarks as 'seems to have the upper indument of *angustifolia* and the leaves of *ladanum*.' It was hoped that an investigation into the varieties listed by Druce (1928) within the British flora would shed some light on these anomalous forms, but rather did this confuse the issue further. The present notes are written with two objects in view; firstly, to clear up the differences between these two species, and secondly to assess the value of the varieties listed by Druce.

Historical

The foundation of most modern work on *Galeopsis* has been the monumental monograph of Briquet (1893). The influence of this, with the inevitable changes of status and additions of infra-specific entities of varying worth, may be seen in all the Continental Floras. These range in their taxonomic concepts from the confusing treatment of Rouy & Foucaud (1909) to the ultra-conservative account by Fiori (1925-9); the most recent truly critical paper is that of Henrard (1919).

Typification of the species

The typification of *G. ladanum* L. presents no difficulty. As has been widely noted, an excellent specimen exists in the Linnean Herbarium at Burlington House. But to the best of my knowledge *G. angustifolia* has never been formally typified.

The name *G. angustifolia* first appeared on exsiccatae which were distributed by Ehrhart in 1792 (No. 137, mis-cited by Briquet, 1893, as No. 132). He published no description, but the name was validated by Hoffmann (1804), who published a short but adequate diagnosis and cited Ehrhart's exsiccata number as the basis of the name. Williams (1910) suggested that in fact Hoffmann published *angustifolia* as a variety of *G. ladanum* and that Persoon (1807) was the first to accord it specific rank. However, it would seem that the 'unnumbered species' listed by Hoffmann (and other older botanists) were intended to take specific rank, though perhaps as species concerning whose status the writer was in some doubt. Mr. J. E. Dandy advises me (*in litt.*, 7 Feb. 1961) that such was his view in compiling the *List of British Vascular Plants.*

Williams makes the following remarks on this exsiccata :

' On p. 246 of the monograph, var. (or subsp.) *angustifolia* is mentioned as having first been described by Ehrhart, *Pl. exsicc.* no. 132 (1792) as a species. This merely refers to a series of specimens (and poor ones) from Ehrhart's garden, bearing Linnean or other names, several of them obviously cultivated examples, but without either descriptions or other references. There seem to have been 160 of them, divided into ten bundles. In Kew Herbarium Library there is a catalogue of the whole series of names, bound up with the first two bundles. But the name of *Galeopsis angustifolia* is not in the list at all. No. 132, which is the plant cited in the monograph, is *Rumex pulcher*; while No. 137, which is the plant cited by Hoffmann, is *Artemisia sieversiana*.'

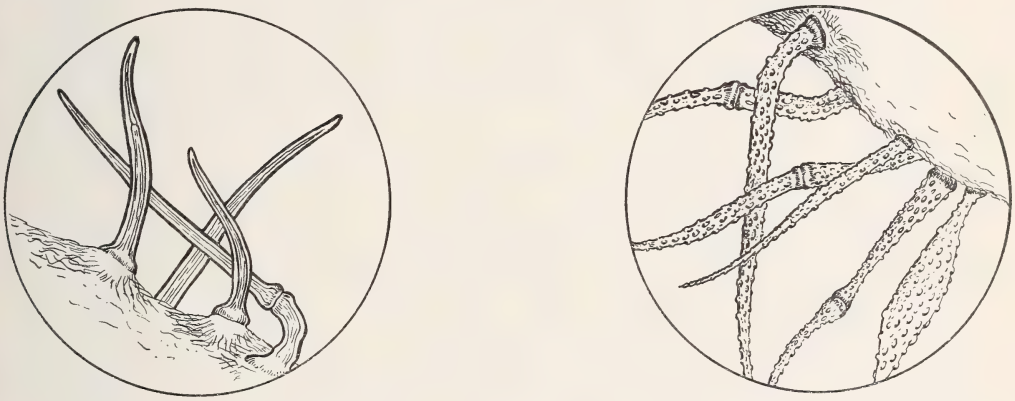
It seemed to me that since the date of circulation of the exsiccata referred to by Williams differed from that cited by Briquet, and the numbers given by Briquet and Hoffmann did not correspond to specimens of *G. angustifolia* in the list which he mentions, it was very probable that there were other sheets distributed by Ehrhart of which Williams was unaware. This view has been vindicated by the discovery of at least two sheets of Ehrhart's *G. angustifolia* No. 137 still extant. These are at Halle (**HAL**) and Goettingen (**GOET**), and by courtesy of Profs. Meusel and Firbas I have been able to examine both. Both agree well with Hoffmann's description, but that from Halle is the more homogeneous, and I therefore formally designate this as the lectotype of *Galeopsis angustifolia* Ehrh. ex Hoffm. (Plate 7a). It has appressed hairs to the calyx and agrees well with specimens of *G. ladanum* subsp. *angustifolia* var. *kerneri* Briq. from Briquet's herbarium at Geneva (**G**) which I have had on loan through the kindness of Prof. Baehni.

Distinction between the two species

The difficulties which have been experienced in distinguishing between *G. angustifolia* and *G. ladanum*, at any rate in British and the Continental material which I have seen, are the result of undue stress on the value of leaf characters. Indeed, Warburg stresses these in italics as the chief means of separating these perfectly distinct species. Yet it has long been realised that *G. angustifolia* frequently has broad-leaved forms. Briquet's variety *odontota* is described as having the leaf superficies with a length : breadth ratio of 3 : 1, which is quite as broad as in many gatherings of *G. ladanum* which I have seen. Rouy & Foucaud described a var. *latifolia* of ' Race *calcarea* ' with ' feuilles ovales-lancéolées ' and Henrard's *G. ladanum* ssp. *angustifolia* var. *calcarea* subvar. *platyphylla* (Plate 7b) is undoubted *G. angustifolia* with a superficies of 4·0 × 1·8 cm. In fact, after examining a large number of gatherings of both species, one is made aware that leaf shape in this species pair is as variable as in, for example, the genus *Mentha*; and as Graham (1954) has done good service in recommending the quashing of all varietal epithets based on leaf shape in *Mentha aquatica* L., so ' varieties ' of, particularly, *G. angustifolia* based on leaf shape are scientifically worthless, as a complete range from broadly ovate to narrowly linear may be found, though lanceolate is probably the commonest shape. Likewise I have seen leaf serration quite as pronounced in *G. angustifolia* as in any *G. ladanum* material which has been examined. However, it may be said that *G. ladanum* does not seem to produce forms with linear or linear-lanceolate leaves, and to this extent leaf-shape would appear a reliable character; the real pitfall is in the broad-leaved *G. angustifolia* forms.

Thus we are left with the other commonly used separating character, that of calyx indument. After testing this on a great number of specimens I am satisfied that, correctly understood, it affords a means of accurate identification. Unfortunately the macroscopic difference is of a nature which is not readily expressed in words, and unquestionably the best means of apprehending it is to ' get one's eye in ' by examining a quantity of authentic material. As is pointed out by Warburg the calyx of *G. ladanum* appears green, while that of *G. angustifolia* appears whitish or canescent. At first sight this appears due to the fact that the hairs on the calyx of *G. ladanum* are patent, thus rendering the tube visible; but if fresh or fairly recent herbarium material is viewed under a lens it is at once apparent that the hairs of *G. ladanum* have a peculiar transparent and glistening appearance while those of *G.*

angustifolia appear a dull harsh white. To ascertain the reason for this, the hairs were examined under the high power of the compound microscope (× 400). It was found that the white colour of the hairs of *G. angustifolia* was due to the crowded, coarse papillae with which the hairs are furnished. In *G. ladanum*, on the other hand, the hairs are for the most part almost devoid of papillae and quite transparent — so much so that the inner walls of the cells of the hair are visible (Fig. 1). All the hairs in *G. ladanum* are not always as smooth as figured, but in material I have examined papillae of sufficient prominence to show any irregularity in the profile of the hair are very rare; it is difficult to determine whether such unevenness in the hair surface as does occur is in fact caused by a very low papilla or a very shallow punctum, and the inner cell walls remain visible. In old herbarium material the glistening appearance under the lens is lost due to the shrinkage of the cells, but is restored somewhat by boiling out. I cannot find any previous notice of this character, which is diagnostic as far as I have been able to test it. It may also be noted that when the indument of the calyx in *G. angustifolia* is so sparse as to render any appreciable area of the tube visible, the hairs are usually short and tightly appressed, glands are few, and there is often development of anthocyanin pigmentation which tints the tube purplish or brownish. In fresh material the glistening appearance of the glands in *G. ladanum* is very striking.



a. b.

Fig. 1. Calyx hairs, × 400, of
(a) *Galeopsis ladanum* L. (b) *Galeopsis angustifolia* Ehrh. ex Hoffm.

Hybrids between the two species have been reported from the Continent, but I have had no difficulty in assigning all the material which I have seen to either one species or the other. *G. ladanum* is clearly a plant of considerable rarity in this country, occurring in waste places, docks, railway tracks, vegetable gardens and other abodes of the casual alien, which is clearly its status in Britain. It is thus hardly to be expected that, in any event, hybrids would be of any but the rarest occurrence with us. According to Briquet, the hybrid recorded by Haussknecht (1884) is in fact typical *ladanum*. Briquet himself cites some intermediates between ssp. *intermedia* and ssp. *angustifolia* ; but since these are for the most part said to approach ssp. *intermedia* in leaf shape probably broad-leaved *angustifolia* forms are involved.

On the varieties listed in Druce's "British Plant List," ed. 2 (1928)

In this list Druce notes only one species, 578/4 *G. ladanum* L., with eight varieties. These will be dealt with seriatim :—

b. *intermedia* (Vill.). *G. ladanum* L. was divided by Briquet into two subspecies, subsp. *intermedia* (Vill.) and subsp. *angustifolia*. It is as clear as can be ascertained in the absence of an authentic specimen in Villars' herbarium at Grenoble that Villars' *G. intermedia* was,

as has been long accepted, a form of *G. ladanum* L. *sensu stricto*. Villars' second and better description (1778), including the phrase 'toute la plante est visqueuse,' considered in conjunction with the plate, which shows a broad-leaved plant with patent glandular hairs on the calyx, can hardly apply to *G. angustifolia*. Villars appears to have regarded his plant as an intermediate between *G. ladanum* and *G. tetrahit* on the grounds of flower size—not a constant character in *G. ladanum*, or in most species of the genus.

c. *angustifolia* (Ehrh.). This becomes the second species, *G. angustifolia*.

d. *latifolia* (Hoffm.). With his original description Hoffmann (1804) cites t. 884 of Sowerby & Smith's *English Botany*. This plate is not only clearly *G. ladanum*, but in the accompanying description it is mentioned that the plant illustrated agrees well with the Linnaean specimen. Thus *G. latifolia* Hoffm., like *G. intermedia* Vill., falls into the synonymy of *G. ladanum* L. *sensu stricto*.

e. *kerneri* Briq. As has been pointed out above, specimens of var. *kerneri* from Briquet's herbarium match the lectotype of *G. angustifolia*. Thus, assuming that two or more varieties are recognised within *G. angustifolia*, 'var. *kerneri*' falls into the synonymy of var. *angustifolia*.

f. *campestris* Timb. This variety is placed by Briquet in the synonymy of his var. *orophila* (an earlier MS. name from an exsiccata distributed by Timbal-Lagrave which he takes up), which is distinguished from 'var. *kerneri*' by the length of the calyx teeth (5 mm. long as compared with 2-3 mm. for the latter variety). That the two names do in fact apply to the same form is clear not only from Timbal-Lagrave's description (1885) : 'lobes du calice aussi longs que le tube . . . . terminés par une épine blanche et longue,' but also from examination of the exsiccata distributed through the Société Dauphinoise on which this was based compared with specimens of var. *orophila* from Briquet's herbarium. Since the epithet *campestris* is the earlier at varietal level, this is the correct one. I do not consider, however, that the variety is worth maintaining. The length of the calyx teeth in *G. angustifolia* varies tremendously, quite independently of other characters. I have seen quite a lot of British material that matches well ' var. *orophila* ' from Briquet's herbarium – e.g., a gathering by E. F. Linton from Diddington Wood, Hunts. (v.c. 31), 29 July 1879, in Cambridge (**CGE**); and also others which provide a good match for the type of *G. ladanum* subsp. *angustifolia* var. *calcarea* subvar. *longidentata* Henrard. These apparently represent the greatest length reached by the calyx teeth in Great Britain. At the other end of the scale are specimens agreeing with the type of *G. ladanum* subsp. *angustifolia* var. *calcarea* subvar. *microdus* Henrard – e.g., a gathering from 'shingle bank between Southampton and Netley,' S. Hants. (v.c. 11), Sept. 1846, from Herb. Babington in Cambridge (**CGE**).

On the Continent greater variation even than this occurs, from var. *spinosa* Benth., with calyx teeth said to be over 8 mm. long, to var. *inermis* (Posp.) Fiori with muticous calyx teeth. I have seen no material agreeing with the original descriptions of these, but they are clearly *angustifolia* forms.

g. *odontota* Briq. This variety is based on leaf shape, Briquet keying it out from 'var. *kerneri*' thus :—

Leaf serration always of irregular, scarcely perceptible or almost non-existent, triangular teeth less than 1 mm. deep.

'var. *kerneri*.'

Leaf serration of stronger, more regular teeth, triangular, 1-1·5 mm. deep.

var. *odontota* (& var. *berteti* Briq.).

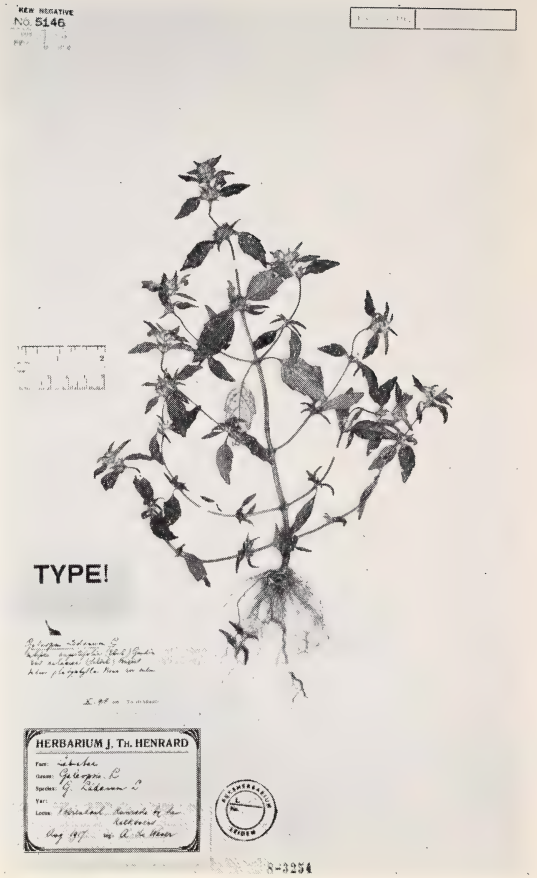
Var. *odontota*, which Briquet himself cites from Miller's Dale, is also said to have broad leaves of which the bases are rounded and shortly attenuate into the petiole. As has been stated above, no useful purpose will be served by maintaining varieties of this species based on leaf shape, and var. *odontota* thus falls into the synonymy of var. *angustifolia*.

PLATE 7A



(a) Lectotype of *Galeopsis angustifolia* Ehrh. ex Hoffm.

PLATE 7B



(b) Holotype of *Galeopsis ladanum* L. ssp. *angustifolia* (Ehrh. ex Hoffm.) Briq. var. *calcarea* (Schonh.) Briq. subvar. *platyphylla* Henrard.

h. *monticola* Lannes. In some areas, particularly on the chalk in eastern and south-eastern England, there occurs a form of *G. angustifolia* which in its extreme state appears very distinct. It is a rather short plant, branched almost from the base, canescent, and with the calyx densely villous with patent, long white hairs. This form was first described without ambiguity by Schönheit (1832), as a species, *G. calcarea*, attention being particularly called to the ' calycis patenti-villosuli.' It is the form often called ' var. *canescens* ' by referees of British exchange clubs, but its correct place under *calcarea* was noted by Salmon (1931). Briquet reduced Schönheit's species to a variety of *G. ladanum* ssp. *angustifolia*. However, since according to the International Code a name has priority only within its own rank, consideration must be given to two varietal names of earlier date which Briquet cites in synonymy here. One of these is var. *monticola* Lannes, the name used by Druce. This, however, is a *nomen nudum* which appeared on a herbarium label, Magnier's *Flora selecta No. 940*. Neither on the sheet nor in the Scrinia which gave notes on Magnier's plants does any description appear. The only note which the label on the specimen bears is ' an *G. monticola* Jord *ined.* ? ' It is undoubtedly *G. calcarea*, but the epithet *monticola* must be discarded as never validly published.

The name *G. angustifolia* var. *arenaria* Gren. Godr. was indicated as the correct one for the form under consideration by Brenan (1956). But what does not appear clear is why Briquet should have placed this name within the synonymy of *calcarea* at all. The original description is very brief : ' Dents du calice plus courtes; plante blanchâtre et parfois glanduleuse dans le haut.' There is no mention of patent hairs on the calyx, and in fact Godron cites *G. canescens* Schultes, which Briquet maintains as a distinct variety, as a synonym. The only two specimens of *G. angustifolia* var. *arenaria* Godr., named by the author, which exist in his herbarium, were kindly sent to me on loan by the Director of the École Nationale Supérieure Agronomique de Nancy. Both bear collection dates later than 1850, the date of publication of Godron's varietal epithet. These two specimens represent diverse elements. Under Briquet's classification, interpreted in the light of specimens from his herbarium at Geneva, one specimen, which has the calyces almost or quite eglandular and totally appressed-hairy, would have been called ' *G. ladanum* ssp. *angustifolia* var. *kerneri* ' (i.e., *G. angustifolia* var. *angustifolia*); the other, which has the calyces considerably glandular and with some patent hairs, would have been called '*G. ladanum* ssp. *angustifolia* var. *calcarea*.' Indications are, therefore, that Godron would have applied his epithet to any reasonably canescent form of *G. angustifolia* irrespective of other characters. What is clear is that whatever was in Godron's mind, he was in fact reducing *Galeopsis canescens* Schultes to the rank of variety. The present writer's views on *G. canescens* are given later in this paper, and these views thus gain some additional support from the fact that Godron appears to have interpreted Schultes' species in the same manner. Thus *G. angustifolia* var. *arenaria* Godr. and *G. canescens* Schultes can now only be regarded as merely representing any ± canescent forms of *Galeopsis angustifolia*. The correct name for the form of *G. angustifolia* with the patent-villous calyces remains *G. angustifolia* var. *calcarea* (Schonh.) C. E. Salmon, based on the beautifully circumscribed *G. calcarea* Schonheit. In addition to the patent calyx hairs, var. *calcarea* is usually considerably glandular around the inflorescence.

Intermediates between var. *calcarea* and var. *angustifolia* certainly occur not infrequently, and it is a matter of opinion as to whether the former should be maintained; in particular, forms with long appressed hairs on the calyx tube, and patent hairs in the region of the teeth and sinuses between them, are clear intermediates. Nevertheless, the appearance of the variety is so distinct in the field, and it is so predominant over large areas of arable chalkland, that it seems worthy of recognition. It may be noted that the hairs of the calyx tend to spread even further on drying and storing.

i. *canescens* (Schultes) (not Schultz, as in the *British Plant List*). This is certainly the most elusive of the varieties of *G. angustifolia*. In the synoptic table which forms chapter XXXI of the *Monograph*, Briquet separates it from vars. *odontota* and *kerneri*, which it is said to resemble in the appressed indumentum of the calyx, in the following manner :—

Plant with branches greenish, pilose or glabrous, but not with a hoary indumentum.
vars. *odontota*, *kerneri* (&c.).

Plant with branches densely and closely hairy, the stem, leaves, bracteoles and calyces likewise being thickly canescent.
var. *canescens*.

The difficulty in resolving precisely what Schultes's plant was is due principally to the fact that no authentic specimen appears to be extant at Munich, Berlin, or other Continental institutions. Fortunately, however, his description is a good and full one.

The plant pictured by Briquet's description on p. 254 of his monograph is one with so thick an indumentum that the whole plant appears ashy-white (though, as often, the specimens in his herbarium so named do not always bear this out). Likewise, the leaves are depicted as having their margins more or less revolute; and in all but one of Briquet's specimens (a specimen from the Somme, ex herb. Schmidely, coll. E. Gonse – this *is* densely white-canescent) the plants have linear, entire or slightly sinuose leaves. In his original description Schultes (1809) clearly states ' caule . . . . *sub*tomentoso . . . . foliis *lanceolatis sub*tomentosis *subserratis*.' Also, in *Oesterreichs Flora*, Schultes gives to his *G. canescens* the vernacular name ' Graugrüner Hohlzahn ' and refers to the stems and leaves as ' *etwas* filzig.' For such a plant as Briquet describes, ' graugrüner ' would hardly be appropriate; ' weisgraulich ' or ' weisgrau ' seem more applicable. It appears to me that *G. canescens* was merely one of the more canescent forms of *G. angustifolia* var. *angustifolia*, and that Godron was correct in using the epithet *arenaria* to cover the same range.

Briquet's plant is said to occur in dry or stony places by the sea, or by lakes. Under such xerophytic conditions many species take on an unusually tomentose appearance (as may be seen in many plants as they occur, for example, at Braunton Burrows); similarly, leaf margins may become revolute. Briquet's form is probably of this kind; but it must be confessed that in this country *G. angustifolia* grows on maritime shingle (as for example at Wolferton, Norfolk, at Dungeness and the Crumbles, Eastbourne) without developing such tomentum, and the variety may prove worth keeping up. If so, the name var. *littoralis* de Vicq & de Brutelette (1864) should be used, as the description of these authors (' velue blanchâtre ') is far more applicable to Briquet's plant than that of Schultes. Mr. Brenan informs me (*in litt.*, 1 March 1957) that ' . . . I have seen what appears to be *canescens* as a sand dune plant in southern France, and it looks very different from anything I have seen in Britain.' I have seen no British material which could be placed here with any confidence.

The confusion which has existed in the past between *canescens* and *calcarea* may well be due to Hegetschweiler (1840), who describes *his G. canescens* as ' die Kelch . . . mit . . . etwas abstehenden Härchen besetzt.' *G. canescens* Heg. is, of course, an illegitimate later homonym.

It is thus proposed that *Galeopsis ladanum* L. agg. in Great Britain be listed thus :
Galeopsis ladanum L.
Galeopsis angustifolia Ehrh. ex Hoffm.
Var. *angustifolia*
Var. *calcarea* (Schönh.) C. E. Salmon.

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CHROMOSOME NUMBER, MORPHOLOGY AND BREEDING BEHAVIOUR IN THE BRITISH SALICORNIAE

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Abstract

Chromosome counts on British *Salicornia* confirm the presence of two series, diploids with $2n = 18$, and tetraploids with $2n = 36$. These two series differ in size of pollen, stomatal guard cells and seeds; and also in general morphology. An attempt is made to correlate these numbers with the taxa generally recognised as being present in the British flora.

The plants are self-compatible, and appear usually to be self-pollinated, though there is limited evidence for occasional anemophily and possible out-breeding. Infra-specific variation may be attributed to the presence of numerous virtually pure-breeding races perpetuated by autogamy.

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Introduction

The genus *Salicornia* has for many years been a source of trouble to systematists, and we may echo the words of Baxter (1839) : ' Botanists of the highest authority differ in opinion respecting the specific distinctions of the British Salicorniae.' This is especially unfortunate in view of the important role played by these plants in the ecology of saltmarshes and similar habitats. In order to achieve a satisfactory understanding of this group, one must take into account various aspects of the plants' general biology such as breeding behaviour and phenotypic plasticity, which until recently have been neglected or altogether ignored. The taxonomic problems presented by this genus cannot be solved by the study of herbarium material alone.

In the present paper attention is directed mainly to the relationship between morphology and chromosome number, together with a discussion of breeding behaviour. The significance of the variation patterns seen in field colonies, and the particular problems of growth habit and taxonomy, will be elaborated elsewhere.

Morphology

Salicornia L., a genus of succulent halophytes belonging to the Chenopodiaceae, is represented in Britain by one perennial and several annual species, limited in distribution to coastal saltmarshes. Free leaves are absent, and the fleshy internodes (' segments ') have apparently been derived from the fusion of the decurrent leaf bases with the outer cortical tissues of the stem (de Fraine, 1913). Branching is regularly decussate, and in large plants

may be of the fourth order. When mature every branch ends in an inflorescence, referred to in this paper as a spike, though perhaps a more correct description would be a ' spike of three-flowered cymules.' Branches which are purely vegetative at maturity are confined to the perennial species.

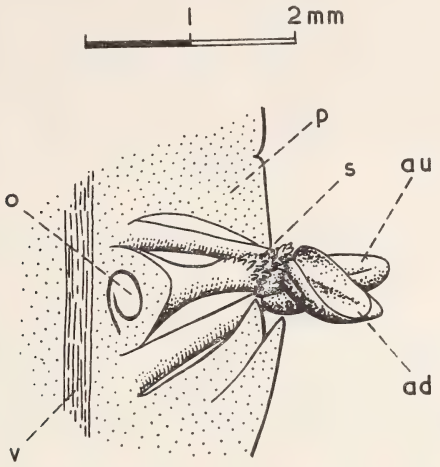


Fig. 1. Longitudinal section through *Salicornia* flower. ad–anther, dehisced, au–anther, unopened, o–ovule, p–perianth, s–stigma, v–vascular strand.

The flowers are much reduced morphologically (Fig. 1), the perianth consisting of three minute flaps and being immersed in the cortical tissues so that its upper surface is flush with that of the stem. Normally each flower contains two stamens, but sometimes only one is present. The solitary ovules (and also the mature seeds) lie transversely in the ovary, parallel to the main axis of the stem, and each with its micropylar end towards the funicle (Fig. 1).

Names used

There is no general agreement as to the number or status of the taxa occurring on our coasts. Illustrative of this variation in personal judgement are the differing treatments of the British species advanced by Tutin (1952,1959) and by Ball & Tutin (1959). Extreme views on the species concept in the genus are those of Wilmott (1939, and unpublished), and König (1960). For reference purposes some taxonomic system must be followed, so the names given by Dandy (1958) are being used in this paper as they conform more closely with the views of the present writer. These are :

Salicornia perennis Mill., Gard. Dict. ed. 8, no. 2 (1768).
S. dolichostachya Moss, New Phytol., **11**, 409 (1912).
S. europaea L., Sp. Pl., 3 (1753).
S. ramosissima Woods, in Henfrey, Bot. Gaz. **3**, 29.
S. pusilla Woods, in Henfrey, Bot. Gaz. **3**, 30 (1851).

Making allowance for the synonymy given by Dandy, these species are interpreted in the sense of Tutin (1952), where references may be found to the appropriate figures in Moss (1914). Ball & Tutin's new species, being published later, are not included by Dandy; reference will be made to these in a subsequent paper.

Chromosome Number

Of the published chromosome counts on European *Salicornia* known to me, those which can be assigned to particular segregates within the genus are included in Table 1.

Table 1.

Chromosome counts for European *Salicornia* species.

	Wulff 1936, 1937	Maude 1939	König 1939	Castro & Fontes 1946	Ludwig 1950	Hambler 1954	Ball & Tutin 1959	Dalby unpublished
S. perennis	—	18	—	18	—	18	—	18
S. pusilla	—	—	—	—	—	16?	18	18
S. ramosissima	—	—	18, 36	—	—	18	18	18, 36
S. europaea	38	—	—	18	18, 36	36	18, 36	36
S. dolichostachya	—	—	36	—	—	36	36	36

Some of the counts given above were recorded for taxa not recognised by Dandy (1958). Such taxa have been grouped as far as possible to conform with the species listed by Dandy.

This table shows clearly that there are two chromosome series present, one diploid with $2n = 18$, and the other tetraploid with $2n = 36$. No triploid hybrids have so far been recorded. There is considerable agreement as to the chromosome numbers for each taxon, apart from *S. ramosissima* and *S. europaea*, both of which appear to contain diploid and tetraploid races. It is clear, from other evidence, that these names are being used to cover a range of forms whose precise taxonomic status is open to debate.

With regard to the aneuploid numbers which have been published, Hambler (1954) was uncertain of his own count of $2n = 16$ for *S. pusilla*, and counts by other authors for this very distinct species give uniformly $2n = 18$. Wulff's (1936, 1937) figure of $2n = 38$ needs some comment. He writes (1937) ' Ich fand in zahlreichen Platten eindeutig $2n = 38$ Chromosomen, wodurch *S. herbacea* L. als polyploide, abgeleitete Form gekennzeichnet ist.' His conclusion as to polyploidy is certainly correct, but it is strange that he did not find any plates with $2n = 36$. No plate that I have examined has shown an aneuploid number, all examples where exact counts were possible proving to be euploid 18 or 36.

In the present study, chromosome counts were made from metaphase plates of mitotic divisions of root-tips,obtained from plants in the field and from seedlings in culture.

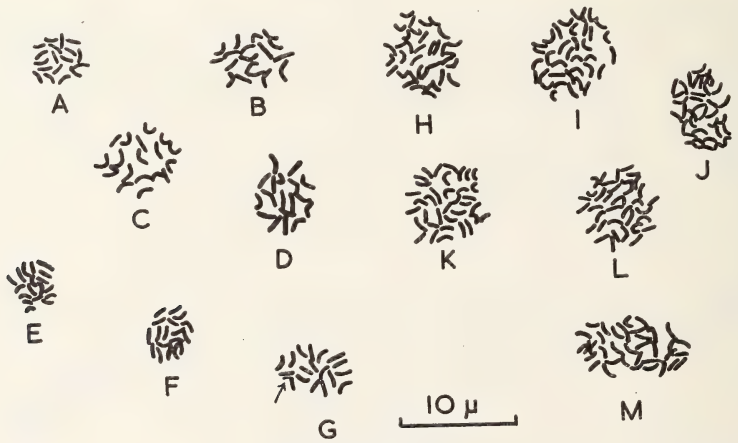


Fig. 2. Metaphase plates from root-tip sections. Diploids ($2n = 18$) A–C, *S. ramosissima*, Hayling Island, Hants (Nos. 68, 55, 69); D, E, *S. ramosissima*, Shingle Street, Suffolk (Nos. 12, 11); F, *S. ramosissima*, Flatford, Suffolk (*s.n.*); G, *S. pusilla*, Hayling Island, Hants (No. 52). Tetraploids ($2n = 36$). H, *S. europaea*, Blakeney Point, Norfolk (*s.n.*); I, *S. europaea*, Colne Point, Essex (No. 35); J, *S. dolichostachya*, Hayling Island, Hants (No. 71); K, *S. europaea*, Hayling Island, Hants (No. 54); L, *S. europaea*, Flatford, Suffolk (No. 19); M, *S. europaea*, Shingle Street, Suffolk (No. 14).

Langlet's modification of Navashin's fixative was used, this fluid also being used for storage until required. The stain used was gentian violet, which was usually taken up well by the chromosomes, and differentiation yielded very satisfactory plates. Some counts were made from acetic orcein squashes of fresh root-tips.

Some examples of metaphase plates are given in Fig. 2. After fixation the chromosomes are small and range from about 0·6 μ to 1·8 μ in length, with very little in the way of distinctive morphology to enable the recognition of homologous chromosomes or particular karyotypes. Nevertheless, diploid plates show sufficient variation in chromosome shape and size to suggest genetic heterogeneity within the scope of the species as recognised in the present study. In two plates at least from plant No. 52 (*S. pusilla*), one chromosome (arrowed in Fig. 2 G) was seen to bear a satellite.

Morphological Differences between Diploids and Tetraploids

It was thought that diploid and tetraploid plants within the genus might well show systematic differences in size or form of their parts, and that this could be used as a primary taxonomic division in the annual species. A range of specimens was therefore examined, including plants from all the species recognised by Dandy (1958). As mentioned above, no definite aneuploid counts were made, and in a few polyploids where clumping made precise counting difficult, they were regarded as having the expected number of $2n = 36$.

(*a*) *Pollen grains*

Pollen grains were taken from mature anthers, and mounted in acetocarmine, their diameters being drawn with a camera lucida at a magnification of × 800. The grains are almost spherical, and their volumes were assumed to be the volumes of spheres with similar diameters. It should be noted that measurements of volume are of greater value than say diameters or lengths, though slightly more difficult to obtain.

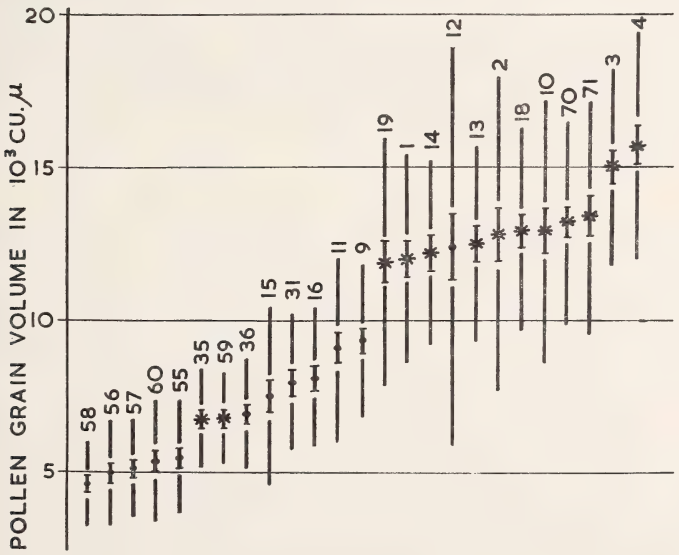


Fig. 3. Pollen grain size for 25 plants of known chromosome number.

Note. In Figs. 3 to 5, dots and asterisks mark the mean values for diploids and tetraploids respectively. The shorter bars above and below mark distances of ± 2 standard error of the mean (non-overlap indicates $p = < 0{\cdot}005$ for samples of similar size). The longer bars mark distances of ± 2 standard deviation, as an estimate of the range. This range will be exceeded by about 1 in 20 in a normal sample.

The data for pollen size are given in Fig. 3, where it is seen that in general the pollen grains are larger in the tetraploids than in the diploids, the change-over being at about $10{\cdot}5 \times 10^3$ cu. μ volume ($27{\cdot}2\ \mu$ diameter).

(*b*) *Stomatal guard cells*

The stomata are rather variable in size, even on a single plant, and vary considerably in frequency, being most numerous towards the tops of the fleshy internodes. They are arranged with their long axes at right angles to the line of the stem, a feature often found in xeromorphs and succulents.

Strips of epidermis were removed from living plants, and placed immediately in absolute alcohol. The length of each stoma was drawn with a camera lucida at a magnification of $\times$ 800, and the volume calculated as that of a sphere with diameter equal to the stoma length. These volumes will always bear a constant relationship to the actual stomatal volumes, provided the stomata are of constant shape. This was assumed to be so.

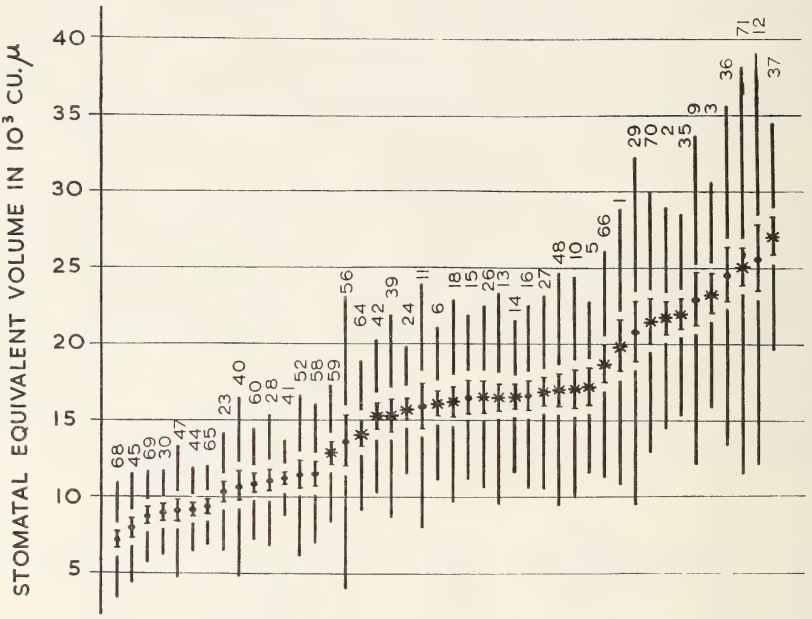


Fig. 4. Stomatal size for 44 plants of known chromosome number. See also note to Fig. 3.

The stomatal sizes are shown in Fig. 4, where, as might be expected, they are generally larger in the tetraploids than in the diploids, the change-over point between the two groups being at approximately 13×10^3 cu. μ for equivalent volume, and $29{\cdot}17\ \mu$ for length. There is however considerable overlap, part of which seems to be due to certain diploid plants having shown unusual vigour in their vegetative growth. These plants, referred to later in this paper, were selected in the field because of their noticeably robust growth and it was expected that they would prove to be polyploids related to, for example, the ' Typ. Nr. 3 ' of König (1939). These plants proved in reality always to be diploids. In this connection, it is interesting that out of four plants whose pollen size was compared with that of their F_1 progeny, the only one to show a significant change in size was one of these robust ' pseudopolyploids.' This was plant No. 11, and the significantly smaller F_1 pollen seemed correlated with poorer vegetative growth.

Clearly pollen size is more closely correlated with chromosome number than is stomatal size in *Salicornia*, but in neither case is the relationship sufficiently precise as to be used alone as a reliable indicator of chromosome number without actually making a count.

(*c*) *Seed size*

Seeds were taken from the central flowers of cymes on heads of plants of known chromosome number. The seeds from lateral flowers would have been equally satisfactory for this purpose, but seeds from central and lateral flowers should not be mixed, as within each cymule the central flower always has a larger seed than has either of the laterals.

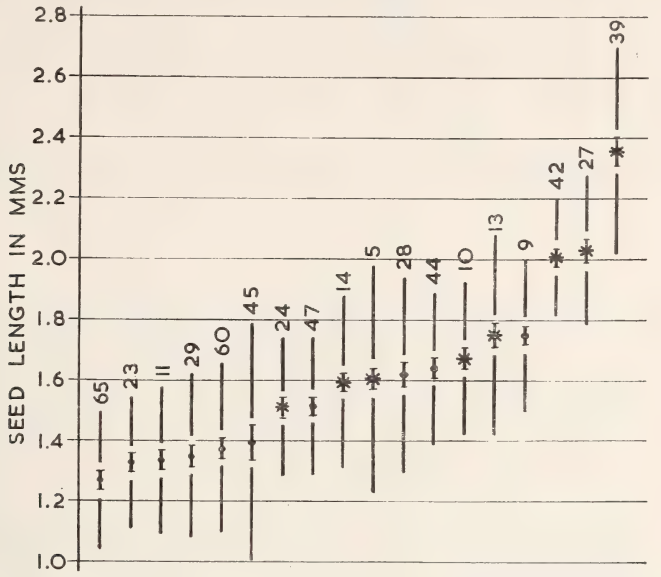


Fig. 5. Seed size for 18 plants of known chromosome number. See also note to Fig. 3.

Seed lengths are shown in Fig. 5, where it is seen that tetraploids have larger seeds than do the diploids, although there is considerable overlapping. The change-over size is at about 1·6 mm. length. Plants 28 and 9 were robust 'pseudopolyploids,' and once again the increase in size of a particular structure seems to follow vigorous vegetative growth in the rest of the plant. The largest tetraploid sample comes from plant 39, a natural mutant of *S. europaea*, in which the cymules are one-flowered. Here, in the absence of competition from the lateral flowers, the central seeds grew to an abnormally large size.

(*d*) *Ratio of numbers of fertile to sterile segments*

The ratio of numbers of fertile to sterile segments shows a break with very little overlap at about 55,* the data being given in Fig. 6. The ' pseudopolyploid ' plants referred to above are labelled 'A' in Figs. 6 and 7. They are all regarded as belonging to *S. ramosissima*,

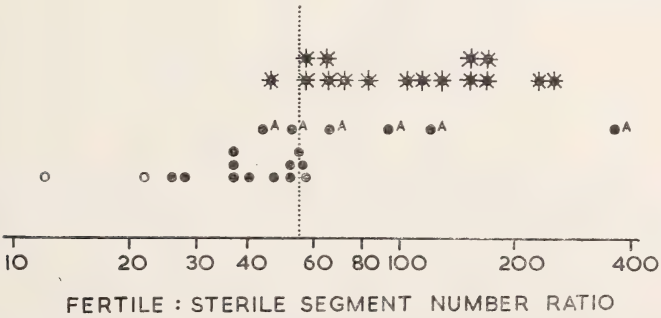


Fig. 6. Ratio of number of fertile to sterile segments for 36 plants of known chromosome number. Rings–diploids (*S. pusilla*), dots–diploids (other than *S. pusilla*), A–robust forms, asterisks–tetraploids. Note. The horizontal scale is plotted logarithmically.

* In this paper, all ratios are expressed as single figures, the second (always 100) being omitted for brevity.

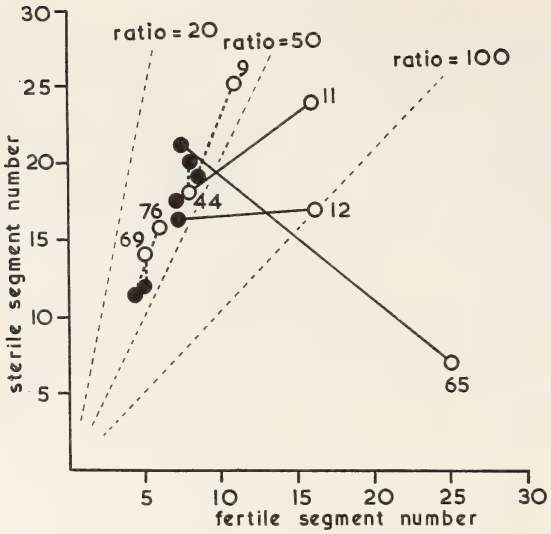


Fig. 7. Change in ratio of numbers of fertile to sterile segments in F_1 progeny in *S. ramosissima*. Open circles–parent plants; solid circles–mean values for F_1 progeny in culture. Lines connecting circles continuous if change is significant ($p = < 0{\cdot}005$), broken if not significant. Plants 9, 11, 12 and 65 were robust 'A' forms, the remainder being of normal size.

some evidence for this being given in Fig. 7, which shows the change in the segment number ratio between several parent plants and their progeny in cultivation. Clearly the 'A' plants lose their high values for the segment number ratio, and assume a constant one of between 40 and 50, typical of normal *S. ramosissima* in the field. One may reasonably assume that in normal circumstances of growth, there is little or no overlap between diploids and tetraploids in their segment number ratio.

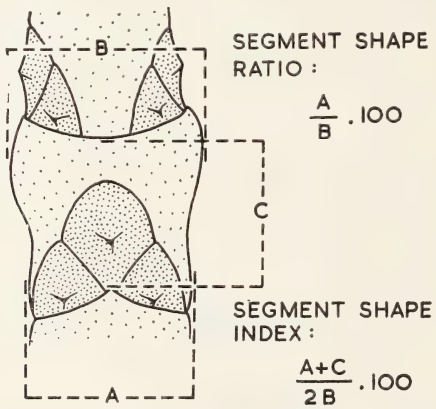


Fig. 8. Derivation of segment shape ratio and index. Means for 2 or 3 segments (central by distance along terminal spike of main axis) used in calculations, except for progeny and field colony samples where only one central segment was measured.

(*e*) *Segment shape index*

A segment shape index (see Fig. 8) also reveals differences between the two groups. The break is seen in Fig. 9 to be at about 65. Very few diploids overlap the tetraploid range, and those that do are in fact all 'A' plants.

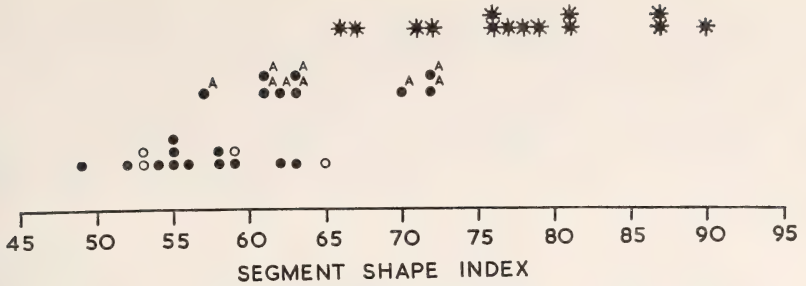


Fig. 9. Segment shape index for 39 plants of known chromosome number. For segment index see Fig. 8. Rings–diploids (*S. pusilla*), dots–diploids (other than *S. pusilla*), A–robust forms, asterisks–tetraploids.

(*f*) *Anthocyanin*

Anthocyanin occurs widely in the European species of *Salicornia*, and its varied distribution and intensity are responsible for their often brilliant autumnal coloration. The presence or absence of anthocyanin in 43 plants investigated is shown in Table 2.

TABLE 2

	Diploids	*Tetraploids*
Anthocyanin present	20	4
Anthocyanin absent	4	15

The correlation between chromosome number and presence or absence of anthocyanin is highly significant, though not absolute (testing for x^2, $p = 0{\cdot}001$). Anthocyanin is almost restricted to the diploids, though it does occur rarely in tetraploids. Strictly however, it is the ability to produce anthocyanin in favourable circumstances that should be measured, rather than its actual appearance. Too much shading prevents the red pigment being developed, a feature sometimes encountered in prostrate forms which are green beneath yet bright red above.

(*g*) *General conclusions*

The results discussed above show that the two levels of chromosome number are quite distinct morphologically for several characters which can be measured with some precision. Other differences may also be noticed (some are listed by Ball & Tutin (1959) and König (1960)), and it is gratifying to observe the general agreement reached here. One striking difference however, is seen in Ball & Tutin's data for pollen size. They regard a pollen diameter of about 29·5 μ as marking the change from diploid to tetraploid, whereas the present writer would put it at 27·2 μ. Approximately half the tetraploids plotted in Fig. 3 come within Ball & Tutin's diploid range for mean grain size. Their data for stoma and seed size are however almost identical with those given in this paper.

The assigning of chromosome numbers to the different species of *Salicornia* is a difficult problem, and will not meet with the same general agreement as has been reached over the correlation between gross morphology and chromosome number. This is because of the instability of the systematic treatments of the genus referred to at the start of this paper. Thus although *S. pusilla* is definitely a diploid, and *S. dolichostachya* is definitely a tetraploid, both *S. ramosissima* and *S. europaea* appear to contain diploid and tetraploid forms. It is from this *S. ramosissima–europaea* complex that several new species have recently been separated, and doubtless others could too with equal justification.

It seems to me that it is in this *S. ramosissima–europaea* complex that we should seek a basic *Salicornia*-type from which the other forms have been derived. This is wholly opposed to Salisbury's (1940) views, where he believed *S. dolichostachya* to be a basic type, allied to *S. perennis*. In the first instance, *S. dolichostachya* is polyploid, and so cannot be regarded as ancestral to the diploid species. Secondly it is very close morphologically to some forms of *S. europaea*, and differs quite markedly from *S. perennis*. These differences are in fact so great as to have led Moss (1948) into transferring the latter species from *Salicornia* to *Arthrocnemum*.

Breeding Behaviour

Genera showing taxonomic difficulties often possess reproductive peculiarities, and as little is known of the reproductive methods in these plants, the remainder of this paper is devoted to the pollination and fertilisation of *Salicornia*.

(*a*) *Pollen fertility*

The fertility of pollen from a number of plants was determined by mounting fresh grains in acetocarmine; those which took up the stain deeply being considered fertile, whilst those which remained colourless or pale, and which were usually mis-shapen or shrunken, were regarded as being sterile. Data for pollen sterility are given in Table 3.

Table 3
Percentage sterility of *Salicornia* pollen.

$2n = 18$ (counted)		$2n = 18$ (inferred from morphology)	
Shingle Street	10·5	Colne Point	8·5*
	8·5	Hayling Island	15·0
	6·0		9·5
	5·5		6·8
	3·0		
Colne Point	1·5		
$2n = 36$ (counted)		$2n = 36$ (inferred from morphology)	
Blakeney	5·0	St. Mary's Bay	100·0**
	3·5		9·1***
	3·3***		1·5
	2·0		1·0
Shingle Street	5·0	Dovercourt	10·3***
	2·5		7·5
	0·0		5·0
Colne Point	82·0		3·0
Hayling Island	2·5		2·0
	1·5		

* – 100 grains examined.
** – 83 grains examined.
*** – c.150 grains examined.
At least 200 grains examined from each plant unless otherwise stated.

From these figures it is seen that normal plants show a fertility of between 90% and 100%, whether they are diploid or tetraploid. From this one may suppose that the tetraploids are, in general, allo- rather than autoploids. The markedly reduced fertility of some specimens indicates some genetic unbalance, possibly resulting from the hybridisation of related, but not identical, biotypes.

Pollen tubes were seen in abundance on gynoecia dissected out and mounted whole, although efforts to germinate pollen artificially met with no success. Fresh stained dissec-

tions have revealed pollen tubes within the stylar tissues, and sections have shown traces of what are probably pollen tubes at the entrance to the micropyle. Such serial sections of flowers cut at and soon after pollination have cast little light on the actual process of the presumed sexual fusion. The embryo sac appears to have eight nuclei, and the embryo develops normally from the micropylar end. An endosperm is formed, though scanty in amount, as is correctly recorded by Volkens (1893), though overlooked by Moss (1914) and Tutin (1952).

(*b*) *Pollination*

Knuth (1909) quotes Schulz as saying that the flowers of *Salicornia* are feebly protogynous, but possess persistent stigmas so that in consequence of the proximity of the anthers automatic self-pollination is easily possible. Moss (1912) says ' The species of *Salicornia* are wind-pollinated; and hybrids are often abundant when allied species grow together.' Ball & Tutin (1959) describe a species *S. obscura* with ' usually cleistogamous flowers.'

My own observations suggest that it is very likely that many of the annual forms are self-pollinated in nature, as ripe dehiscing anthers may be seen in contact with presumably receptive stigmas, and their pollen spilling on to the stigmatic papillae (see Fig. 1).

Usually it seems that *Salicornia* is weakly protogynous, and sometimes it may be markedly so (as for example *S. perennis*). Often, however, stigmas and anthers appear simultaneously, and even when protogynous, pollen from earlier flowers on one part of a plant may be transferred to stigmas on later flowers on another part of the same plant.

The possibility of wind-pollination sometimes happening must therefore be considered, though without an experiment using distinctive marker-genes, it may not be possible to prove. The experiment described below was carried out at Blakeney Point, Norfolk, to help in assessing the possibility of anemophily in *Salicornia*.

Blakeney Point was selected because there is, on the ' *Pelvetia* Marsh,' a great expanse of almost pure *Salicornia* which comes to an abrupt stop on the northern edge of the marsh against sand-dunes, where the vegetation is almost solely *Ammophila arenaria*. On the southern side of the marsh there is about $\frac{1}{2}$ to $\frac{3}{4}$ mile of bare mud or water, and then more saltmarsh with much *Salicornia*.

A day was selected when the wind was blowing steadily from the south, and *Salicornia* on the marsh was shedding its pollen. Microscope slides coated thinly with gelatin contain-

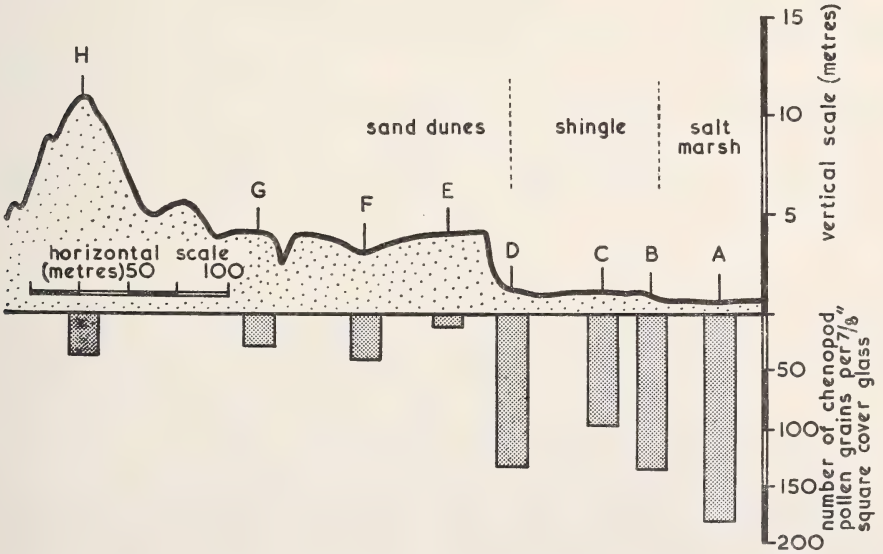


Fig. 10. Wind dispersion of pollen along transect from saltmarsh to sand dunes, Blakeney, Norfolk. The lines marking the sampling points A to H are not drawn to scale vertically.

ing a little acetocarmine were exposed vertically at about one foot above the ground at intervals along a transect running from saltmarsh to dune-crest (see Fig. 10). After 12 hours, the slides were taken indoors, coverslips placed in position and the slides warmed gently to melt the gelatin. The catch for total Chenopodiaceae-pollen is shown below each sampling point in Fig. 10. The catch at D is rather larger than might have been expected, probably because the freshening wind raised grains which had come to rest on the shingle (the slide was covered with wind-blown sand). In contrast, the catch at E is smaller than to be expected, as the wind was deflected clear of this sampling site on rising from the blow-out.

This experiment certainly proves that pollen of Chenopodiaceae is carried by the wind, and knowing that *Salicornia* was by far the most numerous genus at anthesis on the marsh, we may well assume that the majority of this wind-blown pollen did in fact come from that genus. It should be mentioned that related genera in the Chenopodiaceae have very similar pollen grains, differing only very slightly in size and sculpturing of the exine.

(*c*) *Self-compatibility*

The compatibility relationships of several plants were examined by considering specimens gathered from different saltmarshes before the flowers had opened. The flowering branches were washed carefully to remove any grains that might be adhering, and the selected spikes were enclosed in small polythene bags tied loosely over cotton-wool plugs. Other branches were left as controls. When the control branches had set seed, the 'bagged' branches were dissected, and the number of seeds set counted. In all instances counts were restricted to the central flowers of the cymules. The results are set out in Table 4.

TABLE 4.

Effect of ' bagging ' on setting of seed in *Salicornia*.

	Control		*Experimental*	
	Maximum potential seed number	*Number actually set*	*Maximum potential seed number*	*Number actually set*
S. ramosissima				
Hayling Island				
a	—	—	21	17
b	—	—	22	18
Shingle Street				
c	5	2	12	7
d	13	8	18	10
e	16	11	26	12
S. europaea				
Pagham				
f	22	15	26	15
g	33	31	28	23
h	21	17	30	21
S. dolichostachya				
Blakeney				
i	10	10	23	18
j	—	—	28	13

It will be seen that ' bagging ' has caused a slight but significant reduction in the quantity of seed set ($x^2 = 5{\cdot}93$; $0{\cdot}025 > p > 0{\cdot}01$). Assuming reproduction to be sexual, it is clear from the substantial quantity of seeds set that the plants used in the experiment were self-compatible. A further conclusion is that the physical effects of the ' bagging ' (eli-

mination of air currents near the anthers) have reduced the chances of pollination taking place. Thus though these plants are self-compatible, we may assume that in nature some pollen transfer takes place from flower to flower, and possibly from plant to plant.

(*d*) *Apomixis*

There still remains the possibility that some species of *Salicornia* may be apomictic, which might explain their taxonomically critical nature.

Plants of *S. europaea* from Pagham, Sussex, were used in a simple experiment in which the stigmas were removed from 17 protogynous flowers by making a cut parallel to the segment surface. 16 of the experimental flowers failed to set seed during a period when uncut control flowers did so. The single seed set may have been due to pollination having taken place before the experiment began.

This evidence, though scanty, is against autonomous apomixis in *S. europaea*, but would not of course indicate the absence of pseudogamous apomixis. The evidence in favour of sexual reproduction is, however, strong, though not yet conclusive.

(*e*) *General conclusions*

The main significance of the work described above lies in its bearing on specific variation limits in the genus. Hybrids may sometimes occur, although as far as the writer knows there have not yet been any proven records of hybridity in this genus. Hybridisation could certainly be a physical possibility, as *Salicornia* pollen may be carried in considerable quantities for short distances by the wind. The reduced pollen fertility sometimes encountered is evidence for crossing, possibly between related, but not identical, biotypes.

Reproduction is considered to be sexual, whilst the preponderance of self-fertilisation would be expected to produce more or less pure-breeding lines which could be regarded taxonomically as microspecies. Segregates from the occasional crosses between different lines could then act as the sources of new lines. This pattern of variation is wholly in keeping with the views expressed by Stebbins (1958) in considering the advantages to an annual species following self-fertilisation.

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STUDIES IN THE BIOLOGY OF *POA SUBCAERULEA* SM.

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Abstract

Poa subcaerulea has a widespread distribution in Great Britain, being common in the hill country of Scotland and Wales, and in sand dunes along the British coast. It is essentially a plant of moist habitats.

There is considerable variation within populations but all show taxonomic characters of great constancy. *P. subcaerulea* panicles are usually small, with a low number of spikelets, a tendency to two branches at the lowest node and glumes with three nerves. The rhizomes spread extensively and normally have one tiller per tillered node. Leaves are broad and may be hairy.

Pollen diameter is from 30·6–37·5 μ and fertility is high. Seeds are long. Polyembryony has been found in all samples collected.

Chromosome numbers varied between $2n = 54$ and $2n = 109$. Autopolyploidy is widespread and chromosome number varies within populations. Apomixis may be the main method of seed production, and together with vegetative reproduction by rhizomes gives considerable cloning.

Taxonomically *P. subcaerulea* is quite distinct from other species of the *P. pratensis* group occurring in the British Isles, but it is essential to consider vegetative as well as floral characteristics in classification. Transplant studies have shown the great constancy of these taxonomic characters.

Introduction

The critical nature of *Poa pratensis* L. *sensu lato* is now well appreciated and this, together with its economic importance, has attracted much study to this group which is usually classified either into distinct ecological form complexes (e.g. Åkerberg, 1942), or subspecies (e.g. Hiitonen 1933; Hylander 1941, 1953, 1955; Tutin 1952, 1957), or divided into several separate species (e. g. Lindman 1926, Roshevitz 1934; Hultén 1950; Hubbard 1954; Melderis 1955; Dandy 1958). The concept of the last-mentioned authorities is followed in this paper.

Lindman (1926), who was the first to be particularly interested in this group, divided it into five species : *P. pratensis* L. *sensu stricto*, *P. angustifolia* L., *P. alpigena* (Fr.) Lindm., *P. subcaerulea* Sm. and *P. irrigata* Lindm. Hylander (1941, 1953, 1955) has treated these entities as subspecies of *P. pratensis*, and has included *P. subcaerulea* in subsp. *irrigata* (Lindm.) Lindb. f. On the specific level the epithet *subcaerulea* published by Smith in 1802 is much earlier than *irrigata* given by Lindman in 1905. More recently Clausen & Hiesey (1958) have added *P. arctica* R. Br. to this group, as it forms intermediates with *P. alpigena* in Sweden (Nygren, 1950).

Three of these species, *P. pratensis* L. *sensu stricto* (*P. pratensis* L. subsp. *pratensis*), *P. angustifolia* L. (*P. pratensis* subsp. *angustifolia* (L.) Lindb. f.) and *P. subcaerulea* Sm. (*P. irrigata* Lindm., *P. pratensis* subsp. *subcaerulea* (Sm.) Hiitonen. *P. pratensis* subsp. *irrigata* (Lindm.) Lindb. f., *P. pratensis* subsp. *alpigena* auct. flor. brit.) are present in Britain. Both the other species, the low-arctic *P. alpigena* (Fr.) Lindm. (*P. pratensis* subsp. *alpigena* (Fr.) Hiitonen) and arctic-alpine *P. arctica* R. Br. have a circumpolar distribution, but neither occurs in the British Isles.

Melderis has reviewed the taxonomic interest of *P. pratensis*, *sensu lato*, and with regard to *P. subcaerulea* has pointed out that no work has been carried out on this species in Britain, though Löve (1952) has investigated Icelandic populations and Åkerberg a limited number of Swedish plants. Since then data on Welsh populations have been recorded (Barling 1957, 1959).

It would appear from Åkerberg that *P. subcaerulea* is itself taxonomically very variable, for he describes a shore and a forest form, which hybridise with other forms of *P. pratensis*. Indeed the reticulate relationship of the various forms of *P. pratensis, sensu lato*, is well known and a similar pattern appears to exist between many Poae (Gustaffson 1947, Stebbins 1950; Nygren, Melderis, Clausen & Hiesey).

The variety of taxonomic opinions on *P. subcaerulea*, together with the knowledge of hybridisation with other species of the *P. pratensis* group, not to mention the ecological specialisation of species, makes this group a necessary study for a fuller understanding of the complex relationships within the Poae. The present paper is an account of more extensive studies on populations and transplants of British origin.

Material and Methods

Populations of *P. subcaerulea* from centres distributed through most of its latitudinal range in the British Isles have been studied as follows :— v.c. 3, Slapton Sands and Dawlish Warren (sea level); v.c. 34, Hazel Hill and Five Acres (800 ft.); v.c. 41, Cwmdare : Lluestai Llwydion (900 ft.), Tir-Evan-Bach-Traws (600 ft.), Pwll Rhys (600 ft.), Tir Morris (750 ft.), Cefn-y-Gyngon (1,100 ft.), Windber (950 ft.), Bwllfa (950 ft.); v.c. 41, Pen Rhys (800 ft.), Craig-y-Llyn (1,900 ft.), Limeslade (sea level), Jersey Marine (Sea level); v.c. 42, Pontpren (600 ft.), Penderyn (600 ft.); v.c. 44, Pendine (sea level); v.c. 45, Maenclochog (800 ft.), Rosebush (800 ft.), Wolf's Castle (300 ft.); v.c. 46, Ffair-Fach (1,000 ft.); v.c. 60 St. Annes (sea level), Bispham (sea level); v.c. 69, Grange-over-Sands, (sea level), Windermere (800 ft.), Kirkstone Pass (1,500 ft.), Knock Fell (2,200 ft.); v.c. 70, Dunmail Raise (2,000 ft.); v.c. 77, Bailliesmuir (300 ft.); v.c. 90, Montrose (sea level); v.c. 92, Balmoral (800 ft.); v.c. 98, Glenbeg (800 ft.).

The transplants were grown in 8 in. pots immersed in a washed gravel bed situated at Cirencester (Lat. 51° 43′ N., Long. 1° 57′ W.), at an elevation of 440 ft. The soil used was a calcareous loam derived from the Great Oolite.

Distribution and Ecology

P. subcaerulea was described by Smith (1802) from specimens gathered by Rev. H. Davies in Anglesey. In his *English Flora*, Smith (1824) mentioned that this species occurs in mountainous situations in Wales, Anglesey, Westmorland, Cumberland and Scotland. According to Hubbard, *P. subcaerulea* has a widespread distribution in the British Isles, though it is more common in the north than in the south. It is found in a variety of habitats : moist mountain grasslands, stream sides, dune slacks and sea shores, and the last environments have resulted in its distribution along the south coast of England.

Outside the British Isles, this species has been recorded from Fennoscandia, Denmark, the northern part of the European U.S.S.R. and Iceland (cf. Hylander 1953). It seems that this species is common in N.W. Europe, from at least 50°N. to slightly within the Arctic Circle, overlapping over much of this territory with other species of the *P. pratensis* group. An excellent map showing the distribution of *P. subcaerulea* in N.W. Europe is given by Hultén. It is probably at its southern limits in the British Isles and is replaced to the south by the *P. pratensis* complex. This may account for its ecological prevalence in the hill or mountain areas as opposed to lowlands of the British Isles.

Its distribution in the British Isles is incompletely known. Habitats, particularly in South Wales, are as follows :—

1. *Permanent grasslands*. The plant was found in enclosed and open hill grasslands, particularly where *Agrostis tenuis* or fine-leaved fescues (*Festuca rubra* and *F. ovina*) were dominant. In these pastures the plants are not very obvious, their long rhizomes and single tillers giving a very diffuse appearance. It is most noticeable in flower, or where conditions may lead to local concentration as on pathways.

   It has been recorded in tussocky swards of *Molinia caerulea*, usually as isolated plants with very long culms and rather poor vegetative development, and also amongst swards where *Juncus effusus* is prominent.

TABLE 1. Morphological data from wild populations in *P. subcaerulea*

Origin	*Habitat*	*Inflor. length* mm.	*Branches lowest node*	*Spikelets per panicle*	*Height of culm* mm.	*Tillers/tillered node*
Slapton Sands	Shore	36·46 ± 1·93	2·60 ± 0·12	31·35 ± 1·20	126·60 ± 9·65	—
Dawlish Warren	Fixed dune	52·67 ± 2·26	3·30 ± 0·14	50·40 ± 4·20	148·40 ± 7·17	—
Windber	Waste tip	27·35 ± 1·79	2·00 ± 0·00	23·17 ± 1·48	107·65 ± 8·09	—
Cefn-y-Gyngon	Sheep shelter	40·40 ± 2·47	2·47 ± 0·24	28·15 ± 2·21	100·46 ± 10·12	1·00 ± 0·00
Craig-y-Llyn	Road verge grassland	38·24 ± 4·78	2·18 ± 0·13	27·82 ± 2·59	137·77 ± 15·60	—
Penderyn	Grassland	45·20 ± 2·61	2·10 ± 0·10	33·04 ± 2·31	155·80 ± 13·05	1·00 ± 0·00
Five Acres, Forest of Dean	Grassland	52·10 ± 1·69	2·63 ± 0·14	46·73 ± 2·76	136·00 ± 7·10	1·00 ± 0·00
St. Anne's	Fixed dune	53·72 ± 1·89	2·72 ± 0·11	50·65 ± 2·19	198·43 ± 11·99	1·00 ± 0·00
Bispham	Cliff top	43·20 ± 0·97	2·60 ± 0·22	39·65 ± 2·65	82·95 ± 3·85	1·00 ± 0·00
Helvellyn	Grassland	38·72 ± 1·61	2·15 ± 0·06	29·31 ± 1·83	122·90 ± 6·01	1·06 ± 0·02
Kirkstone Pass	Grassland	47·14 ± 2·00	2·31 ± 0·08	36·14 ± 2·46	175·45 ± 11·25	1·00 ± 0·00
Montrose (Tay Fisheries)	Fixed dune	51·46 ± 2·08	2·20 ± 0·09	43·34 ± 2·72	284·48 ± 18·95	1·14 ± 0·04
Glenbeg	Grassland	32·07 ± 1·30	1·90 ± 0·12	27·40 ± 1·99	75·30 ± 5·23	1·04 ± 0·04
Balmoral	Road verge	45·85 ± 1·19	2·15 ± 0·10	37·03 ± 1·82	179·60 ± 6·74	1·00 ± 0·00

2. *Road-verge grasslands.* On the hill areas the fertilising effects of road dust has led to the formation of improved swards a few yards wide in what is often rough grassland dominated by *Nardus stricta* or *Molinia*, and on these areas *P. subcaerulea* is frequently found.
3. *Sheep shelters.* Where localised shelter or " camping " is taken by sheep, as under walls, banks or stunted hawthorn, then the heavy trampling and faeces concentration result in localised modification of the flora. On these small areas bare ground is obvious, and *P. subcaerulea* is frequently found, often in well developed mats, together with such species as *Agrostis tenuis*, *Poa annua* and *Stellaria media.* These modifications are often isolated amongst large acreages of rough grazings.
4. *Waste places and walls.* Plants have been found growing on walls at a variety of sites in north Glamorgan and south Breconshire. *P. subcaerulea* has been repeatedly found on tips of colliery waste, where the loose weathered shale allows the spread and development of long rhizomes and provides conditions similar to the sand dune environment. It is also found in swards developed on the stable areas of colliery tips where it may be accompanied by *Agrostis tenuis* and *Festuca ovina.*
5. *Sand dunes. P. subcaerulea* is frequently found on sand dunes, particularly on fixed dunes and slacks. In the present study plants have been collected from Dawlish Warren, Jersey Marine, St. Anne's and Montrose. Plants are sometimes found in the shifting sand and also in the turf of nearby golf courses. It is also common on walls, cliff top grassland, and gravelly shores in these areas. At Dawlish it is found on fixed dunes and also in slacks among such species as *Spiranthes spiralis.*
6. Other habitats in which the plant has been found include the ballast of railway tracks, roadside gutters, garden pathways and hedgerows.

Plant Characters

Wild populations were selected from a wide range of geographical and ecological environments to provide representative data (Table 1). Plants follow a regular pattern with short inflorescences and a low spikelet number. There was usually one tiller per tillered node, and rhizomes were difficult to excavate in dense swards, and much rotting of rhizomes was found. However, long rhizomes easily excavated were characteristic of sand dunes, and the somewhat similar waste-tip areas.

Culms were short in grazed grasslands but where they were sheltered by unpalatable herbage, such as tufts of *Juncus effusus*, they might be very tall as at Cwmdare where heights of 510, 505, 460 and 425 mm. were found. The lengthening of fertile tillers is due to internode elongation which increases to a maximum in the node below the panicle. Two branches at the lowest node is common but 1–5 branches may be found in wild or transplant panicles. Data for transplants is found in Table 2. The number of panicle nodes seldom exceeds twelve (Barling 1959) and the glumes are both three-nerved.

Table 2
Inflorescence data in transplants of *P. subcaerulea*

Origin	*Culm height* mm.	*No. basal branches*	*No. spikelets*	*Panicle length* mm.
Lluestai llwydion grassland	350·18 ± 13·83	2·41 ± 0·13	41·13 ± 2·43	60·93 ± 1·92
Craig-y-Llyn	408·60 ± 17·08	2·42 ± 0·14	43·72 ± 3·89	70·17 ± 3·42
Cefn-y-Gyngon	319·29 ± 8·08	2·76 ± 0·08	42·96 ± 2·01	57·09 ± 1·80
Knock Fell	316·57 ± 10·39	2·48 ± 0·08	40·73 ± 2·84	62·87 ± 2·98

Rhizomes are produced as early as February and actively during March, April and May. Internode length measured has varied from 15·33 ± 0·59 mm. to 22·85 ± 2·45 mm., which is usually shorter than that found in *Poa angustifolia*, and the number of tillers per tillered node is also less (Table 3).

TABLE 3
Tillers/Tillered Node.

Origin	*No. tillers/tillered node*													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
P. subcaerulea														
Windber														
a. waste tip	116	12	8	–	–	–	–	–	–	–	–	–	–	–
b. path	122	20	4	–	–	–	–	–	–	–	–	–	–	–
Jersey Marine	70	4	–	–	–	–	–	–	–	–	–	–	–	–
Slapton Sands	356	5	–	–	–	–	–	–	–	–	–	–	–	–
Dawlish	360	17	1	–	–	–	–	–	–	–	–	–	–	–
P. angustifolia														
Cirencester	–	–	5	14	7	8	11	7	9	8	2	3	2	2
P. pratensis														
Cirencester	26	21	19	4	1	1	–	–	–	–	–	–	–	–
Steadings	4	8	14	14	6	2	2	–	–	–	–	–	–	–

Roots are actively produced from the end of February to early May. Leaves are produced from March onwards and the number of green leaves found at Windber was 3·9 ± 0·3 in August, none in December and 1·48 ± 0·2 in March. Hairiness of the blade is frequently found and is a ready means of finding biotypes. Leaf blade length increases then decreases on fertile tillers.

Plants of *P. subcaerulea* that are kept in a heated greenhouse in autumn remain vegetative the next season, but if kept in the open and then placed inside during January they head in the greenhouse. Heading is usually accelerated by the higher temperatures. There is quite obviously a response to late autumn low temperature and daylength similar to that reported for *P. pratensis* by Peterson & Loomis (1949). Inflorescence primordia have been found in late December and January.

Floral Biology and Breeding Mechanism

Anthesis in *P. subcaerulea* commences about two thirds of the way up the panicle at about the seventh or eighth node. Other spikelets flower above this node, and then at lower nodes, flowering at the lowest node last of all. The basal floret of a spikelet opens first and the top floret often does not open at all. Details of anthesis have been described elsewhere (Barling 1959) and it follows, essentially, that of typical cross-pollinating species.

Pollen grain size was measured as the greatest diameter, and for ten transplants had

TABLE 4
Seed production in enclosed and open pollinated panicles of *P. subcaerulea.*

Origin	*No. selfings*	*Average seeds/panicle*		*Seeds set/spikelet*	
		enclosed	*open*	*enclosed*	*open*
Lluestai llwydion 1	3	68	66	2·1	2·6
Lluestai llwydion 3	3	47	60	1·2	3·0
Tir-Evan-Bach-Traws 1	5	66	70	2·6	2·8
Tir Morris 1	3	49	68	1·7	2·4
Windber 1	3	96	95	3·8	3·9
Bwllfa Farm	3	372	391	3·9	4·0
Penderyn 5	5	124	165	2·7	3·5

a mean of 34·66 μ with a range of 26 – 45 μ, whilst 4 wild plants had a mean of 33·38 μ and a range of 27·5 – 40 μ. Pollen fertility, determined by staining, was a mean of 89% in the transplants and 81·75% in the wild material.

The seed production of open-pollinated and selfed panicles was determined for a number of plants (Table 4). The yield of many of the selfed panicles compares favourably with that found under open pollination of transplants or field material.

Seed, Germination and Polyembryony, and Seedlings

Seed length was longer than found in *P. angustifolia*, and hand threshed samples from six wild populations gave an average mean of 3·30 $\pm$ 0·045, mm. and from six transplant populations 3·25 $\pm$ 0·044. mm.

Seed samples were collected from a wide range of sixteen centres in 1958 and were germinated on moist filter paper in petri dishes at room temperature and full illumination; twelve transplant samples were similarly sown. The wild samples totalled 1,485 seeds which gave 1,055 seeds with one seedling, 110 seeds with two, and 4 seeds with three seedlings. Polyembryony was present in all samples and amounted to 7·7%, with germination equal to 78·8%. The transplant seeds totalled 1,174 with 758 single, 114 twin and 11 triplet seedlings, having 10·7% polyembryony and 75·2% germination.

Selfed seed was obtained from various transplants and generally germinated well. However, some samples contained much light seed and a comparison with more normal-sized seed was made (Table 5).

Table 5
Germination data for selfed seed samples of *P. subcaerulea*.

Date	*Penderyn* (*thin*)						*Slapton* (*full*)				
	Seedlings/seed				% *Poly-embryony*	% *Germ-ination*	*Seedlings/seed*			% *Poly-embryony*	% *Germ-ination*
	1	2	3	4			1	2	3		
10 Sept. 1958	(*Seed sown*)						(*Seed sown*)				
25 Sept. 1958	9	6	–	–	6	15	73	10	1	11	84
29 Sept. 1958	13	7	–	–	7	20	73	9	2	11	84
3 Oct. 1958	22	9	–	–	9	31	73	9	2	11	84
6 Oct. 1958	67	13	–	–	13	80	73	9	2	11	84
9 Oct. 1958	64	17	2	4	23	87	73	9	2	11	84

Fifty seeds of each known transplant of varied geographical origin were sown half an inch deep in John Innes Seed Compost, together with some from transplants of *P. angustifolia*. It was found that the first leaves of *P. subcaerulea* and *P. angustifolia* were very similar but that the second leaf was wider and generally shorter in *P. subcaerulea*. Width differences were quite clear to the eye in the second leaf stage (Table 6). The leaf blade colour of *P. subcaerulea* was of a darker or bluer green. Also in *P. subcaerulea* the first tiller was found exclusively in the axil of the first leaf whereas in *P. angustifolia* it was found in the second leaf in many cases. In *P. subcaerulea* the first tiller either penetrated the sheath of the first leaf giving typical extra-vaginal tillering, or emerged sideways or took a very small angle pushing the sheath and blade towards the soil, whilst the second tiller was normally found in the axil of the second leaf and was intra-vaginal. In *P. angustifolia* the tillering was exclusively intra-vaginal.

This early extra-vaginal tillering was the most obvious of all the features recorded and revealed the characteristic tendency to a creeping as opposed to a bunched habit. Although the measurements of leaf blade width offered some hope of quantitative discrimination it was felt that for rapid work and single seedling identification it was unreliable in itself, and should be backed by colour features if discernible, as well as tiller behaviour.

TABLE 6
Seedling data in *P. subcaerulea* and some *P. angustifolia*

Origin	1st leaf		2nd leaf	
	Width (mm.)	Length (mm.)	Width (mm.)	Length (mm.)
P. subcaerulea				
Cefn-y-Gyngon	0·82	36·25	1·44	46·00
Craig-y-Llyn	0·55	22·40	1·17	39·60
Knock Fell	0·68	20·14	1·02	36·40
Pontpren	0·76	29·40	1·38	44·50
Penderyn	0·60	22·00	1·26	34·20
Lluestai llwydion	0·66	36·20	1·13	32·00
P. angustifolia				
Deer Park 1	0·55	18·83	0·89	43·67
Deer Park 2	0·55	23·38	1·00	46·00
Deer Park 3	0·51	23·83	0·89	46·67

CYTOLOGY

In the present work mitosis has been studied in root tips and meiosis in pollen mother cells. The root tips were stained in aceto-orcein or Feulgen and then squashed and irrigated in the stain if necessary when the counts were being made. Metaphase plates invariably contained large numbers of small, densely arranged chromosomes. In some cases there was difficulty in determining the exact number, but counts were made of three cells for each plant. PMC smears were stained with aceto-orcein.

Mitosis counts have given high numbers and it is possible to get widely different chromosome numbers within relatively small areas. Thus at Cefn-y-Gyngon, plants from different sheep shelters gave the different numbers of 70 and 98. Other numbers determined were Dawlish Warren 1, $2n = 92$; Dawlish Warren 2, $2n = 84$; Slapton Sands 1, $2n = 54$; Cwmdare, $2n = 65$; Lluestai llwydion grasslands 1, $2n = 72$; Lluestai llwydion tip, $2n = 90$; Tir-Evan-Bach-Traws, $2n = 105$; Bwllfa Farm, $2n = 56$; Limeslade, $2n = 92$; Penderyn 8, $2n = 83$; St. Anne's Airport, $2n = 109$; Grange over Sands, $2n = 98$; Knock Fell 1, $2n = 84$.

At meiosis univalents are commonly seen at first division when they usually lag at anaphase, they may divide and some are excluded from the interphase nuclei. Multivalents are common at first metaphase and segregation of chromosomes is clearly uneven in some mother cells. At second division lagging is again common and exclusion has been seen in some cells in the tetrad stage. The pattern is identical with that illustrated for north American *P. pratensis* by Nielsen (1945, Figs. 22–46). The number of univalents for various transplants was : Slapton Sands $2{\cdot}90 \pm 0{\cdot}18$, Lluestai llwydion grassland $2{\cdot}70 \pm 0{\cdot}20$, Penderyn 8, $1{\cdot}85 \pm 0{\cdot}16$, Jersey Marine 1, $3{\cdot}20 \pm 0{\cdot}27$, Knock Fell $2{\cdot}80 \pm 0{\cdot}20$.

In Icelandic *P. subcaerulea*, Löve found chromosome numbers of $2n = 82$–147. Within an area of 10 metres diameter he found plants with $2n = 82$, 84, 91, 105, 111, 112, 113 and 119 chromosomes and provides the most detailed evidence of variation within populations. In addition, Åkerberg has given numbers of $2n = 87$ (for a form of *P. pratensis* which comes close to *P. subcaerulea*), 90, 90–95, for Swedish material.

TRANSPLANTS

Transplants have been much quoted already in the data on plant characters and it remains to mention the major features of genetic and taxonomic value derived from their study at Cirencester. An obvious factor was the genetic variation within and between populations. It would be difficult to show that the morphological variation revealed has

any adaptive value, but it shows that apomixis where present is not a barrier to variation.

The transplants have shown that many characteristics seen in the wild such as short culms, small spikelets and small panicles, are usually environmental effects. Thus greater values for the features measured have been recorded in transplants (Tables 1 & 2), and many of the extremes seen in the field are not seen under cultivation. When studied together the transplants from widely scattered localities show no great differences in gross morphology. It was not possible to detect differences according to altitude. Three-nerved acuminate glumes have been constant. Branching at the lowest panicle node has been variable within clones with a tendency to a greater number of branches than found in the wild. The number of spikelets, panicle length and number of panicle nodes all usually show much lower values than in *P. angustifolia*, but in some clones there are approaches in quantity to this species. These inherited tendencies are found within populations. The vegetative character of great constancy is the single tillering per node which has been recorded in all transplants. Hairiness of the leaf blade is a ready means of detecting population variability and it is inherited in clones. Hairs at the collar of the leaf blade are also constant in all transplants. Fig. 1 compares characters in *P. angustifolia* and *P. subcaerulea* transplants.

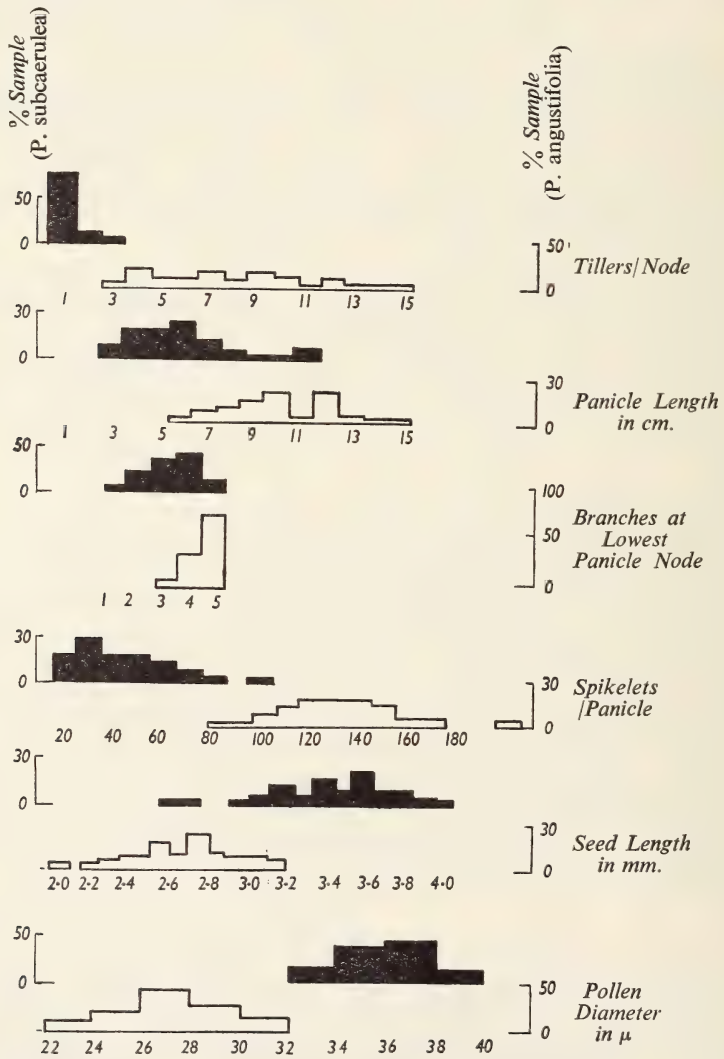


Fig 1. Taxonomic characters in *P. subcaerulea* (solid black) and *P. angustifolia* (outline)

Discussion

One of the obvious conclusions that can be made from these studies is that *P. subcaerulea* forms a morphological and ecological complex of widespread distribution in the British Isles, possessing characteristics of great similarity to related forms.

All the morphological features are important in the taxonomy of the group and are seen to rest on vegetative, inflorescence and seed characters. The outstanding vegetative feature is the production of single tillers on spreading rhizomes, which contrasts markedly with *P. angustifolia* (Barling 1959). Leaf blades may be hairy, a ready means of seeing variability in populations. The inflorescence is characteristically short, with a low number of spikelets and a tendency towards two branches at the lowest node. The number of nodes is also low and all these characters contrast with the values found in *P. angustifolia* (Barling 1959). Whilst these may be the general and focal features of taxonomy, the expected variability about these features is easily found. Panicles with spikelet numbers and branches similar to *P. angustifolia* may be seen though they are combined with the usual vegetative features of *P. subcaerulea*. Whilst these characters are more typical of related complexes, the decision to include such plants in *P. subcaerulea* is based on their presence within field populations of the group, their three-nerved acuminate glumes, and their conspicuous vegetative behaviour. The taxonomic difficulty is due to the retention of a basic type of inflorescence, long rhizomes, and hairy seed bases throughout the species of the *P. pratensis* group, in spite of the tremendous variability in ecological and physiological directions.

The cytology of the group shows high polyploidy and there is a wide range of numbers and variation within the same habitat, features found in other populations of *P. subcaerulea* (Löve, Åkerberg) and *P. angustifolia* (Barling, Åkerberg). If one considers the chromosome numbers of complexes in relation to their typical habitats, then the higher polyploids are of the wetter and more extreme climates. Such ecological variation within races has been reported by Winge (1940) and Jones (1958), amongst others. It is likely that increasing polyploidy in *P. pratensis*, *sensu lato*, has allowed some of its forms to survive in areas with more adverse conditions. However, the situation is far from clear as wide ranges of chromosome numbers have been reported from within each of the distinct taxa (see Melderis), and also from within populations (Löve). Thus it would be necessary to consider the average polyploidy of British populations on an altitudinal basis, and also to compare these with data from more northerly areas (Löve). Hagerup (1931) proposed that since the majority of polyploids have a better adaptability than diploids then an increase in polyploids could be expected in the flora of areas of more extreme climate. In this work no discussion of the degree of polyploidy, only its incidence, was undertaken. Löve & Löve (1958) have discussed this aspect and whilst supporting Hagerup's hypothesis, point out that the degree of polyploidy is only connected with distribution in exceptional circumstances. It appears that the apomictic Poae may present suitable material for studying the degree of polyploidy in relationship to environmental extremes, such as latitudinal and altitudinal distribution might involve. Thus the range of chromosome numbers reported by Löve for Icelandic material is greater than that found in the more limited work of the present study.

In spite of this high polyploidy there is little disturbance at meiosis, and the occurrence of univalents and multivalents at metaphase of the first division appears to be insufficient to affect pollen fertility. There is good seed production when inflorescences are selfed and this, together with the constancy of polyembryony in seed from all sources, is probably indicative of apomixis. Åkerberg has shown sexual and apomictic forms in Swedish material and Löve apomixis in Icelandic plants. The effects of this on the breeding system are similar to those discussed for *P. angustifolia* (Barling 1959), and the opportunity may now be taken of discussing this feature in relationship to *P. pratensis* as a whole.

Löve has reported a range of chromosome numbers from $2n = 82–119$ in a sample area of ten metres diameter. A similar situation, on a less detailed basis, is found in the present work. There is no difference in visible taxonomic characters associated with this range, though certain features such as pollen diameter, height, etc., do show correlation

in Icelandic material. It seems that these taxonomic characters depend upon genes that are not lost by loss of chromosomes, and this is undoubtedly due to autopolyploidy of a high degree bringing about much repetition of basic hereditary material (multivalents at meiosis support this point). The same appears to hold for other forms of *P. pratensis, sensu lato*, and this autopolyploidy and its association with apomixis have been discussed in a thorough fashion by Darlington (1956).

There is obviously much ecological and physiological differentiation between these forms of *P. pratensis* which is of a genetic nature and this may have occurred at a much earlier period than the inception of the present levels of polyploidy, much nearer to the presumably diploid and sexual ancestors. The present differences in average polyploidy that seem to occur between *P. angustifolia* and *P. subcaerulea* are not the only reasons for their distinctiveness. If they have chromosomes in common they also have complex genetic differences, as their ecology shows.

P. subcaerulea is distributed widely in Britain in two major habitats of contrasting altitude, namely hill and mountain grasslands and dune slacks and shores. Both are essentially moist environments. Large gaps are nevertheless present in its distribution and these are probably the result of unfavourable habitat, though the under-recording that would arise from its critical nature may complicate the issue. The species is common in Icelandic grasslands and north west Europe, and is undoubtedly at the southern edge of its range, in much the same way as *Lolium perenne* is at its northern edge in the British Isles. This might account for its greater tendency, in the dense competitive grassland environment, to occur in hill areas, habitats of more extreme climate, and so behave as *P. pratensis, sensu stricto*, does in southern Europe and north Africa (Tutin) when it is at its southernmost points. The uncommonness of the form in the south of England (Hubbard), and its more or less restricted occurrence in the specialised maritime habitats, lend further support, and fits with many of Salisbury's (1932) generalisations.

Clausen & Hiesey suggest a latitudinal zonation of the forms of *P. pratensis*, with *P. arctica*, *P. alpigena*, *P. subcaerulea* and *P. pratensis* replacing one another from north to south. Whilst this is broadly true – for example *P. arctica* and *P. alpigena* are not known in Great Britain – it is not completely so since in many areas they are sympatric. Much overlap occurs in Sweden (Åkerberg) and certainly on a broad basis in the British Isles between *P. angustifolia*., *P. subcaerulea* and *P. pratensis*.

This tendency to geographical, coupled with ecological, specialisation in the polymorphic *P. pratensis* allows widespread colonisation and the development and maintenance of distinct physiological forms simultaneously. But the fact that the group is basically pastoral introduces a complexity of distribution since the variety of agricultural practices will lead to a modification of ecological barriers, and *P. pratensis, sensu stricto*, the main agriculturally useful form, will migrate to areas which, under more natural conditions, might be more suitable for others. Similarly, if there is a tendency for various pasture types to merge, there may be some areas in which the forms may be brought into very close contact, and even pollinating distance.

In conclusion it appears that in Britain *P. subcaerulea* is a species with a tendency to inhabit damp environments, hill grasslands and fixed dunes and shores. It is relatively easy to distinguish the typical panicles from other forms of *P. pratensis, sensu lato* but variation is such that panicle details may be similar to *P. pratensis* or *P. angustifolia* and so it is necessary to examine glume and vegetative characters. However, work in relationship to *P. alpigena* is much needed. A fuller and more detailed account of the distribution of *P. subcaerulea* in Great Britain would be of value in assessing the complex relationships of the other species of the *P. pratensis* group, and could indicate to what degree apomixis has permitted a fragmentation of distribution to small but suitable habitats. There is, even at this stage, much to suggest that *P. subcaerulea* and *P. angustifolia* are more or less extreme forms of *P. pratensis, sensu lato*, whether considered ecologically, cytologically or taxonomically.

Acknowledgments

It is a great pleasure to record my thanks to Dr. A. Melderis for his interest and suggestions, as well as his help in the final stages of the work. Thanks are also due to Principal F. H. Garner for facilities, and to Mr. J. Stevens for aid from time to time.

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Flora of New Zealand. Vol. 1 : *Indigenous Tracheophyta: Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones.* H. H. Allan. Pp. liv. + 1095, with 4 maps in colour on end papers and 40 figures in text. Government Printer, Wellington, 1961. Price £5 5s. 0d. (New Zealand currency).

The flora of New Zealand is remarkable for the high proportion of endemics, complex hybrid populations, the large number of attractive species contributed to horticulture, and the impressive spread of introductions. The publication of the late Dr. H. H. Allan's new *Flora* of a country with a climate so similar to our own is an event of considerable interest to British botanists.

The previous most recent work is the second edition of Cheeseman's *Manual* issued in 1925. The first volume of the new *Flora* describes 1457 species, whereas of the same groups Cheeseman described 1363. But statistics alone cannot convey the measure in the advance in knowledge of New Zealand plants in the last 35 years, or of the higher technical standards used in its presentation. Cheeseman's book stood high amongst the most useful Floras of the world; Allan's entirely new work is a great advance on Cheeseman and should take its place in every botanical library.

Most of the features of the best Floras are included. There are dichotomous keys to families, genera and species – combined with clear warnings in the more difficult genera about their limitations. Original descriptions are cited for all species and varieties, and latin descriptions of new taxa collected together at the end of the volume. Characters are set out clearly, and measurements and numbers cover extremes as well as normal specimens. A most commendable feature is citation of type localities and the location of type specimens. Many of the latter are in Britain, and thus this feature will be especially valuable to workers in this country. The task of critically reexamining type material must have involved an immense amount of work, but it is probably in this that Dr. Allan's work makes its biggest advance on Cheeseman's; many misinterpretations have been corrected, while the very full critical notes added in small type to so many genera and species will pave the way for further advances. As an example of the value of this approach Allan's account of *Crassula* (*Tillaea*) *helmsii* is appropriate, as this species was discussed at length in the last part of *Watsonia*. Allan gives the type locality as near Greymouth, and the type as collected by R. Helms in the herbarium of the Dominion Museum, Wellington, and refers to a paper by Court stating that this type has been compared with Victorian specimens of *Crassula recurva* (Hook. f.) Ostenf. and that no specific differences between the two were found. Full citations like this will save future workers much time, encourage sound nomenclature, and facilitate future research.

The present volume includes only species accepted as indigenous though this must considerably reduce its practical use as " a means of identifying plants," which, as is pointed out in the preface is the " primary purpose of a regional Flora." Visitors and resident botanists will find many plants which are not mentioned in this book. Even aliens like the blackberries and sweet briar which occur in great quantity are excluded. If a Flora is to serve adequately its purpose as a means of identification it should include all established species to be found at the time of publication. To limit the scope to those regarded as indigenous is to ignore the changes which have taken place during the past two centuries, and to involve users in failing to find names for many of the plants they find, or, even worse, making erroneous determinations simply because they were unaware that they were dealing with an introduced species. This treatment is the more surprising as Dr. Allan wrote *A Handbook of the Naturalized Flora of New Zealand* published in 1940, and was responsible for other valuable publications on aliens. Even if it is intended to include description of introductions in the second volume – and Cheeseman listed them in an appendix – this will be less useful than including them in systematic order.

Dr. Allan died in 1957 leaving a manuscript which included all the indigenous vascular plants except the monocotyledons. We are indebted to his colleague Miss Lucy B. Moore for filling in gaps, making final checks, seeing the volume through the press and adding a useful section of supplementary notes including abstracts of very recent papers. It is to be regretted that there is no reference in the preface or on the dust-cover to any arrangements for completing the work. Monocotyledons form such a relatively small proportion of the New Zealand Tracheophyta that the labour of preparing Volume 2 should be very much less than for the volume now in our hands.

The selection of type and standard of printing reflect great credit on the Government Printer, but it is unfortunate that such thin paper was chosen. This is too flimsy for satisfactory use in library or herbarium, and unpractical for consultation in the field. Portability is extremely desirable for a Flora but the fact has to be faced that a paper has yet to be invented which will give 1150 pages of print easy to handle in a volume less than one inch thick. From the heavy paper of Cheeseman, the Government Printer has gone to the other extreme in company with other publishers of modern floras – it should not be difficult to find a paper of intermediate weight which would be more serviceable.

Dr. Allan and Miss Moore have given us a first class new Flora which will be valued by workers in many countries.

J. E. Lousley

p. 65. Line 6 from bottom of page, *for* Mullett *read* Mullet.

p. 66. Line 1, *for* Mullett *read* Mullet; line 3, *for* Glosh *read* Glash; line 4, *for* Mollet *read* Mullet

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THE TAXONOMY OF *POLYGONUM AVICULARE* AND ITS ALLIES IN BRITAIN

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Abstract

The taxonomic history of *Polygonum* species in the section *Polygonum* (*Avicularia*) relating to the British flora is outlined. The merits of the various morphological characters used by authors to separate taxa in previous treatments is discussed. Evidence is produced, supported by results of biometrical, ecological and cytological studies, that the British and W. European forms of the weedy *Polygonum aviculare*, *sensu lato* comprise four species and a reclassification of these is proposed. Problems in the related British species in the group are discussed and clarified. A key to the British species is included.

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1. Historical introduction

As the nomenclatural problem encountered in the taxonomy of *P. aviculare*, *sensu lato* is complicated and confused, a more detailed historical taxonomic sketch than usual of the species concerned is necessary for a full understanding of the problem as it exists today. This however includes only the barest detail relevant to the species described.

Linnaeus (1753) includes *P. aviculare* in a division of the genus :

'**Polygonum* foliis indivisis, floribus octandris.'

As the other sections are given names by him, e.g. *Persicaria*, *Helxine*, *Bistorta*, it seems clear that he intended *Polygonum* as the sectional name for this group. In it he includes the following species: *P. aviculare*, *P. erectum*, *P. articulatum* and *P. divaricatum*. Of these *P. aviculare* is the best known, the commonest and also one which stands first in the group. It is therefore proposed to make *P. aviculare* the type species of the genus and *Polygonum* should be regarded as the name of the section according to the *International Code of Botanical Nomenclature* (1956), replacing later names.

The section was named *Centinode* by De Candolle (1815) with a brief description which was later amplified by Meisner (1826) who called it *Avicularia*.

None of the characters given separate this section sharply from others in the genus. However, there should be little difficulty in recognizing species belonging to it; the axillary flowers alone are a sufficient guide. There is a tendency for certain of the species, e.g. *P. arenarium* Waldst. & Kit. and *P. ramosissimum* Michx., to have the flowers aggregated at the upper nodes only of the leafless branches, forming long spike-like racemes. The fruit characters of these species are however similar to those of the more typical species of this section.

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Polygonum aviculare, sensu lato

Linnaeus (1753) used the binomial *P. aviculare* and gives the following very brief description :

' *Polygonum* floribus octandris trigynis axillaribus, foliis lanceolatis, caule procumbente herbaceo.'

This is an extremely broad description of the plant and would include all the species of the section. The closely related *P. maritimum* appears in the group headed ' *Persicaria* pistillo bifidis,' but the diagnosis is :

' *Polygonum* floribus pentandris trigynis axillaribus, foliis lanceolatis, caule stipulis obtecto fruticoso.'

Linnaeus also gives 4 varieties to *P. aviculare*, which are impossible to relate to any species which have been subsequently described in the aggregate.

The first ' species ' to be separated from *P. aviculare* L. was *P. littorale*. The original place of publication of this binomial is often wrongly cited. H. F. Link (in Schrader 1800) states in a letter written while on a journey to Portugal that he has seen a variety of *P. aviculare* which is similar to *P. maritimum*, and which has thick juicy leaves and the branches covered wholly with sheaths. This note of Link's does not however contain any name but some authors have referred to it as being the place where *P. littorale* was first published.

The first publication of the epithet *littorale* is in fact by Persoon (1805) when he gives **P. littorale*† with the following description,

' foliis crassis succulentis, caule minus ramoso.'

He cites Link's original plant in Schrader.

Link (1821) later described *P. littorale* with:

Caule procumbente suffruticoso, foliis oblongis acutis venosis carnosis, vaginis ciliatis internodiis multo brevioribus. Hab. in Europae maritimis.

Caulis suffrutescens angulatus. Foliis petiolo brevissimo lamina 10 " 5 " acuta. Cor. alba. Vulgo pro *P. maritimo* colitur at hujus vaginae internodiis aequilia. A. *P. aviculari* differt foliis latioribus magis carnosis, caule suffruticoso.'

From this one learns that the main differences between *P. littorale* and *P. aviculare* are slight, as it is said to differ in only the broader fleshy leaves and the woody or shrubby stem. *P. maritimum* differs in having ochreae as long as or longer than the internodes.

Since this time the plant has sometimes been given the status of a species, sometimes as subspecies or as a variety. Koch (1837) reduces it to that of a variety of *P. aviculare* whereas Meisner (1826) gives it the status of full species.

It is difficult to visualize the kind of plant which Persoon first described and its origin is not quoted in the diagnosis. Many authors of later works have included it under *P. maritimum*. Lindman (1896) contends that Persoon may have in fact described a form of *P. maritimum*.

Babington (1922), Lindman (1912), Moss (1914) and Rechinger (1958) follow Koch in retaining the plant as a maritime variety of *P. aviculare*. Tutin (1952) retains it as a ' microspecies ' in the *Polygonum aviculare* aggregate distinguished by characters of the fruit.

It is interesting to note that in the last five years A. & D. Löve (1956 a, & b), Chrtek (1956), Scholz (1959) and Pauvels (1959) do not mention this plant, and its status as a species may be taken as doubtful (see later).

I have made exhaustive attempts to trace the type specimen of *P. littorale* on the Continent. Unfortunately, Persoon's herbarium is apparently lost and almost all Links' specimens at the Berlin-Dahlem Herbarium, including the *Polygonaceae*, were destroyed during the last war. A specimen named by Koch *P. aviculare* var. *littorale* has been seen from the Rijksherbarium, Leiden (L), which fits *P. aviculare*, *sensu stricto*. The specimen exhibited the characteristic fleshiness of the leaves and stems associated with plants growing under halophytic conditions. It seems necessary, therefore, to treat *P. littorale* as a *nomen dubium*.

†Species given by Persoon with an asterisk appear to him to be uncertain or obscure

An investigation of British maritime forms in *P. aviculare sensu lato* has shown that no plants answering to the description of *P. littorale* Pers. exist in this country. A number of herbarium specimens labelled under this name exhibited great morphological differences and were a mixture of either *P. aviculare*, *sensu stricto*, or *P. arenastrum*. Living plants of the group collected by myself had rather fleshy, glaucous stems and leaves, but these phenotypic differences did not persist in cultivation.

Persoon (1805) also named plants collected by Thiébaud in the *P. aviculare* group as **P. monspeliense* with the following description :

' P. erecta, foliis ellipticis crenulatis, caule erecto stipulis scariosis incisis. Hab. Monspelii; Thiébaud. Distincta species videtur.'

Many later authors in floras have cited Thiébaud as the authority for the name but this is incorrect. It is the earliest name for the taxon *P. aviculare*, *sensu stricto* (*P. heterophyllum* Lindm.) if the Linnean name is rejected for any reason (see p. 205). I have obtained a photograph from the De Candolle Herbarium at Geneva (**G – DC**) of *P. monspeliense* collected by Thiébaud, and it is typical of plants which I today call *P. aviculare*, *sensu stricto*. This name will be considered later.

Besser (1822) described a species that he collected in ' Volhynia and Podolia ' (now the Ukraine, Russia), which he called *Polygonum neglectum*. He gives the following description :

' P. floribus 7 octandris, trigynis, subspicatis, foliis lanceolatis, ochreis laceris, internodiis brevioribus, caulibus diffusis patentibus ramosis mihi.'

There have been several different interpretations of this description and it has been the centre of much confusion. Although the plant has never been listed as a member of the British flora, a discussion of its taxonomy is relevant from the point of view of nomenclature.

Besser does not describe the fruit of the plant he collected and later authors describe it differently. Ledebour (1850) gives *P. neglectum* as a synonym of *P. arenarium* Waldst. & Kit., whilst Meisner (1856) includes it *pro parte* under this species and *pro parte* under his own *P. aviculare* var. *angustissimum*. Boreau (1857), on the other hand, suggests that it might be an earlier name for Jordan's *P. rurivagum*.

Several of the more recent treatments of the variation in this group have included *P. neglectum* as a full species. Notable examples of these are Komarov (1936), Lembke (1948), A. & D. Löve (1956) and Scholz (1959). Whilst A. & D. Löve record the plant as being common in Canada, the other three authors are all concerned with its occurrence in eastern Europe. This species will be discussed later.

The Russian botanists Meyer & Bunge (in Ledebour (1824)) first described *P. oxyspermum* from the island of Ösel in the Baltic. Their description is :

' Foliis lineari-lanceolatis subeveniis, floralibus diminutis, ochreis laceris internodiis brevioribus, caule ramoso, ramis erecto-patulis, corollae laciniis apice concavis patulo-conniventibus, semine acuminato corollam superante.'

P. oxyspermum is kept as a species by Meisner in De Candolle (1856), and is placed in the herbaceous section with *P. aviculare*, whereas the very closely related *P. raii* is placed in the suffruticose section with *P. maritimum*. The name appears in several of the older east-European Floras. A plant was named *P. acadiense* by Fernald (1914) as an endemic in N. America but Ostenfeld (in Fernald (1916)) states that after examining Danish and Scandinavian material labelled as *P. raii* he discovered that many of the plants referred to this were in fact *P. acadiense*. He found it to be widely distributed along the coasts of the Baltic and gives records for Denmark, Sweden, Gulf of Riga and arctic Norway. True *P. raii* is according to him confined to the channel coasts (England and France) and neighbouring areas.

Samuelsson (1931) identified *P. acadiense* as conspecific with *P. oxyspermum* after examining the type of Meyer & Bunge in Leningrad. *P. oxyspermum* was recorded in Great Britain during the last century and will be discussed later.

A ' species ' of a most dubious nature, *P. robertii* was described by Loiseleur-Deslongchamps (1827). Specimens were gathered by a M. Robert from a locality near Toulon, France and sent to Loiseleur for determination. The description is :

' Planta caulibus herbaceis procumbentibus diffusis, foliis ovato-lanceolatis virentibus, stipulis membranaceis acutis, floribus 2–3 axillaribus pedunculatis.'

No indication is given of the character of the fruit, but from Rouy (1910) one gathers that the main differences between this plant and *P. aviculare* are to be found here. In *P. robertii* the fruits are small and shining, and the plant is said to be a biennial or perennial. This species is of interest to British botanists in that the name has been frequently quoted as a synonym of *P. raii* Bab. and has been taken by some to be the correct name for this species. C. E. Britton, however, commenting on a specimen gathered from the Killiney Sands, Co. Dublin (v.c. H21) and labelled *P. raii* Bab. 1920, mentions : ' The two names are not synonymous. *P. robertii* is a plant of the Mediterranean area apparently not reaching the British shores, and distinguished by its biennial or perennial root. The achenes are much smaller than in *P. raii* and polished almost as much as *P. maritimum*.'

Babington (1836) described *P. raii** as a new species from plants sent to him from Marazion Bay, Cornwall, as follows :

' Caule procumbente herbaceo, ochreis 2-partitis ovatis demum laceris venis paucis distantibus simplicibus, floribus axillaribus, caryopside laevissima perianthio longiore.'

He was considerably confused about the existence of *P. robertii* and mentions in a letter to W. J. Hooker ' *P. robertii* appears to be a plant that is quite unknown to all botanists except its author and I am quite unable to state whether it is the same as my *P. raii*.'

No authentic material of *P. robertii* could be traced in France. Specimens in the Herbarium, Laboratoire de Phanérogamie, Paris (**P**) labelled as such were not *P. raii* but maritime forms of *P. aviculare*, *sensu lato*.

However, Reynier (1905) states ' Mutel, ayant examiné dans l'herbier de Robert la plante authentique, la décrit variation à tiges herbacées moins dures du *P. maritimum*.' Lindman (1904) mentions that a specimen of this ' species ' in the State Museum, Stockholm, labelled *P. robertii* Loiseleur, Toulon, ' belongs decidedly to *P. aviculare s.s.*' I feel sure that M. Robert's plant was merely a form of *P. aviculare* with rather more shining fruits than normal.

As no authentic specimens of this species are extant this name must be treated as a *nomen dubium*.

Boreau (1857), incorporating the researches of Jordan, threw the problem of nomenclature in the *P. aviculare* aggregate into even greater confusion by adding five new names and elevating other varietal names to specific status. The four binomials of Jordan (previously unpublished) are *P. agrestinum*, *P. humifusum*, *P. microspermum* and *P. rurivagum*, whilst Boreau himself described *P. arenastrum* as a new species as well as *P. polycnemiforme* (Lecoq & Lamotte) Bor. based on *P. aviculare* var. *polycnemiforme* Lecoq & Lamotte, and *P. denudatum* (Desv.) Bor. based on *P. aviculare* var. *denudatum* Desv.

Two of the binomials given by Boreau are relevant to the work on the British plants. These are *P. rurivagum* Jord. and *P. arenastrum* Bor. The relevant parts of his description are given here for purposes of typification.

' *P. rurivagum* Jord. ex Bor. Tige de 1 à 5 dec. grêle, flexueuse, dressée . . . . à nervures saillantes, gaînes brun-rougeâtres. . . . fruit brun mat, un peu luisant, finement chagriné, trigone, à faces excavées, ovoïde, aigu au sommet . . . Champs sablonneux après la moisson.'

' *P. arenastrum* Bor. Tiges très rameuses à rameaux longs étalées, sur le sol, tous très garnis de feuilles rapprochées, petites, ovales ou ovales oblongues, gaînes courtes. . . . fruit brun châtain, assez luisant, court, terminé en pointe. Sables, graviers etc.'

**P. rayi* or *raji* are mistaken orthographies adopted by many Continental, Scandinavian and American botanists, but no employed by Babington in his original diagnosis

These two names have been taken up as being the correct ones for taxa in the British flora.

Lange (1880) after a botanical expedition to Greenland described a new variety *P. aviculare* var. *boreale* which was later elevated by Small (1895) to specific rank. Lange's original description is as follows :—

'Foliis petiolatis, ½–1 pollicaribus, elliptico-obovatis, obtusiusculis; glomerulis 2–5 floris, floribus pedicellatis, pedicello fere perigonii longitudine; ochreis latis, acutis v. obtusiusculis, apice fissis.' North America, Siberia, Iceland, Faeroes.

Druce in this country was much puzzled by populations which he encountered from the Shetland Islands, subsequently called by him (1922) *P. aviculare* var. *grandiflora*, and this led me to an investigation of the plants of this group occurring in these islands. A number of populations have been obtained from the Shetlands and most of these on investigation have been found to form a distinct taxon. The plants agree with Lange's type collection in the petiolate leaves and in the large fruit and persistent perianth. They have also been compared with gatherings from Iceland, Greenland and Northern Scandinavia. It is regarded here as a distinct species, *P. boreale*, new to the British Isles.

An effort to produce a more satisfactory taxonomic treatment for the species occurring in Europe was attempted by Lindman (1904, 1912). He studied the plants over a greater area of their range than any previous workers and made the group the object of special investigation to which many more recent authors have referred.

He divides the group into three species, *P. calcatum* Lindm., *P. heterophyllum* Lindm. and *P. aequale* Lindm., with a number of varieties. He first separated *P. calcatum* (1904) and later (1912) published the other names in dividing up the forms remaining under *P. aviculare*. It is regrettable, however, that the differences between *P. calcatum* and *P. aequale* are not clear from his description. Lindman states furthermore, that *P. calcatum* is as common in Scandinavia as *P. aviculare*, (including *P. aequale*). The relevant features of Lindman's description of *P. calcatum* are :

'Annual, prostrate, leaves tending to be small elliptical, ovate or obovate. . . Peianth united to the middle, compressed, tubular; segments pale green edged with white. Stamens 5. Nut small 2–2½ mm long, broadly ovate-lanceolate, gradually narrowing at the tip, compressed trigonous, the sides convex, smooth.

Those of *P. aequale* are :

'Annual, stem erect or prostrate, leaves of main stem and flowering branches equal or differing in size, all commonly the same shape. . . Perianth segments equalling the length of the fused base or twice as long. . . Persistent perianth as long as the fruit or a little shorter. Fruit trigonous *c.* 2–3 mm long, ovate or lanceolate, black.'

Lindman's other species, *P. heterophyllum*, is a more satisfactory entity, and is distinguished from the others by the heterophyllous nature of the leaves and by the fruit which is larger, generally up to 3 mm, with three dull, concave sides. Lindman gives five varieties of the latter with the name *rurivagum* as one of them. Hybrids between all species of the group are said to occur. It is presumed that Lindman used new binomials for these taxa on the grounds that the Linnean *Polygonum aviculare* is a *nomen ambiguum*, but nowhere in the literature does he state this.

Moss (1914) follows Lindman very closely in his extensive treatment of the group in Britain but raises *P. rurivagum* to full specific rank.

Tutin (1952) in our most recent Flora treats the Linnean *P. aviculare* as an 'aggregate species' and includes the following as segregates, *P. aviculare* L., *sensu stricto* (= *P. heterophyllum* Lindm.), *P. littorale* Link, *P. rurivagum* Jord., *P. aequale* Lindm., *P. calcatum* Lindm. His account is based on that of Moss (1914) but less detail of the morphology and distribution of the plants in Britain is given.

The four latest studies by specialists on the taxonomy of this difficult group have all appeared since this present work was begun in 1956. The conclusions of these workers differ to some extent among themselves and from my own. There is, however, some measure of agreement over such issues as the number of taxa into which the variation pattern of

P. aviculare in the wide sense can be divided if allowance is made for the areas in which these taxonomists have worked. There is, however, still great confusion and difficulty over the question of the correct binomials which are to be used in naming these taxa. Every effort has been made to discuss the more difficult problems with them. These discussions have helped in reaching the conclusions included in this present treatment, which I believe to be the correct ones.

A. & D. Löve (1956) have worked on Canadian plants and base their reasons for the delimitation of taxa mainly on cytological evidence. They give little detail of the morphology of the species they include and this has made exact comparisons with them and the British taxa difficult in most cases. These authors retain *P. heterophyllum* Lindm., *P. aviculare* L. (= *P. aequale* Lindm.) and *P. rurivagum* Jord. (!). They include also *P. neglectum* Bess. and state that it ' has been introduced, and is common in Canada.' *P. calcatum* Lindm. is reduced to a subspecies of *P. aviculare* L. *P. boreale* is treated as a subsp. *boreale* of *P. heterophyllum*. No reason is given by A. & D. Löve for equating *P. aequale* Lindm. with *P. aviculare* L.

The interest of the work by A. & D. Löve lies in the fact that they are the first workers in this field to attempt a complete correlation of cytological observations with morphological differences in these plants. Their work, however, contains several counts of chromosome numbers which are not consistent with those made on the same taxa in this country. A discussion of these differences will appear later.

The treatments of Chrtek (1956) and Scholz (1958–59) may be considered jointly since they have both worked in eastern Europe. Although the rank of the taxa they propose is considerably different and a new binomial is introduced their results are similar. Chrtek proposes four groups at the level of subspecies. These are subsp. *monspeliense* Pers., subsp. *rectum* Chrtek, subsp. *calcatum* (Lindm.) Thell. (new to Czechoslovakia) and subsp. *aviculare* (= *aequale* Lindm.). The name subsp. *rectum* is a new one to the already long list of names in the aggregate, and Scholz (1959) elevates it to specific rank in his treatment* and keeps the taxa above as full species together with *P. neglectum*.

The value of Chrtek and Scholz's work is difficult to assess since they each seem to have worked in a vacuum and have referred to existing literature rather than specimens on which to base their conclusions. Types have been entirely neglected.

Pauvels (1959) has been able to establish the existence of two separable taxa in *P. aviculare*, *sensu lato* in the Belgian flora. He contends that plants gathered from different localities in Belgium fall easily into two groups, *P. aviculare* L., *sensu stricto*, and *P. aequale* Lindm. which are both extremely variable.

2. Analysis of taxonomic characters

(a) *Vegetative Characters*

Habit.

The habit and size of the plant have been frequently used in the past as diagnostic for a particular species, (Boreau 1857, Ascherson & Graebner 1913, Chrtek 1956). Habit varies with the age of the plant and is a most variable feature depending on environmental conditions, and I consider it to be of little taxonomic significance.

Ochreae.

The hyaline outgrowths at the nodes which characterize the family *Polygonaceae* are of only limited use as taxonomic criteria in the *P. aviculare* aggregate. The ochreae of *P. rurivagum* are however longer than those of the other species recognized.

Ochrea-length and the type and number of veins are, on the other hand, highly significant characters in the separation of *P. raii* and *P. maritimum*; those of *P. maritimum* are frequently as long as the upper internodes, and silvery in colour, with 8–12 branched

*He drops this name later (1960) in a key to the species in this group.

veins. Those of *P. raii* are shorter; the mean length of a population from Hayling Island, S. Hants (v.c. 11), was 0·6 cm, with up to a maximum of 6 unbranched veins.

Leaf size and shape: Heterophylly

The leaves are all simple and entire from 0·3 cm to 5·5 cm in length, and 0·1 cm to 1·8 cm wide, varying in shape from very narrowly lanceolate, to oblong-lanceolate and ovate-spathulate. The petiole is evident only in *P. boreale* where it is longer than, and protrudes beyond, the enveloping ochrea. Stress has been laid on leaf-characters by previous workers, and they are frequently the only ones mentioned in their keys, (e.g. Boreau 1857). Because of the caducous nature of the foliage, leaf characters must be used with caution, and in this work they have always been related to other more stable features such as fruit-size and length of the fruiting perianth.

Two characters were used for biometrical data :

1. A linear measurement of the length and breadth of the largest stem leaf. The length was measured from the point of insertion of the leaf, including the petiole if present, to the apex. The width was taken at the broadest part of the leaf.

2. The index of heterophylly for each plant in any given sample was obtained by dividing the length of the main stem leaf obtained in 1 by the length of the lowest leaf of the branch subtended by this stem leaf.

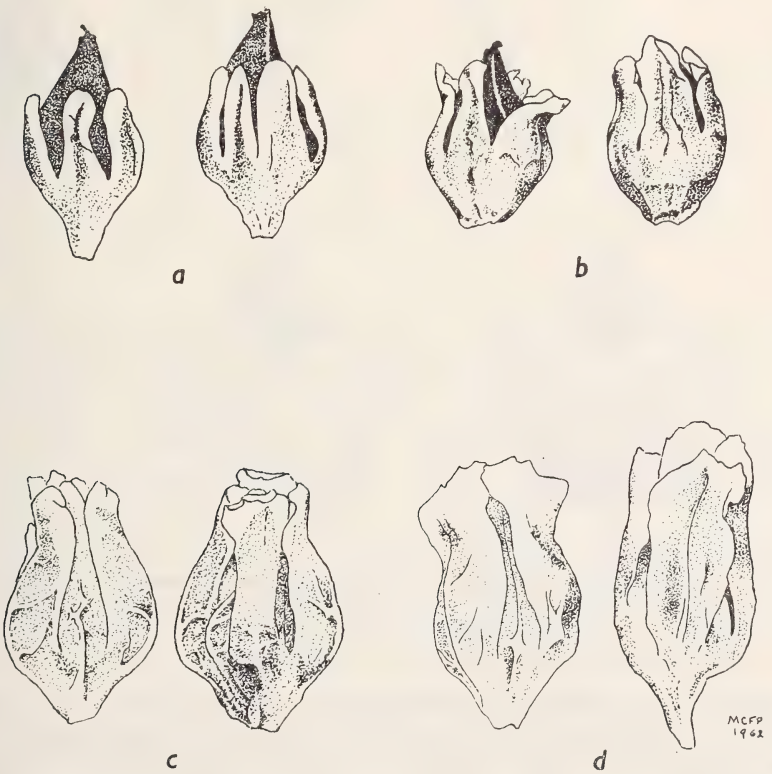


Fig. 1. Camera lucida drawings of fruiting perianths of *Polygonum* spp., × 8.
(a) *P. rurivagum*, Devil's Dyke, Cambs. (b) *P. arenastrum*, Chedworth, Glos.
(c) *P. aviculare*, Brill, Bucks. (d) *P. boreale*, nr. Scalloway, Shetland Is.

(b) *Flower and Fruit Characters*

It is very probable that the small size of the flowers and fruits and their insignificant position in the axils of the leaves is a reason for their having been neglected as taxonomic criteria by many earlier authors. The very striking differences between the fruits of *P. maritimum* and *P. aviculare* are not mentioned by Linnaeus. The flowers of the *Polygonaceae* are monochlamydeous. In the species in this section there are 5 (rarely 4 or 6) perianth segments which vary in length according to the species. The perianth segments have a green midrib and a red, pink or greenish-white petaloid border. The width of this border varies, being greater in the two littoral species *P. raii* and *P. maritimum*, and in *P. boreale*, than in the other species. Colour-differences between the species have been given as diagnostic by many authors in the past, but the present study has revealed that there is no correlation between colour and the different species.

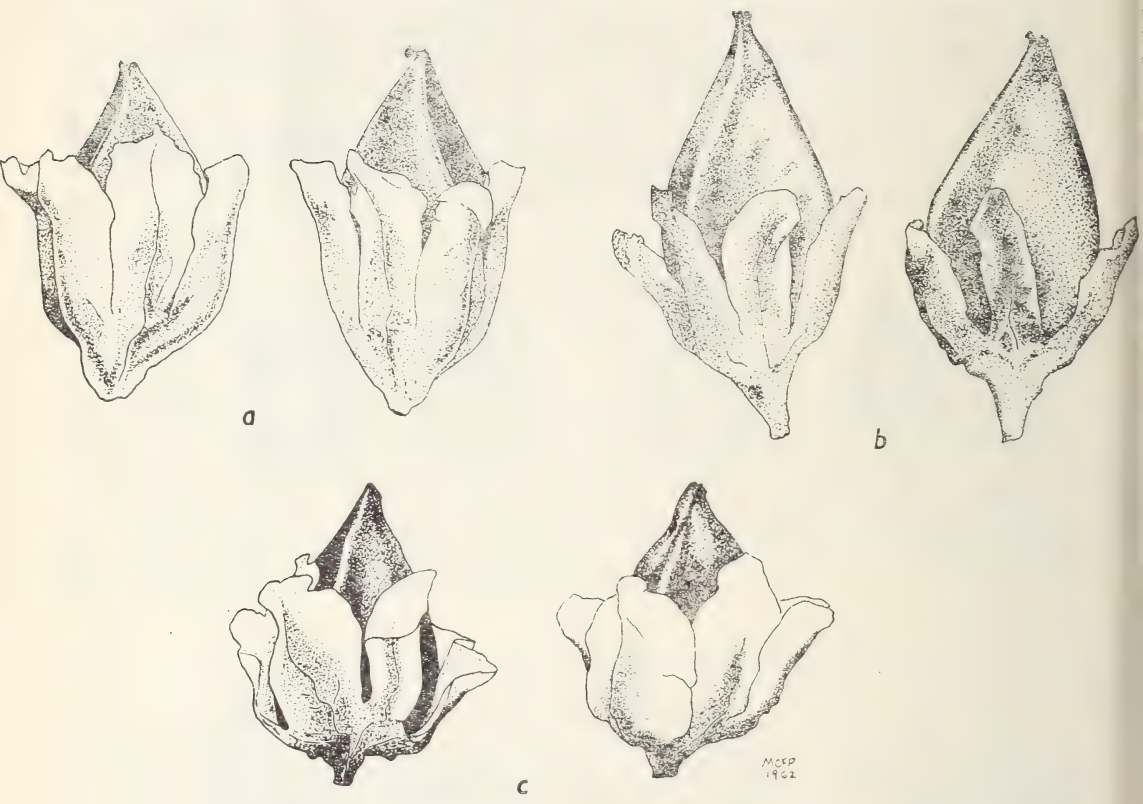


Fig. 2. Camera lucida drawings of fruiting perianths of *Polygonum* spp., × 8.
(a) *P. raii*, Hayling I., S. Hants., (b) *P. oxyspermum*, Irevik, Gotland, Sweden.
(c) *P. maritimum*, Herm, Channel Is.

The perianth is persistent and encloses the fruit forming an enveloping cover. It is dispersed with it when mature. The length of the fruiting perianth segments shows a considerable amount of variation. In some species the perianth is divided almost completely to the base of the flower so that there is practically no tube, whereas in others it is less deeply divided. The tube is then longer, sometimes three quarters of the total perianth length. The length of the persistent perianth, the length of its fused portion and the length of the perianth segments have been found to be diagnostic. (See Fig. 1 & 2). The following

parameters were measured using a low-power binocular microscope with a × 10 eye-piece containing a calibrated micrometer scale and a × 3·4 objective.

3. Length of the persistent perianth.
4. Length of the perianth segments, obtained by subtracting the length of the joined portion of perianth from the total perianth length.
5. The ratio $\frac{\text{Total perianth length}}{\text{Perianth segment length}}$

Stamen number

Lindman (1912) states that *P. heterophyllum* has generally eight stamens, five in an outer whorl and three in an inner, whereas *P. aequale* has five, a whorl of three and another of two. Three typical populations were analysed in detail for this character. There is wide variation in the number of stamens in the flowers of any one plant in all three species (Table 1). Stamen number seems to vary with the age of the flower in the inflorescence. Also flowers developed late in the year were found on the whole to have a lower number than earlier formed ones.

TABLE 1.
Percentage frequency of stamen number in flowers of 3 different species.

Species	*Number of stamens*						*Total No. of flowers*	*No. of plants*
	4	5	6	7	8	9		
P. aviculare, sensu stricto	1·26	1·95	7·36	27·8	59·6	1·95	163	52
P. arenastrum	2·82	42·4	8·02	11·26	35·4	0	148	48
P. rurivagum	0	2·58	7·22	20·6	68·0	1·03	194	50

Fruit

The fruit develops from a tricarpellary ovary to form a nut which is usually three-sided. It may be examined by removing the persistent perianth with a sharp scalpel. Absolute length of the fruit has been used by many botanists to segregate species in the past, as in *P. microspermum* for very small fruited specimens, and *P. heterophyllum* (= *P. aviculare* L., *sensu stricto*) with large fruit. On the whole the longer fruits tend to be broader, so that fruit-size offers a supplementary character to that of fruit-length. I therefore measured the following parameters using the method mentioned above.

6. *Fruit length*, from the base of the apex of the fruit, but not including the trifid style which is sometimes found persisting.
7. *Fruit size* (fruit length × breadth). The length of the fruit as measured above multiplied by its greatest width when the fruit is lying on its broadest face.

Perhaps one of the most interesting features of the fruit is the strong correlation between size and shape as seen in cross-section. (See Fig. 3, a-e). It is at once noticeable that the longer fruits of heterophyllous plants almost always have all three sides of the fruit concave, and that one of them is broader than the other two. The more homophyllous plants tend, on the other hand, to have smaller fruit of a different shape. In this case it exhibits in cross-section two convex sides with the third side concave. This third side is narrower than the other two. The narrowness of the concave side, recognisable in the

fruit of certain plants, was the reason for Lindman (1904) separating *P. calcatum* as a species from the Linnean *P. aviculare* complex. It is difficult to obtain biometric data on variation of the width of this concave side. As there is variation in the narrow side from ' narrow – very narrow – ridge like ' in populations referable to *P. arenastrum* it is considered that *P. calcatum* Lindm. as a taxonomic entity does not exist.

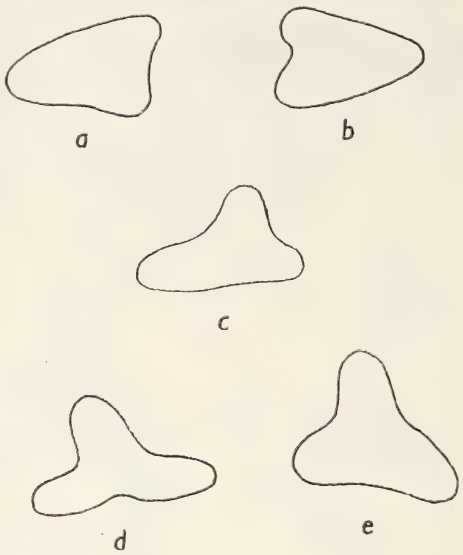


Fig. 3. Camera lucida drawings of cross sections of fruits of *Polygonum* spp., × 8.
(a) *P. arenastrum*, Chedworth, Glos. (b) *P. arenastrum*, Newborough Warren, Anglesey. (c) *P. rurivagum*, Babraham, Cambs. (d) *P. boreale*, Shetland Is. (e) *P. aviculare*, Caernarvon, N. Wales.

The fruits of *P. aviculare*, *sensu stricto*, are always lustreless and dull with rows of punctate dots. The sides of the fruit are concave. Occasionally four-sided fruits are found. Populations of *P. arenastrum* have fruits which vary considerably from completely shining to shining only on the edges. *P. rurivagum* has fruits which are as long as those of *P. aviculare*, *sensu stricto*, but narrower; they also are shiny on their edges.

The surfaces of fruits of the two maritime species, *P. raii* and *P. maritimum*, are very distinctly shining and highly polished. This, together with their larger size, makes them distinguishable from plants of *P. aviculare*, *sensu lato*.

A feature which has caused some difficulty in the past is the fact that the fruits of plants in *P. aviculare sensu lato* may be totally included within the persistent perianth or may project very slightly from it. This has, however, during the course of the work, been found to be variable in any population of either *P. arenastrum* or *P. aviculare*, *sensu stricto*. The fruits of *P. rurivagum* are always exserted, a point noted by Moss (1914). Those of any single plant are usually all of one type, but even on a single plant there may be variation, since fruits formed late in the year are nearly always slightly exserted. This will be further considered. The fruits of *P. raii* are always markedly exserted from the persistent perianth whereas those of *P. maritimum* are enclosed, or only slightly exserted.

3. Biometrical studies

As a basis for my biometrical studies, I decided to take as my primary groups for preliminary investigation those given by Tutin (1952), who has followed in the main the treatment by Moss (1914), in order to see if they presented differences enough to warrant their delimitation as taxa in this country. The groups are *P. heterophyllum* Lindm. (now



Fruits of *Polygonum* spp., × 2·5. (a) *P. rurivagum*, Babraham, Cambs. (b) *P. arenastrum*, Chedworth, Glos. (c) *P. arenastrum*, Newborough Warren, Anglesey. (d) *P. aviculare*, Brill, Bucks.



Fruits of *Polygonum* spp., × 2·5. (a) *P. boreale*, Easterhoull, Shetland Is. (b) *P. raii*, Hayling I., S. Hants. (c) *P. oxyspermum*, Laeso, Denmark. (d) *P. maritimum*, Figueira da Foz, Portugal.

P. aviculare, sensu stricto), *P. aequale* Lindm. (now *P. arenastrum*), *P. rurivagum* Jord., *P. calcatum* Lindm. and *P. littorale* Pers. *P. microspermum* was also included as this binomial is given by Dandy (1958). I examined in detail a very large number of specimens of the group from British and European herbaria, to ascertain the variation of the plant from many localities over its entire range in this country and western Europe.

From this study it was apparent that there is a very great variation in general morphology and habit of the plant according to the type of habitat and degree of sheltering, trampling and crowding to which the plants are exposed, and many characters used by previous authors appeared to be very unreliable, or showed such variability from one plant to another as to be taxonomically useless. Certain features of the fruit and persistent perianth which lend themselves easily to biometric treatment were found to be more constant over a larger number of specimens. Measurement made on non-random samples produced evidence that at least three groups could be defined on these characters. The variation patterns, for instance of linear measurements of fruit, perianth-segment- and perianth-length, fruit size and certain ratios, showed marked discontinuities between the three groups. These corresponded to Tutin's *P. heterophyllum*, *P. aequale* and *P. rurivagum*.

A cursory examination also revealed that the larger-fruited *P. heterophyllum* tended to possess leaves of a larger size, whereas *P. aequale* which is small-fruited (by comparison) has shorter, narrower leaves. Thus a possibility existed of correlating the very variable vegetative characters with those of the fruit which are less variable (see scatter diagrams, Figs. 8–10).

I have gathered a large number of random samples from throughout the range of the plant in Great Britain and from as many ecologically different habitats as possible. All species in the group are gregarious and found in patches (often alone on bare ground), or intermixed with other weeds. Sampling was done by gathering plants from a transect cutting through the centre of a patch and from around the edges so that a true representative collection was made of all forms. Composite data for all populations of the four taxa proposed is presented.

In the herbarium the samples were analysed for the quantitative parameters already discussed. Their arithmetical means ($\bar{x}$), standard deviations (σ) and ranges (after Heslop-Harrison 1952) were obtained. Data for a number of samples are presented in Tables 2–6. The same measurements were made on all plants*. Certain other qualitative characters, such as surface-texture and shape of the fruit, which it was not found possible to treat biometrically, have already been discussed.

Analysis of Individual Characters

An idea of the differences between populations of the same group can be gained from a study of Tables 2–6. In these tables the correct names for the groups have been applied and will be used in the discussion here of their variability.

Fruit Characters

Sample data for the linear measurements of the fruits, as seen in the tables, show that the means for the different populations in the same group agree remarkably well in this dimension. i.e. $\bar{x} = 3{\cdot}88$ for the Chedworth population, 3·85 for that of Clevedon and 3·79 for that at Brill (Table 2).

In this research where I have used large samples, the significance of the difference between the means was determined by calculating the standard error of the difference. If the difference between the two means is greater than twice the standard error then the means may be taken to be significantly different ($P = 0{\cdot}05$). The fruit length of *P. arenastrum* is significantly smaller and that of *P. boreale* (Table 5, Shetland plants) significantly larger than *P. aviculare, sensu stricto*. The fruit of *P. rurivagum* is as long as that of *P. aviculare* and the range of variation is almost completely overlapping. The means for the

*The measurements in the tables are given in arbitrary units, where one arbitrary unit = 0·793 mm.

TABLE 2. Statistical data for four random samples of *P. aviculare*, *sensu stricto*
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Chedworth, Glos.* †$N = 45$			*Clevedon, Somerset** $N = 50$			*Caernarvon** $N = 35$			*Brill, Bucks.* $N = 40$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·88	0·61	3·30–4·60	3·85	0·59	3·40–4·45	3·96	0·58	3·40–4·40	3·79	0·71	3·40–4·60
2. Fruit size	9·65	1·48	6·93–12·60	10·41	1·56	9·50–13·60	10·70	1·52	9·36–13·44	9·68	1·48	7·52–12·30
3. Persistent perianth length	5·01	0·57	3·90–5·90	4·96	0·47	4·10–5·80	4·79	0·49	4·00–5·80	4·97	0·44	4·20–5·70
4. Segment length	3·60	0·19	2·50–4·50	3·55	0·16	2·75–4·20	3·37	0·16	2·60–4·25	3·46	0·16	2·70–4·10
5. Per. length/seg. length	1·39	0·21	1·24–1·61	1·41	0·21	1·27–1·60	1·41	0·21	1·27–1·61	1·43	0·20	1·34–1·62
6. Leaf length (cm)	3·28	2·76	2·40–4·50	3·18	2·64	1·82–4·40	3·54	3·20	2·60–5·30	3·09	2·76	1·90–4·20
7. Leaf breadth (cm)	0·82	0·71	0·44–1·35	0·78	0·46	0·58–0·95	0·87	0·77	0·60–1·60	0·75	0·42	0·55–0·98
8. Index of heterophylly	0·63	1·41	1·16–2·32	1·54	1·31	1·21–2·14	1·58	1·32	1·23–2·12	1·51	1·31	1·23–2·05
9. Branch leaf length (cm)	2·00	1·37	1·50–2·80	2·08	1·41	1·50–2·90	2·24	1·48	1·60–3·20	2·03	1·45	1·40–2·80

* As *Polygonum 'littorale'*

† N = number of measurements of individual plants for each parameter.

TABLE 3. Statistical data for samples of *P. arenastrum* Bor.
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Oxford (By-pass)* $N = 50$			*Bognor, Sussex* $N = 36$			*Oxford (Jackdaw Lane)* $N = 50$			*Berrow, Somerset** $N = 44$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·13	0·56	2·70–3·40	2·73	0·36	2·40–3·10	2·78	0·39	2·30–3·20	3·06	0·47	2·50–3·50
2. Fruit size	6·31	1·34	4·72–7·70	4·58	1·21	3·50–5·51	4·57	1·32	3·10–6·20	5·57	1·35	4·20–7·65
3. Persistent perianth length	3·44	0·59	2·85–3·95	3·14	0·61	2·50–4·00	2·98	0·52	2·30–3·60	3·43	0·54	2·80–4·20
4. Segment length	1·93	0·09	1·45–2·45	1·70	0·08	1·40–2·25	1·75	0·89	1·20–2·20	1·80	0·10	1·30–2·40
5. Per. length/seg. length	1·78	0·15	1·57–2·12	1·85	0·13	1·60–2·10	1·70	0·16	1·50–2·00	1·91	0·18	1·50–2·25
6. Leaf length (cm)	1·68	1·41	1·38–2·40	1·27	1·45	0·97–1·56	1·03	1·84	0·65–1·60	1·36	2·07	0·75–2·10
7. Leaf breadth (cm)	0·43	0·31	0·30–0·58	0·25	0·36	0·12–0·59	0·19	0·30	0·10–0·28	0·37	0·35	0·20–0·60
8. Index of heterophylly	1·31	0·21	1·20–1·61	1·24	0·27	1·00–1·43	1·19	0·21	1·00–1·56	1·15	1·41	0·65–1·85
9. Branch leaf length (cm)	1·10	1·41	0·82–1·50	1·08	1·27	0·78–1·38	0·87	1·31	0·50–1·25	1·18	0·21	1·04–1·68

* As *Polygonum 'littorale'*

TABLE 4. Statistical data for three random samples of *P. rurivagum* Jord.
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Seaford, Sussex* $N = 32$			*Wytham, Berks.* $N = 35$			*Babraham, Cambs.* $N = 50$		
	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·86	0·71	3·40–4·80	3·90	0·65	3·40–4·50	3·76	0·48	3·20–4·20
2. Fruit size	8·86	1·39	6·65–11·20	8·52	1·37	6·54–12·10	8·29	1·49	6·08–11·20
3. Persistent perianth length	4·30	0·61	3·60–5·20	3·93	0·52	3·20–4·87	3·77	0·51	3·00–4·50
4. Segment length	2·63	0·10	1·90–3·40	2·48	0·09	1·64–3·20	2·36	0·12	1·70–3·00
5. Per. length/seg. length	1·62	0·19	1·36–1·87	1·63	0·23	1·34–1·88	1·59	0·18	1·37–1·83
6. Leaf length (cm)	2·42	2·59	1·70–3·40	2·84	3·61	1·94–3·96	3·11	3·17	2·60–4·20
7. Leaf breadth (cm)	0·24	0·65	0·15–0·35	0·28	0·74	0·14–0·41	0·31	0·64	0·20–0·45
8. Index of heterophylly	1·68	0·25	1·35–2·43	1·57	0·23	1·24–2·53	1·94	0·28	1·40–2·40
9. Branch leaf length (cm)	2·05	1·58	0·70–1·90	1·77	1·41	1·14–2·09	1·59	1·43	1·28–2·11

TABLE 5. Statistical data for four random samples of *P. boreale* from the Shetland Islands. Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

Parameter	*Burra Voe* $N = 38$			*Scalloway* $N = 50$			*Easter Quarff* $N = 40$			*Vassa South Nesting* $N = 45$		
	$\bar{x}$	σ	range	$\bar{x}$	σ	range	$\bar{x}$	σ	range	$\bar{x}$	σ	range
1. Fruit length	4·72	0·83	4·10–5·70	4·14	0·73	3·70–4·60	4·12	0·75	3·80–4·80	4·42	0·81	4·00–5·40
2. Fruit size	12·80	1·54	10·00–18·00	11·49	1·47	8·93–14·95	10·80	1·39	8·80–12·20	11·73	1·50	9·76–16·31
3. Persistent perianth length	5·90	0·54	4·80–7·30	5·35	0·57	4·50–6·30	5·35	0·52	4·60–6·10	5·49	0·52	4·42–7·10
4. Segment length	4·30	0·15	3·30–5·60	3·95	0·12	3·20–4·80	3·88	0·12	3·20–4·60	4·04	0·13	3·20–4·70
5. Per. length/seg. length	1·35	0·11	1·25–1·45	1·35	0·13	1·25–1·44	1·37	0·12	1·30–1·47	1·35	0·12	1·25–14·7
6. Leaf length (cm)	3·45	3·10	2·70–4·40	3·52	3·92	2·70–5·00	3·28	3·51	2·30–4·50	3·29	3·40	2·55–4·15
7. Leaf breadth (cm)	1·15	0·51	0·90–1·50	1·17	0·54	0·80–1·70	1·14	0·55	0·75–1·65	1·14	0·55	0·83–7·04
8. Index of heterophylly	1·48	0·31	1·22–1·90	1·84	0·35	1·47–2·31	1·91	0·42	1·20–2·30	1·52	0·41	1·20–2·27
9. Branch leaf length (cm)	2·32	1·42	1·90–2·70	1·91	1·71	1·50–2·80	1·71	1·45	1·47–2·57	2·02	1·68	1·75–2·64

TABLE 6. Composite statistical data for the four taxa, *P. aviculare*, *P. arenastrum*, *P. rurivagum*, *P. boreale* (all samples)
Measurements in arbitrary units, one unit = 0·793 mm, unless otherwise stated.

	P. aviculare, sensu stricto			*P. arenastrum*			*P. rurivagum*			*P. boreale*		
Parameter	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*	$\bar{x}$	σ	*range*
1. Fruit length	3·86	0·62	3·40–4·50	2·92	0·37	2·45–3·40	3·83	0·66	3·32–4·50	4·35	0·74	3·95–5·20
2. Fruit size	10·00	1·50	8·00–12·78	5·30	1·34	2·85–6·76	8·55	1·36	6·42–11·70	11·75	1·54	9·51–15·42
3. Persistent perianth length	4·96	0·48	4·03–5·80	3·33	0·53	2·61–3·93	4·00	0·55	3·26–4·84	5·54	0·51	4·65–6·55
4. Segment length	3·47	0·16	2·60–4·26	1·78	0·09	1·34–2·32	2·49	0·10	1·74–3·20	4·05	0·15	3·50–5·26
5. Per. length/seg. length	1·33	0·20	1·28–1·61	1·80	0·15	1·53–2·12	1·61	0·18	1·35–1·86	1·35	0·12	1·25–1·45
6. Leaf length (cm)	3·30	3·63	2·31–4·66	1·33	2·47	0·93–1·92	2·78	3·14	2·08–3·84	3·42	3·32	2·60–4·70
7. Leaf breadth (cm)	0·82	0·64	0·53–1·35	0·28	0·35	0·18–0·52	0·27	0·66	0·16–0·40	1·15	0·54	0·82–1·62
8. Index of heterophylly	1·57	1·30	1·21–2·16	1·21	0·24	1·05–1·61	1·73	0·25	1·33–2·45	1·74	0·35	1·29–2·18
9. Branch leaf length (cm)	2·09	1·42	1·50–2·93	1·06	1·30	0·68–1·49	1·80	1·45	1·04–2·03	1·98	1·48	1·63–2·69

aggregate data can be seen in Table 6. There is a significant difference between the means 3·86 for *P. aviculare*, *sensu stricto* and 2·92 for *P. arenastrum*. Fruits from plants that I gathered in Brill (Table 2) and grew the next year in the experimental garden showed a range in length from 3·50 to 4·50, and plants from fruits collected on the Oxford by-pass gave offspring with the same range in fruit-length as the parent plants. This character therefore appears to be very stable under different conditions.

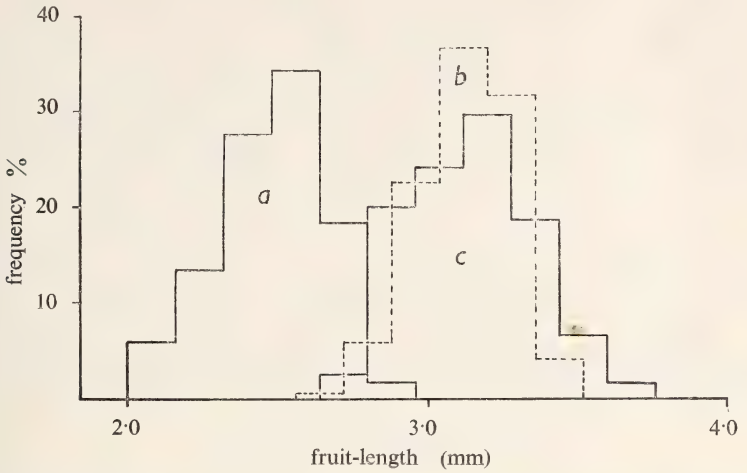


Fig. 4. Variation in fruit-length in (a) *P. arenastrum*, (b) *P. rurivagum* and (c) *P. aviculare*.

Fruit-length and -breadth have been multiplied together to give numbers which express size more adequately than either linear dimensions. The fruits of *P. boreale* are both broader and longer than those of *P. aviculare*; the product is therefore greater. Although there is some degree of overlap the two have significantly different means. Variation in fruit size between *P. arenastrum* and *P. aviculare* is almost discontinuous.

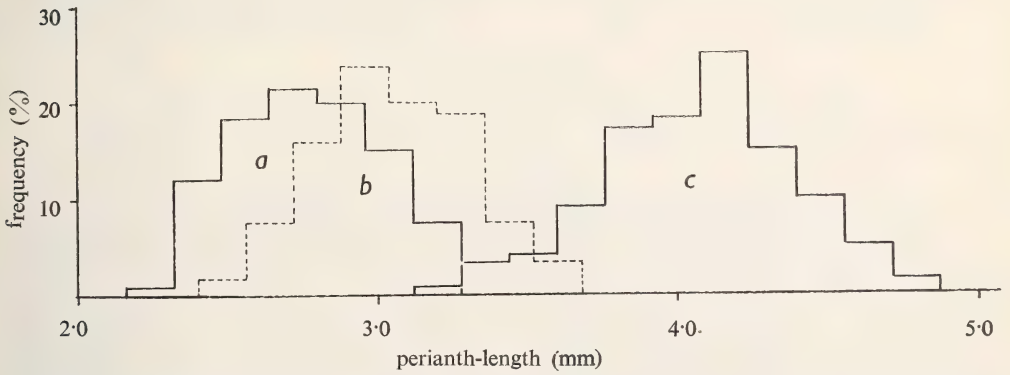


Fig. 5. Variation in perianth-length of (a) *P. arenastrum*, (b) *P. rurivagum* and (c) *P. aviculare*.

Perianth Characters

The variation of perianth-length in the different groups follows the same pattern as fruit length. From the tables it is seen that perianths of *P. aviculare*, *sensu stricto* are longer ($\bar{x} = 4{\cdot}96$) than those of *P. arenastrum* ($\bar{x} = 3{\cdot}33$) and *P. rurivagum* ($\bar{x} = 4{\cdot}00$). The

distributions of the last two are almost coincident (Fig. 5). Perianth-length in *P. boreale* ($\bar{x} = 5{\cdot}40$) is the longest in the group and differs significantly from that of *P. aviculare* although there is again some overlap in the variation Fig 6. The range of this character in the group is great.

The length of the tube in relation to the total length of the perianth is very interesting and significant in the taxonomy of the group. This relationship has been expressed as a ratio. In *P. arenastrum*, which has a comparatively short perianth and long fused portion, up to half its length, with consequently shorter perianth segments, this ratio approaches and exceeds, in some cases, 2 in the fruiting stage. *P. aviculare*, on the other hand, has a longer perianth and short tube with correspondingly longer perianth segments. In this species the ratio is nearer unity. Study of the results shows that *P. aviculare*, *sensu stricto* has a mean value of 1·33, whereas in *P. arenastrum* it is as high as 1·80. Variation in this ratio is great, however (see Fig. 7, and Tables 2–4). The population of *P. arenastrum* from Berrow showed variation from 1·50 to 2·25, and another from Oxford (By-pass) varied from 1·57 to 2·12. In *P. aviculare* the Chedworth population varied from 1·24 to 1·61, and that from Brill between 1·34 and 1·62. From the histogram of the variation of this ratio it is clear that two well defined groups may be demarcated. *P. rurivagum* has, as already stated, a perianth length approaching that of *P. arenastrum* ($\bar{x} = 4{\cdot}00$ and 3·33 for aggregate data) but has the short tube of *P. aviculare*. In respect of this ratio, therefore, *P. rurivagum* is intermediate and the mean value from the composite data is 1·61.

The length of the perianth segments is greatest in flowers of *P. boreale* ($\bar{x} = 4{\cdot}05$);

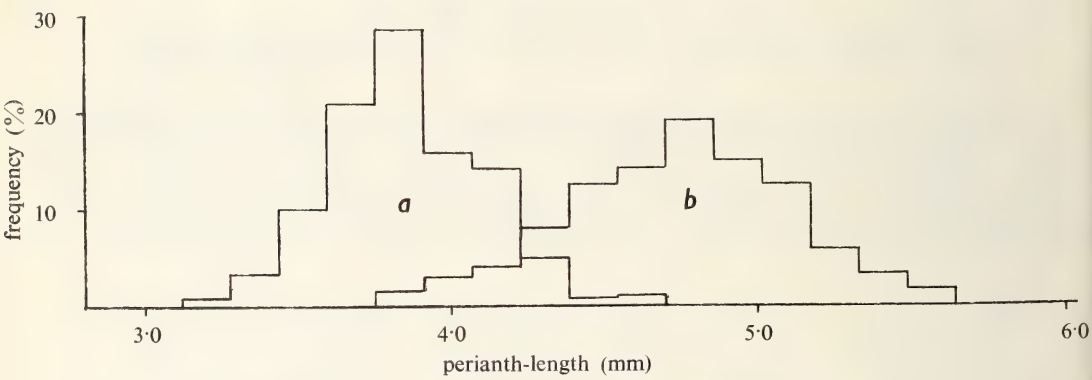


Fig. 6. Variation in perianth-length of (a) *P. aviculare* and (b) *P. boreale*.

this is significantly different from the mean (3·47) for *P. aviculare*, *sensu stricto* (see Tables 2, 6). The shortest perianth segments occur in *P. arenastrum* with $\bar{x} = 1{\cdot}78$.

Lindman (1904) mentions that *P. calcatum* has the perianth fused up to half its length whereas *P. aequale* has the perianth segments as long as the fused portion or twice as long (see Table 3). Therefore the ratio mentioned above should always be approximately 2 for *P. calcatum* whereas that for *P. aequale* would be more variable. In no population have I found this to be constantly the case and as already mentioned this ratio varies considerably, from 1·50 to 2·20, and there is variation from one flower to another on the same plant.

Vegetative Characters

The four species may be identified on leaf size and shape, although as previously pointed out these characters must be used with caution. Populations of *P. aviculare sensu lato* are extremely variable (Styles 1960); from the tables it is seen that plants of *P. rurivagum*

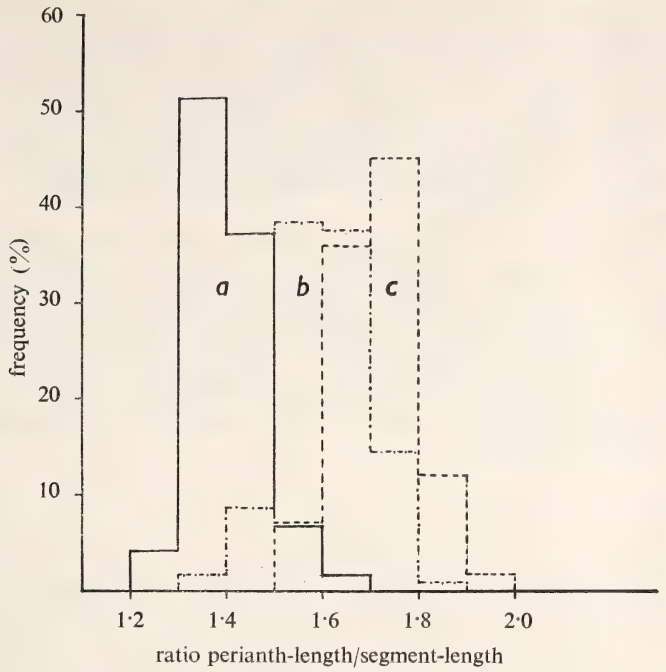


Fig. 7. Variation in the ratio perianth-length: segment-length in (a) *P. aviculare*, (b) *P. rurivagum* and (c) *P. arenastrum*.

are separable from those of *P. aviculare* on leaf breadth, ($\bar{x} = 0{\cdot}27, 0{\cdot}82$), although on this character alone they would be indistinguishable from *P. arenastrum* ($\bar{x} = 0{\cdot}28$). The leaves of *P. rurivagum* are, however, longer, $\bar{x} = 2{\cdot}78$ to $\bar{x} = 1{\cdot}35$ in *P. arenastrum*, and there would be no difficulty in recognizing either in the field. From the Index of Heterophylly for the four species it is seen in the tables that *P. arenastrum* is more homophyllous than the others, although this feature varies widely from population to population owing to factors already mentioned (p. 183).

TABLE 7.

Parameters of population of plants from Arthur's Seat, Edinburgh named *P. calcatum* ($N = 25$)

Measurements in arbitrary units, unless otherwise stated.

Parameter	$\bar{x}$	σ	*range*
Fruit length	2·98	0·58	2·40–3·40
Fruit size (l. × b.)	6·22	1·34	4·65–7·80
Persistent-perianth length	3·57	0·63	2·90–4·20
Segment length	1·96	0·12	1·70–2·60
Per. length/Seg. length	1·71	0·13	1·55–2·05
Stem leaf length (cm)	1·63	2·10	1·25–2·58
Leaf breadth (cm)	0·33	0·32	0·22–0·47
Index of heterophylly	1·36	0·21	1·20–1·44
Branch-leaf length (cm)	1·24	1·38	1·05–1·48

In Table 7 are presented data for a population from Arthur's Seat, Edinburgh (v.c. 83). Mr. B. L. Burtt tells me that they were gathered from a spot which is 'traditionally' known as a station for *P. calcatum*. The appearance of the plants in the first instance gave me no reason to suspect that they were any different from plants in other populations named *P. arenastrum*. This proved to be the case when I examined certain of the characters quantitatively. None of the significant characters mentioned by Lindman could be seen only in these plants and not in others. The same is true of samples of Lindman's own specimens obtained from Stockholm.

Some British authors have taken *P. calcatum* to have fruits which are two-sided (bi-convex) instead of normally 3-sided. During my biometrical analysis of many populations of *P. arenastrum* I discovered that a certain percentage of fruits of this species were always bi-convex, the highest being for a sample of plants collected from the sand-dunes at Berrow, Somerset with 7·72% (see Table 8). These are not constantly found on single plants, and when I raised plants from 10 of such fruits they yielded normal trigonous fruit. This atypical fruit shape is almost certainly due to their development from ovaries with two styles instead of three.

Table 8.

Percentage of bi-convex fruits in populations of *P. arenastrum*

Sample	*No.*	*% of population*
Jackdaw Lane, Oxford v.c. 23	5	2·70
Berrow v.c. 6	17	7·72
Bognor Regis v.c. 14	12	6·60
Oxford by-pass v.c. 23	8	2·20

In 1958 I obtained from the Jardin Botanique de l'État, Brussels (**BR**), six authentic specimens of Jordan's *P. microspermum*. I have analysed these biometrically in order to ascertain whether they are in fact different morphologically from small plants in populations I had named *P. arenastrum* (see Table 9).

Table 9.

Statistical data from six herbarium specimens named by Jordan *P. microspermum*

Measurements in arbitrary units, unless otherwise stated.

Parameter	$\bar{x}$	σ	*range*
Fruit length	2·94	0·35	2·70–3·40
Fruit size (l. × b.)	5·94	1·38	4·48–6·40
Persistent-perianth length	3·12	0·51	1·80–3·70
Segment length	1·70	0·12	1·60–1·90
Per. length/Seg. length	1·68	0·18	1·50–1·85
Stem-leaf length (cm)	1·02	1·81	0·94–1·35
Leaf breadth (cm)	0·15	0·25	0·10–1·28
Index of heterophylly	1·10	0·25	1·00–1·25
Branch-leaf length (cm)	0·92	1·27	0·72–1·24

Even though this sample is very small, from the data for fruit and perianth characters there is no evidence that these plants form a distinct taxon, or that the plants are any different from ones which fall in the normal range of *P. arenastrum*.

As already indicated the fruits of the four species in the *P. aviculare* aggregate differ somewhat in shape and this is, in some respects, a more useful discrimination than size. Unfortunately, however, no method of presenting this feature in quantitative terms could be devised.

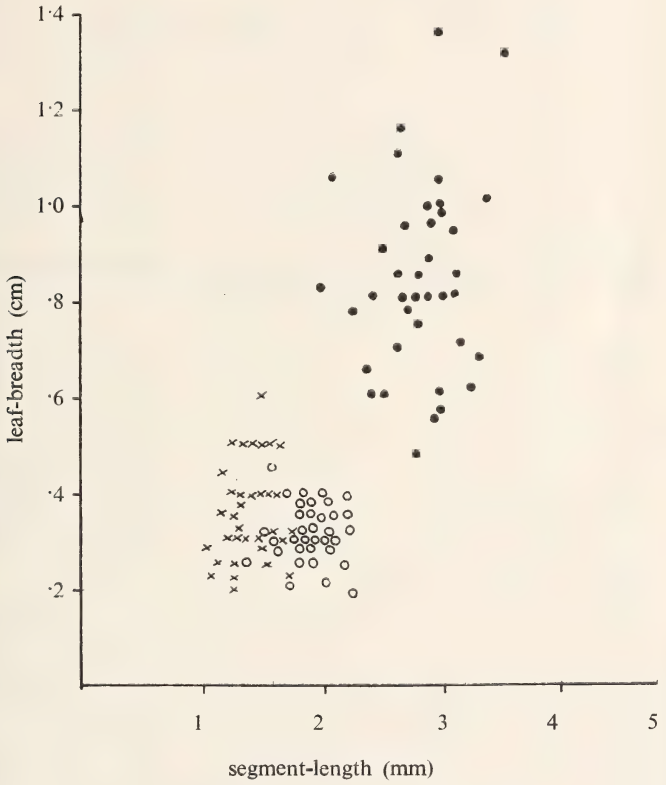


Fig. 8. Scatter diagram to show the relationship between leaf-breadth and segment-length in *P. aviculare* (solid dots), *P. arenastrum* (crosses) and *P. rurivagum* (open circles).

From Fig. 8 separation of the three species *P. aviculare*, *P. arenastrum* and *P. rurivagum* is possible using leaf breadth and perianth-segment length. Fig. 9 deals with the separation of *P. arenastrum* and *P. aviculare*, *sensu stricto* on leaf-length and the size of the fruit. *P. boreale* may be distinguished from *P. aviculare* in general by the larger size of its floral and fruiting parts, although the separation is not complete on these characters alone (Fig. 10).

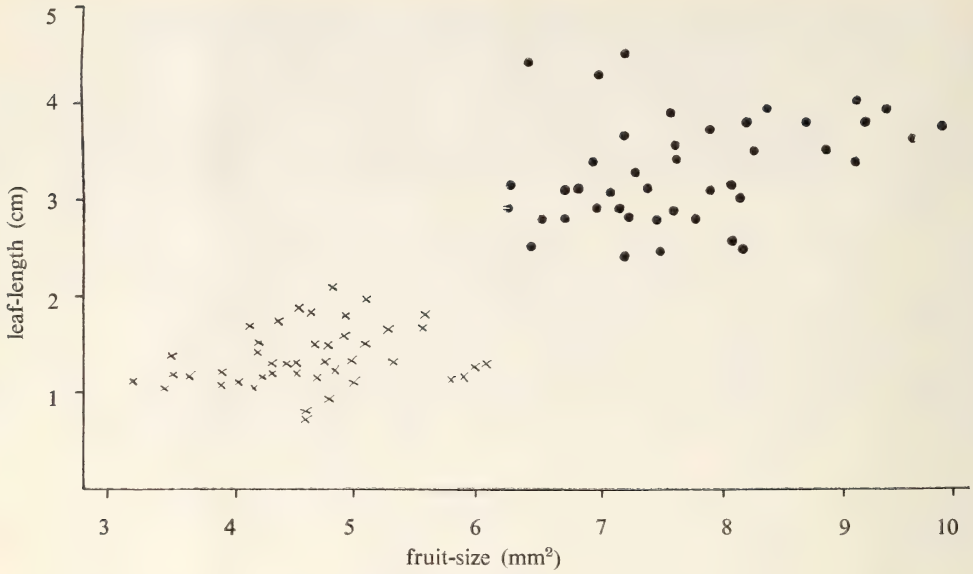


Fig. 9. Scatter diagram to show the relationship between fruit size and leaf length in *P. aviculare* (dots) and *P. arenastrum* (crosses).

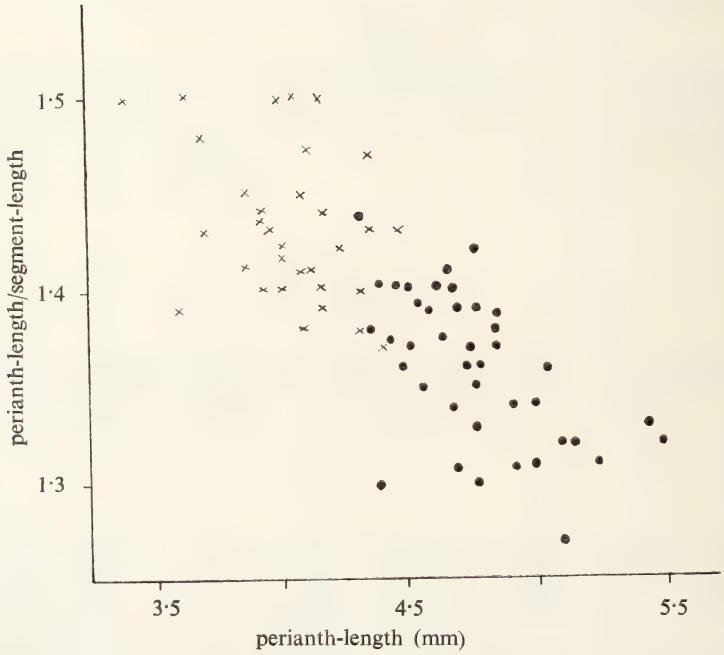


Fig. 10. Scatter diagram to show the relationship between perianth-length and the ratio perianth-length : segment-length in *P. aviculare* (crosses) and *P. boreale* (dots).

TABLE 10. Chromosome records in the section *Polygonum* (all diploid members, 2*n*).

Species	*Jaretzky (1928) (Germany)*	*A. and D. Löve (1942b) (Scandinavia)*	*Andersson (1942, 1948) (Scandinavia)*	*Pólya (1948) (Hungary)*	*A. and D. Löve (1956a and b) (Canada & Iceland)*	*Pauvels (1959) (Belgium)*	*Scholz (1960) (Germany)*	*Styles (Great Britain)*
P. aviculare, sensu lato	40	40	40, 60	40	20, 40, 60	40, 60	40, 60	40, 60
P. aviculare, sensu stricto (*P. heterophyllum*)		40	60		60	60	60	60
P. arenastrum (*P. aequale*)			40		40	40	40	40
P. rurivagum					20		60	60
P. boreale					60 (Iceland and Canada)			40
P. littorale					60			
P. calcatum					40		40	
P. raii					60	40		40 (also Norway)
P. maritimum	20 (Rome)							20 (also Portugal and France)
P. oxyspermum					80			40 Denmark
P. neglectum					40			

4. Cytology and breeding systems

Chromosome Numbers

Results of previous cytological investigations on *Polygonum aviculare* and its allies are summarized in Table 10. Jaretzky (1928) confined his work to six species which he apparently obtained from botanic gardens rather than natural habitats. As he gives no details of the morphology of the plants he studied the value of his observations is very limited. The tetraploid number for his species *P. monspeliense* Pers. is surprising, since the type of this plant is easily referred to *P. aviculare*, *sensu stricto*, and might have been expected to be hexaploid. The tetraploid number is given for a form of *P. aviculare*, to which, he states, he is unable to give a name as he is not conversant with the very many varieties of this species.

A. & D. Löve (1942a) working in Sweden record the tetraploid number for plants labelled '*P. aviculare*' with a remark that the specimens studied seemed to be nearer *P. heterophyllum* Lindm. In a later publication (1956), however, they state that the identification of the voucher specimens was erroneous since they belong to *P. neglectum* Bess. As this species has never been mentioned in any Scandinavian Flora its existence here is considered most doubtful. Andersson (in A. & D. Löve 1942b) published the numbers $2n = 40$, 60 for plants in *Polygonum aviculare, sensu lato* and later in A. & D. Löve (1948) gave the former number for plants identified as *P. aequale* and the latter for plants approaching *P. heterophyllum*.

Both Pólya (1948) and Pauvels (1959) have published results consistent with these findings, and the latter also discovered *P. raii* new to Belgium with a chromosome number of $2n = 40$.

The most important work published on the cytogenetic and taxonomic variability within and between species of *Polygonum* is that by A. & D. Löve (1956a) on the Icelandic flora and (1956b) on plants in eastern North America. As will be seen from the table several of their chromosome counts do not agree with my own or those of other workers in this field. Perhaps the most interesting is the fact that they record the diploid number of $2n = 20$ for *P. rurivagum* with the other species in the aggregate forming a polyploid series with an octoploid of $2n = 80$. The littoral species *P. raii* is also given as hexaploid with $2n = 60$, as is *P. boreale* from Iceland. In both these reports the nomenclature is confused and will be discussed later.

Very recently Scholz (1960) has published chromosome counts substantiating my own records.

Cytological investigations on the British taxa recognised in *P. aviculare*, *sensu lato* were carried out on germinating seedlings, fruits having been gathered from naturally occurring populations, widely distributed ecologically and geographically. Plants of the littoral species *P. raii*, *P. maritimum* and *P. oxyspermum* have been examined from only a limited number of populations. This was due mainly to the fact that, in the case of the first two, the species are rare or very rare, and in the last because authentic material from stations abroad was not forthcoming, although the greatest possible effort was made to obtain viable seed from several north-European and Scandinavian countries. Great difficulties were experienced in obtaining a sufficient germination, and a method following that published by Justice (1941) was finally used to raise the germination rate to about 60%.

A method of obtaining metaphase chromosome counts was developed from squash techniques following Darlington & La Cour (1947). Translucent root-tips were treated in 1% colchicine or *p*-dichlorobenzene for 12 to 24 hours and chromosomes stained using the Feulgen technique, with 6–8 minutes hydrolysis. The chromosomes are extremely small with a slight variation in size from 0·8–1·2 μ. Lists of the British taxa with their chromosome numbers are given in Tables 11 and 12.

The diploid number $2n = 20$, given by A. & D. Löve for *P. rurivagum*, was not found in any British populations of this species which all proved to be hexaploid with $2n = 60$. This agrees with the results of Scholz (1960). As the British plants agree very well morpho-

TABLE 11.

Chromosome records of species recognized in *P. aviculare, sensu lato* in Britain.

Species	*Locality*	*v.c.*	*Chromosome number 2n*
P. aviculare, sensu stricto	Foreshore shingle, Caernarvon	49	60
	Farmyard, University Farm, Wytham	22	60
	Waste ground, building site, Brill	24	60
	Entrance to gateway, Chedworth, Glos.	33	60
P. arenastrum	Between flagstones, northern by-pass, Oxford	23	40
	Sand dune, path to sea, Berrow, Somerset	6	40
	Rough cart track, Bodmin, Cornwall	2	40
P. rurivagum	Barley stubble, Gog Magog Hill, Cambs.	29	60
	Chalky cornfield, Seaford, Sussex	14	60
	Bean field, University Farm, Wytham	22	60
P. boreale	Shetland Islands	112	40

TABLE 12

Chromosome records for British and European plants of *P. maritimum*, *P. raii* and *P. oxyspermum*

Species	*Locality*	*Origin*	*Chromosome number 2n*
P. maritimum	Sea shore, Herm	Channel Isles	20
	Sea shore, Figueira da Föz	Portugal	20
	Banyuls, Pyrenees	S. France	20
P. raii	Shingle, West Town, Hayling Island, Hants. (v.c. 11)	England	40
	Sandy beach, Maenporth, Cornwall (v.c. 2)	England	40
	Sands, Tromsoe Island	Norway	40
P. oxyspermum	Leudrig Strait, Laeso, Copenhagen	Denmark	40

logically with specimens of the same name from Jordan's herbarium at Lyon it can only be supposed that the Canadian plant is something other than *P. rurivagum* Jord. and perhaps indigenous there. Plants of *P. arenastrum* and *P. aviculare* from this country were consistently found to be tetraploid and hexaploid respectively. Specimens from populations of varying morphology of the two species were studied and counts were made on as many root tips as possible per population. Plants of *P. boreale* obtained from the Shetland Isles through the courtesy of Mr. W. Scott were consistently found to be tetraploid with $2n = 40$. This observation does not agree with that of A. & D. Löve. The identification of their plants is however suspect. Among weedy species of *Polygonum*, therefore, there do not appear to be any intraspecific chromosome races.

Diploid ($2n = 20$) and tetraploid ($2n = 40$) numbers were found in *P. maritimum* and *P. raii* respectively in both British and European populations whilst a single population of *P. oxyspermum* from Denmark was also tetraploid.

The number for *P. maritimum* thus agrees with the observations of Jaretzky on plants from the Mediterranean. The number for *P. raii* and *P. oxyspermum* differ from the $2n = 60$ and 80 respectively given by A. & D. Löve. These authors mention that eastern Canadian plants of *P. raii* come nearer the race named subsp. *norvegicum* Sam. which is stated to be more northern, having blue-green foliage, shorter internodes, flowers which are white rather than pink or greenish white, and somewhat broader achenes. They suggest that there may be two races of differing chromosome numbers : a British–west-European–Channel race which is tetraploid and a northern Scandinavian and east Canadian race which is hexaploid. My own counts on Norwegian plants do not, however, support this view. It is possible that the Canadian populations do differ from the European ones in chromosome number; the same may be true of *P. oxyspermum*, but my efforts to obtain viable fruits of these species from several Canadian botanical institutions were unsuccessful.

Both Andersson and A. & D. Löve record $2n = 50$ for supposed hybrids between *P. aviculare*, *sensu stricto* and *P. arenastrum* but I have never met with a plant I suspected to be a hybrid either from its morphology or its chromosomes.

Breeding Systems

P. aviculare agg. and the other species of this section are inbreeding and the flowers appear to be always self-fertilized. This mechanism leads to difficulties in their taxonomy. On many occasions populations have been carefully observed in the field, but no insect visitors have been recorded. The flowers are scentless and their inconspicuous size, colour, and position on the plant show no adaptations to out-breeding. Frequently in the course of emasculation experiments unopened buds were found to contain two or three stamens already dehisced, and many flowers especially at the ends of the older branches open when still enclosed in the ochreae. They then behave as though they were cleistogamous.

My own attempts to obtain hybrids between the various species in the aggregate were not conclusive, due mainly to technical difficulties. Such results as were obtained suggested that hybridity is extremely rare among species of this group.

A. and D. Löve (1956b) have pointed out that a low degree of apomixis cannot be ruled out. I could not verify this suggestion but I am of the opinion that it does not occur in this group. It is in any case extremely rare among annual weeds (Warburg 1960). The condition whereby the fruits formed in late autumn become swollen and much exserted from the persistent perianth does not so far as I am able to tell have anything to do with apomixis. The embryos and endosperm of these fruits appear to be almost twice as large as normal and they are not as A. & D. Löve state ' inflated and mostly empty.' Samples of these swollen fruits from several populations were grown in the experimental garden at Oxford but the plants raised from them were normal in every way. I can offer no explanation for this abnormal development, and I know of no cases of similar developments among other genera.

The possible origin of these species in the *P. aviculare* aggregate presents an interesting problem. Many plants are known to have spread from their original areas through the induction of polyploidy (*Poa* spp., *Paeonia* spp.). It is interesting to note that the mediterranean species *P. maritimum* never behaves as a weed and only survives in a natural (littoral) habitat. It is thought that weedy species have been derived through hybridization and allopolyploidy of this diploid with one or more unknown species. The place of origin of the weedy species of *Polygonum* is, however, uncertain. It is interesting to note that certain North American diploid species (e.g. *P. achoreum* Blake, *P. buxiforme* Small and *P. prolificum* (Small) Robins) are also confined to maritime zones such as sand-dunes and salt-marshes.

5. Taxonomic revision and discussion

From the morphological and cytological evidence presented it is clear that the differences between the groups which can be delimited as species within *P. aviculare*, *sensu lato* are relatively clear-cut and well defined. This is perhaps surprising, considering the chaos and uncertainty which exist in many floras regarding the number of taxa which can be recognized in this group. It is now proposed to discuss very briefly the chief causes of difficulty in the taxonomy of *P. aviculare*, and the reasons for calling the groups species. Finally an account of the taxonomy of the group as it now stands after this revision is presented. The synonomy is complete except for some varietal names, which, however, have not been used in accounts of *Polygonum* in the British flora.

I have found the fruit and persistent perianth the most useful and stable criteria in the group and they are the most reliable for classification. There is, however, wide variation in size even on a single plant, and the extent of this can only be ascertained by extensive measurements. The fruits are inconspicuous and concealed in the more evident vegetative parts of the plant. Old plants of *P. aviculare*, *sensu lato* are especially difficult to identify since they are frequently reduced to bare stems by the dropping off of the leaves. All species therefore tend to have the same facies and the fruits are then the only guide.

Care must also be exercised with specimens gathered in the late autumn because of the enlargement of the fruit, a condition mentioned previously. Maritime forms of *P. aviculare* in this condition have frequently been called *P. raii*.

A. & D. Löve mention that the recognition of the tetraploid *P. arenastrum* and hexaploid *P. aviculare* as species is ' beyond discussion.' I am in full agreement with these authors on this point. Not only are they morphologically distinct on a number of reliable taxonomic characters but the numerical chromosome differences result in an effective sterility barrier. Hybrids between them appear to be extremely rare in nature. The two species have also different ecological niches, though some intermingling does occur.

P. rurivagum has the same chromosome number as *P. aviculare* but my hybridization experiments have shown that there is probably a sterility barrier. Morphologically the plant differs from the other taxa in a number of characters. The extreme narrowness of the leaves, the longer ochreae and short perianth serve to distinguish it from typical forms of *P. aviculare*, *sensu stricto*. Both occur in cultivated fields but remain distinct. *P. rurivagum* seems, also, to be confined to basic soils in this country and west Europe and has a limited distribution.

Plants of *P. boreale* are among the most robust I have found in the aggregate. This is surprising since it is the most northerly of all the species. *P. boreale* is separable from all the others by the large size of the fruit and perianth, and is recognized as a species mainly because it differs in having the very evidently petiolate leaves and the tetraploid chromosome number.

P. arenastrum is perhaps the most distinct morphologically of all the species in the aggregate. *P. aviculare* and *P. rurivagum* are probably closely related. *P. boreale*, though tetraploid, exhibits many of the features of *P. aviculare*. *P. maritimum* and *P. raii* are less variable than the weedy species in the group; this is possibly due to the fact that they are

always confined to littoral habitats. The differences between them are well-marked. Hybrids of these have not, so far as I can trace, ever been recorded.

1. P. AVICULARE L., Spec. Pl., 362–3 (1753).

P. centinodium Lam., Fl. Francaise **3**: 237–8 (1778). nom. illegit.

P. erectum Roth., Beitr. Bot. **2**: 131 (1783) nom. illegit.

P. monspeliense Pers., Synop. Plant. 439 (1805).

P. aviculare var. *vulgare* Desv., Obs. Pl. Angers 98 (1818).

P. aviculare var. *littorale* Koch, Syn. Fl. Germ. Helv. 618 (1837).

P. aviculare var. *polycnemiforme* Lecoq & Lamotte, Catal. Rais. Pl. 322 (1848).

P. provinciale K. Koch, Linnaea **22**: 204 (1849).

P. aviculare β *erectum* Ledeb., Fl. Ross. **3**: 532 (1850).

P. aviculare δ *vegetum* Ledeb., Fl. Ross. **3**: 532 (1850).

P. aviculare var. *angustissimum* Meisn. in DC. Prodr. **14**: 98 (1856).

P. denudatum (Desv.) Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. agrestinum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. polycnemiforme (Lecoq & Lamotte) Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. humifusum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857) nom. illegit.

P. heterophyllum Lindm., Svensk Bot. Tidskr. **6**: 690–1 (1912) nom. illegit.

P. aviculare subsp. *heterophyllum* (Lindm.) Aschers. & Graebn., Synops. Mitteleur Fl. **4**: 848 (1913).

P. aviculare subsp. *rectum* Chrtek, Preslia **28**: 365 (1956).

P. aviculare subsp. *monspeliense* (Pers.) Chrtek, Preslia **28**: 365 (1956).

P. rectum (Chrtek) Scholz, Ber. Deutsch. Bot. Ges. **72**: 65–66 (1959).

[*P. littorale* auct.].

Annual. Plant robust, erect, prostrate or spreading, heterophyllous when young; stems up to 2 m long. Leaves lanceolate to ovate-lanceolate, 2·5–5 cm × 1·5 cm, subacute, those of the main stems 2–3 times as long as those of the flowering branches: petioles short (up to 2 mm) or almost absent, included in the ochreae. Ochreae silvery when young, *c.* 6 mm, becoming lacerate with age. Inflorescence 3–6–flowered. Perianth-segments united at the base only, distinctly veined and overlapping in fruit, pink, purple or white at the edges. Stamens (5)–8–(9). Fruit 2·5–3·5 mm, half as broad, punctate, dull brown, with three ± equal concave sides, (rarely 4-sided), included or sometimes slightly projecting from the persistent perianth. Flowering the whole season, from July to November.

Holotype in the Linnean Herbarium (**LINN**), London.

2. P. ARENASTRUM Bor., Fl. Centre France, Ed. 3, **2**: 559 (1857).

P. microspermum Jord. ex Bor., Fl. Centre France, Ed. 3, **2**: 560 (1857).

P. calcatum Lindm., Bot. Not. 139 (1904).

P. aequale Lindm., Svensk Bot. Tidskr. **6**: 692 (1912).

P. aviculare subsp. *aequale* (Lindm.) Aschers. & Graebn., Synops. Mitteleur. Fl. **4**: 848 (1913).

P. aviculare subsp. *calcatum* (Lindm.) Thell., Ber. Schweiz. Bot. Ges. **22**: 120 (1913).

P. × *lindmanii* Druce Rep. Bot. Soc. Exch. Cl. **8**: 873 (1928).

[*P. aviculare* subsp. *aviculare sensu* Chrtek, Preslia **28**: 366. (1956)].

[*P. aviculare* auct. (Komarov 1936, Lembke 1948, A. & D. Löve 1956a & b) non L.].

Annual. Plant usually 5–50 cm, forming a dense prostrate mat or sometimes erect. Leaves elliptic or elliptic-lanceolate, up to 2 cm long and 0·5 cm wide, those of the main stem and flowering branches ± equal in size, subsessile. In old specimens the leaves are often more or less crowded towards the ends of the branches. Ochreae short, *c.* 4 mm. Inflorescence 2–3-flowered. Flowers smaller than in *P. aviculare*; stamens (4)–5–(8). Segments of the persistent perianth united for up to half their length, greenish-white or pink. Fruit 1·5–2·5 mm, dull, but sometimes shining on the edges, with two convex and one narrowly concave sides, (rarely with two sides concave and one convex), or sometimes biconvex, brown to black, not or only a little exserted from the persistent perianth. Flowers July to November.

Holotype not traced (but see later).

The taxonomy of these two species is best considered together both from the point of view of nomenclature and their geographical distribution.

The nomenclatural problems of the two species are most involved. In splitting the Linnean *P. aviculare*, Lindman (1912), according to the *International Code of Botanical Nomenclature*, should have kept the latter binomial for one of his segregated species. Instead, however, he published two new names, *P. heterophyllum* and *P. aequale*, giving *P. aviculare* L. *pro parte* under both. In trying to equate *P. aviculare* with one of these names in order to conform with the accepted rules, some authors (Komarov 1936, Lembke 1948, Chrtek 1956 and A. & D. Löve 1956) have given the name *P. aviculare* to *P. aequale*, whereas others (Moss 1914, Tutin 1952, Dandy 1958 and Rechinger (in Hegi 1958)) have given it to *P. heterophyllum*. Those authors who take *P. aequale* Lindm. to be *P. aviculare* L., retain *P. heterophyllum* as the name for the other species. This name, however, is illegitimate since Lindman himself includes under it subsp. *rurivagum* based on the earlier *P. rurivagum* Jordan ex Boreau. A. & D. Löve and Chrtek give no reasons for retaining *P. aviculare* L. as the correct name for *P. arenastrum*.

In the Linnean herbarium under *P. aviculare* there are 5 specimens but only one bears the name *P. aviculare* in Linnaeus' handwriting. It is a large leaved heterophyllous plant with fruit *c.* 3 mm and a persistent perianth with segments divided almost to the base. This is *P. heterophyllum* Lindm. and the Linnean name must therefore stand for it. The specimen falls well within the range of variation of British and west-European plants that I call *P. aviculare*, *sensu stricto*. Since the phrase-name in *Hortus Cliffortianus* is not cited by Linnaeus in *Species Plantarum*, this specimen may be regarded as the type. It seems better to retain this well-known name since it has been used correctly by many British and European botanists. *P. monspeliense* is the correct name if *P. aviculare* is rejected, since *P. centinodium* is illegitimate.

The name *P. aequale* Lindm. cannot be retained because earlier names are available. I have obtained specimens of *P. aviculare*, *sensu lato*, from Boreau's herbarium at Angers, but unfortunately there is no specimen here which can be taken as the type of his *P. arenastrum*. Plants however, collected and labelled as this (in what is taken to be Boreau's handwriting) at a date later than 1857 fall very well into the range of variation exhibited by British plants. There thus seems no doubt of Boreau's intentions as all specimens labelled *P. arenastrum* in his herbarium belong to the same species. I propose therefore to use this name, *P. arenastrum* Bor., for the taxon usually called *P. aequale* Lindm. *P. arenastrum* was frequently used by botanists in this country prior to the publication of the name *P. aequale* by Lindman either as a specific name or as a variety of *P. aviculare*.

Although the names *P. arenastrum* and *P. microspermum* were published at the same time by Boreau (1857) I retain the former in that it refers to plants with broader leaves which are the commoner form. The two names have not been combined previously so far as I am able to discover.

Scholz (1959) rejects the name *P. aviculare* L. on the grounds that it is a *nomen ambiguum* and replaces *P. heterophyllum* by *P. monspeliense*. As already mentioned, the latter is, in fact, the correct name for this species if *P. aviculare* is not used. As I have

been able to typify the Linnean species, there is no reason why the name should not be retained.

I do not at the present time propose to recognize any infraspecific categories within the two taxa. As is well known in plants where a high degree of inbreeding is prevalent, homogeneous populations occur which differ only slightly from other populations. This has often led to the description of numerous meaningless microspecies in *Polygonum* as in other common weed species. Both *P. aviculare* and *P. arenastrum* are very polymorphic and are markedly affected by habitat conditions. They also show great genetic plasticity in all their morphological characters. Until more controlled breeding experiments can be carried out it is perhaps best to consider them as two variable groups with the status of species in the 'Linnean' sense.

Ecotypic forms of *P. arenastrum* are recognizable and these show a certain degree of constancy in habitats of the same type. These showed some morphological differences when their offspring were raised in the experimental garden.

I have found that *P. calcatum* Lindm. cannot be maintained as a distinct taxon in this country at least. The differences between it and *P. aequale* are not clearly stated by Lindman (1904, 1912) and those attributed to it by Moss (1914) and other authors have not been found sufficiently constant to warrant its maintenance as a species or even subspecies (see p. 196 above and Table 7). Professor H. Nannfeldt of Uppsala (*in litt.*) states that in Sweden also many botanists agree that this plant is not a distinct species.

It is also suggested that *P. microspermum* Jord. is not a distinct taxon. Measurements of a small number of plants named by Jordan as this have been obtained from several European herbaria. These plants were analysed but were found to be inseparable from forms of *P. arenastrum*. In this country narrow-leaved plants with small fruits have been given this name. Small-fruited forms are biometrically inseparable from the overall variation pattern of this character in *P. arenastrum* (see Table 9).

A study of the type of Besser's *P. neglectum* from Kiev (**KW**) shows that it is a different form from any met with in west Europe. The specimen is a poor one but agrees fairly well with the figure given by Lembke (1948) from Polish specimens. It has proved impossible to obtain an idea of the morphological range of this species owing to its being very poorly represented in European herbaria, and hopelessly confused in the literature. It is probable that it has a more easterly distribution and could have been introduced into Canada.

Geographical Distribution

British Isles

Both species are very common as weeds throughout the whole of this country. Druce (1932) records *P. aviculare, sensu lato*, for every vice-county in Great Britain, mentioning that the common plant is *P. heterophyllum* Lindm.

I have seen specimens of both species in British herbaria from every vice-county; I have also received many records besides from the BSBI Distribution Maps Scheme.

It is clear that the two species have different ecological preferences. The estimated percentages in Table 13 must be regarded as only a very rough guide since not all habitats fall clearly into any of the categories listed. These results were obtained from data compiled during my field work on approximately 200 habitats in Great Britain. The two species are often found growing together forming mixed populations. *P. aviculare* occurs most commonly in cultivated areas, cornfields, etc. (87%), whereas *P. arenastrum* tends to be found at the edges of fields, in bare patches, and on paths and roadsides (82%). It is on the whole a smaller plant, and most frequently prostrate, which seems to account for the ecological differences. *P. arenastrum* appears to be able to tolerate a greater amount of treading and trampling than *P. aviculare*. The former has been observed on footpaths which were trampled on daily by human beings and farm animals, but the plants were not eliminated. In maritime areas, I have noticed too that the two species occur in about the same frequency, but again *P. arenastrum* survives in places where trampling is most severe.

TABLE 13.
Ecological preferences of *P. aviculare* and *P. arenastrum*.

Habitat	P. aviculare	P. arenastrum
Cornfields	66%	10%
Other cultivated fields e.g. potato fields, *Brassica* crops, legumes	21%	34%
Tracks and roadsides (pavements, metalled streets, footpaths)	1%	36%
Waste ground (farmyards, building sites, etc.)	4%	12%
Maritime habitats	6%	6%
Other habitats (gardens, etc.)	2%	2%

On the whole the latter species thrives in drier situations than *P. aviculare*, as on gravel drives, roadsides, pavements and tracks.

Foreign Distribution

P. aviculare agg. has a world-wide distribution except for the Antarctic, and it is presumed that the two species *P. aviculare* and *P. arenastrum* have similar geographical distributions though with some ecological differences. I have seen herbarium specimens of both from most European countries and there are records for many parts of Asia. *P. plebejum* is, however, said to replace *P. aviculare* in some parts of India, Ceylon and parts of Africa. *P. aviculare* and *P. arenastrum* are now well established in N. America, but detailed information on their occurrence in S. America and Australasia is lacking.

3. P. RURIVAGUM Jord. ex Bor., Fl. Centre de la France, Ed. 3, **2**: 560 (1857).

P. aviculare var. *rurivagum* (Jord. ex Bor.) Gentil, Inv. pl. Sarthe, 218 (1892).

P. heterophyllum subsp. *rurivagum* (Jord. ex Bor.) Lindm., Svensk Bot. Tidskr. **6**: 691 (1912).

Annual. Plant very slender, flexuous, suberect, seldom more than 30 cm, heterophyllous. Leaves linear-lanceolate to linear, acute, 1·5–3·5 cm long and 0·5–1·4 mm wide. Ochreae brownish-red below, *c.* 10 mm long, longer than in related species. Inflorescence 1-2-flowered, seldom more. Perianth segments narrow, shorter than *P. aviculare*, reddish, not overlapping. Fruit 2·5–3·5 mm × 1·5–2 mm, exserted from the persistent perianth, with 3 concave sides, scarcely shining. Fruit as long as, but narrower than that of *P. aviculare*. Flowers from August to November.

Holotype not seen (but see below).

There are no Jordan specimens of *P. rurivagum* in the Boreau herbarium, but there are others, the collector of which is unknown (the handwriting is evidently not that of Jordan). I have, however, seen three specimens of the latter from his own collections at Lyon gathered by himself in 1860. This is three years after the publication of Boreau's *Flore du Centre de la France* (Ed. 3). As the specimens in the two herbaria are the same plant I propose to keep the name *P. rurivagum* for this species.

Geographical Distribution

British Isles

This species is not well known, and is probably overlooked in Great Britain. Its distribution needs further investigation. I experienced considerable difficulty in tracing populations of this plant and have found very few records of it.

P. rurivagum occurs most frequently in cornfields and cultivated places, and so far as is known, only on chalky or other light soils. All my records are from the south and south-west of England. It is easily recognizable from *P. aviculare*, with which it sometimes grows, by its slender and flexuous habit, very narrow acute leaves and long reddish brown ochreae.

I have gathered material myself from vice-countries 8, 13, 14, 22 and 29, and further localities have been provided by the BSBI Plant Distribution Maps Scheme or herbarium specimens from v.c. 7, 9, 11, 16, 17, 18, 24, 30, 31, 54 and 58. There are specimens from all of these except 54 and 58 where the determinations must remain doubtful.

Moss (1914) gives the plant's further distribution as Leicestershire, Durham, Dumbarton and Perthshire. These records again need confirmation.

Foreign Distribution

The species was first recorded from France by Jordan. I have seen many French specimens and there are duplicates of these in the herbarium at Munich (**M**). It will probably prove much more common with further searching and will no doubt be found to occur in most western European countries.

As stated above, A. & D. Löve record *P. rurivagum* from Canada with the diploid chromosome number ($2n = 20$). The achenes of this plant are stated to be small, from 1–1·5 (rarely up to 2 mm) long, whilst British plants of this species have fruits which are as long as in *P. aviculare* but narrower. I have sent British specimens of this species to Professor A. Löve for examination and he agrees that they differ from the Canadian plants to which he gives this name.

4. P. BOREALE (Lge.) Small, Bull. Torr. Bot. Club **21**: 479 (1894).

P. aviculare var. *boreale* Lge., Medd. om Groenl. **3**: 105 (1880).

[*P. islandicum* Meisn. ex Small, Mem. Dept. Bot. Columbia Coll. **1**: 108, et tab. 41. (1895) nom. illegit.].

P. heterophyllum var *boreale* (Lge.) Lindm., Svensk Bot. Tidskr. **6**: 691 (1912).

P. heterophyllum subsp. *boreale* (Lge.) A. & D. Löve, Acta Hort. Gotoburgensis **20**: 216 (1956).

Annual. Plant up to 100 cm, erect or suberect, simple or sparingly branched, markedly heterophyllous. Stem leaves oblong-obovate to spathulate, the lower blades 3–5 cm long and 0·5–1·8 cm broad; petioles 4–8 mm, projecting from the ochreae. Ochreae 5–8 mm, silvery or brownish, only slightly lacerate. Flowers large, *c.* 4–5 mm. Petaloid margins of perianth segments broader than those of *P. aviculare* L., pinkish or white. Segments inclined to open in fruit, longer than in the other species, *c.* 2·5–3·0 mm. Fruit triquetrous, punctate, dull, light or dark brown, 3·5–4·5 mm × *c.* 2·5 mm broad, with 3 broadly concave sides (sometimes 4), included, or with the apex just protruding from the lax perianth segments. Flowers June to October.

This species has the largest fruit yet observed in plants of the *Polygonum aviculare* aggregate, and has flowers approaching *P. raii* and *P. maritimum* in size.

Holotype, Botanical Museum, Copenhagen, Denmark (**C**) Legit J. Lange, Greenland, 1880.

Geographical Distribution

British Isles

This species is new to the British Isles, although Druce (1912) used the name *P. aviculare* var. *boreale* for plants gathered at Loch Leven, Fife (v.c. 85). There was, however, at the time great confusion between this variety and the plant then known as *P. littorale*. It is at present only known from the Shetlands and Orkney Islands. Druce (1922) records a forma *grandiflora* [*sic*] of *P. aviculare* var. *littorale* from Uyea Sound, Shetland, and it was from a study of this specimen and others in the Druce Herbarium, Oxford, that I decided to investigate the Shetland populations further.

Foreign Distribution

I have seen harbarium specimens of this species from Iceland, Faroes, Greenland and Northern Scandinavia.

A. & D. Löve's records for northern Canada need to be checked but may well be correct, since the description of the Canadian plants studied agrees with European and Greenland plants but differs from their earlier description of plants from Iceland.

Small (1894), after raising Lange's variety *boreale* of *P. aviculare* to full specific rank, published the name *P. islandicum* in 1895. It is apparent that after having published the first of the binomials he received a sheet of *P. boreale* from De Candolle's herbarium at Geneva collected from Iceland in 1866 by M. E. Jardin labelled by Meisner as *P. islandicum* The latter author, however, never published this name and it is therefore not valid. The name *P. boreale* (Lge.) Small must be retained for this species. Further work is needed to establish the extent of the distribution of *P. boreale* in northern Scotland.

5. P. RAII Bab., Trans. Linn. Soc. Lond. **17**: 458–9 (1836).

P. dubium Deakin, Florig. Brit. **2**: 576 et tab. 656 (1845), nom. illegit.

P. maritimum β *raii* (Bab.) Lloyd, Fl. Ouest France, ed. **2**: 430 (1868).

[*P. littorale sensu* Gren. & Godr., Fl. de France **3**: 51–2 (1855), non Link].

P. raii subsp. *norvegicum* Sam., Acta Hort Bergiani **11**: 72 (1931).

[*P. robertii* auct.].

Annual. Plant prostrate, glabrous, sometimes glaucous and slightly fleshy, 10–100 cm. Stems more or less woody at the base. Leaves 1–3·5 cm, elliptic-lanceolate to linear-lanceolate, usually flat, though the young ones sometimes appear revolute. Ochreae shorter than upper internodes, laciniate, *c.* 5 mm, hyaline and silvery in the upper part with 3–6 unbranched veins. Inflorescence 2–6-flowered. Flowers large, pink or white. Perianth segments *c.* 3 mm, with broad petaloid margins. Stamens 8. Fruit 5–6 mm long × 3–3·5 mm broad, light brown, flattened, smooth, shining, much exceeding the persistent perianth. Flowers from June to September.

Holotype in the University Herbarium, Cambridge (**CGE**). Legit Borrer. Sands between Marazion and Penzance, Cornwall, 1836.

Geographical Distribution

British Isles

P. raii is an interesting Atlantic species which formerly occurred fairly frequently on sands and shingle in maritime areas just above the high tide mark around the coasts of Britain (see Fig. 11).

Associated species growing with *P. raii* at Freshwater Bay, Pembrokeshire (v.c. 45) were *Euphorbia paralias*, *E. portlandica*, *Salsola kali*, *Cakile maritima*, *Ammophila arenaria* and *Chenopodium* spp.

From records received by the BSBI Distribution Maps Scheme there is evidence that it is decreasing in frequency in this country. I have searched for it, without success, in many of the localities in Wales and in the west and south of England where it has been recorded in the literature as common. The plant was very local in two areas (Hayling Island, S. Hants (v.c. 11), and Maenporth, Cornwall (v.c. 1)). It was formerly common locally along the coasts of south England, Wales, west Scotland and the Hebrides and on the east from Durham to Angus. It has been recorded from nearly all the coastal counties in Ireland. Druce gives the following vice-county records of the species in the British Isles.

S, 1–6, 9–11, 13–16, 18, 34, 37, 41, 44–46, 48–52, 53, 54, 58–60, 66–76, 82, 83, 85, 87, 90, 97–99, 100–104, 110 H, 1–3, 5–6, 9, 12, 15–16, 20–22, 27, 31, 34, 35, 38–40,

I have added the plant new to v.c. 106, where it was recorded by Marshall at Ballintore, E. Ross in 1910, but named by him *P. aviculare* var. *littorale* Link (**BM**). I have seen specimens from all the above vice-counties except 34, 37, 53 and 54. The last two records are suspect. Vice-county 37 is inland (Worcs.), but the occurrence of *P. raii* is possible since the river Severn is tidal along its lower reaches.

Foreign Distribution

Moss (1914) gives the extra-British distribution of *P. raii* as southern Scandinavia, Denmark, Germany, Belgium, France, northern Russia, Spain, Italy and the west coast of North America. Specimens are extant from the following; north-west France, Belgium, north Germany (Heligoland) (Scholz 1957), Norway and Denmark. Dr. Bengt Pettersson tells me (*in litt.*) that *P. raii* does not occur in Sweden where it is replaced by *P. oxyspermum*. Specimens tentatively named *R. raii* from Portugal by Dr. A. R. Pinto da Silva were *P. maritimum* (atypical). I have been unable to trace specimens or records for Spain and Italy, and, as the species appears to have an exclusively Atlantic distribution, I regard them as having been based on misidentified material.



Fig. 11. Distribution in Europe of *P. maritimum* (solid line), *P. raii* (dashes) and *P. oxyspermum* (dots).

P. raii is recorded from northern Russia by Komarov (1936). The name *P. raii* is given in certain east-European Floras, Savălescu (1952), Stoyanoff & Stefanoff (1933) for plants collected around the Black Sea. I have seen specimens named *P. raii* from this area. They are morphologically very close to west-European plants to which I give this name and I am investigating them further. Chrtek (1960) has described two new species in the group from this area. One of these also seems to be very close to *P. raii*.

The north American records present a problem. Many recent Floras and Manuals of selected areas of this continent, *e.g.* Fernald (1950), Gleason (1952) and Roland (1947), give accounts of it but it appears that it may be a different cytological race. I have seen specimens in the Kew herbarium (**K**) which are undoubtedly *P. raii*.

I can find no basis for retaining Samuelsson's subspecies *norvegicum* (1931) of *P. raii*. The differences attributed to it are small. It differs from the type in having more flowers in the inflorescence and narrower non-overlapping perianth segments with a broad white edge. All of these characters are most variable and are not of great taxonomic significance within the section. Both pink and white flowers occur in plants of *P. raii* from Great Britain. Plants from Norway have been called exclusively subspecies *norvegicum*.

Many British, Continental and American botanists during the latter half of the last century named plants belonging under *P. raii* Bab. as *P. robertii* Lois. The confusion arose in this country in the first instance because no British botanists had seen authentic material of the latter, while Meisner (in De Candolle 1856) states that material sent to him by Loiseleur-Deslongchamps was a mixture of *P. raii*, *P. littorale* and *P. aviculare* and that the name ought to be completely abolished. Loiseleur's species was described from maritime sands of the Mediteranean, and since *P. raii*, according to Rouy (1910), does not occur south of the shores of the English Channel, it is hardly probable that the plant collected by Robert on the sands near Toulon is identical with the northern one. Furthermore, Rouy maintains *P. robertii* is a very distinct plant of the Mediterranean sands with shining achenes 2–3 mm long. Under these circumstances it is correct to keep the name *P. raii* for Babington's plant, and no change in the binomial is proposed.

6. P. OXYSPERMUM Mey. & Bge., in Ledebour, Ind. Sem. Hort. Acad. Dorpat. Suppl. **2**: 5 (1824).

P. acadiense Fernald, Rhodora **16**: 188 (1914).

After examining a number of specimens of *P. oxyspermum* from Denmark, Sweden and Scotland, I feel that the status of this plant as a full species is doubtful. Many of the differences given by Samuelsson are based on characters which show great variability. Although I was able to detect the colour differences of the achenes and perianth on plants collected in 1957, I found this impossible in older specimens. The narrowness of the fruit is an important feature, but I was unable to separate *P. raii* from it on this character alone.

Although *P. oxyspermum* has a Baltic distribution (neglecting Canadian records) there is considerable overlap of this species with *P. raii* in southern Scandinavia and Denmark (Fig. 12). Before any taxonomic conclusion can be made on the distinctness of these two species more information is required on their behaviour in these areas of overlap. There is a chance of hybridization since the plants occupy similar types of habitat, the flowers are larger and more attractive than those of *P. aviculare, sensu lato* and the European populations have the same chromosome number.

I think that *P. oxyspermum* and *P. raii* may be better treated as geographical subspecies of one species, but until more information is forthcoming on the facts mentioned above the question must remain unanswered. The two are being grown under experimental conditions and I hope to publish a fuller account of these two species later.

There are several specimens in Herb. Mus. Brit. which have been labelled by Samuelsson as *P. oxyspermum*, although the original collectors identified them as *P. raii*. The localities are: Gosfort, Haddington 1850 (v.c. 82); Mornfar, Forfar, 1845 (v.c. 90); Carnoustie, Angus, 1845 (v.c. 90); Musselburgh, W. Lothian, 1842 (v.c. 83).

There is also another, originally named as *P. aviculare* var. *littorale*, collected from a salt marsh, Warrenly, Yorks., v.c. 62, which is also called ? *P. oxyspermum* by Samuelsson.

I have studied these specimens, but at the moment feel uncertain about their correct determination. They are all old and the colour and narrowness of the fruit is not evident. The Carnoustie plant (the same form was also obtained from Dundee), did not have red borders to the flowers, which is given as diagnostic for the species by Samuelsson (1931), and I could not see that the perianth segments were any narrower than in specimens of *P. raii*. There are no very evident differences in leaf morphology and internode length, which are very variable characters in the group.

7. P. MARITIMUM L., Sp. Pl. 361 (1753).

P. maritimum var. *confusum* Rouy, Fl. France **12**: 110 (1910).

A glabrous, glaucous, prostrate or erect shrubby (in south Europe) perennial, 10–50 cm; root stock woody and stout at the base. Leaves 0·5–2·5 cm, elliptic-lanceolate, greyish-green, margins usually revolute. Ochreae very conspicuous and silvery-white above, usually

longer than the upper internodes which they envelop, 2-lobed at first but eventually becoming lacerate, with 6–12 strong branched veins. Inflorescence 1–4-flowered. Flowers twice as large as those of *P. aviculare*. Perianth segments *c.* 2–2·5 mm, with pink or white broad petaloid margins. Stamens 8. Fruit 4–4·5 mm long × *c.* 2·5 mm broad, ovoid, acute, reddish chestnut-brown, smooth, shining, as long as or slightly exceeding the persistent perianth. Flowers July to September.

Holotype in Linnean Herbarium (**LINN**), London.

Geographical Distribution

The British Isles

This species is now thought to be extinct on the mainland of Great Britain, since no plants have been found since about 1939 (coll. C. West nr. Mullion, Cornwall, v.c. 1) in spite of the increased activities of the members of the BSBI engaged in the Maps Scheme. The well known colony of approximately 30 plants was seen on Herm, Channel Islands in 1961. They were growing in bare unstable coarse shell-sand just above the high tide mark with *Beta vulgaris* subsp. *maritima*, *Carex arenaria* and *Brachythecium albicans* as associate species.

Although never very abundant in any one locality in this country, I have seen herbarium specimens from the following vice-counties in the south of England :

S. (Guernsey, Herm) 1 (including Scilly Isles), 2–5, 6, 9, 11.

Druce also gives the following v.c. records in brackets : 13, 28, 46, 49, 75. All are suspect and no specimens are available for their confirmation.

P. maritimum is a Mediterranean species which reaches its northernmost limits in Great Britain. As in many other plants at the edge of their geographical range, the British specimens are not quite typical and differ in certain characters from the main body of the Continental material. The Herm plants are more herbaceous than those obtained from Sacavém, Portugal and Banyuls, Pyr.-or., France and have shorter ochreae with less conspicuous veins. The British populations on Herm (*fide* Mrs. F. Le Sueur) behave as perennials but other specimens seen from Braunton Burrows suggest from their herbaceous appearance that the plant might have behaved as an annual on the mainland.

It is quite possible that fruits of *P. maritimum* could be carried by ocean currents and thereby washed up on to the shore by tides. I have no doubt that the plant could become established again in the south and west of England given the right conditions.

Foreign Distribution

P. maritimum occurs frequently on sandy shores and shingle in the following European areas from which I have seen specimens : western (Manche) and southern France, Iberian Peninsula, Macaronesia, Mediterranean Europe, Corsica; also in Asia Minor and north Africa. Moss (1914) gives the following further records, Cape Colony, South Africa (rare), North America (Massachusetts to Florida) and South America. I have seen no specimens nor can I trace records from the first and last continents mentioned, and consider the occurrence of the plant here most doubtful. The North American records are, according to Fernald (1913), all based on wrongly identified material. Linnaeus (1753) includes American plants with his frutescent Mediterranean species *P. maritimum*, saying 'Habitat Monspelii, in Italia, Virginia, [perennial].' Several American authors, Pursh (1814), Torrey (1843) and Small (1895), have included *P. maritimum* in their Floras and Manuals but it is now fairly certain that the American plant referred to by Linnaeus is in fact *P. glaucum* Nutt. This species is an American endemic and differs from *P. maritimum* in that it is always annual and herbaceous, with shorter ochreae, 7–10 mm, and in the fruits, which are distinctly smaller, 3–4 mm long and 1·6–2·2 mm wide. It is very probable that Linnaeus included his American plants of this species under *P. maritimum*. There is still much confusion in American floras over the maritime species in this section and experimental work on their taxonomy is urgently needed.

Artificial key to the British species*

1. Fruit dull, striate, enclosed by or slightly longer than the persistent perianth. *3*
   Fruit smooth, distinctly shining, as long as or longer than the persistent perianth. *2*
2. Ochreae with 4–6 unbranched veins, shorter than the upper internodes; fruit 5–6 mm long, exceeding persistent perianth. 5. *raii* †
   Ochreae with 8–12 branched veins, as long as upper internodes; fruit 4–4·5 mm long, enclosed by or slightly projecting from persistent perianth (very rare). 7. *maritimum*
3. Branch leaves much smaller than stem leaves; persistent perianth divided almost to base; fruit trigonous, with 3 concave sides. *4*
   Branch and stem leaves ± equal; persistent perianth divided for half its length; fruit with 2 sides convex, one concave. 2. *arenastrum*
4. Stem leaves narrow, linear-lanceolate, 1–4 mm broad; perianth segments and fruit narrow. 3. *rurivagum*
   Stem leaves 5–18 mm broad; perianth segments overlapping; fruit broad. *5*
5. Stem leaves ovate-lanceolate, subsessile or with petioles *c.* 2 mm included in the ochreae; fruit 2·5–3·5 mm long. 1. *aviculare*
   Stem leaves obovate-spathulate; petioles 4–8 mm, projecting from ochreae; fruit 3·5–4·5 mm long (Shetland). 4. *boreale*

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*Identifiable with certainty only if ripe fruit and stem leaves at least at 2nd or 3rd node are present.
† see also 6. *oxysperum*

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NOTES ON BRITISH HIERACIA. II. THE SPECIES OF THE ORKNEY ISLANDS

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During the period 1920 to 1933 more than a dozen new species and varieties of *Hieracium* from the Orkneys were described by H. Dahlstedt, based on specimens sent to him for identification by the late H. H. Johnston. Many of these have been ' lumped ' by H. W. Pugsley (1948). We have made a special study of the hawkweeds of this area in an attempt to discover how far there was justification for Dahlstedt's new species and for their treatment by Pugsley.

All the specimens on which these new species were founded are in the collections made by H. H. Johnston and J. Sinclair. We are grateful to Mr. Sinclair for allowing us to examine the specimens in his private herbarium, and to the Regius Keeper of the Royal Botanic Garden, Edinburgh, for the loan of Johnston's material. A few specimens from other collections have also been examined.

As a result of a careful examination of all the available material we have found that we are in general agreement with Pugsley that many of Dahlstedt's species can be matched with species already described. It is well known that certain species of *Hieracium* are extremely variable and not easily distinguishable from one another, especially when poorly grown or late-flowering. Johnston often sent Dahlstedt few specimens of inadequate, late-flowering material. This and the fact that Dahlstedt was not well acquainted with the British Hieracia may account for the large number of names he applied to Johnston's plants.

We recognise in all twelve species of *Hieracium* from the Orkney Isles. Ten of these species belong to the Subgenus *Hieracium*, namely *H. anglicum* Fries and *H. iricum* Fries (Sect. *Cerinthoidea* Fries); *H. argenteum* Fries, *H. orimeles* Hanb. ex W. R. Linton and *H. scoticum* Hanb. (Sect. *Oreadea* Fries); *H. sarcophylloides* Dahlst. (Sect. *Suboreadea* Pugsley); *H. euprepes* Hanb. and *H. caledonicum* Hanb. (Sect. *Vulgata* Fries); and *H. latobrigorum* (Zahn) Roffey and *H. maritimum* (Hanb.) Hanb. (Sect. *Foliosa* Fries). The other two species, *H. pilosella* L. and *H. aurantiacum* L. *sensu stricto*, belong to the subgenus *Pilosella* Tausch.

Of these twelve species *H. aurantiacum* and *H. pilosella* present no difficulty. *H. aurantiacum* is a garden escape of central European origin, easily recognised by its reddish-orange ligules. *H. pilosella* is widespread in the British Isles and continental Europe but is absent from the Shetlands, Faeroes and Iceland. Its stoloniferous, scapigerous habit makes it a plant easy to identify.

H. latobrigorum and *H. maritimum* differ from the rest by their very leafy stems. *H. maritimum* shows little variation in form, and elsewhere occurs only in a few places in N. Scotland, the Shetlands (as *H. obesifolium* Pugsl.), Ireland and Scandinavia. *H. latobrigorum*, on the other hand, is a very variable plant to which several names have been applied. It is widely distributed in northern Britain, north-eastern Ireland and central Europe.

H. anglicum and *H. iricum* can usually be separated from the remainder by their semi-amplexicaul cauline leaves, very pilose-tipped ligules and furcate inflorescence of large heads. They may however be difficult to distinguish from each other, and their differences can only be fully appreciated by examination of a series of authentic herbarium sheets. *H. iricum* normally has more numerous stem leaves, and is more shaggy in appearance, but plants of *H. anglicum* occur (var. *amplexicaule* Backh.) that superficially

resemble it. In fact, among the specimens we examined there were several of *H. anglicum* which had been labelled *H. iricum*. *H. anglicum* is not uncommon in northern Britain and Ireland, but is extremely rare in Wales. It occurs in the Faeroes (as *H. perampliforme* Dahlst.) and in Iceland (as the variety *vestmannaense* Omang). It is absent from the Shetland Isles and the Continent. *H. iricum* occurs in Scotland, northern England, Ireland and the Faeroes (as *H. peramplum* Dahlst.), but is not recorded from the Shetlands, Iceland or continental Europe.

The remaining six species are variable and are not easy to distinguish from one another, especially when poorly grown or late flowering.

H. argenteum Fries is most readily distinguishable by the characteristic leaden colour of its leaves. *H. pseudomicrodon* Dahlst., which was founded on exsiccatae from Hoy, is, as Pugsley (1948) rightly pointed out, identical with this species. *H. argenteum* is widely spread throughout Scotland, northern England, and Scandinavia, and is of local occurrence in Ireland, Wales and Iceland (as *H. microdon* Dahlst.). It has not been found in the Shetlands or in the Faeroes.

H. orimeles Hanb. ex W. R. Linton, which is abundant in the Shetlands (as *H. beebyanum* Pugsl.) and local in western Scotland, northern England and Wales, is known only from a single locality in the Orkneys. This species closely resembles *H. argenteum*, both having narrowly ovate to lanceolate basal leaves, 1–3 usually spreading cauline leaves, and narrow acute phyllaries. It can however be distinguished from *H. argenteum* by the colour and clothing of its leaves.

H. sarcophylloides Dahlst. which was originally described from the Faeroes, is identical with *H. dasypodum* Dahlst. from the Orkneys. *H. sarcophylloides* is the older name. It is a variable species, which in its typical form can be separated from the other Orcadian species by its rather broadly ovate, truncate-based leaves. The type material of *H. sinclairii* Dahlst. matches *H. sarcophylloides* so closely that it is not easy to understand why Pugsley claimed, even with some reservation, that it was closely allied to *H. oistophyllum* Pugsl. *H. pycnodon* var. *acutidens* Dahlst. is based on specimens of *H. sarcophylloides* with leaf bases which are less truncate than usual. The Scandinavian *H. pycnodon* Dahlst. may also be referable here, but the material we have seen is insufficient to enable us to arrive at a definite opinion. *H. sarcophylloides* also occurs in Sutherland, Argyll and the Faeroes.

Although *H. euprepes* is so variable that it is not easy to pick out any definite distinguishing characters, the general facies of a well-grown plant with its elliptical, dark green leaves, tall wiry stem with 1–3 rather narrow stem-leaves, and rather condensed inflorescence of narrow, often geminate heads, is characteristic. We agree with Pugsley (1948) in placing a number of Dahlstedt's species under *H. orcadense*, but we consider that species to be indistinguishable from *H. euprepes*. The type specimen of *H. sagittatum* subsp. *sagittatum* var. *abrasum* Dahlst., which was considered by Pugsley to be a variety of *H. oistophyllum*, bears little resemblance to that species. It is without doubt *H. euprepes*. *H. euprepes* is not uncommon in Scotland and Wales, and has a local distribution in north-east Ireland and the Faeroes (as *H. ardisodon* Dahlst.). It has not been recorded from the Shetlands, Iceland or the Continent.

In Wales, northern England, northern Ireland, and the greater part of Scotland, *H. caledonicum* can be recognised by its thick, ovate, caesious leaves and broad, truncate-tipped phyllaries, but in the extreme north of Scotland, the Orkneys and the Faeroes (as *H. subrubicundum* Dahlst., *H. perintegrum* Dahlst., *H. cordifrons* Dahlst., *H. leniscotum* Omang, *H. subcordifrons* (Zahn) Omang) it shows many modifications of form. A variety (var. *austroislandicum* Omang) of *H. perintegrum* Dahlst. has been described from Iceland, but we have seen no specimens of it. *H. caledonicum* is not known from the Shetlands or the Continent.

H. scoticum can usually be distinguished by its numerous (2–7) dark green stem-leaves and long deflexed hairs on the base of the stem. It is of local occurrence in Wales, northern England, Scotland, north-west Ireland and the Faeroes (as *H. scoticiforme* Dahlst.), but is not recorded from Iceland, the Shetlands or the Continent.

H. anglicur

H. iricum

H. argentei

H. scoticun

H. orimeles

H. sarcophy

H. euprepes

H. caledoni

H. latobrig

H. maritim

H. pilosella

H. aurantia

TABLE 1. The Distribution in Europe of the species of *Hieracium* which occur in the Orkneys

Species	Mainland of Scotland	Northern half of England	Southern half of England	Wales	Ireland	Shetland Isles	Faeroes	Iceland	Scandinavia	Continental Europe
H. anglicum	+	+	—	+ R	+	—	+ as *H. perampliforme* Dahlst.	+ as var. *vestmannaense* Omang	—	—
H. iricum	+	+	—	—	+	—	+ as *H. peramplum* Dahlst.	—	—	—
H. argenteum	+	+	—	+	+	—	—	+ as *H. microdon* Dahlst.	+	—
H. scoticum	+	+ R	—	+ R	+	—	+ as *H. scoticiforme* Dahlst.	—	—	—
H. orimeles	+	+ R	—	+	+	+	—	—	—	—
H. sarcophylloides	+ R	—	—	—	—	—	+	—	? as *H. pycnodon* Dahlst.	—
H. euprepes	+	—	—	+	+	—	+ as *H. ardisodon* Dahlst.	—	—	—
H. caledonicum	+	+	—	+	+	—	+ as { *H. subrubicundum* Dahlst. *H. perintegrum* Dahlst. *H. cordifrons* Dahlst. *H. leniscotum* Omang *H. subcordifrons* (Zahn) Omang	? as *H. perintegrum* var. *austroislandicum* Omang	—	—
H. latobrigorum	+	+	—	—	+	—	—	—	—	+
H. maritimum	+ R	—	—	—	+ R	as *H. obesifolium* Pugsl.	—	—	+ R	—
*H. pilosella**	+	+	+	+	+	—	—	—	+	+
H. aurantiacum, sensu lato†	+ N	+ N	+ N	+ N	+ N	—	—	—	+ N	+

\+ = present — = absent R = rare N = naturalised

**H. pilosella* also occurs in Asia Minor and Siberia.

†*H. aurantiacum, sensu lato*, occurs as a naturalised plant in North America.

In the Orkney Isles the Hieracia are mainly distributed along the south coast of the Mainland and on the island of Hoy, usually occurring on rocks, banks of streams or low sea cliffs, where there is a high humidity and good drainage, and where they are protected from the depredations of grazing animals, particularly sheep.

If the distribution of the Orkney species of the Subgenus *Hieracium* is considered, it will be seen from Table 1 that all the species occur on the Scottish mainland while many are to be found in Ireland, Wales and the north of England. They are completely absent from central and southern England. Perhaps the most striking feature is that the only species represented in the Shetlands are *H. orimeles* and *H. maritimum*.

When considering the European distribution of the group we have attempted to assign to what we consider to be their proper place certain specific and varietal names created by Dahlstedt and Omang from material gathered in the Faeroes and in Iceland. The Orcadian species are well represented in the Faeroes whereas only two or possibly three have been recorded from Iceland. They are very poorly represented in Continental Europe, only *H. argenteum*, *H. maritimum* and possibly *H. sarcophylloides* occurring in Scandinavia, and only *H. latobrigorum* in central Europe.

Not a single species of the Sect. *Alpestria* has been found in the Orkneys, in spite of the fact that numerous species of this section are common in the Shetlands, Faeroes, Iceland and Scandinavia. *H. sparsifolium* Lindeb. (*H. stictophyllum* Dahlst. ex W. R. Linton) of the Section *Tridentata* Fries is common in the Shetlands (as *H. pseudo-protractum* Pugsl. non Notø.), the Faeroes (as *H. faeroense* Dahlst. and *H. epileucoides* Dahlst.), Iceland and Scandinavia, but is absent from the Orkneys.

The following key may help visitors to the Orkneys to identify the species of *Hieracium* which are known to occur there. Identifications should always be confirmed by comparison with authentic specimens. Early to mid-July is probably the time to see most species at their best, but *H. pilosella* and *H. aurantiacum* usually flower about a month earlier while *H. latobrigorum* and *H. maritimum* may not flower until late July or early August. After the key the full synonymy of each species and a list of all the Orkney specimens we have examined are given. The National Grid References are only given as a guide to the locality and may not denote the exact spot where the plant was found.

Artificial key to the species of Hieracium recorded in the Orkneys

1.	Ligules orange-red	*H. aurantiacum*
	Ligules yellow (sometimes with red stripe on back)	2
2.	Plant stoloniferous; ligules usually with red stripe on back	*H. pilosella*
	Plant not stoloniferous; ligules concolorous	3
3.	Cauline leaves usually more than 12	4
	Cauline leaves usually less than 7	5
4.	Leaves mostly ovate to elliptic-lanceolate; phyllaries with many microglands, a number of very small glands and a few simple hairs	*H. latobrigorum*
	Leaves narrowly oblong; phyllaries with very few, very small glands, and/or an occasional simple hair, or glabrous	*H. maritimum*
5.	Ligules strongly pilose-tipped; cauline leaves semi-amplexicaul	6
	Ligules glabrous; cauline leaves not amplexicaul	7
6.	Large cauline leaves rarely more than 2, hairs of stem long but not shaggy	*H. anglicum*
	Large cauline leaves usually more than 3; hairs of stem long and shaggy	*H. iricum*
7.	Phyllaries narrow and ± acute	8
	Phyllaries broader and ± obtuse	10
8.	Leaves yellowish-green, rather broadly ovate, often with a truncate base, cauline usually 0, rarely 1	*H. sarcophylloides*
	Leaves rather glaucous (leaden) or light green, narrowly ovate or lanceolate, ± cuneate-based, cauline 1–3	9
9.	Leaves rather glaucous (leaden), almost glabrous above	*H. argenteum*
	Leaves light green, densely short-setose above	*H. orimeles*

10. Leaves rather dark green, ± elliptic, base cuneate or attenuate, cauline 0–3; phyllaries c. 10 mm. long, linear-lanceolate *H. euprepes*
Leaves caesious, ± ovate or elliptic, base rounded or cuneate, cauline 0–3; phyllaries 10–12 mm. long, broad linear-lanceolate, truncate-tipped *H. caledonicum*
Leaves rather dark green, ± ovate or occasionally elliptic, base cuneate, cauline 2–7; phyllaries 11–12 mm. long, linear-lanceolate *H. scoticum*

Subgenus HIERACIUM

Section Cerinthoidea Fries

Hieracium anglicum Fries (1848) 93; Fortescue (1882) 370; W. R. Linton (1887) 154; E. S. Marshall (1901) 269; Spence (1914) 43; Johnston (1914) 209; Pugsley (1948) 68.
[*H. iricum sensu* Spence (1914) 41 *pro parte*.]
H. anglicum var. *cerinthiforme* Backh., Bennett (1915) 55.
H. mougeotii subsp. *anglicum* var. *cerinthiforme* (Hanb.) Zahn, Johnston (1928) 12.
H. mougeotii subsp. *anglicum* forma *acutifolium* (Backh.) Zahn, Johnston (1928) 12.
H. patens Dahlst. in Johnston (1934) 473 (Lectotype: west side of Nowt Bield, Ward Hill, Hoy, 10 July 1933, H. H. Johnston No. 4742 (**E**)).

Southwest side of Berriedale, Hoy, 30/1901, 8 August 1927, H. H. Johnston nos. 3651 and 3655A (**E**). Near the Kame, Hoy, 30/1904, 9 August 1886, H. H. Johnston (**E**). Ward Hill, Rousay, 12 August 1880, H. H. Johnston (**E**); 28 August 1883, H. H. Johnston (**E**); 10 August 1886, W. R. Linton (**BM**); 23 July 1907, M. Spence (**E**); 30 August 1916, H. H. Johnston no. 426 (**E**); 26 July 1927, J. Sinclair no. 436 (herb. Sinclair); 31 July 1928, J. Sinclair no. 591 (herb. Sinclair & E). Valley Burn, Hoy, 12 July 1928, J. Sinclair no. 571 (herb. Sinclair) and H. H. Johnston nos. 4006 and 4008 (**E**). Burn of Segal, Hoy, 30/2002, 11 July 1933, H. H. Johnston no. 4749 (**E**). Lenders Fea, Skecking Gill, Hoy, 30/2004, 25 July 1925, J. Sinclair no. 155 (herb. Sinclair), H. H. Johnston no. 3120 (**BM**). Braebuster Burn, Hoy, 30/2105, 7 July 1928, J. Sinclair no. 568 (herb. Sinclair) and H. H. Johnston no. 3990 (**E**). Glen of Gair (Greor), Ward Hill, Hoy, 30/2203, 20 August 1885, H. H. Johnston (**BM**). West side of Sel Wick, Hoy, 30/2205, 7 July 1928, J. Sinclair no. 566 (herb. Sinclair), H. H. Johnston no. 3987 (**E**). Trowie Glen, Hoy, 30/2300, 28 July 1925, H. H. Johnston no. 3138 (**E**, **BM**); 5 August 1927, H. H. Johnston no. 3644B (**E**). Nowt Bield, 30/2301, 5 August 1927, H. H. Johnston no. 3646 (**E**); 2 August 1932, H. H. Johnston no. 4340 (**E**); 10 July 1933, J. Sinclair no. 954 (herb. Sinclair) and H. H. Johnston nos. 4740, 4741 and 4742 (**E**); 1953, C. West (**CGE**). Junction of the burn of the Nowt Bield and the Trowie Glen, Hoy, 30/2300, 16 July 1928, H. H. Johnston no. 4046 (**E**). Burn of Quoys, Hoy, 30/2402, 1 August 1927, H. H. Johnston no. 3616 (herb. Sinclair) and no. 3616A (**E**); 5 August 1927, J. Sinclair no. 457 (herb. Sinclair); 6 July 1928, J. Sinclair no. 637 (herb. Sinclair). Dwarfie Hamars, July 1953, C. West (**CGE**). Red Glen, between Burandie and Dwarfie Hamars, Hoy, 30/2500, 10 August. 1886, H. H. Johnston (**E**). Bring Head, Hoy, 30/2701, 15 August 1937, J. Sinclair no. 481 (herb. Sinclair). Scapa, August 1875, J. Boswell-Syme (**BM**). Westerow, Rackwick, Hoy, 39/2098, 14 July 1928, J. Sinclair nos. 578 and 639 (herb. Sinclair), H. H. Johnston nos. 4025 and 4025A (**E**). South Burn, Hoy, 39/2099, 14 July 1928, H. H. Johnston no. 4039 (**E**); 20 July 1932, H. H. Johnston no. 4515 (**E**). Pegal Bay, 39/3097, August 1880, J. B. Fortescue (**CGE**, **BM**); 22 August 1894, H. H. Johnston (**E**); 16 July 1912, H. H. Johnston (**E**); 3 August 1927, J. Sinclair no. 453 (herb. Sinclair & **E**); 7 July 1933, H. H. Johnston nos. 4727 and 4728 (**E**).

Hieracium iricum Fries (1848) 60; Spence (1914) 41 *pro parte*; Pugsley (1948) 80.

Burn of the Nowt Bield, Hoy, 30/2300, 2 August 1932, H. H. Johnston no. 4540A (**E**). Dwarfie Hamars, Hoy, 30/2400, 10 August 1886, H. H. Johnston (**E**, **BM**). Burn of Quoys, Hoy, 30/2402, 3 July 1926, J. Sinclair no. 328 (herb. Sinclair); 1 August 1927, H. H. Johnston no. 3616 (**E**); 6 July 1928, J. Sinclair no. 634 (herb. Sinclair); 1953, C. West (**CGE**).

Section Oreadea Fries

Hieracium argenteum Fries (1848) 99; Pugsley (1948) 92.
[*H. rivale* var. *dasythrix sensu* Johnston (1920) 32.]
H. pseudomicrodon Dahlst. in Johnstone (1929a) 5 (Lectotype: Grassy rocky crags at

burnside in a ravine on the southwest side of Berrie Dale, below a waterfall, Hoy, alt. 280 ft., 8 July 1927, H. H. Johnston, no. 3657 (**E**)); Johnston & Sinclair (1930) 24.
[*H. saxifragum sensu* Dahlst. in Johnston (1933a) 3; *sensu* Johnston (1933b) 23, *sensu* Johnston (1934) 472.]

Southeast side of Enegars, Kame, Hoy, 30/1904, 19 August 1932, J. Sinclair no. 770 (herb. Sinclair & **E**); 8 July 1933, H. H. Johnston no. 4731 (**E, BM**). Berrie Dale, Hoy, 30/2001, 7 September 1914, H. H. Johnston no. 362 (**E**); 8 July 1927, H. H. Johnston no. 3657 (**E**); 8 August 1927, J. Sinclair no. 471 (herb. Sinclair); 26 August 1928, H. H. Johnston and J. Sinclair (herb. Sinclair & **E**); 1 August 1932, J. Sinclair no. 760 (herb. Sinclair & **E**).

Hieracium scoticum Hanb. (1888) 206; Spence (1914) 42 and 130; Johnston (1914) 220; Johnston (1925) 6; Pugsley (1948) 98.
[*H. gothicum sensu* Johnston (1882) 370.]
[*H. rubicundum sensu* Johnston (1914) 210 (*quoad loc.* Malsetter).]
H. scoticum var. *submaculatum* Dahlst. in Johnston (1929b) 5 and (1930) 24 (Lectotype: Heathery rocky ravine at burnside, Roonie (? = Runcie) Gill, Hoy, 210 ft. alt., 15 August 1929, H. H. Johnston no. 4241 (**E**)).

Berrie Dale, 30/2001, 22 August 1929, H. H. Johnston no. 4280 (herb. Sinclair & **E**). Burn of Sowa Dee, Sandwick, 30/2314, 26 August 1912, H. H. Johnston (**E**); 15 July 1913, H. H. Johnston (**E**); 23 July 1925, H. H. Johnston no. 3107 (**E, CGE**); 30 June 1928, J. Sinclair no. 645 (herb. Sinclair); 1954, N. D. Simpson no. 54/153 (herb. Simpson). Hangarback, Gyre, Orphir, 30/3403, 18 August 1885, H. H. Johnston (**E**). North Hill, Westray, 30/4048, 15 July 1883, H. H. Johnston (**E**); 28 August 1913, H. H. Johnston (**E**). Roonie (? = Runcie) Gill, Hoy, 39/2299, 15 August 1929, H. H. Johnston no. 4241 (**E**). Malsetter, Waas, Hoy, 39/2789, 11 August 1913, H. H. Johnston (**E**). North-east side of Aith Hope, South Walls, Hoy, 39/2989, 21 July 1913, H. H. Johnston (**E**); 25 July 1913, H. H. Johnston (**E**); 4 August 1913, H. H. Johnston (**E**); 9 August 1928, J. Sinclair no. 597 (herb. Sinclair & **E**); 2 August 1929, J. Sinclair no. 663 (herb. Sinclair & **E**); 20 August 1929, H. H. Johnston no. 4259 (**E**). West side of Fara, South Isles, 39/3195, 30 July 1924, H. H. Johnston no. 2669 (**E**).

Hieracium orimeles Hanb. ex W. R. Linton (1901) 106; Pugsley (1948) 102.

Waulkmill Bay, 30/3806, July 1953, C. West (**CGE**).

Sect. Suboreadea Pugsley

Hieracium sarcophylloides Dahlst. in Warming (1903) 629 (Holotype: Osteró, Kodlen ad Eide at 400 m., 17 July 1895, H. G. Simmons in Herb. Copenhagen).
[*H. pallidum sensu* Johnston (1882) 370.]
[*H. silvaticum* var. *tricolor sensu* Spence (1914) 131; *sensu* Johnston (1914) 211.]
[*H. caesium sensu* Spence (1914) 43.]
[*H. murorum sensu* Spence (1914) 43.]
[*H. britannicum sensu* Spence (1914) 42; *sensu* Johnston (1925) 6.]
[*H. sarcophyllum* var. *expallidiforme sensu* Bennett (1915) 55; *sensu* Johnston (1920) 32.]
[*H. rubicundum* var. *boswellii sensu* Johnston (1920) 31.]
H. dasypodum Dahlst. in Johnston (1929a) 5 (Lectotype: Heathery crags on hillside between Grut Fea and the Glen of Button, Hoy, 12 July 1928, H. H. Johnston no. 4012 (**E**)); Johnston (1929b) 3; Johnston & Sinclair (1930) 24; Pugsley (1948) 115.
H. pycnodon var. *acutidens* Dahlst. in Johnston (1929a) 4 (Lectotype: Grassy, rocky banks of burn, White Glen, Ward Hill, Hoy, 16 August 1928, J. Sinclair no. 602 (**E**)); Johnston (1929b) 3; Sinclair (1930) 25.
H. sinclairii Dahlst. in Johnston (1932) 5 (Lectotype: Moist mossy soil on sandstone cliffs, Dwarfie Hamars, Hoy, 24 July 1931, J. Sinclair no. 706 (**E**)).

Between Grut Fea and the Glen of Button, Hoy, 30/1901, 12 July 1928, J. Sinclair no. 575 (herb. Sinclair) and H. H. Johnston no. 4012 (**E, BM**). South of the meadow of the Kame, Hoy, at 750 ft., 39/1904, 11 September 1914, H. H. Johnston no. 373 (**E**) and Enegars, south-east of Kame, 880 ft., 30/1904,

8 July 1933, H. H. Johnston no. 4735 (**E**). Ward Hill, Hoy, 30/2301, 31 July 1928, J. Sinclair no. 590 (herb. Sinclair & **E**); 16 August 1928, J. Sinclair no. 602 (herb. Sinclair & **E**); 22 August 1929, H. H. Johnston no. 4274 (**E**); 14 August 1938, J. Sinclair no. 1234 (herb. Sinclair); July 1953, C. West (**CGE**). Dwarfie Hamars, 30/2400, 28 August 1883, H. H. Johnston (**E**); 14 July 1900, E. S. Marshall no. 2328 (**BM**) and as Linton Set no. 178 (**BM, CGE**); 22 July 1912, H. H. Johnston (**E**); 24 July 1925, J. Sinclair no. 147 (herb. Sinclair); 26 July 1929, J. Sinclair no. 661 (herb. Sinclair & **BM**); 24 July 1931, J. Sinclair no. 716 (**E, BM**) and no. 715 (herb. Sinclair & **E**); 2 August 1932, H. H. Johnston nos. 4534 and 4535 (**E**); July 1953, C. West (**CGE**). Bring Head, Hoy, 30/2702, 4 July 1877, H. H. Johnston (**E**); 7 July 1933, H. H. Johnston no. 4726 (**E**) and J. Sinclair no. 952 (herb. Sinclair).

Sect. Vulgata Fries

Hieracium euprepes Hanb. (1892) 206 (Lectotype: Craig Dulyn, Caernarvon, 28 July 1891, F. J. Hanbury (**BM**)); Pugsley (1948) 166.

[*H. vulgatum sensu* Fortescue (1882) 370, *sensu* Johnston (1882) 370; *sensu* Spence (1914) 42.]

H. orcadense W. R. Linton (1893) 196; Johnston in Cryer (1913) 264; Johnston (1914) 211; Spence (1914) 41 and 131; Pugsley (1948) 168.

[*H. orarium* var. *fulvum sensu* Marshall in Marshall & White (1901) 638.]

[*H.* ? *caesium sensu* Spence (1914) 43.]

[*H. buglossoides sensu* Spence (1914) 130; *sensu* Johnston (1914) 211.]

[*H. schmidtii* var. *crinigerum sensu* Spence (1914) 41; *sensu* Johnston (1925) 6.]

[*H.* ? *orarium sensu* Bennett (1915) 55.]

[*H. silvaticum* var. *subtenue sensu* Johnston (1926) 300.]

[*H. holopleurum sensu* Dahlst. in Johnston (1928) 11; *sensu* Johnston (1929b) 3; *sensu* Johnston (1929c) 619.]

H. sagittatum subsp. *sagittatum* var. *abrasum* Dahlst. in Johnston (1929a) 6 (Lectotype: Heathery, sandy banks of Valley Burn, Hoy, 50 ft. alt., 12 July 1928, H. H. Johnston no. 4007 (**E**)); Johnston & Sinclair (1930) 35.

H. subalpestrifrons Dahlst. in Johnston (1929a) 7 (Lectotype: Grassy, heathery banks of the Burn of Quoys, Hoy, 6 July 1928, J. Sinclair no. 565 in herb. Sinclair); Johnston (1929b) 4; Johnston and Sinclair (1930) 25.

H. paraliaeforme Dahlst. in Johnston (1932) 7 (Lectotype: Moist mossy soil on sandstone cliffs, Dwarfie Hamars, Hoy, 24 July 1931, J. Sinclair no. 717 in herb. Sinclair).

H. kalsoense subsp. *burnense* Druce & Zahn in Druce (1932 for 1931) 559 (Holotype: South Burn near Rackwick, Hoy, August 1931, G. C. Druce (**OXF**)).

H. sagittaticeps Dahlst. in Johnston (1932) 4 (Holotype: Heathery banks of the Burn of Segal, Hoy, 8 August 1931, H. H. Johnston no. 4425 (**E**)).

H. subexpallescens Dahlst. in Johnston (1933 a) 3 (Lectotype: Heathery freestone sea-cliffs, Enegras, Craig Gate, southeast of Rackwick, Hoy, 1 August 1932, H. H. Johnston no. 4532 (**E**)); Johnston (1933 b) 23.

H. oistophyllum var. *abrasum* (Dahlst.) Pugsl. (1948) 159.

North Geo, between Bre Brough and The Sow, 30/1802, 13 August 1929, J. Sinclair no. 671 (herb. Sinclair). Grut Fea, Hoy, 30/1901, 7 August 1938, J. Sinclair no. 1233 (herb. Sinclair). Enegars, south-east of the Meadow of the Kame, Hoy, 30/1904, 8 July 1933, J. Sinclair (herb. Sinclair) and H. H. Johnston no. 4734 (**BM**). South-west side of Berriedale, Hoy, 30/2001, 26 August 1928, J. Sinclair no. 699 (herb. Sinclair). Burn of Segal, Hoy, 30/2001, 8 August 1931, H. H. Johnston no. 4425 (**E**); 1 August 1932, J. Sinclair no. 761 (herb. Sinclair) and H. H. Johnston no. 4533 (**BM**). Trowie Glen, Hoy, 30/2300, 5 August 1927, J. Sinclair no. 462 (herb. Sinclair). West side of Nowt Bield, Ward Hill, 30/2301, 8 July 1929, J. Sinclair no. 660 (herb. Sinclair). Dwarfie Hamars, 30/2400, 14 July 1905, E. S. Marshall and W. A. Shoolbred as Linton Set no. 142 (**BM, CGE**); 1921, G. C. Druce (**BM**); 24 July 1931, J. Sinclair no. 717 (herb. Sinclair & **BM**); 2 August 1932, H. H. Johnston no. 4536 (**E**). Burn of Quoys, Hoy, 30/2402, 31 July 1894, F. J. Hanbury (**BM**); 6 July 1928, J. Sinclair no. 565 (herb. Sinclair). West side of Waulkmill Bay, Orphir, Mainland, 30/3706, 15 August 1881, H. H. Johnston (**E**); 17 July 1900, E. S. Marshall no. 2331 (**CGE**); 20 July 1912, H. H. Johnston (**BM, CGE**); 9 August 1933, J. Sinclair no. 959 (herb. Sinclair); July 1953, C. West (**CGE**); 1954, N. D. Simpson no. 54/084 (herb. Simpson). Enegras, Craig Gate, south-east of Rackwick, 39/1998,

1 August 1932, J. Sinclair no. 759 (herb. Sinclair) and H. H. Johnston no. 4532 (**BM, E**). South Burn, Hoy, 39/2099, 12 June 1929, H. H. Johnston no. 715 (**BM**); 23 August 1927, J. Sinclair no. 486 (herb. Sinclair); 14 July 1928, H. H. Johnston no. 4038 (**BM**). Roonie (? = Runcie) Gill, 39/2299, 26 July 1929, J. Sinclair no. 662 (herb. Sinclair); 15 August 1929, H. H. Johnston nos. 4241A (**E**) and 4245 (**BM**); 21 August 1938, J. Sinclair no. 1235 (herb. Sinclair). Valley Burn, Hoy, 12 July 1928, J. Sinclair no. 572 (herb. Sinclair) and H. H. Johnston no. 4007 (**BM, E**).

Hieracium caledonicum Hanb. (1889) 75; E. F. & W. R. Linton (1893) 178; W. R. Linton (1905) 26; Johnston (1913) 263; Spence (1914) 130; Johnston (1914) 210; Pugsley (1948) 106.

H. rubicundum Hanb. (1892) 208; E. F. & W. R. Linton (1893) 178; Johnston in Cryer (1913) 262; Johnston (1914) 210 *pro maximo parte*; Spence (1914) 130.

H. boswellii E. F. Linton (1893) 178.

[*H. pulchellum sensu* Spence (1914) 43.]

[*H. ? murorum sensu* Spence (1914) 43.]

H. rubicundiforme (Zahn) Roffey (1925) 26 no. 1028.

Grut Fea, Hoy, 30/1901, 8 August 1927, H. H. Johnston no. 2659 (herb. Sinclair). South-east of Enegars, Kame, Hoy, 880 ft. 30/1904, 19 August 1932, J. Sinclair no. 769 (herb. Sinclair). Berriedale, Hoy, 30/2001, 7 September 1914, H. H. Johnston no. 360 (**E**); 8 August 1927, J. Sinclair no. 470 (herb. Sinclair) and H. H. Johnston no. 3655 (**E**). West side of Waulkmill Bay, Orphir, 30/3706, 19 and 20 July 1912, H. H. Johnston (**E, CGE**); 3 August 1924, R. J Burdon (**CGE**); July 1953, C. West (**CGE**); 1954, N. D. Simpson nos. 54/085, 54/088 and 54/339 (herb. Simpson). Ward Hill, Rousay, 30/3829, 30 August 1916, H. H. Johnston no. 422 (**E**); 23 July 1917, M. Spence (**E**). Fitty Hill, Westray, 30/4244; 3 August 1934, H. H. Johnston no. 4948 (herb. Sinclair & **E**). Sea-cliff, Scapa, St. Ola, Mainland, 30/4308, 5 July 1912, H. H. Johnston (**E, CGE**); 1953, C. West (**CGE**). Scapa Pier, 30/4408, 18 July 1894, F. J. Hanbury (**CGE**); 17 July 1900, E. S. Marshall and W. A. Shoolbred as Linton Set no. 131 (**CGE**).

Sect. Foliosa Fries

Hieracium latobrigorum (Zahn) Roffey (1925) 29 no. 1230; Pugsley (1948) 272.

[*H. strictum sensu* Johnston (1882) 370; *sensu* Fortescue (1882) 370; *sensu* Bennett (1915) 55.]

H. strictum var. *amplidentatum* Hanb. *pro parte* (1894) 232 (*quoad loc.* Pegal Burn); *sensu* Spence (1914) 42.

[*H. corymbosum* var. *salicifolium sensu* Spence (1914) 42; *sensu* Johnston (1920) 43 and (1925) 6.]

[*H. auratum sensu* Spence (1914) 42; *sensu* Johnston (1925) 7.]

H. inuloides subsp. *striatum* var. *pseudauratum* Zahn (1921) 901; Johnston (1927) 411.

[*H. inuloides* subsp. *strictum* var. *amplidentatum sensu* Johnston (1929a) 8.]

[*H. crocatum* var. *normale sensu* Druce (1932 for 1931) 561.]

H. aestivum subsp. *hemitrachys* Druce & Zahn in Druce (1932 for 1931) 561 (Holotype: Pegal Bay, Hoy, August 1931, G. C. Druce (**OXF**)).

H. johnstonii Dahlst. in Johnston (1932) 8 (Lectotype: north side of Pegal Head, 13 August 1931, H. H. Johnston no. 4461 (**E**)).

H. polyphyllum Dahlst. in Johnston (1933a) 2 & 5 (Lectotype: Grassy sea cliffs between Lee Craig and Stanger Head, Hoxa Sound, Flotta, 15 August 1932, H. H. Johnston no. 4560 (**E**)); Johnston (1933b) 24; non Willd., Enum. hort. Berol., Suppl., 54 (1813).

H. subpolyphyllum Pugsl. (1946) 347 and (1948) 279 (Lectotype: that of *H. polyphyllum* Dahlst. non Willd.).

Hobbister Rocks, Orphir, 30/3805, August 1873, J. B. Syme (**BM, E**) and 1874 and 1879 (**BM**); August 1880, J. B. T. Fortescue (**BM**); July 1953, C. West (**CGE**); 1954, N. D. Simpson no. 54/098 (herb. Simpson). Pegal Bay, North Walls, Hoy, 39/3098, August 1880, J. B. T. Fortescue (**CGE, OXF**); 22 August 1894, H. H. Johnston (**E, CGE, OXF**); 9 August 1926, H. H. Johnston, no. 3484 (**E**); 20 August 1929, J. Sinclair no. 678 (herb. Sinclair); 13 August 1931, H. H. Johnston no. 4461 (**E**) and J. Sinclair no. 724 (herb. Sinclair); August 1931, G. C. Druce (**OXF**). Between Lee Craig and Stanger Head, Hoxa Sound, Flotta, 39/3793, 26 September 1924, H. H. Johnston no. 2847 (**E**); 15 August 1932, J. Sinclair no. 763 (herb. Sinclair) and H. H. Johnston no. 4560 (**E, BM**).

HIERACIUM MARITIMUM Hanb. (1904) 267; Pugsley (1948) 289.
[*H. inuloides* subsp. *strictum* forma *angustifolium sensu* Dahlst. in Johnston (1929a) 8; *sensu* Johnston & Sinclair (1930) 26; *sensu* Johnston (1934) 472.]

Aith Hope, South Walls, Hoy, 39/2989, 9 August 1928, J. Sinclair no. 596 (herb. Sinclair); 20 August 1929, H. H. Johnston no. 4258 (**E**, **CGE**).

Subgen. PILOSELLA Tausch

Sect. PILOSELLINA Fries

HIERACIUM PILOSELLA L. (1753) 800; Fortescue (1882) 370; Spence (1914) 41; Pugsley (1948) 314.

Bu Farm, Hoy, 30/2304, 5 July 1926, J. Sinclair no. 330 (herb. Sinclair). Swanbister, 30/3405, July 1849, J. T. Syme (**BM**). St. Andrews, Rousay in Spence (1914). Not uncommon on Mainland and Hoy according to J. T. Syme in Fortescue (1882).

var. TRICHOSCAPUM (Naeg. & Peter) Pugsl. (1948) 315.

Near Maeshow, Mainland, 30/3112, August 1880, J. B. Syme (**BM**).

Sect. COLLININA Naeg. & Peter

HIERACIUM AURANTIACUM L. (1753) 801, *sensu stricto*; Johnston (1927) 415.

Top of a stone wall, 90ft. alt., near the garden of Holland House, Papa Westray, 30/4851, 22 June 1926, H. H. Johnston no. 3330 (**E**).

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A STUDY OF VARIATION *EUPHRASIA* BY MEANS OF OUTDOOR CULTIVATION

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Abstract

Samples of *Euphrasia* from populations at six localities on chalk or limestone in the Midlands and south-east of England were cultivated in the garden in order to compare them without interference from environmental effects. The variation between populations in the wild and in cultivation is described. It was concluded that five samples were more or less normal *E. nemorosa*, differing only slightly from one another; also that one of them was mixed with, and apparently hybridising with, *E. stricta* (not previously known in Britain, and possibly an alien introduction). One population appeared to represent a slightly divergent ecotype of *E. nemorosa* and another an extreme ecotype of the same species. A hybrid between the latter and *E. pseudokerneri* appeared among the plants cultivated. Four more samples were grown a year later and it was concluded that these comprised three normal forms of *E. nemorosa* and a form of *E. confusa*.

Two forms of *E. anglica* showed fairly marked differences although growing only three-quarters of a mile apart. The differences may have been caused by hybridisation at one of the localities.

The cultures provided instructive information on interspecific and intraspecific variation in a taxonomic group in which the most closely related species are very similar to one another and in which variation within species is considerable.

Introduction

Owing to the fact that the species of *Euphrasia* are annual and semi-parasitic plants they show great variations in vigour. These may be seen within populations, but overall differences of vigour occur between populations as well. Ignorance of the effects of this variation on morphology suggested that the sampling of wild populations for morphological study would be unreliable. A large-scale garden trial cultivation was therefore undertaken to investigate variation in *E. nemorosa*. A small trial of *E. anglica* was carried out at the same time, and further populations of *E. nemorosa* were later compared by the same method.

The species of *Euphrasia* are variable, ill-defined, and subject to hybridisation, though each has several characters by which it normally differs from its nearest relatives (Yeo, 1955). In spite of the difficulty of recognizing even species on the basis of small and relatively inconstant characters, *E. nemorosa* was subdivided by Pugsley (1930) into five varieties, and Warburg (1952) stated that three of them were distinct ecologically and might prove to be worthy of treatment as subspecies. It was thought that the cultures might help in the understanding of some of these varieties, especially of var. *calcarea* Pugsl., since most of the samples of this species were collected from chalk or limestone.

Comparison of seven Euphrasia samples grown in the garden

Description of experiment

The ' whalehide pot ' method of cultivation was used in this experiment, which was carried out at Leicester in 1953. Each bituminized paper pot was planted in March with one seedling of *Euphrasia* and one of *Plantago lanceolata* ; the pots were then embedded in the garden; *Euphrasia* and host plants that died during the few days occupied by this process were replaced at once. The aim of the experiment was to compare the offspring

*Most of the work here described was done during the tenure of a Research Scholarship at the then University College of Leicester.

of wild populations from six localities when grown in the same environment. Six samples were grown in a set of randomised blocks, an arrangement which permits an analysis of variance to be made on the statistical data. There were six blocks, each consisting of six rows of fourteen *Euphrasia* plants each. Each sample of *Euphrasia* was represented by one row in each block. The individual plants were assigned to the blocks at random, and the order of the rows in each block was also chosen at random. A seventh sample, of which few seedlings were available, was grown in a row of ten plants near the main experiment.

On four occasions from mid-May to mid-June a record was made of the survival of the Euphrasias, signs of establishment on the host, and signs of disorder in the plants.

Leaves and flowers were taken from the plants and mounted on cellulose tape on glass. From each plant two leaves were taken, one subtending the last-but-one normally-developed branch or pair of branches (called ' leaf 2 '), and one from the fourth node above the uppermost branch or pair of branches (called ' bract 4 '). One flower from each plant was mounted; the aim in collecting these was to obtain mature full-sized flowers which had not begun to wrinkle or shrink. Most of the flowers chosen were therefore ones which had not been shed but which could be pulled off easily. The mounting was begun on 29 July 1953. Between 27 August and 7 September all the plants were pressed, except for some which were pressed early because they were wilting.

The height of the pressed plants was measured, and various measurements were made on the mounted leaves and flowers. For this purpose, the lantern-plate cover-glasses on which they were mounted were put into a projector and measurements were made on their enlarged images. In addition, photographs were taken of individual plants in the garden, and photographic contact-prints were made of the mounted leaves and flowers.

The *Euphrasia* seed for this experiment was extracted from many different plants of large or fairly large gatherings of herbarium specimens. The samples will be referred to by their serial numbers. The six samples used in the main part of this experiment were :

E151A	Juniper Top, Box Hill, Surrey, v.c. 17; flinty, rabbit-grazed turf on chalk;
E166	Watlington Hill, Oxon., v.c. 23; chalky field;
E167A	near Medmenham, Bucks., v.c. 24; chalky field (with E167B, see below);
E210	Waltham Quarry, Waltham on the Wolds, Leics., v.c. 55; grassland on oolite;
E211	near Croxton Kerrial, on Leics.-Lincs. border, v.c. 53/55; grassy track on oolite, about 6 miles from E210;
E215	Bedford Purlieus, Northants., v.c. 32; woodland ride on oolite, about 19 miles from E211 and about 17 miles from E210.

The additional group of 10 plants grown nearby, numbered E167B, was from the same locality as E167A and was growing mixed with it; all samples, with the probable exception of E167A, were considered to be *Euphrasia nemorosa*. At Box Hill the population of E151A was in contact with and apparently hybridising with *E. pseudokerneri*. Plants thought to be hybrids were excluded from the gathering.

Effect of replacement of dead seedlings

Many seedlings of *Euphrasia*, and some of the host, were replaced from 22 to 26 April, about four weeks after the initial potting-up and early replacement of the Euphrasias and hosts. Survival during May and June was slightly less good where replacements had been made, but the percentage of survivors probably established on the host was approximately the same whether replacements had taken place or not.

Variation between populations in survival and establishment

Table 1 shows that there was considerable variation in survival up to 31 May between the different samples. This variation was greater than that between the blocks, each of which contained all the samples. The table shows a similar result for establishment on the

host. These figures show that the populations differed from one another in characters affecting their establishment on the host provided and their survival in the garden at Leicester.

TABLE 1. Survival and establishment of *Euphrasia* in 1953 in the garden

	% of Euphrasias alive on 22-26 April that survived until 31 May	*% of surviving Euphrasias probably established on host on 31 May*
Sample		
E151A	50	44
E166	73	83
E167A	81	84
E210	93	85
E211	92	94
E215	82	67
Block		
1	83	74
2	85	75
3	87	75
4	77	81
5	75	80
6	74	81

Deaths of plants later in the season, after they had become established on the host, were mostly due to fraying of the stem base, which in turn was probably the result of attacks of damping-off fungi upon the young seedlings. Many plants which did not die wilted readily in dry weather from this cause. However, the sample E151A, which suffered the heaviest mortality before establishment, showed no ill effects from stem-fraying, apparently because of its dwarf habit.

Variation between populations in habit

Variation in habit is illustrated by photographs of some of the living plants, and by height measurements. Some of the leaf characters will also be considered here.

The plants grew with great luxuriance, and as a result all samples were much more bushy than their wild parents had been. Sample E151A (Plate 10a) was dwarf, with short internodes, few branches, and flowering from a relatively low node. The leaves were very thick and readily developed anthocyanin; their green colour was pale and they were not shiny. The areas between the veins were flat on the upper surface of the leaves and very slightly concave beneath; the veins appeared on the upper surface as narrow grooves. In all these characters E151A was different from all the other samples, except E167A, which resembled it in its development of anthocyanin.

Sample E166 (Plate 10b) was characterised in habit by its small leaves which left the branches more exposed than in other samples.

The remaining samples were all very similar in habit, but E167A (Plate 10c) was distinguishable by its leaf-shape, which will be described later, and by the considerable development of anthocyanin in its leaves.

The other three samples, E210, E211 and E215, could not be distinguished from one another in the garden by habit and foliage. It can be seen from Plate 10d, that the leaf surface was similar to that of E166 and E167A.

The measurements of plant height, together with numerical data obtained for ten other characters (Table 2), have been subjected to an analysis of variance. This work was kindly carried out by Dr. D. A. Wilkins at the Scottish Plant Breeding Station. It was found that, in all eleven characters, differences existed among the populations significant at the 0·1% level of probability.

For the character of plant height (character 1), Tables 2 and 3 show that E151A was significantly shorter than all other samples, and that sample E167A was significantly shorter than the two tallest samples. Table 2 shows that E151A was in fact only about half the height of E210 and E211.

Variation between populations in leaves

The leaves of the populations are illustrated in Fig. 1 a-f. Differences between samples E166, E210, E211 and E215 are not very noticeable in the silhouettes, but E151A and E167A are conspicuously distinct. E151A (Fig. 1a) has disproportionately few teeth for the size of its leaves and the teeth are necessarily relatively large (Table 2, character 5). The same applies to E167A (Fig. 1c) in lesser degree, but this sample has the longest teeth of all. The leaves of E167A are also more elongated and have the teeth directed more towards the apex than in other samples. Table 3 shows which of the measured or counted differences are statistically significant. It is noteworthy that there are no significant foliar or habit differences between E210, E211 and E215, which were the samples that could not be distinguished by these characters when they were being grown. A comparison of the figures for the length and breadth of the leaves (Table 2) indicates a variation between the samples in leaf shape.

TABLE 2. Averages of measurements made on *Euphrasia* plants

(Measurements in cm for character 1, in mm for characters 2-11; greatest and least averages for each character are in bold type)

	Population					
	E151A	E166	E167A	E210	E211	E215
Habit character						
1. Height of plant after pressing	**12·7**	22·7	18·9	**25·4**	25·0	22·6
Foliar characters						
2. Length of ' bract 4 ' (see p. 225)	**9·41**	10·2	**13·2**	12·2	11·9	10·7
3. Breadth of ' bract 4 '	11·2	**10·4**	11·9	**13·0**	12·0	11·7
4. Greatest no. of teeth on a side of ' bract 4 '	**0·53**	0·91	0·73	**1·10**	0·97	1·02
5. Length of distal side of a tooth on the widest part of ' bract 4 '	1·90	**1·56**	**2·09**	1·97	1·74	1·91
Floral characters						
6. Length of upper lip of corolla plus tube	7·31	**6·56**	7·79	7·56	7·60	**7·93**
7. Length of lower lip of corolla plus tube	8·19	**7·60**	9·04	8·74	8·67	**9·17**
8. Length of mid-lobe of lower lip of corolla	**2·90**	**2·13**	2·76	2·70	2·67	2·71
9. Depth of emargination of mid-lobe of lower lip of corolla	**0·59**	0·60	0·81	0·79	0·90	**0·99**
10. Breadth of base of mid-lobe of lower lip of corolla	1·3	**1·2**	1·5	**1·7**	1·6	1·6
11. Greatest breadth of mid-lobe of lower lip of corolla	2·27	**1·97**	2·37	2·71	2·73	**3·07**

TABLE 3. Characters in which pairs of *Euphrasia* samples showed a statistically significant difference ($P = 0{\cdot}1\%$)

(Characters numbered as in Table 2)

Pairs of samples	*Characters in which pairs of samples differed significantly*		
	Habit	*Foliar*	*Floral*
E151A and E166	1	4, 5	6, 7, 8, 11
E151A and E167A	1	2, 4	6, 7, 9
E151A and E210	1	2, 3, 4	7, 9, 10, 11
E151A and E211	1	2, 4	8, 9, 10, 11
E151A and E215	1	4	6, 7, 9, 10, 11
E166 and E167A		2, 4, 5	6, 7, 8, 9, 10, 11
E166 and E210		3, 4, 5	6, 7, 8, 9, 10, 11
E166 and E211			6, 7, 8, 9, 10, 11
E166 and E215		5	6, 7, 8, 9, 10, 11
E167A and E210	1	4	10, 11
E167A and E211	1	4, 5	11
E167A and E215		2, 4	9, 11
E210 and E211			9
E210 and E215			9, 11
E211 and E215			7, 11

Leaves of two untypical plants, plant 1 of E151A (counting from left to right) and plant 2 of E167A, have been included in Fig. 1. These will be discussed later.

The number of teeth on a side of ' bract 4 ' attained for each population the following maxima :—

E151A	4 teeth	(attained by about $\frac{3}{4}$ of plants)
E166	7 teeth	(attained by about $\frac{1}{2}$ of plants)
E167A	6 teeth	(attained by about $\frac{1}{8}$ of plants)
E210	9 teeth	(attained by about $\frac{1}{5}$ of plants)
E211	8 teeth	(attained by about $\frac{1}{6}$ of plants)
E215	8 teeth	(attained by about $\frac{1}{3}$ of plants)

When the two untypical plants were omitted, each population produced its maximum tooth-number in each of the six blocks of the field trial. It seems, therefore, that there was a characteristic maximum tooth-number for each population, which was not attained by all individuals. It is interesting to note that E210 had a greater maximum tooth-number than E211 and E215, which it closely resembled (p. 226).

Variation between populations in flowers

This variation is also shown by Tables 2 and 3, and some flowers are illustrated in Fig. 2 a-f, p. 230. It is clear that samples E151A and E166 were the most distinctive in flower shape : E151A by its fan-shaped lower lip with the lobes shallowly emarginate and weakly dilated in relation to their length, and E166 by its small size and narrowly emarginate lobes, the lobules on either side of the emargination tending to turn in. E210, E211 and E215, with no significant habit or foliar differences, were also found to differ in their flowers. The tables show that E210 has a less deeply emarginate mid-lobe than the other two, E215 has a longer lower lip and tube than E211, and E215 has a wider (more dilated) mid-lobe than either E210 or E211.



Fig. 1. Leaf silhouettes of *Euphrasia*, $\times \frac{2}{3}$. a–g, ' bract 4 '; h and i, ' bract 6.' a, E151A; b, E166; c, E167A; d, E210; e, E211; f, E215; g, E167B; h, E168; i, E219.

Variation within populations

Dr. Wilkins calculated the standard deviations of each of the six populations for one foliar and one floral character. These are given in Table 4; they show that E210 and E211 were the most variable populations. The wild populations at the localities of E210 and E211 were numerically larger than the other four populations, and they were certainly sampled over a larger area than the others, except possibly E167A, which also formed an extensive population although it was not extremely abundant.

Population E151A was very uniform. However, it included one untypical plant that stood out sharply from the rest. Compared with the other plants of this population, it will be seen from Fig. 1a that this plant had 5 teeth on a side of ' bract 4 ' instead of 3 or 4. In addition the corolla lobes were broader, the leaf surface not so flat, the habit more branched, and the flowers more abundant.

This untypical plant was evidently a hybrid between E151A and *E. pseudokerneri* which grew at the same locality, and it seems likely that it was an F1 hybrid, in view of the effort made to exclude hybrids from the original collection of E151A.



Fig. 2. Corollas of *Euphrasia*, upper and lower lips separated. a, E166; b, E151A; c, E167A; d, E210; e, E211; f, E215; g, E219; h, E168.

TABLE 4. Standard deviations for *Euphrasia* populations
(Unit of measurement = 1 mm)

Population	*Standard deviation for length of 'bract 4'*	*Standard deviation for greatest width of mid-lobe of lower corolla-lip*
E151A	0·97	·217
E166	1·83	·181
E167A	1·62	·374
E210	2·34	·390
E211	1·96	·501
E215	1·62	·326

The other plant with an untypical leaf shape belonged to population E167A. The leaf of this plant was, however, similar in shape to those of the populations E166, E210, E211 and E215; it was the only 'bract 4' produced by E167A with more than six teeth on one side. Leaves of this shape also occurred in plants 1, 2, 3, 4 and possibly 6 of E167B (Fig. 1g), counting from left to right). The leaves of the only other two survivors out of the original ten plants of E167B were like those of E167A , though the leaf of plant 5 is perhaps intermediate, as were some of the leaves of E167A. The occurrence of intermediate leaf-shapes suggests that the two forms were hybridising.

Comparison of wild and cultivated plants

The wild plants of E151A were extremely dwarf and compact, but freely branched. The leaves were few-toothed, and fleshy-looking but shiny. The plants were seeding freely when collected on 24 July 1952, which is an early date for *E. nemorosa* to be in such an advanced condition. E166 was taller and had longer internodes than E151A, but was dwarfer and had smaller leaves and flowers than the other populations. E167A had a distinctive leaf-shape, but was otherwise rather similar in habit to the remaining three populations. The latter were all collected on the same day, and appeared to differ slightly from one another, E211 having stout, dense flowering spikes, and E215 particularly long internodes, compared with E210.

Population E151A, which was the most distinct in the field, was also the most distinct in cultivation. Its few leaf-teeth, dwarf habit, and early flowering were shown to be hereditary, although the internodes were not quite as short in cultivation as in nature. The leaves became even more fleshy in cultivation, and developed a flat, non-shiny surface.

In cultivation, population E166 was little different from E210, E211 and E215, except in its small leaves and flowers; it looked about as distinct as it did in the wild. E167A in the main retained its characteristic leaf-shape in cultivation. The slight differences which E210, E211 and E215 showed in the wild disappeared in cultivation, where they could not easily be distinguished by eye. E215 was in fact the shortest of these three in cultivation, in spite of having had the longest internodes in the wild. On the other hand small differences between these samples were detected statistically.

CULTIVATION OF FURTHER SAMPLES IN 1954

In 1954 an attempt was made to repeat the 1953 experiment on a smaller scale, using another five *Euphrasia* populations. The plants were grown at Cambridge by the method used at Leicester, but conditions were apparently less favourable, and very few plants survived. However, a fairly good idea of the characters of four of the populations was obtained. These were believed to be *E. nemorosa* and were as follows :

E417 between Warslow and Elkstones, Staffs., v.c. 39; long grass and stony patches by roadside on acid moorland but accompanied by some more or less calcicolous plants;
E421 Friday Street, Surrey, v.c. 17; sandy field;
E429 West Harling Heath, W. Norfolk, v.c. 28; calcareous sandy soil;
E430 Devil's Dyke, Cambs., v.c. 29; on part of chalk dyke levelled in 1943.

In general appearance the cultivated plants of three populations (E417, E421 and E430), although distinguishable by eye, were much like E210, E211 and E215 grown in 1953. E417 showed the closest resemblance to the 1953 samples just mentioned, being very vigorous and rather large-leaved. E430 and E421 were rather smaller plants with somethat narrower leaves, E421 differing from E430 in that its branches diverged for a greater proportion of their length and became vertical only at the tips. The fourth population, E429, had smaller leaves and thinner stems than the others, and it was not so tall as E417. Most of the E429 plants were quite luxuriant, however, for they produced a great profusion of branches; these were usually widely spreading and somewhat flexuous.

The flowers were largest in E417 and smallest in E430, and the flowers of E429 differed from those of the other samples in being lilac instead of white. The flower-shape was different in each sample.

Wild populations of the 1954 culture

The differences between the 1954 samples in cultivation were mostly similar to differences seen in the wild plants from the same localities. The distinctive features of the cultivated E429 were all evident in the wild except for the low spreading habit.

Comparison of samples of E. anglica grown in the garden

Two samples of *E. anglica* were grown in the garden at Leicester in 1953. There were ten ' whalehide ' pots for each sample, and each pot was planted with two *Euphrasia* seedlings and a plant of *Luzula campestris*. The pots of each sample were arranged in a row, the two rows being side by side. The seed of the two samples (E168 and E219) was collected from two localities three-quarters of a mile apart in Charnwood Forest, Leicestershire.

The two populations differed in habit in cultivation, E168 having shorter internodes than E219. The average height after pressing of the 13 surviving plants of E168 was 7·2 cm (range : 3·3–9·3 cm), and that of the 16 survivors of E219 was 11·1 cm (range: 4·4–16·5 cm).

' Bract 6,' defined in the same way as 'bract 4' (p. 225), was mounted for each plant (Fig. 1h, i). In E168 the bracts did not attain so large a size as in E219, and they also had fewer teeth, the greatest number of teeth on a side of ' bract 6 ' averaging 5·0 in E168 (range: 4–6) and 6·2 in E219 (range: 5–7).

The flowers of E168 were smaller, but more uniform in size, than those of E219, and they also differed from them in shape (Fig. 2g, h, p. 230). Some measurements were made on the flowers. The depth of emargination of the mid-lobe of the lower lip averaged 0·39 mm in E168 and 0·67 mm in E219. In E168 the width of the mid-lobe averaged 1·29 mm at the base and 1·63 mm at the widest point, while in E219 it averaged 1·49 mm at the base and 2·23 mm at the widest point.

Taxonomy

The three most distinct forms of supposed *E. nemorosa* that were cultivated were E151A, E167A and E429. In order to look for further populations of the type of E151A I spent two days in 1954 at Box Hill and Mickleham Downs. The area from which E151A had been collected was revisited and the same form collected again. Several other gatherings of *E. nemorosa* from both grassy fields and dry chalky slopes were made, but none was at all like E151A. They appeared to be fairly normal forms of *E. nemorosa*, although

PLATE 10



a



b



c



d

Euphrasia plants growing in the garden; the plants were luxuriant and each photograph shows only a portion of a plant. a, E151A; b, E166; c, E167A; d, E211.

those from the poorest habitats were the most dwarf. The form represented by E151A appears to deserve taxonomic recognition on morphological grounds, but it does not seem to be worth while to accord it such recognition when only one colony is known. In view of its similarity to *E. nemorosa* in leaf-outline and flower-size, it seems best to regard it as an extreme ecotype of that species.

Regarding the plants from Medmenham (E167A and B), I consider that two species were present, *E. stricta* Lehm., represented by nearly all the cultivated plants of E167A, and *E. nemorosa*, represented by one cultivated plant of E167A and four or five of E167B. Other samples of *E. stricta*, obtained from foreign sources, that I cultivated, had long, very acute leaf-teeth, similar to those of E167A, and they were usually rather few in number. The upper cauline or lower floral leaves were usually rather narrow, and some had a rather rounded base, but others were truncate. Usually *E. stricta* has rather large lilac flowers, and few short erect branches. These two characters were lacking in E167A. However, they are not always present in *E. stricta*, and Professor W. Rothmaler, to whom I sent plants of the same type as E167A, collected in 1954 from the same locality, considered that they were *E. stricta* forma *parviflora* Sag.

After the publication of Wettstein's (1896) monograph, *E. stricta* was widely reported from Britain. In Pugsley's (1930) revision, however, *E. stricta* was not accepted as occurring in Britain; plants previously identified as *E. stricta* were referred by him to *E. nemorosa*, *E. confusa* and *E. pseudokerneri*. I find these identifications acceptable, but I have encountered a few populations of *E. nemorosa* in which there were resemblances to *E. stricta*, and it may be that *E. stricta* was formerly in Britain, or has been introduced from time to time, but has in most places been unable to maintain itself as a distinct entity. Probably *E. stricta* was introduced at Medmenham, possibly at the same time as another alien that was growing with it, namely *Prunella laciniata*. A description of *E. stricta* follows.

EUPHRASIA STRICTA, Wolf ex J. F. Lehmann, Primae linae Florae Herbipolensis, 43 (1809), *emend.* Host, Flora Austriaca, **2**, 185 (1831).

Stem erect, usually with 0–4 pairs of erect branches, cauline and few to many of the lower floral internodes 1½–3 times as long as the leaves, upper floral shorter than the leaves; flowering commencing at the 7th to 12th node. Leaves glabrous or nearly so, usually strongly pigmented with anthocyanin; cauline ovate or narrowly ovate, obtuse or acute, up to *c.* 14 mm long, with up to 5 pairs of obtuse, acute or aristate teeth; floral leaves relatively broader, ovate or rhombic, acute, more or less rounded or cuneate at base, with 4–6 acute or aristate teeth, teeth of upper cauline and floral leaves directed towards the apex of the leaves. Calyx 4·5–6 mm long, with long slender aristate teeth. Corolla white or lilac with the usual markings, (5·5–) 8–11 mm long, measured from base of tube to apex of upper lip. Capsule rounded, truncate or retuse at apex, 4–6 mm long, almost always distinctly shorter than the calyx-teeth.

E. stricta is widespread in Europe as a plant of dry grassland. It is best distinguished from *E. nemorosa* and *E. pseudokerneri*, its nearest allies in Britain, by its habit and foliage.

The National Grid Reference of the locality at Medmenham, Bucks., v. c. 24, is 41/8186. The plant was collected from a chalky pasture and a rough field by a wood on 12 August 1952 (Yeo, no. E167A, E169A) and 19 August 1953 (Yeo, no. E401A, E402A).

The small leaves, short internodes, ascending main stem, and abundant, spreading and often flexuous, branches of E429 are characters of *E. confusa*. Wild plants from the Breckland locality of E429 differed from the cultivated E429 in being more erect and *nemorosa*-like in habit. Excursions to the Breckland, made since 1954, have shown that plants which are identical with *E. confusa* from the West of England occur there; in addition, there are many populations which, although similar to *E. confusa*, show some resemblance to *E. nemorosa*. Most of these populations are probably best referred to *E. confusa*, a species which was first identified as occurring in the Breckland by Pugsley in 1939 (specimen in **CGE**).

The experiments described here have emphasized the differences between these three distinctive forms. The hereditary character of the distinctive habit of E151A has been confirmed and a number of lesser differences which together have a considerable effect on the appearance of the cultivated plants have been brought out; the distinctive leaf-shape of E167A was easier to appreciate in the luxuriant cultivated plants; the small leaf-size of E429 was still evident in the luxuriant plants, while habit differences from *E. nemorosa* were increased.

The remaining samples of *E. nemorosa* were all slightly different from each other in cultivation but the differences were not always the same as the ones they showed in the wild; the experiment thus revealed examples of phenotypic and genotypic variation between populations of generally similar plants. This general similarity was evident among samples collected over a fairly wide geographical area. The most distinct population among these was the small-leaved, small-flowered E166 from Watlington Hill. Its characters are probably a response to the dryness of the habitat, and the form can thus be regarded as an ecotype of *E. nemorosa*, though a much less extreme one than E151A.

The differences shown by the two populations of *E. anglica* that were grown are quite considerable in view of their separation in the wild by only three-quarters of a mile. However, *E. nemorosa* was growing with E219, but not with E168.

Conclusions

Cultivation showed that all samples compared differed genetically. This indicates some degree of reproductive isolation, which in most cases must be due to the spatial separation of colonies. Where the differences are slight they can tentatively be attributed to chance; where they are rather larger and have been classed as ecotypic they can be attributed to response through selection to special habitat conditions. The differences, of a similar magnitude to the ecotypic ones, between the two populations of the diploid species *E. anglica* which were compared may well be due to introgressive hybridisation, for the tetraploid *E. nemorosa* was growing with E219, but not with E168. There is evidence (Yeo 1956) that introgression takes place from tetraploid species into diploid species of *Euphrasia*, and it is, therefore, possible that this had occurred at the locality of E219.

Another population of *E. anglica*, growing some miles away from E168 and also unmixed with any other species, was cultivated in the greenhouse with additional plants of E168 and, although found to differ from it in flower-shape, leaf-shape and habit, the differences were never greater, and were mostly smaller, than those between E168 and E219.

The differences between sample E167A and the samples of *E. nemorosa* compared with it are considered to indicate that E167A is *E. stricta*, while the differences between E429 and samples referred to *E. nemorosa* are considered to indicate that E429 is *E. confusa*.

There were indications that hybridisation was taking place between *E. nemorosa* and *E. stricta*, two rather similar species with the same chromosome number which would be expected to hybridize freely, judging by the behaviour of other *Euphrasia* species.

The observations on variation within *E. nemorosa* can do no more than provide a useful initial contribution to the material required for the evaluation of the varieties of this species.

Cultivation was considered necessary in order to eliminate the effects of phenotypic variation in vigour before making morphological comparisons. However, the results of comparing the very well-grown plants of rather uniform vigour suggest that at least leaf-shape and flower-shape can be reasonably satisfactorily compared in wild material on the basis of selections of the more vigorous individuals.

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THE BRITISH FORMS OF *TUBERARIA GUTTATA* (L.) FOURREAU

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Abstract

An account is given of the variation in British *Tuberaria guttata*, and of its previous taxonomic treatment : the taxonomic value of various characters is examined. Most of the Welsh and Irish plants including the type population of *Helianthemum breweri* Planch. differ from *T. guttata* as it occurs in the Channel Isles and northern France in their shorter stature, the more common presence of bracts and other characters. All the characters said to distinguish *breweri* intergrade continuously with those of typical *guttata* in both herbarium and cultivated material, and are only loosely correlated. The more compact Welsh and Irish plants appear to be comparable with plants in similar exposed coastal habitats in north-west France. It is concluded that *T. guttata* shows ecotypic differentiation in relation to exposure on the Atlantic coast of Europe, and that the populations combining short diffuse habit and numerous bracts may be of polytopic origin. It is suggested that they should not be given formal taxonomic recognition.

1. Introduction

Like a number of other widespread Mediterranean species, *Tuberaria guttata* extends northwards up the west coast of Europe to a northern limit in the British Isles. Up to the north coast of France its distribution is more or less continuous, and the Channel Islands lie on the northern fringe of this essentially continuous area. But north of the English Channel its range is disjunct, and it occurs only in widely separated colonies on the coasts of north Wales and western Ireland. Plants from the best known of these colonies, on Holyhead Mountain in Anglesey, were described by Planchon in 1844 as a new species, *Helianthemum breweri*, and, as a variety or subspecies, *breweri* has become firmly established in the British literature. Authors have differed considerably in the value they have attached to the various characters said to separate it from typical *T. guttata*, and in the British populations that they have referred to *breweri* and to *guttata*. Most seem to have assumed that it was deserving of taxonomic recognition, and that all British plants could be assigned satisfactorily either to *breweri* or to *guttata*. The purpose of this paper is to show that none of the delimitations of *breweri* proposed hitherto is completely satisfactory, and that the variation pattern in *T. guttata* in Britain and neighbouring parts of the Continent is more complicated, and taxonomically intractable, than has usually been assumed.

2. The History of Helianthemum breweri Planch.

The Holyhead colony of *Tuberaria guttata* was discovered by Samuel Brewer in 1726 (see Hyde 1930). Dillenius wrote to Brewer on 31 May 1727 ' I desire him (i.e. the Rev. Mr. Green) to look after the plant you sent from Holyhead . . . . It is a *Cistus* and seems to be new.' Brewer received further specimens of the plant from Mr. Green on 5 August 1727. Dillenius had evidently intended to describe the plant himself, but, in the event, it was first mentioned in print over half a century later by Hudson (1778), as '*Cistus guttatus* . . . . Habitat *in pratis arenosis*, *in monte* Llech ddû *prope* Holyhead *in insula* Mona.' Curtis (1775–98) figured under the same name a bracteate and spotted-petalled plant, but did not say whether it was wild or cultivated, and gave the Isle of Man as a locality, evidently mistranslating ' Insula Mona.' In this he was followed by Sowerby & Smith (1790–1814, t. 544), who figure a rather stiffly formal little plant with numerous bracts and say that ' Having no hopes of obtaining wild specimens in a state fit for drawing, we have been

obliged, like Mr. Curtis, to have recourse to a garden one, communicated by the Rev. Mr. Watts, F.L.S. of Ashill, Norfolk . . . ' Smith (1800) gave the localities ' In Jersey, Sherard. In the Isle of Man, Mr. Brewer. Huds.' and his description notes ' . . . saepius ebracteati, interdum bracteis lanceolatis, solitariis, ad basim pedicellorum.' Later (1825), quoting the Rev. H. Davies, he correctly gave the locality as Anglesey. Supposedly Manx plants were distributed by Dickson (*Hortus Siccus Britannicus*), 1793–9, but the specimens are tall slender plants quite unlike any other British examples of *T. guttata*. As far as I know, there is no other evidence that they actually came from the Isle of Man, and they are probably garden specimens to which the name of the (supposed) best-known British locality was attached.

Planchon knew *T. guttata* well in the south of France, and saw specimens of the Holyhead plant in the herbarium of W. Wilson of Warrington. He says (Planchon 1844) ' the straggling mode of growth, with short, numerous and dichotomous bunches of flowers, the existence of bracteas even to the upper flowers, and of pedicels, which at first bend down, but rise up when the fruit is ripe and stand at an angle of forty-five degrees to the axis of the cluster, such were the characters, which at first glance, suggested the idea that the plant was specifically distinct from *H. guttatum*.' Planchon knew that cultivation made no difference to ' the main point,' the presence of bracts. He gives a terse diagnosis, followed by a longer Latin description:

HELIANTHEMUM BREWERI, Planchon

Helianthemum (e sectione Tuberaria); annuum a basi ramosum subdiffusum viscidulo-hispidulum, pedicellis bracteatis, defloratis subdeflexis, fructiferis erecto-patentibus, petalis angustis immaculatis, staminibus 8–12, seminibus quam in H. guttato majoribus.

Citus guttatus, *Huds. Fl. Angl.*, p. *232*, *ex local. citat.*

Cistus guttatus, *Smith Fl. Brit. t. 2, p. 573, (pro parte et quoad plant. Brewerian, non Engl. Bot.).*

HAB. Anglesey, Mr. Brewer, (Hudson), Holyhead Mountain, *Rev. Mr. Williams*, and also near Amlwch, *Rev. H. Davies*, *W. Wilson*, *Esq.*

Herba a basi ramosa, vel, axi abbreviato pluricaulis, viscidulo-hispida. Caules 4–6, subdiffusi, semel bis-trichotomi, in racemos laxos, bracteatos desinuentes. Folia pauca, opposita, sessilia ,inferiora 4–6, rosulata, late obovata, semipollicaria, obtusissima; caulina stipulata, lineari oblonga, obtusiuscula, omnia pilis stellatis simplicibus intermixtis, utrinque hispidula. Bracteae conspicuae, lineares, non raro falcatae, inferiores 3–4 lin. longae, hinc ad summos flores gradatim minores, nunquam deficientes. Pedicelli graciles, 6–8 lin. longi, floriferi subdeflexi, deflorati diu sic persistentes, tandem, maturo semine, erecto-patentes. Calyx ut in *H. guttato*. Sepala conspicue nigropunctata; trium majorum alterum latus in praefloratione tectum, petaloidea-membranaceum. Petala in flore unico observata, angusta, lutea, immaculata. Stamina definita (8–12) pistillo vix longiora. Ovarium et fructus vix *H. guttati*, sed semina pauciora et evidenter majora.

Planchon emphasised the short diffuse habit of growth and the presence of bracts as the most important characters of his new species. He had seen an imperfect specimen of the Jersey plant, and considered it ' merely a hispid variety of *H. guttatum*.'

The *Annals and Magazine of Natural History* for the same year contains an account of a meeting of the Botanical Society of London, at which W. R. Crotch exhibited specimens of Planchon's new species, and a note by C. C. B[abington] reporting ' true *H. guttatum*,' collected at Three Castles Head by Miss H. Townsend.

H. breweri appeared in the second edition of Babington's *Manual of British Botany* (1847) as a separate species, the presence of bracts being given as a diagnostic character. Bentham (1858) says rather non-committally ' . . . the Anglesea specimens are rather stunted, with the leaves broader than usual, and have been published as a species under the name of *H. Breweri*.' Hooker and Arnott (1860) give *breweri* as a variety under *H. guttatum*. In the seventh edition of the *Manual* (1874), Babington reduced *breweri* to a variety of *guttatum*, and altered the description to ' Racemes with or without bracts on the same plant.' Syme (1864) and Hooker (1870) rank the plant as a subspecies of *H. guttatum*. Inishbofin, W. Galway, was added to the list of localities of var. *breweri*

by A. G. More (1876), and appeared in the ninth edition of Babington's *Manual* (1884); according to Praeger (1901) ' The var. *Breweri* accompanies the type at Three Castles Head and Inishbofin, and alone grows on Inishark.' (see below for detailed list of localities).

Planchon's conclusions seem to have been generally accepted by British botanists, who contrasted *breweri* with the Channel Islands plant : indeed tall ebracteate plants from the *locus classicus* of *breweri* were named *guttata* by J. G. Baker (Druce 1890, 1891). But Griffith (1895) says ' I have sown seeds of the supposed *H. guttatum* and seeds of undoubted *H. Breweri* from the same place in rich soil in my garden, with the result that they all turned out to be the same – viz. *H. Breweri.*' In this conclusion he is strongly supported by Druce (1902) who considered that ' . . . the characters given to *H. breweri* both by its original describer and subsequent writers will need amending; as those of bracteate inflorescence, diffuse growth, and unspotted petals given by Planchon are found to be inconstant . . . . Still, the Anglesey plant has a different facies from the *H. guttatum* of Jersey, the leaves being broader and more obovate, and of a more coriaceous texture . . and I think it to be a good geographical race.' Druce had earlier (1893) named the ebracteate plants from Holyhead ' f. *ebracteata.*'

Grosser (1903), regarding *T. guttata* on a continental scale, united populations on the west coast of Europe from Wales and Ireland to Portugal in var. *breweri.* The main diagnostic characters of his variety are low, diffuse habit, and the pubescence of the leaves, which are described as hispid and densely stellate-tomentose on both surfaces : he makes no mention of bracts. The distribution of the variety is given as ' Strandgebiete von West-England und Nord-West-Frankreich entlang der westfranzösischen Kuste bis in das maritime Nord- und Mittel-Portugal (Sierra de Cintra).' He cites *Welwitsch It. Lusit.* (1840) *nos.* 433, 1317, 1526 and (1851) *no.* 49, and includes *H. guttatum* var. *maritimum* Lloyd and *H. litorale* Rouy and Fouc. as synonyms. As he included England among the localities for his var. *genuina*, it seems that he accepted the opinion of British botanists that at least the Channel Islands material belonged to typical *T. guttata.*

Warburg (1952) accepts Grosser's statement of the Continental distribution of *T. guttata* var. *breweri*, and his description and account of its British distribution follow accepted British opinion. In my account of *T. guttata* for the *Biological Flora* (Proctor 1960), I suggested that the name *breweri* should be limited to the Welsh and Irish populations; though recognising that the taxon so defined was not completely satisfactory. At my suggestion, Dr. Warburg adopted this delimitation of subsp. *breweri* in the second edition of the *Flora* (1962).

3. The variation in British T. guttata

(*a*) *Distribution*

I believe the following list of the British localities of *T. guttata* is substantially complete: I have cited specimens and literature records only in the case of less well-known localities, or where the record is otherwise interesting.

V.c. S. CHANNEL ISLANDS. Jersey: West Mount, St. Helier; Noirmont; St. Brelade's Bay; Beauport; La Moye; Portelet; Corbière; Petit Port; headland north of Petit Port; L'Etac (Lester-Garland 1903); above Pinnacle Rock, between L'Etacq and Grosnez (F. Le Sueur, March 1960); ' observed in Jersey by Mr. Sherard on the west-side of the Island near Grosnez Castle.' (Ray 1690 p. 238); Grosnez (Lester-Garland 1903). Alderney: south coast, on cliff top west of Val du Sud. (Except where specific references are given, specimens from all localities are in either **K**, **BM** or **CGE**).

49. CAERNS. Mainland opposite Bardsey I. (1938, W. Hughes D'Aeth), 1939 (and det.) Miss B. M. Morgan (*Rept. Bot. Soc. Exch. Cl.* for 1943–4, 705 (1946)).

52. ANGLESEY. Holyhead Mountain, S. Brewer, 1726, and many more recent collectors; near Porthdafarch, C. C. Townsend, 8 July 1952 (herb. Townsend); ' Lady Verney tells me she has found this [*H. breweri*] in another locality about three miles from the *locus classicus* in Anglesey.' (Druce 1919) (Perhaps the same locality as the last); between Clegyr Mawr and the

sea, Llanrhyddlad (Griffith 1895, as *H. breweri*); Gader [Trwyn y Gader = Carmel Head] in the parish of Llanvair in Cornwey [Llanfairynghornwy] at the north end of the Island facing the Skerries about half a mile from the sea upon the rocks where the soil is not deep, among the *Scilla bifolia* and *Sedum rubens:* it flowers in June. Mr. Williams [undated] (BM); . . . . . Amlwch, i.e. N.W. of the Village among Heath, before the discovery of the great copper mine, plentifully, H. Davies [undated] (BM).

H3. W. CORK. Three Castles Head (Babington, 1844; Moore & More, 1866, as *H. guttatum*); *ibid.*, type and var. *breweri* (Colgan & Scully 1898; Praeger 1901); Calf Islands (Praeger 1934).

H16. W. GALWAY. Inishbofin (type and var. *breweri*), Inishark (var. *breweri*) (Colgan & Scully 1898; Praeger 1901).

H27. W. MAYO. Inishturk (Praeger 1934).

(*b*) *Cultivation experiments*

My own cultivation experiments were begun in 1953, the most extensive being carried out in 1956, 1959 and 1961 (see Figs. 3–6). It was found most convenient to grow plants singly in four-inch pots (1956) or in rows in boxes (1959, 1961). The seeds are hard-coated, and it often proved difficult to germinate enough seeds from all the populations at nearly enough the same time for the seedlings to be comparable. Plants grown from wild-collected seedlings were several weeks more forward than those grown from seed germinated in the garden, and all plants took much longer to flower and fruit than in the wild. Indeed in Cambridge it was often difficult to induce the Three Castles Head plants to flower at all.

T. guttata is a plastic species, and the different conditions of different years produced very different-looking plants, so that comparisons cannot be made between populations grown in different seasons. However, the relative differences between populations in any one season were not greatly affected. From comparison of several years' results I am satisfied that the main conclusions set out below are generally true, though further experiments would quite probably produce results differing in detail from mine. In spite of some difference in the age of the seedlings, plants from any one population were generally rather uniform in size and other characters, and I found no evidence for the coexistence of two taxa in any British population.

In a number of cases seed was saved from cultivated plants for later experiments. This was made easier by the fact that the plants grown were apparently all normally self-pollinated: as additional precautions, plants kept for saving seed were isolated as far as possible, or seed was used which had set when other populations were not in flower.

(*c*) *General observations on the taxonomic characters*

Of the characters emphasised by Planchon, the ' narrow unspotted petals ' were based on observation of only a single, aberrant, flower. Seed size has received little attention. Seed lengths for a number of samples of *T. guttata* are given in Table 1. There is an evident tendency for the northern and western populations to have somewhat larger seeds, but there is too much local variation, both in north and south Europe, for this to be a useful diagnostic character.

The presence of bracts was recognised to be inconstant by Babington and Druce, and the size and number of bracts produced depends at least in part on environmental conditions. Thus on the one hand it is possible to find ebracteate individuals in populations of generally bracteate ' *breweri*,' while on the other hand plants of *T. guttata* from Jersey grown in Exeter produced numerous bracts. The bracts are of two kinds. Broad leafy bracts are sometimes seen in the lower part of the inflorescence, and it is not always easy to differentiate between these and the uppermost leaves. Higher up the inflorescence the bracts resemble the narrow outer sepals in shape and texture. These small bracts may become almost constant in the upper parts of inflorescences which are wholly ebracteate below (e.g. from about the fifth flower in La Moye plants, and the third in Holyhead

TABLE 1.
Seed length in some populations of *Tuberaria guttata.*

Provenance	*Number of seeds measured*	*Mean length* (mm)	*Standard deviation*
Messina, Sicily	5	·584	·042
Monte Nuovo, Naples	6	·534	·045
Appenines between Florence and Bologna	5	·699	·066
Sintra (Estação Agronómica Nacional)*	10	·559	·044
Sintra (I. A. Williams)*	10	·688	·060
Welwitsch It. Lusit. 433	5	·501	·037
Toulon	5	·613	·054
Montpellier	4	·613	·046
Lyon, à la Pape	5	·598	·042
Mouilleron-en-Pareds, Vendée	5	·662	·053
Croisic, Loire-inf.	5	·560	·035
Baie des Trépassés, Finistère*	10	·636	·030
Corbière, Jersey*	10	·621	·038
L'Etacq, Jersey*	10	·608	·041
Ffynnon Fair, Caerns.*	10	·739	·070
Holyhead, Anglesey*	10	·702	·073
Clegyr Mawr, Anglesey*	10	·675	·048
Inishbofin (Middle Quarter)*	10	·703	·045

For further details of populations marked with an asterisk, see appendix. The other measurements are from herbarium specimens in **CGE**.

TABLE 2.
Measurements of herbarium specimens of British *T. guttata*. This table is based mainly on material in **BM**, with some Welsh and Irish material from **CGE**, **EXR**, **K** and herb. C. C. Townsend.

Provenance	*Specimens examined**	*Height* (*cm*)		*% diffuse habit*	*% pedicels with bracts*	*% with stellate pubescence on upper leaf surface*
		mean	*s.d.*			
Channel Isles						
Jersey (S. Coast)	21	10·47	4·64	50	9	100
Jersey (W. Coast)	49	9·49	3·57	35	3	96
Alderney	2	15·0	—	0	0	100
Wales						
Opposite Bardsey Island	5	3·2	0·75	0	—	100
Holyhead	59	3·49	1·96	21	60	94
Porthdafarch	9	10·22	2·35	0	62	89
'Gader'	12	5·17	2·33	8	21	100
Clegyr Mawr	5	7·2	2·49	0	20	100
Ireland						
Three Castles Head	13	6·08	2·04	31	19	23
Inishbofin	14	5·86	1·72	24	29	79

*These are the numbers of specimens whose height was measured : in several cases it was not possible to score all of these for bract number and stellate pubescence. Several of the small sets of data are based on one or a few gatherings, and in these cases the figures given are not suitable for a significance test of the difference in height between populations, since season-to-season differences contribute variation which may not be adequately reflected in the standard deviations.

plants, among material cultivated in 1961), so there is a general tendency for the proportion of bracts to flowers to rise as the season advances (see Table 3). There is a negative correlation, but not a close one, between plant height and bract number ($r = -0.24$ in cultivated material in September 1961 (not statistically significant, $P > 0.3$): if the La Moye plants are ignored as possibly aberrant, $r = -0.75$; $P \simeq 0.05$).

TABLE 3.

Height and bract frequency of plants of *T. guttata* cultivated in 1961. The upper measurement in each row was made on 8 Aug. 1961, the lower on 8 Sept. 1961.

Population	*Number of plants measured*	*Height (cm)*		*% pedicels with bracts*
		mean	*s.d.*	
Brittany				
Baie des Trépassés	4	7·5	2·0	0
	3	12·3	0·47	0
Channel Islands				
La Moye	2	15·0	1·0	23
	2	16·5	1·5	47
Corbière	9	10·6	2·27	7
	8	13·1	0·93	13
L'Etacq	9	4·1	1·37	—
	8	10·6	0·70	36
Wales				
Holyhead	6	3·8	0·69	—
	2	9·0	1·0	63
Clegyr Mawr	8	5·9	3·1	0
	7	9·7	1·7	13
(Clegyr Mawr*)	7	14·9	0·84	19
Ffynnon Fair	6	5·2	0·69	—
	5	10·0	1·6	32
Ireland				
Inishbofin	10	3·0	—	—
	6	6·3	0·94	53

Druce considered relative leaf-width a more useful and more constant character of Holyhead *breweri* than any of the foregoing. However, if the logarithm of leaf-width is plotted against the logarithm of leaf-length, the points for all populations fall near to a straight line. This suggests that the relation of leaf-breadth to leaf-length is allometric, and that the essential difference between the '*breweri*' populations and typical *guttata* is the obvious one of size. Environmental factors evidently affect the relation between leaf-breadth and -length, and the leaves of plants in cultivation are regularly wider than those of plants in wild habitats.

There remain the characters of stature and habit. The size of the plant depends greatly on environment, so that although stature differences may be striking in the field, cultivation experiments are necessary to assess their significance. In cultivation, different

*Wild-collected seedlings, measured 8 Aug. 1961.

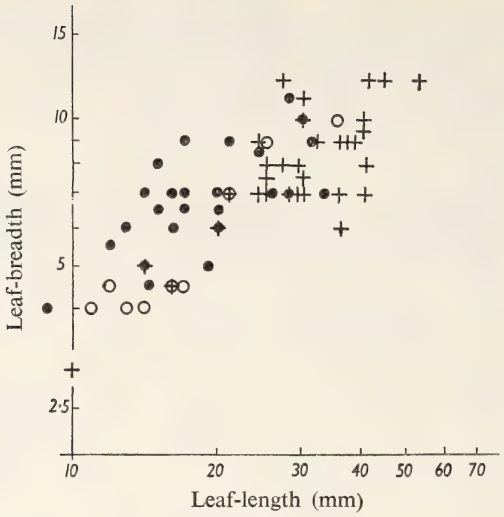


Fig. 1. Log leaf-breadth plotted against log leaf-length for lower cauline leaves of 68 herbarium specimens of *T. guttata*. Crosses, Channel Isles material; solid dots, Wales; open circles, Ireland.

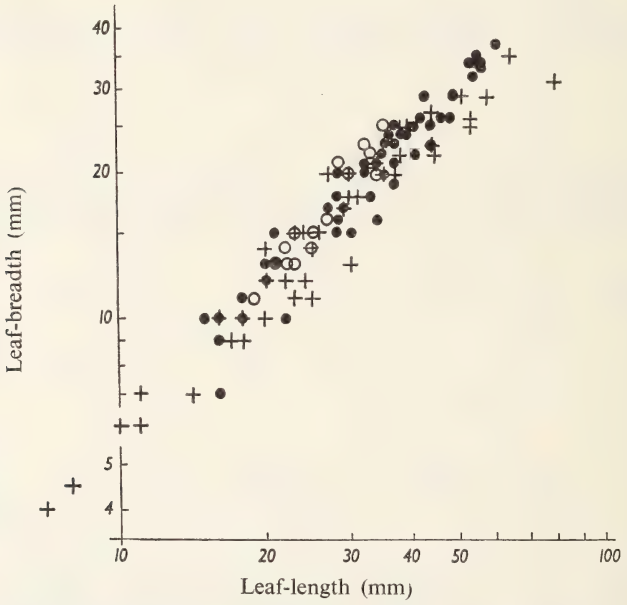


Fig. 2. Log leaf-breadth plotted against log leaf-length for basal rosettes of *T. guttata* in cultivation. The graph is based on two measurements, taken on 8 and 20 June 1961, of the longest rosette-leaf of each of 62 plants. The measurements are taken from the same material as Figs. 5 and 6. Symbols as in Fig. 1.

populations matured at different rates, southern plants in general developing more rapidly and flowering earlier than those from further north. Hence it was possible for plants to be similar in size and habit in the rosette stage and at maturity, but strikingly different at any one moment in the intervening period (see figs. 3–5). These differences in rate of maturation are obviously important taxonomically and physiologically : so far as possible I have avoided their incidental effects on other characters by making comparative

measurements on mature plants. Diffuse habit of growth is not as useful a character as it appears at first sight. Simple individuals can be found in all populations of *T. guttata*, especially in dry seasons. All the populations I have grown become more diffuse in cultivation, and, given sufficient water, more diffuse as the season progresses, and the differences observed in the field are probably very largely a direct reflection of habitat conditions, especially water-supply and competition. The inflorescence does not appear to me to provide any clear characters apart from length which might separate *breweri* from typical *guttata*: the pedicels in all the British populations appear to behave in the same way as Planchon describes for *H. breweri*.

It is interesting, as Druce (1919) points out, that cultivation tends to accentuate several of the features usually considered characteristic of *breweri;* diffuse habit, broad leaves, and the occurrence of bracts. Without cultivated plants of typical *T. guttata* for comparison this undoubtedly presented Planchon and Griffith with an even more striking picture of the difference between Holyhead *breweri* and Channel Islands *T. guttata* than that which really exists.

(*d*) *Comparison of British populations*

The Channel Islands plants do not differ in any taxonomically significant way from the plants of neighbouring parts of the French coast, and they are the standard by which other populations have generally been judged by British botanists. Tall sparingly branched plants from Jersey can be matched closely in habit, leaf shape, and inflorescence with plants from as far afield as Spain and Calabria; but taken as a whole the Channel Islands plants are shorter and more branched than south European populations. Typically they range from about 5–15 cm in height, with 3 or 4 pairs of opposite cauline leaves above the basal rosette. Even vigorous individuals are often sparingly branched; but plants showing diffuse branching from the base are also common. The leaves are pilose or hispid on both surfaces, and stellate-hairy below; and almost invariably show a greater or lesser amount of stellate tomentum above. They are usually said to be ebracteate, but bracts occasionally occur in wild plants, often several on one individual (see Table 2). Their scarcity in wild material probably reflects the fact that flowering is over much earlier in Jersey than in the more northern and western localities. There are usually one or more alternate, lanceolate, stipulate leaves between the opposite-decussate lower cauline leaves and the first flowers. In cultivation, plants from Jersey show substantial variation in size and in the number of bracts produced.

Plants from the *locus classicus* of *breweri* at Holyhead are shorter (usually less than 10 cm), and vigorous examples are normally diffusely branched. However, small impoverished plants are usually simple, and in fact diffuse branching was found to be substantially *less* frequent in herbarium material from Holyhead than in that from the Channel Islands. There are most commonly 3 pairs of opposite-decussate cauline leaves, and the alternate, stipulate, upper cauline leaves are often absent. As Druce observes, the leaves are dark green, rather coriaceous in texture, and relatively wider than those of Jersey plants (but see pp. 241–2). Stellate hairs are usually present on the upper surface of the leaf, forming a sparse felt, at least near the apex. Bracts are usually present, subtending some or all of the pedicels, but by no means constantly so. The Holyhead plants have a rather distinctive appearance, with their short rigid spreading inflorescences, and their compact dark green vegetative growth. They remain shorter than the Channel Islands plants in cultivation. Their habitat, in the bare patches between wind-cut heathers on the steep slopes above the cliffs facing South Stack, is extremely exposed.

The Caernarvonshire locality opposite Bardsey Island is equally exposed : specimens I have seen from here are similar in stature to Holyhead plants (2–4 cm), but simple and more slender in habit. In cultivation they differ in their untidier and more vigorous vegetative growth, fewer bracts, and in the less coriaceous texture and paler colour of the leaves: they become almost as tall as the most compact of the Jersey plants (l'Etacq).

Plants from the Clegyr Mawr colony are similar in stature, but with laxer inflorescences (mean distance between successive pedicels in 1961 experiment 8·66 mm, against 7·20 mm in material from Ffynnon Fair; difference significant at $P < 0{\cdot}05$), and the presence of bracts is much less constant. Some herbarium specimens can scarcely be distinguished from the largest plants collected at Holyhead, while others do not differ in any significant respect from small Channel Islands plants, which plants from this population resemble in cultivation. The Clegyr Mawr population grows among low wind-cut heather on a slight rocky knoll in the shallow valley leading from Clegyr Mawr to the sea, and is probably considerably less exposed than either the Holyhead or Lleyn populations. The exact location of Williams's population ' Gader . . . . facing the Skerries . . . . ' is not certain. His specimens resemble the Clegyr Mawr plants, and it is perhaps possible that the locality is the same. His description suggests a position near Carmel Head (*c.* Nat. Grid Ref. SH 296924), where there is certainly suitable-looking ground, but if *T. guttata* occurred here I have been unable to refind it. In any case the habitat must have been less exposed than at Holyhead.

Irish plants from Three Castles Head, Inishbofin, and Inishturk are all diffuse in habit when well-grown, though they are extremely plastic and, as in Wales, starved specimens are often simple. Bracts are often present, though less regularly than in the Holyhead plants: they appear to be significantly more frequent on Inishbofin than at Three Castles Head. I have not seen herbarium material from the Calf Islands, but there seems to be little variation in size and habit in Irish *T. guttata* from the remaining localities beyond that due to plasticity (though there is a surprisingly tall, simple, specimen from Three



Fig. 3. 1956 cultivation experiment; silhouettes of representative plants, × ¼. a, Jersey; b, Baie des Trépassés; c, Clegyr Mawr, Anglesey; d, Holyhead, Anglesey; e, Three Castles Head, Co. Cork.

Castles Head in Babington's herbarium (**CGE**)). Plants grown from seed from Three Castles Head and Inishbofin uniformly produced very dense much-branched leafy rosettes, with many short inflorescences late in the summer.

TABLE 4.

Ranking of cultivated material of six populations of *T. guttata* by seven characters (1961 experiment).

Population	*Height (tall-short)*	*Bract frequency (few-many)*	*Leaf colour (dark-light)*	*Stem pubescence (sparse-dense)*	*Number of branches (many-few)*	*Order of flowering (early-late)*	*Seed length (small-large)*
Corbière	1	1	1	1	2	1	2
L'Etacq	2	4	2	5	6	3	1
Ffynnon Fair	3	3	6	6	4	6	6
Clegir Mawr	4	2	4	3	5	4	3
Holyhead	5	6	3	2	1	2	4
Inishbofin	6	5	5	4	3	5	5



Fig. 4. 1959 cultivation experiment; silhouettes of representative plants, × ¼. a, Sintra, Portugal, 20 July; b, *ibid.*, 27 Aug.; c, Jersey, 20 July; d, *ibid.*, 28 July; e, *ibid.*, 4 Aug.; *f*, Holyhead, 20 July; g, *ibid.*, 4 Aug.; h, Ffynnon Fair, 28 July; i, *ibid.*, 27 Aug.; j, Middle Quarter Hill, Inishbofin, 28 July; k, *ibid.*, 18 Aug.; l, *ibid.*, 27 Aug.; m, West end of Inishbofin, 18 Aug.; n, *ibid.*, 27 Aug.; The dates given are when plants were pressed.



Fig. 5. 1961 cultivation experiment : material from Brittany and the Channel Islands, $\times \frac{1}{4}$. a, Baie des Trépassés, Brittany, 8 Sept.; b, La Moye, Jersey, 8 Aug.; c, Corbière, Jersey, 8 Aug.; d, *ibid.*, 8 Sept.; e, L'Etacq, Jersey, 8 Aug.; f, *ibid.*, 8 Sept.

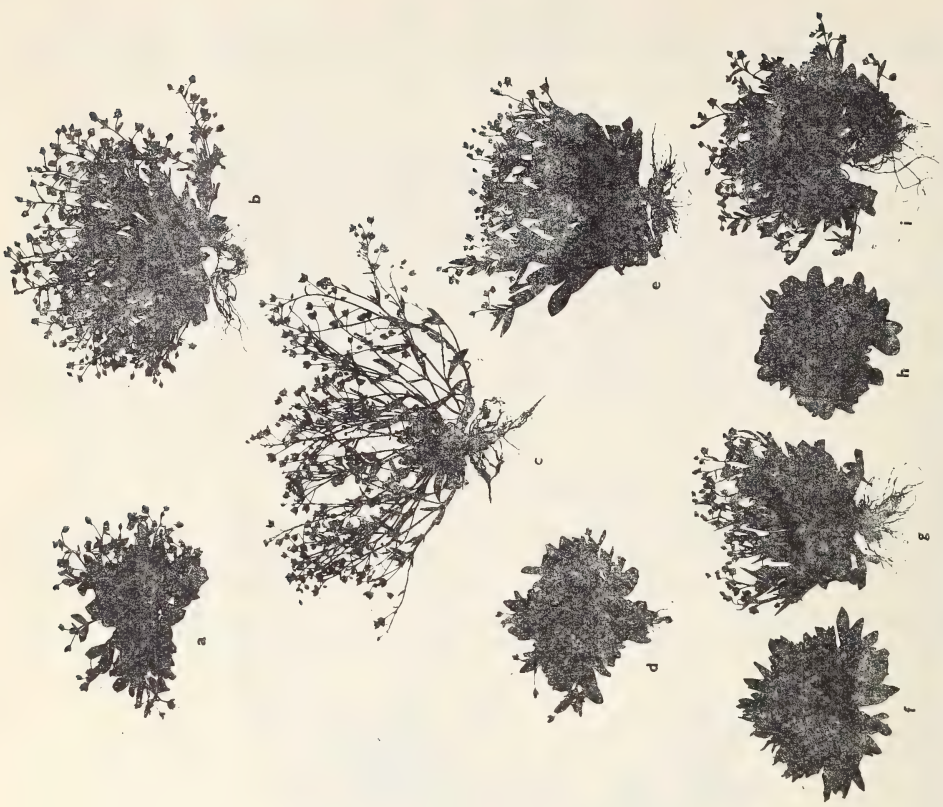


Fig. 6. 1961 cultivation experiment: material from Wales and Ireland, $\times \frac{1}{4}$. a, Holyhead, 8 Aug.; b, *ibid.*, 8 Sept.; c, Clegyr Mawr, 8 Aug. (from wild-collected seedlings); d, Clegyr Mawr, 8 Aug.; e, *ibid.*, 8 Sept.; f, Ffynnon Fair, 8 Aug.; g, *ibid.*, 8 Sept.; h, Middle Quarter, Inishbofin, 8 Aug.; i, *ibid.*, 8 Sept.

TABLE 5.

Spearman rank correlation coefficients calculated from the data of Table 4. Only in the cases of the correlations between flowering date and leaf colour and stem pubescence, and between seed length and leaf colour is ρ great enough to establish a significant correlation between two characters with $P < \cdot 05$. However, in all the remaining cases the departure from unity demonstrates the *absence* of close correlation.

	Bracts	*Colour*	*Pubescence*	*Branching*	*Flowering date*	*Seed length*
Height	·71	·60	·09	— ·24	·43	·60
Bracts		·26	·20	— ·24	·15	·31
Colour			·66	·14	·94	·89
Pubescence				·66	·83	·37
Branching					·43	— ·37
Flowering date						·71

In size and habit the populations form a graded series from the tallest plants from Jersey (La Moye) to the most compact Irish plants from Inishbofin. The relation between height and some other characters is illustrated in Tables 4 and 5. Of these characters, only bract number and leaf colour are markedly correlated with height, and even here the correlation is not statistically significant at the 5% level. In general, each character is correlated with not more than four others: two characters (e.g. bract frequency and leaf colour) may both show correlation with a third character (e.g. height), without themselves being closely correlated. The whole body of data suggests a network of loose correlations in several unrelated directions, in which no single direction of variation predominates strongly over the others. It is noteworthy that in Table 5 the variation associated with leaf colour and flowering date appears to be at least as important as that associated with the more familiar and obvious characters of height, and frequency of bracts.

(*e*) T. guttata *in north-west France*

Plants on the exposed coasts of Brittany and the Bay of Biscay are characteristically short in stature and diffuse in habit, usually with rather denser stellate and simple pubescence on the upper surface of the leaves than in the British populations. Some (including the only sample I have had in cultivation) closely resemble the Channel Islands plants and are more or less ebracteate; but populations exist which appear to be very comparable with the populations at Holyhead and in the west of Ireland : low-growing much-branched plants, with short bracteate inflorescences, e.g. Rochers mar. de Pornichet à Chemaulin (Loire-inf.), July 1874, Herb. E. Gadeceau (**BM**); St. Brevin (Loire-inf.), 23 June 1856, *J. Lloyd* (**BM**); Croisic (Loire-inf.), 23 June 1880 *J. Lloyd* (**BM**); *ibid.*, June 1851, *Drs. Thuret & Broceaux* [?], Herb. Gaston Genevier (**CGE**). These variable west coast plants were described by Lloyd (1876) as *H. guttatum* var. *maritimum*.

> *maritimum*. H. alyssoides Pesn. cat., 59, non Vent. Plante de 5–10 cent. rameuse, étalée, hérissée, blanchâtre; rac. epaisse, dure, mais [annuelle]. Rochers marit.

Rouy & Foucaud (1895) call the plant *Helianthemum litorale*, citing Lloyd's name as a synonym, and they give stature and presence of stellate pubescence on the upper surface of the leaves as diagnostic characters. The habitat is given as " Rochers maritimes des bords de la Manche et de l'Océan." Neither Lloyd nor Rouy & Foucaud mention bracts. The specimens mentioned above, collected by Lloyd and named var. *maritimum*, are bracteate, but the name evidently included taller and more or less ebracteate plants

as well, e.g. Falaise de Carteret, (Manche), 31 May 1888, Herb. L. Corbière (**K**), which is very like material from the more exposed localities in Jersey. What is particularly significant is Lloyd's comment after his description of var. *maritimum:* 'Revient graduellement au type, à mésure que l'on s'éloigne de la mer.'

It appears, then, that in north-west France we have the common pattern of a widespread species passing gradually into a dwarf maritime ecotype on exposed rocky cliffs; a correlation between the '*breweri*' characters and exposure is also apparent in Britain, and it seems reasonable to suppose that the disjunct British populations represent scattered fragments of a similar pattern. A similar pattern may also exist on exposed coasts in N. Spain and Portugal: the plants cited by Grosser provide little evidence of it, but two very short compact flowering specimens (*c.* 1·5–2 cm high) in the Kew Herbarium (Adjuda Hill, Lisbon, May 1935, *S. C. Atchley* Fl. Portugal 401; Foothills facing the Atlantic between Estoril and Cintra, May 1935, *S. C. Atchley*, Fl. Portugal 402), look much more likely to be comparable with British '*breweri*.' They differ from any British or French material in their very dense grey stellate tomentum with only sparse simple bristles. The common feature running through the extreme west coast forms of *T. guttata* is the short much-branched growth habit, often associated with bracteate inflorescences: in fact the characters emphasised by Planchon as distinguishing *breweri*. This may be due to a tendency for other, non-adaptive, characters to show developmental correlations with the characters responding to selection for short stature, and perhaps for long vegetative period; and if this is so, the '*breweri*' characters are likely to be of polytopic origin in the various populations. The differing indumentum of British and French (and Portuguese) plants, and the variation in frequency of bracts and other characters in the British populations, are consistent with this possibility. It would be interesting to know something of the morphogenesis of the leaf and shoot pattern in *T. guttata*.

4. Discussion

The question arises whether these diverse populations can be distributed into useful taxa. The two extreme, and simple, possibilities are either to limit the name *breweri* to the Holyhead population, or to follow Grosser and adopt a wide delimitation of *breweri* to include a range of Atlantic coast plants, of varying stature, with or without bracts. The first possibility would logically require similar separate taxonomic recognition of the Caernarvonshire, Irish and north-west French *breweri*-like forms, and although there are zoological precedents for a treatment of this kind in dealing with isolated small populations within the British Isles, I feel that this would be of little scientific value in the case of a generally variable species like *T. guttata*. On the other hand, Grosser's delimitation of *T. guttata* var. *breweri* provides no satisfactory line of distinction from typical *guttata*. Stellate pubescence on the upper surface of the leaves is commoner near the Atlantic coast, but it is found in a proportion of plants throughout much of the range of the species (and in the British Isles it is least constant at Three Castles Head !). Grosser's delimitation results in the abandonment of virtually all the characters of Planchon's original *H. breweri*. Willkomm's figure of *T. variabilis* var. *cinerea* ('ad specimen Welwitschianum delineatam') is certainly rather like the Welsh and Irish plants, and has a few bracts; but specimens at Kew and Cambridge show *Welwitsch It. Lusit.* (1840) *No.* 433 (which Willkomm and Grosser cite) to be a rather tall plant (11–23 cm), having little in common with the Holyhead plant. The Channel Islands plants can scarcely be excluded from Grosser's variety, though by implication he seems to include them in typical *guttata*; and they were specifically excluded from the original delimitation of *breweri* and included in typical *guttata* by Planchon.

Any intermediate treatment breaks down over one or both of two difficulties: the difficulty of providing usable and taxonomically meaningful lines of demarcation, and the fact that most of the possible groupings of the populations obviously lack genetic coherence. The extreme populations are certainly strikingly different from typical *T. guttata*, but on

analysis their characters reduce to the slight, and obviously adaptive, one of stature, in which they intergrade with the typical form of the species. Other characters, which might be expected to be taxonomically more reliable, do not correlate at all closely with this, and do not appear to show any major taxonomically significant pattern of their own.

There is a strong argument for simply recognising the existence of a pattern of ecotypic differentiation in north-west European *T. guttata* in relation to exposure, and not attempting any formal taxonomic treatment of it. On the present evidence I am forced to the conclusion that no orthodox taxonomic treatment of the variation in these *T. guttata* populations is practicable or of any real value.

Acknowledgments

The work on which this paper is based was begun during the tenure of a research studentship from the Nature Conservancy. I would like to thank all those who helped by providing seed, living plants, herbarium material, or in other ways; and the botanic garden staffs at Cambridge and Exeter and Miss M. A. Turner for their care and patience with experimental material.

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Appendix : Material of T. guttata used in cultivation experiments

Jersey. Seed from cultivated plants, probably originally from near Corbière. D. McClintock.

Near Corbière, Jersey, 22 March 1960, Mrs. F. Le Sueur.

Above Pinnacle Rock, between L'Etacq and Grosnez (on granite), Jersey, 14 March 1960, Mrs. F. Le Sueur.

Exposed slope above cliffs facing Bardsey Island, near Ffynnon Fair, Aberdaron, Lleyn Peninsula, Caerns., April, 1958.

Holyhead Mountain, opposite South Stack, 31 Aug. 1954, D. E. Coombe (and later collections by M.C.F.P.).

Bare patches between wind-cut *Calluna* and *Erica cinerea*, on low rocky knoll between Clegyr Mawr farm and the sea, near Llanrhyddlad, Anglesey, July 1955. Seedlings collected 1 April 1961.

Summit of Three Castles Head, W. Cork, on open rocky ground (Devonian slates). Patches of more closed vegetation (from which *T. guttata* is absent) with *Calluna*, *Erica cinerea*, *Cladonia* spp., 14 Aug. 1952, S. M. Walters.

Sloping bank, edge of pool below Three Castles Head, with *Calluna*, *Erica* and into marsh with *Drosera*, *Sphagnum*, *Potamogeton polygonifolius* etc., 14 Aug. 1952, S. M. Walters.

Bare patches in *Calluna* heath near summit of Middle Quarter Hill, Inishbofin, W. Galway, 14 Aug. 1958.

Rock outcrop in pasture near west end of Inishbofin, facing Inishark, 14 Aug. 1958.

Dry short turf on cliffs above Baie des Trépassés on the Pointe du Van, near the Pointe du Raz, Finistère, France, July 1952, C. D. Pigott.

Sintra, Mercês, Estremadura, Portugal (from Estação Agronómica Nacional, Sacavém).

Roadside, Pe. da Sena, towards Sintra, Portugal, 12 Oct., 1957, I. A. Williams.

LUZULA × *BORRERI* IN ENGLAND

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Abstract

The hybrid *Luzula* × *borreri* was studied using the procedures for determining introgressive hybridisation. Most of the hybrids were sterile and intermediate in their characteristics between the parents, *L. pilosa* and *L. forsteri*. A few plants, however, were found that showed characteristics similar to *L. pilosa* and occasionally a few seeds were produced by the hybrids. This similarity between some of the hybrids and *L. pilosa* as well as the rare production of seeds indicates that occasionally there is some gene flow between these two species.

Luzula pilosa and *L. forsteri* are woodland species which belong to the subgenus *Pterodes*. Both are wide-ranging taxa that occur in Europe, with *L. pilosa* having a more northern distribution. The range of *L. forsteri*, however, overlaps that of its more northern relative and through most of this region hybridisation has been reported. The hybrid was first described under the name *L. Borreri* by Babington (1851) who inserted it doubtfully as a species. He further mentioned that only two seeds were found on the specimen. This taxon was later considered by Syme (1872) to be a variety of *L. pilosa*. However, Buchenau (1890) was the first to recognise it as a hybrid.

Generally this hybrid is completely sterile. Richards (1952) mentions that *Luzula* × *borreri* is not uncommon with the parents, and that it resembles *L. pilosa*, although it is often taller. According to him the capsules of the hybrids are much shorter than the perianth and always sterile. In recent hybridisation experiments, Nordenskiold (1957) indicates that *L. forsteri* ($2n = 24$) and *L. pilosa* ($2n = 66$) can be crossed readily. In all cases the hybrids were completely sterile. It was also indicated that in the F_1 hybrid the 33 small chromosomes of *L. pilosa* sometimes pair with the 12 larger chromosomes of *L. forsteri*.

Although the hybrid is usually sterile, occasionally a few seeds develop. Therefore there is a chance for the transfer of genes between parents. To determine if there is gene flow between these two species, the procedure described by Anderson (1949) for determining introgressive hybridization was used. The present study is primarily confined to collections of these taxa and their hybrid from England.

Materials and Methods

This study was based on herbarium material consisting of more than 100 collections from England. Also, over 200 European specimens were examined to sample the total variability of the two taxa. Fruiting specimens were used for all measurements and the results were plotted on a scatter diagram to show the variability of both species and their hybrid. Material used in this study was obtained from the Gray Herbarium (**GH**), the Royal Botanic Gardens, Kew (**K**) and the United States National Museum (**US**).

Discussion

Luzula pilosa and *L. forsteri* are morphologically distinct from one another. *L. forsteri* has a short projecting mucro extending from the callose tip of the leaves; the basal leaves are usually less than 3 mm wide; the cauline leaves are usually more than 4 cm long; the pedicels of the fruiting inflorescence are erect to slightly spreading; and the caruncle of the seeds is erect and does not exceed 0·6 mm in length. In contrast,

L. pilosa lacks a projecting mucro on the callose tip of the leaf, the basal leaves are over 4 mm wide, the cauline leaves are less than 3 cm long, the pedicels of the fruiting inflorescences are strongly spreading to reflexed; and the caruncle of the seeds is strongly curved and over 0·6 mm long.

In most of the above traits the hybrid is intermediate between the two species. The projecting mucro on the callose leaf-tip may or may not be present and the cauline leaf length is usually between 3 and 5 cm. The curvature of the pedicels is also variable, but they are usually strongly spreading as in *L. pilosa*. In contrast, the basal leaf width is more than 4 mm, similar to that of *L. pilosa*. The distinctive difference, however, is that the seeds of the hybrid are generally small and abortive.

Measurements of the length of the cauline leaves and the width of the basal leaves were made on all available specimens of these two species and their hybrids from England. Observations were also made on the presence or absence of a projection on the callose tip of the leaf, the curvature of the pedicels, and the presence or absence of seeds. These results were then plotted on a pictorialised scatter diagram (Fig. 1) in which the abscissa represents the width of the basal leaves and the ordinate the length of the cauline leaves. A line radiating from the top left of the circle indicates that there is a projecting mucro on the callose tip of the leaf, and a line radiating to the right indicates that the pedicels of the inflorescence are erect, or nearly so. Plants with abortive seeds are indicated by solid circles while plants with normal seeds are represented by open circles.

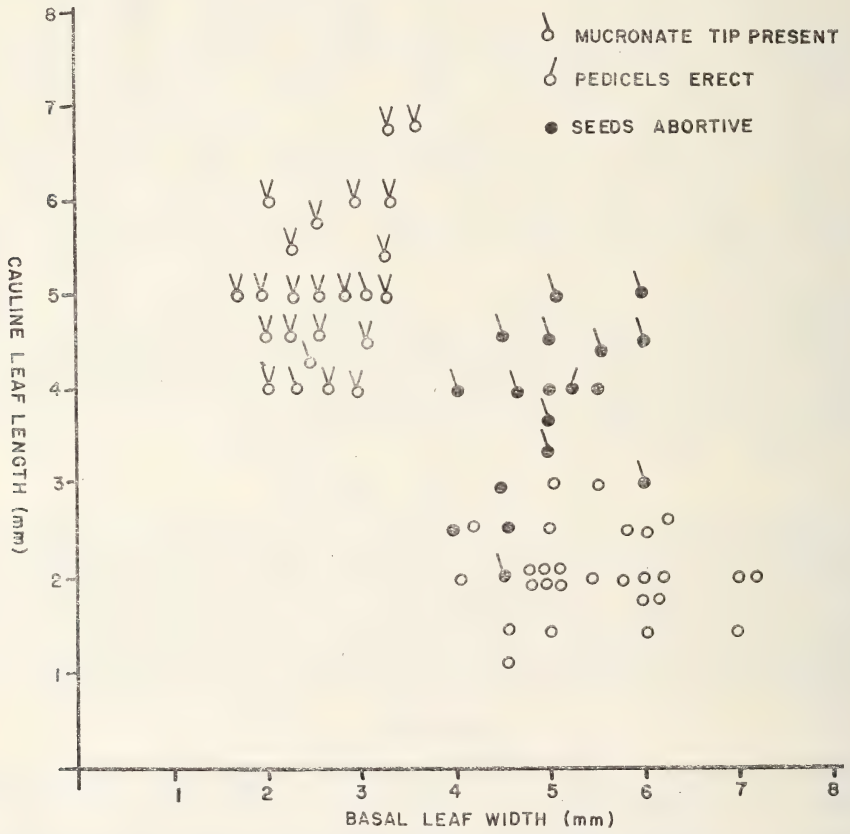


Fig. 1. Pictorialized scatter diagram showing the relationship of cauline-leaf length to the basal-leaf width in *Luzula pilosa*, *Luzula forsteri* and their hybrid. The bar radiating to the left of the circle indicates that there is a projecting mucro on the callose tip of the leaf, while a line radiating to the right of the circle indicates that the pedicels of the inflorescence are erect to slightly spreading. An open circle indicates that seeds are present while a solid circle indicates that the seeds are abortive.

As can be seen from the diagram (Fig. 1) three fairly definite groups are present. The group at the upper left represents *Luzula forsteri*, the group at the lower right represents *L. pilosa* and the group lying between these two species, with solid circles, represents the hybrid. The hybrid apparently resembles *L. pilosa* more than *L. forsteri*, and the similar leaf measurements as well as the other traits indicate that occasionally the hybrid back-crosses with *L. pilosa*. Five specimens with abortive seeds have the same leaf measurements and the spreading pedicels of *L. pilosa* [*J. P. M. Brenan 6248*; *C. E. Britton* (16 May 1909); *R. W. Butcher* (17 May 1925); *Milne-Redhead 6135*; *B. M. Watkins 1170*]. Of these five, three also lack a projecting mucro on the callose tip of the leaves. In addition, on two of the hybrids a few seeds were found [*A. Bromfield* (12 Aug. 1850); *E. C. Wallace* (27 May 1933)]. In both instances there were no more than four seeds, and no more than two to any one capsule. It is not known whether these seeds are viable, and it was not possible to determine this during the present investigation as only herbarium material was used. However, these seeds were as large as those of *L. pilosa* and the embryos were well developed. These plants with a few seeds are also represented by solid circles on the diagram. Furthermore, all of the plants with abortive seed, including these two specimens on which a few seeds were found (all specimens represented by solid circles), are considered to be *L.* × *borreri*.

Though the seeds of the hybrid are generally abortive, the anthers are well developed. They are very long (usually 1·5 mm), three times as long as the short filaments. By contrast, the anthers of *Luzula pilosa* are about 1·0 mm long, half the length of the filaments while the anthers of *L. forsteri* are slightly shorter. Though the anther lengths in both species are variable, in no instance are they as long as in the hybrid. Furthermore, the pollen of the hybrid is similar to that of the two species though slightly larger.

Conclusions

It has generally been considered that the hybrid between *Luzula pilosa* and *L. forsteri* is completely sterile, but present information indicates that occasionally the hybrid sets a few seeds, and may back-cross with one of the parents. Most of the hybrids are intermediate between the two parents and have abortive seeds. However, five specimens were found that, though they usually had abortive seeds, had the same leaf measurements and the spreading pedicels of *L. pilosa* and three of these also lack a projecting mucro on the callose leaf-tip. This similarity between some of the hybrids and *L. pilosa* as well as the rare formation of a few seeds on the hybrid indicates that occasionally there is some gene flow between these two species.

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Representative specimens

Luzula forsteri (Smith) DC., Syn. Pl. Fl. Gall. 150 (1806).

ENGLAND : *A. Bennett 1002* (US); *C. R. Billups 1549* (K); *G. C. Druce* (June, 1914) (GH); *J. S. Gamble 18768* (K); *A. G. Gregor* (26 May 1926) (K); *J. D. Grose* (31 May 1939) (K); *A. B. Jackson* (May 1937) (K); *Jackson & Green 1656* (K); *J. E. Little 2* (K); *B. T. Lowne* (19 May 1906) (K); *A. G. More* (May 1855) (K); *C. E. Moss* (1913) (K); *W. B. Turrill* (2 May 1926) (K); *V. S. Summerhayes 1936* (K); *C. Waterfall* (14 May 1919) (K); *D. P. Young 3992* (K).

Luzula × borreri Bromf. ex Bab., Man. Br. Bot. Ed. 3., 333, (1851).

ENGLAND : *J. P. M. Brenan 6248* (**K**); *A. Bromfield* (12 Aug. 1850) (**US**); *C. E. Britton* (16 May 1909) (**K**), (23 May 1909) (**K**); (16 May 1926) (**K**); *R. W. Butcher* (17 May 1925) (**K**); *C. B. Clarke* (25 June 1891) (**K**); *J. S. Gamble 26063* (**K**), *28500* (**K**); *P. Hall 2299* (**K**); *J. E. Lousley* (18 June 1939) (**K**); *Marshall & Sandwith* (29 May 1918) (**K**); *Milne-Redhead 6135* (**K**); *E. C. Wallace* (27 May 1933) (**K**); *B. M. Watkins 1170* (**US**); *R. Yindlay* (April 1927) (**K**).

Luzula pilosa (L.) Willd., Enum. Hort. Berol. 393 (1809).

ENGLAND : *C. C. Babington* (2 June 1852) (**K**); *R. A. Blakelock* (7 May 1939) (**K**); *C. E. Britton* (21 May 1893) (**K**); *H. E. Bunker 141* (**K**); *B. Burtt 234* (**K**); *J. Cunnack 13536* (**K**); *P. E. Goodliff* (30 March 1957) (**K**); *C. E. Hubbard 12667* (**K**); *J. H. Lewis* (19 July 1877) (**GH**); *F. K. Makins 1910* (**K**); *A. Meebold* (June 1924) (**K**); *Milne-Redhead 6136* (**K**); *H. K. A. Shaw* (18 May 1930) (**K**); *T. A. Sprague* (1 May 1932) (**K, US**); *V. S. Summerhayes 2159* (**K**); *D. P. Young 3993* (**K**).

BOOK REVIEWS

Plant Communities of the Scottish Highlands. Donald N. McVean and Derek A. Ratcliffe. Pp. xiii + 445, with 36 figures and 34 maps in text, 26 plates, and two folding maps in end-pocket. Monographs of the Nature Conservancy, No. 1. H.M.S.O., London, 1962. Price £3 17s. 6d. net.

The tradition of descriptive ecology which culminated in Sir Arthur Tansley's *The British Islands and their Vegetation* has not been prominent in Britain since the War, and for that reason alone the appearance of this book would be a notable event, and one to be welcomed. It sets out to give a monographic account of the vegetation types of the area north of the ' Highland Line ' (but excluding the largely agricultural country to the east, and coastal habitats) – an area which is extensive even by Continental standards. The work which this survey records grew out of Prof. M. E. D. Poore's phytosociological work in Breadalbane, and the authors' methods and concepts closely follow his.

After a brief introductory chapter the greater part of the text is occupied by description and discussion of the communities recognised – 77 of them, not counting facies and a number of vegetation types which are not formally defined and named. These are grouped partly in life-form categories, partly ecologically: forest and scrub, dwarf-shrub heath, grass-heaths, herb and fern meadows, moss heaths, ombrogenous mires or bogs, soligenous mires, and springs and flushes. Chapter 10 tentatively relates the vegetation units described to the phytosociological classification used by the Scandinavian ecologists, and briefly compares Scottish and Scandinavian mountain vegetation. There follows a thoughtful chapter on climate and vegetation, a chapter on soils, and a brief chapter on plant-geographical factors.

Floristic analyses of the communities are set out in 60 tables, which take up 170 pages of the book – about as much as the text. The tables are a tribute to the care and thoroughness of the authors' field-work, and, quite apart from their primary purpose, will be a mine of information to anyone interested in the ecological or geographical distribution of vascular plants, bryophytes or macrolichens in the Highlands. The distribution of a number of selected communities is shown in a series of maps, which illustrate some of the main trends of vegetational variation; and a series of vegetation charts indicate the occurrence and altitudinal range of the main communities in a series of representative areas. The book is completed by twelve pages of soil and mire-water analyses, lists of calcicole, calcifuge and indifferent species, a summary of the distribution and soil preferences of the communities described, 26 photographs of representative pieces of vegetation (all at least adequate and some magnificent), an excellent index, and two folding maps showing the present and reconstructed past distribution of oak, pine and birch woodland in Scotland.

Two points which emerge forcibly from the authors' work are the large number of recognisable vegetation types to be found even on acid mountains, and the richness in species of many of these. Thus even the species-poor *Rhacomitrium* heath of exposed summits averages 16 species (vascular plants, bryophytes, and macrolichens) in the 11 samples listed; not many of the communities average less than 20 species in a sample (usually 4 m^2), and a number of the richer ones average between 40 and 50. In general, the character of the vegetation types emerges clearly from the descriptions and tables, and many of them will be recognised by those who have searched for plants in the Highlands. There is certainly a strong phytosociological element in the intuitive ' feel ' that one acquires for the habitat of a plant, and it is interesting to compare ones field experience with the summary of constant and dominant species and indications of fidelity in the described communities in tables 1 and 2, and with the floristic tables and the comments in the text. Thus *Loiseleuria*, *Salix lapponum*, *Athyrium alpestre*, *Dryas* and *Carex saxatilis* are all constant and more or less faithful species of particular noda, and many of the rarer species are confined, or nearly so, to particular communities.

The authors have attempted so much, and in the main succeeded so well, that any criticism virtually amounts to an attempt to define the standard at which a study of this sort should aim. First there is the question of comprehensiveness. The authors have specifically excluded coastal vegetation, and they have not dealt with rock-face communities, which they consider are best dealt with in terms of the autecology of the species concerned, or with aquatic communities – some of which are certainly interesting and characteristic in the Highlands. Then there are the epiphytic bryophyte communities of woodland and scrub, and this brings one back to the mosaics and bryophyte micro-communities within some of the vegetation types already recognised. A line must be drawn somewhere. However, at least some rock-crevice communities lend themselves to phytosociological treatment in other areas, and it would have been interesting to

have some account of the main types found in the Highlands; is there any regularity in the associates of *Woodsia alpina*, or *Asplenium septentrionale* ? The number of noda recognised is large, and in some cases noda seem to be separated on rather tenuous grounds. However, the authors have undertaken a difficult and unusual task in providing a set of vegetation units to cover an area embracing as much climatic and edaphic variation as the Highlands – a problem which is not faced in quite the same way by the various regional compilations published on the Continent. As they point out, the choice is between a smaller number of more homogeneous units of local distribution, individually well-characterised, but difficult to separate from their equivalents in neighbouring areas, or between a smaller number of widely distributed but variable units which are difficult to characterise. This is a general problem which has no completely satisfactory solution, and compromise is necessary. With the vegetation analysed into a number of noda, the reader is then faced with the problem of synthesis. The authors have taken a great deal of trouble to meet his needs in the maps and vegetation charts, with their explanatory text. Nevertheless, the reader's task would probably have been made easier by a summary chapter outlining the main types of pattern shown in the charts, and the principal trends illustrated in the maps. This need is partly met in the chapters on climate and soils; but much of the relevant information has to be extracted piecemeal from the descriptions of the individual plant communities. One hopes that we shall be given the opportunity to study in more detail the evidence on which the two woodland maps are based. Finally, a minor point; if Latin names are to be used for plant communities, surely the usual forms 'Agrost*i*do-Festucetum' and 'Vaccin*i*etum' are etymologically preferable to the forms used here ?

It is rather refreshing to find that the authors have not added to the tiresome and sterile controversy which tends to surround discussion of phytosociological work, but have let their results stand as their own justification. Phytosociology has generally been discussed in terms of ecology in Britain, but it has as much or more to offer to those whose interests are in floristics or phytogeography. Systematic and thorough phytosociological study obviously has much to add to our knowledge of British vegetation. The authors have managed a nice balance between the coherent formal (but sometimes over-rigid) framework of Continental phytosociology, and commonsense empirical (but sometimes vague) approach of pre-1939 British ecology. It would be a pity if descriptive work in Britain were now to be tied too closely to the ideas that have served some of the major Continental schools for the past few decades, or if it were to divert too much effort from related subjects. On the other hand, there is much scope for descriptive work on vegetation in Britain; Continental phytosociology represents one substantial body of experience on which to draw, and there are now encouraging signs both in Britain and on the Continent of convergence between traditional descriptive methods and recent applications of multivariate techniques.

The book is well printed on good paper, and the layout of the text and illustrations is clear and pleasing; misprints are few. The problem of printing extensive floristic tables has been well handled, and in spite of the small type-size the tables are admirably clear. *Plant Communities of the Scottish Highlands* is undoubtedly the most important post-war contribution to descriptive ecology in Britain, and it is fitting that it should be the first of the Monographs of the Nature Conservancy. It sets a high standard.

M. C. F. Proctor

Flora of the British Isles. Second Edition. A. R. Clapham, T. G. Tutin and E. F. Warburg. Pp. xlviii + 1269, with 87 figures in the text. Cambridge University Press, 1962. Price £3 10s. 0d.

Publication of the new *Flora of the British Isles* in 1952 has proved to be the most important event for a generation in the study of British plants, and the second edition was eagerly awaited. The large number of corrections and additions which have been made is to a considerable extent due to the stimulus to new work prompted by the first edition. The book has been largely re-written, and completely re-set in a new format, and, excellent as it was before, it is greatly improved.

The new format is an outstanding improvement. The first edition was produced as a compromise between a work to be used in the field and one suitable for a library, and was far from ideal for either purpose. Printed on thin paper, more suitable for a Bible to be read at leisure than for a Flora to be consulted in haste under difficult conditions, many copies of the old ' CTW ' became soiled and tattered shortly after purchase. The shorter and more portable *Excursion Flora* is now available for use in the field, and the *Flora of the British Isles* is printed on good paper with a larger page size entirely suitable for the herbarium and library. Although the second edition contains about 320 pages less than the first, the contents are more, better displayed, and easier to consult.

Some genera or parts of genera have been completely re-written in line with recent work. *Polypodium, Salicornia, Oxalis, Ulmus* (reduced from 7 species to 3), *Gentianella, Rhinanthus* (reduced from 8 species to 3), and *Sparganium* are examples. The new account of *Rubus* is more suitable for most users of the book, leaving specialists to consult W. C. R. Watson's *Rubi of the British Isles* for detailed accounts of the species. The revision of Orchidaceae, and especially *Dactylorchis*, is outstanding, but surely *Platanthera bifolia* is characteristically found on more acid soils than *P. chlorantha* and the description of habitats on p. 1033 requires correction. Many readers will be pleased to find *Polygala oxyptera* sunk in synonomy, and *Cochlearia alpina, Daucus gummifer*, and *Epilobium lamyi* reduced to subspecies.

In contrast to the first edition, there are few names which will be unfamiliar to most British botanists, though some of the scientific names introduced then are not retained. As the authors acknowledge in their preface, the work of J. E. Dandy is a step towards nomenclatural stability, and the names used are in general those of the *List of British Vascular Plants*. In the *Flora*, unlike that work, *Scirpus* is split up into *Trichophorum, Isolepis, Eleogiton, Holoschoenus* and *Schoenoplectus*. Changes based on careful study and tending towards stability are necessary but frequent alterations are difficult to justify. If the fern known as *Dryopteris spinulosa* is to be called *D. carthusiana*, the recent change to *D. lanceolatocristata* would appear to have been too hasty. Fortunately similar examples are few. At the time the first edition appeared the spelling of certain specific epithets with a small initial letter was highly controversial, and these were indicated by repeating the name with an initial capital. The new practice is now so generally accepted by British botanists (though still regretted by a few) that the cases where initial capitals are appropriate are no longer indicated. Another change in the second edition is that illustrations are no longer cited for each species. The justification for this is the production of the companion volumes of *Flora of the British Isles Illustrations*, of which two volumes have appeared, but these do not cover, and will not cover, all the species described, and not all the illustrations are as good as those formerly cited. It is to be hoped that the authors will consider restoring this very useful feature in the next edition.

The preface is dated as long ago as November 1958 and in bringing the book up to date the authors were handicapped by the length of time the pages were in the press. This is particularly evident with the paragraphs dealing with distribution, since although they were able to incorporate the major additions revealed by the work of the BSBI Distribution Maps Scheme, they had not got the advantage of the *Atlas* to check the overall pattern or the detail. The distribution of plants found in the Channel Islands is especially defective – for example, *Ranunculus paludosus* is not ' Found only in dry places near St. Aubyns,' *Silene conoidea* is not ' established in Jersey ' (and never has been), and *Spergularia bocconii* is far more plentiful and widespread in Jersey and Guernsey than in any of the counties listed, though its occurrence is recognised by an ' S.' A protest too must be lodged against the use of ' Scilly Is.' to refer to the archipelago officially known as the ' Isles of Scilly.' For a shortened form ' Scilly ' is adequate, more acceptable to the residents, and runs no risk of being tautologous.

The treatment of alien plants has been immensely improved but even so it remains by far the weakest feature of the *Flora*. Many aliens in the first edition which are now seldom seen have been dropped, but some of those in the Cruciferae and Compositae still retained would be more appropriate in a Victorian Flora than in one published in 1962. Similarly there are statements on distribution, which are fifty or more years out of date, such as that *Herniaria hirsuta* is ' Naturalized on sandy ground at Christchurch, Hants.', and that *Reseda phyteuma* is ' Well established in Surrey.' In general the statements about occurrences are too vague to be useful and the means of introduction are seldom mentioned. Later workers will have great difficulty in checking claims of persistence where no locality where the species is established is mentioned. For example, the statement that *Arabis caucasica* is ' occasionally naturalized ' is vague. A reference to its spread since 1890 on limestone rocks in Derbyshire would indicate that in at least one district it is thoroughly established. For aliens for which special studies have been published there can be little excuse for some of the statements given. Thus Lacey's paper on *Galinsoga* which appeared in 1957 must have been available when the entries that *G. parviflora* is ' Well established . . . . in London and elsewhere in S. England ' and *G. ciliata* ' A casual recently recognized in S. England and S. Wales ' were checked for the new edition and left unaltered. They are very much more widespread than this and still spreading, as the entries in Plant Records show.

The selection of alien species for inclusion is always a difficult matter since every botanist's experience differs, but there can be little doubt about the lack of merit of some of the plants included, and the claims of some of those left out. *Inula britannica, Filago arvensis*, and *Crepis nicaensis* are examples of those included in large type. *Centaurea diluta, Erigeron bonariensis* and *Salvia reflexa* are commoner plants which the reader is much more likely to find, while *Juncus pallidus* has current claims for inclusion as established. To include *Erodium botrys*, and leave out several equally common species of the same genus, and to describe ten alien species of *Oxalis* and only two of *Amaranthus* are clearly anomalous. It seems strange that the annual *Ambrosia artemisiifolia*, which seldom persists for long, is given space while the

perennial *A. psilostachya*, which has been at St. Annes for 75 years, is not mentioned. Woody aliens, on the other hand, receive very much better treatment, and this is the best account of them which has yet appeared.

This new edition of ' CTW ' is a first-class work which can hold its own by comparison with any overseas Flora of similar size. In general the revision is thorough and brought as nearly up to date as the timetable for printing allowed. Very few errors escaped notice in the proof reading (though " the Isle of Dogs, Kent " on page 227 should not have been missed). This is a work which no British botanist can afford to be without.

J. E. Lousley

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THE NOMENCLATURE OF *ALCHEMILLA MINOR* AUCT. BRIT.

By M. E. Bradshaw, P. D. Sell and S. M. Walters

This paper attempts to elucidate the various names applied to the taxon described in Clapham, Tutin & Warburg (1952) as *Alchemilla minor* Huds. sec. Wilmott, and to find its correct name. The problem has been tackled before by Wilmott (1939), Rothmaler (1941 and 1944), Samuelsson (1943) and Hylander (1945). Our conclusions disagree with those of Rothmaler and Wilmott and support those of Samuelsson and Hylander. We are very grateful to Mr. J. E. Dandy for all the time and trouble he has taken to answer numerous problems of nomenclature and typification.

The first name to be considered is *A. hybrida* (L.) L. (1756) (*A. alpina* var. *hybrida* L. (1753)). The diagnosis given for the basionym reads '*Alchemilla alpina pubescens minor. Tournef. inst. 508. Pluk. phyt. 240 f. 1.*' The name *A. alpina pubescens minor* " H.R.P." was actually first published by Plukenet (1692) under his plate 240, fig. 2 (not 1 as quoted by Linnaeus), and then in his text (1696). It was later published by Tournefort (1719) who also attributed it to " H.R.P." Plukenet's figure (reproduced in Fig. 1) was based on a specimen in his herbarium now on fol. 22, vol. 95, of Herb. Sloane at the British Museum (Plate 11a). This specimen, which is incomplete (lacking basal leaves), originated in the Botanic Gardens at Paris (' Hort. Reg. Paris.'), from which it would have been sent to Plukenet by Tournefort. In the Tournefort herbarium at Paris (**P**) is a better specimen labelled '*Alchemilla alpina, pubescens minor hort reg Par*' (Plate 12a) which is definitely identifiable with *A. lapeyrousii* Buser (1893). There being nothing to the contrary, it may safely be assumed that Plukenet's specimen is a duplicate of Tournefort's and is therefore also referable to *A. lapeyrousii*. There are no specimens in Linnaeus' own



Fig. 1. Plukenet's figure of '*Alchemilla alpina pubescens minor*.'

herbarium, but there are two sheets in his *Hortus Cliffortianus* at the British Museum. The *Hortus Cliffortianus* is not cited in the original publication of the name *A. alpina* var. *hybrida*, but the specimens were certainly seen by Linnaeus before 1753. Both are labelled with the Tournefort descriptive name '*Alchemilla alpina, pubescens minor*' and both are in our opinion *A. lapeyrousii* Buser (though Rothmaler (1962) refers one to the species we are here considering). There is thus little doubt which taxon Linnaeus meant by *A. hybrida*.

The next name that has been applied is *A. minor* Huds. (1762). Under this species is cited exactly the same synonym as under *A. alpina* var. *hybrida* L., i.e. '*Alchemilla alpina pubescens minor. Tourn. 508. Pluk. Ph. t. 240 f. 1.*' Consequently the publication of *A. hybrida* as a species in 1756 makes Hudson's name a superfluous *nomen illegitimum*. As to what British plant Hudson had in mind it is difficult to tell, as none of his specimens has been traced, but the taxon we are discussing has never been found in Westmorland and Hudson's plant is more likely to have been *A. vestita* (Buser) Raunk.

Next is *A. pubescens* Lam. (1791) which is also a superfluous *nomen illegitimum*, as is *A. montana* Willd. (1809). Both make either direct or indirect reference to *A. hybrida* (L.) L. These superfluous names probably arose because the authors concerned did not know that Linnaeus had raised his variety *hybrida* to specific rank.

This brings us to the name *A. glaucescens* Wallr. (1840), which is the correct specific name of the taxon under discussion. This name first appears on page 134 of *Linnaea* in 1840. Here Wallroth says that, owing to the heterogeneous nature of the specimens labelled *A. montana* in the Willdenow herbarium, he will from now on call the plant he had described as *A. montana* in 1815 *A. glaucescens*. Thus the type description of *A. glaucescens* is that published as *A. montana* in 1815. Later in the year 1840 Wallroth published in the same work (p. 549) a new variety of *glaucescens*, var. *alpestris*. From his notes below this description it is clear that he names his type variety *alpina*, and the only original specimen which we have as yet been able to trace is one of Willdenow's specimens of *A. montana* in the Berlin herbarium (**B**) Plate (11b), annotated by Wallroth as *A. glaucescens* var. *alpina*. This specimen is referable to the taxon here discussed and it is proposed to select it as a lectotype until other material can be found with a better claim.

As all the names here discussed apply to one or the other of two taxa it is proposed to set out their synonymy and give comparative descriptions and distributions.

ALCHEMILLA GLAUCESCENS Wallr. (1840) 134 (Lectotype : Willdenow specimen in Herb. Berlin annotated by Wallroth); Samuelsson (1943) 31; Hylander (1945) 205; Clapham, Tutin & Warburg (1960), 10, fig. 588.

[*A. montana sensu* Wallr. (1815) 26 (*quoad descript. exclud. syn.*).]

A. glaucescens var. *alpina* Wallr. (1840) 549.

[*A. pubescens sensu* Salmon (1928) 345; *sensu* Druce (1928) 36, no. 190 : 1.]

[*A. hybrida sensu* Butcher & Strudwick (1930) 131, plate 144; *sensu* Rothmaler (1962)]

[*A. minor sensu* Wilmott (1939) 249; *sensu* Walters (1949) 9, 16; *sensu* Warburg in Clapham, Tutin & Warburg (1952) 506; *sensu* Ross-Craig (1956) **9**, plate 1; *sensu* Dandy (1958) 55, no. 220 : 3 : 1.]

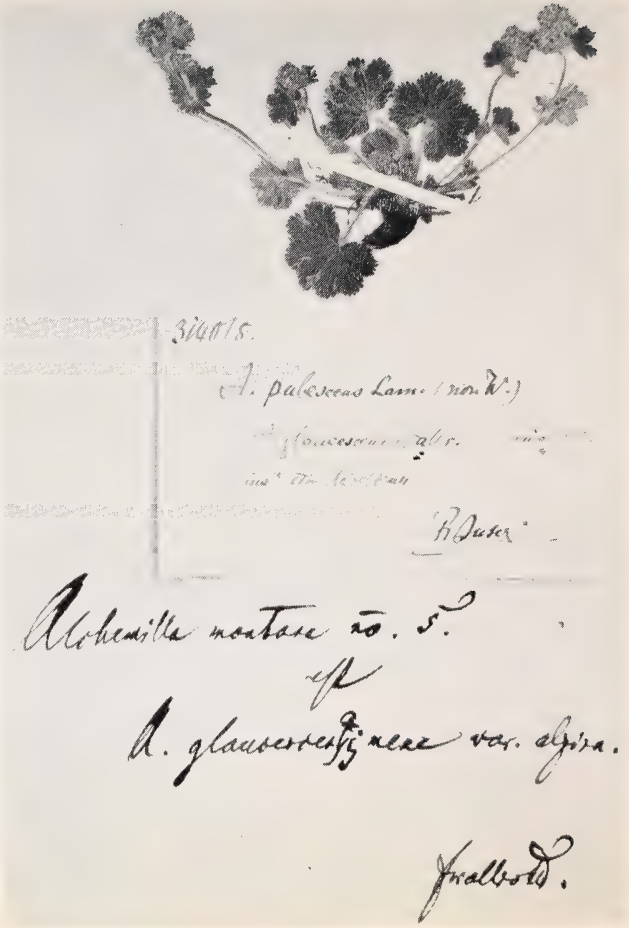
Plant small, up to 20 cm tall, grey-green, silvery. Stem fairly stout, with strong lateral branches giving a dichotomous appearance, yellow-green, often reddening in the summer, densely hairy with spreading or slightly ascending hairs. Radical leaves small, 3–5 cm broad, usually round in outline, basal sinus usually closed, basal lobes often overlapping; lobes 7 or incompletely 9, short, $\frac{1}{4}$–$\frac{1}{3}$ radius of leaf, broad, semicircular, often overlapping at the base; teeth large, subobtuse, 6–7 on each side of lobe; upper surface usually densely hairy, lower very densely hairy with long, silky, silvery hairs; petioles densely hairy with long spreading or slightly ascending hairs. Cauline leaves small, reniform, incompletely 5-lobed, the lobes broad and rounded, densely hairy on both surfaces and with few large teeth. Flowers in dense clusters appearing silvery; pedicels, calyx and outer surface of the sepals densely hairy.

PLATE 11a.



Type specimen of *Alchemilla alpina* var. *hybrida* L. (1753).

PLATE 11b.



Lectotype of *Alchemilla glaucescens* Wallr.

PLATE 12a.



Specimen of ' *Alchemilla alpina pubescens minor* ' in Tournefort Herbarium.

PLATE 12b.



Lectotype of *Alchemilla lapeyrousii* Buser.

Distribution : Austria, Belgium, British Isles (N. England, Scotland and W. Ireland), Bulgaria, Corsica, Czechoslovakia, Denmark, Finland, France (but not Pyrenees), Germany, Switzerland, Hungary, Italy, Jugoslavia, Netherlands, Norway, Poland, Roumania, Russia and Sweden.

ALCHEMILLA HYBRIDA (L.) L. (1756) 49.
A. alpina var. *hybrida* L. (1753) 123 (Holotype : Plukenet specimen on fol. 22 of vol. 95 in herb. Sloane (**BM**)).
A. minor Huds. (1762) 59 (superfluous *nomen illegitimum* for *A. hybrida* (L.) L.).
A. pubescens Lam. (1791) 347 (superfluous *nomen illegitimum* for *A. hybrida* (L.) L.).
A. montana Willd. (1809) 170 (superfluous *nomen illegitimum* for *A. hybrida* (L.) L.
A. lapeyrousii Buser (1893) app. 2, 18 (Lectotype : Sommet du Puy-de-Dôme, France, 27/9/1892, J. Héribaud in herb. Boissier (Herb. Genève (**G**) Plate 12b).
A. anglica Rothm. (1937) 167 (superfluous *nomen illegitimum* for *A. minor* Huds.).

Differs from *A. glaucescens* Wallr. : plant larger, up to 25 cm tall, generally less hairy in all its parts, especially the flowers; stem not bifurcating nor reddening in summer, and the branches less strong; radical leaves reniform, flat, sinus open, lobes longer, c. $\frac{1}{3}$ radius of leaf, more triangular, teeth smaller, more acute and more connivent; pedicels with few hairs or glabrous; and calyx and sepals not densely hairy.

Distribution : France (Pyrenees, Cévennes and Auvergne); Spain (Pyrenees).

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CIRCAEA IN THE BRITISH ISLES

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Although the three European taxa of *Circaea* — *C. alpina* L., *C.* × *intermedia* Ehrh. and *C. lutetiana* L. — have in general been well understood on the Continent, the distinction between *C. alpina* and *C.* × *intermedia* has been a persistent source of confusion and subject of discussion in the British Isles (Baker 1951, p. 306). The result of this confusion has been the classification of a number of individuals of *C.* × *intermedia* as *C. alpina* and the consequent obscuring of some remarkable patterns of distribution. It is the aim of this paper to re-examine the British distribution of *C. alpina* and its relation to the hybrid origin and spread of *C.* × *intermedia*.

Characters distinguishing the three entities

Although the three taxa of *Circaea* considered here (Figs. 1-3) are usually quite distinct, there has in the past been some confusion among them, particularly, as noted above, in Britain. Early in the course of the present study, it was discovered that the most useful character separating *C. alpina* from the others was the nature of its inflorescence. In *C. alpina* the rachis of the inflorescence does not elongate until after the open flowers have dropped; consequently, all of the open flowers are clustered at the stem apex (Fig. 1a). In *C. lutetiana* on the other hand the rachis elongates before the flowers open, and the open flowers are well spaced (Fig. 1g). In *C.* × *intermedia*, the spacing of the flowers is similar to that of *C. lutetiana*, but the inflorescence is somewhat more contracted (Fig. 1d). This character is well shown by Ross-Craig (1958, plates 35-37). When its importance was realised, it was found to be correlated with a number of other features, some stressed in earlier descriptions. Many of them are enumerated in the following table on p. 263.

Comment is necessary on some of these characters. Bracteoles are found with a very low frequency in *C. lutetiana*, but I have not seen them in British or Irish specimens. The disc, which is shown in *C. lutetiana* in Fig. 1h, is a prominent, elevated, nectar-secreting ring at the apex of the hypanthium. The flowers of this species are frequently visited by small flies, and, as the anthers are held away from the stigma, self-pollination is probably a relatively exceptional event, although Mr. P. M. Benoit informs me that the plants of this species he tested were self-compatible. In fine weather the anthers of *C. lutetiana* begin to shed pollen an hour or two after the flowers open. In *C. alpina*, on the other hand, no disc is present, and consequently no nectar, and the anthers often deposit pollen on their own stigma before the buds open, which doubtless causes a high degree of self-pollination. In fact, it is common for the later flowers of *C. alpina* not to open; instead, the buds become large and pale and eventually produce fruit cleistogamously. In *C.* × *intermedia* the disc is usually present but low and obscure.

Evidence of the hybrid nature of *C.* × *intermedia* is found in its complete morphological intermediacy between the two parents, as shown by the preceding table. In addition it is absolutely sterile. The anthers of *C.* × *intermedia* often fall undehisced, and I have never seen a single well-filled, morphologically normal, pollen grain in a plant of this taxon. Likewise, plants of *C.* × *intermedia* fail to produce mature fruit. On the other hand, the plants of *C. alpina* and *C. lutetiana* generally set full complements of seed, and those that I examined, with the exception noted below, were consistent in having pollen more than 90 per cent fertile.

	lutetiana	× *intermedia*	*alpina*
Rhizomes	thick	intermediate	slender, forming terminal tubers in autumn
Overwintering portion	entire rhizome	most of rhizome	only tubers
Stolons from lower axils	absent	present	present
Stem height	15–60 cm	10–45 cm	5–30 cm
Stem pubescence	dense, appressed below	more sparse	absent below
Petioles	hairy all round	hairy above, subglabrous below	glabrous
Leaf base	truncate or slightly cordate	shallowly cordate	cordate
Leaf apex	acuminate	abruptly acuminate	subacuminate or acute
Leaf margin	mostly remotely denticulate	dentate	deeply dentate
Leaf pubescence	strigulose along veins and margins	subglabrous	glabrous
Inflorescence elongation	before flowers fall	before flowers fall	after flowers fall
Bracteoles	absent	present, setaceous	present, setaceous
Pedicels	densely glandular-pubescent	sparsely glandular-pubescent	glabrous
Hypanthium	1–1·2 mm long, about equal to ovary in length	0·5–1·2 mm long, shorter than ovary	0·1–0·2 mm long, much shorter than ovary
Disc	conspicuous, dark, 0·2–0·4 mm high	shallow, rarely to 0·2 mm high	absent
Sepals	pale green; densely glandular-pubescent	whitish; sparsely glandular-pubescent	white; glabrous
Petals	2–4 × 2·2–5 mm, deeply notched	1·8–4 × 2–3·5 mm, deeply notched	0·6–1·4 × 0·4–0·9 mm, often shallowly notched
Petal base	truncate to rounded	rounded to cuneate	cuneate
Filaments	2·5–5·5 mm long	2–5 mm long	1–1·5 mm long
Pollen	fertile	sterile	fertile
Fruits	3–4 × 2–2·5 mm, bilocular	up to 2 × 1·2 mm, falling immature	2 × 1 mm, unilocular
Fruit hairs	0·7–1·1 mm long, dense	0·5–0·6 mm long, dense	0·1–0·5 mm long, more sparse



Fig. 1 a–c. *Circaea alpina:* a, inflorescence; b, flower; c, bud. d–f, *C.* × *intermedia:* d, inflorescence; e, flower; f, bud. g–i, *C. lutetiana.* g, inflorescence; h, flower; i, bud. Inflorescences, × 1; flowers and buds, × 6.

A few British collections, morphologically referable to *C. lutetiana* f. *cordifolia* Lasch, are intermediate between *C. lutetiana* and *C.* × *intermedia* in their cordate leaf-bases and in being relatively glabrous. Although these plants often appear to have full seed set, some of them had only about 50 per cent normal pollen. They may have originated from hybridisation between *C.* × *intermedia* (presumably as the seed parent) and *C. lutetiana*, and this possibility should be investigated further by those in a position to do so. On the other hand, a single plant from Goat Fell, Arran, collected in 1883 (collector unknown; herb. Edinburgh), had the floral characteristics of *C.* × *intermedia* but fruit like that of *C. alpina* and might have been of hybrid origin between them.

Some of the characters used to distinguish the species of *Circaea* in Britain are of little or no value. Amongst them may be mentioned the winged petioles supposed to be found in *C. alpina* and the distinctions in the stigmas described for these species. As shown, for example by Ross-Craig (1958, plate 37), even *C. alpina* may have a two-lobed stigma. Mr. P. M. Benoit has informed me that when the flowers of *C. lutetiana* are not fertilised, the papillose stigmas become swollen and up to 1·5 mm in diameter; stigmas of this sort are frequent in the sterile *C.* × *intermedia*. The seed in one cell of the fruit of *C.* × *intermedia* often begins to develop (as shown by Ross-Craig 1958, plate 36); however, as mentioned above, fruits in this species are not known to reach maturity. It may be added at this point that the plants illustrated by Roles (Clapham, Tutin & Warburg 1960, fig. 722), Butcher (1961, fig. 699), and by Fitch & Smith (1924, fig. 354) as *C. alpina* are in fact small plants of *C.* × *intermedia*.

Chromosomes

The chromosome numbers of the taxa involved have been determined a few times from Continental plants (cf. Löve & Löve 1961), and I have been able to confirm them using British material. All plants of *Circaea* that have been examined to date have had the same chromosome number, $2n = 22$. I determined this number in root-tips of a plant of *C. alpina* from Pennant Dyfi, Merioneth. Some cells in these root tips were tetraploid, with $2n = 44$, but were obviously exceptional in a diploid individual. Meiosis was studied in dividing pollen mother cells of *C. lutetiana* from Llanbedr, Merioneth (*Raven & Benoit* 16301 (**BM**); Fig. 2a), and was regular, with a gametic chromosome number of $n = 11$. Finally, what I believe to be the first observations of meiosis in *C.* × *intermedia* were obtained from plants collected along the roadside in *Fraxinus-Acer* woodland ¼ mile north of Llanymawddwy, Merioneth (*Raven & Condry* 16297 (**BM**); Fig. 2b). Pairing and division of the chromosomes in the plant examined, however, appeared completely normal, with 11 bivalents. In view of the hybrid origin of *C.* × *intermedia*, part of its sterility might have been associated with the presence of meiotic irregularities. The only aspect



Fig. 2. Meiotic chromosomes of *Circaea* at metaphase I, spaced. a, *C. lutetiana;* b, *C.* × *intermedia*. Both × 2000.

in which the meiosis of this plant differed from that of *C. lutetiana*, however, was that two of its bivalents were clearly heteromorphic (one of them is visible in the cell drawn in Fig. 2b), indicating that size differences present in the chromosomes of the parents may have been partly preserved in the hybrid. It does appear from the illustrations of mitotic chromosomes in the three taxa presented by Uddling (1929, Figs. 1–5), that the chromosomes of *C. alpina* are in fact somewhat smaller than those of *C. lutetiana*. Despite this, it would appear that the sterility of *C.* × *intermedia* must be attributed to genetic factors, and certainly not to the kinds of major chromosomal rearrangements that have been so prominent in the evolution of certain other genera of Onagraceae. This is particularly significant in view of the fact that *C. alpina* and *C. lutetiana* seem to be as completely differentiated morphologically as are any two species of *Circaea*.

Distribution of the taxa in the British Isles

As may be seen from an examination of the maps (Figs. 3, 4 and 5), the woodland species *C. lutetiana* is found nearly throughout the British Isles but becomes rarer northward; the hybrid *C.* × *intermedia* likewise has a wide range in the west and north of Great Britain, the Inner and Outer Hebrides, the Isle of Man and northern Ireland, becoming rarer southward; whereas *C. alpina* occupies a much more restricted area than has heretofore been supposed, being relatively common only in the Lake District and on Arran,

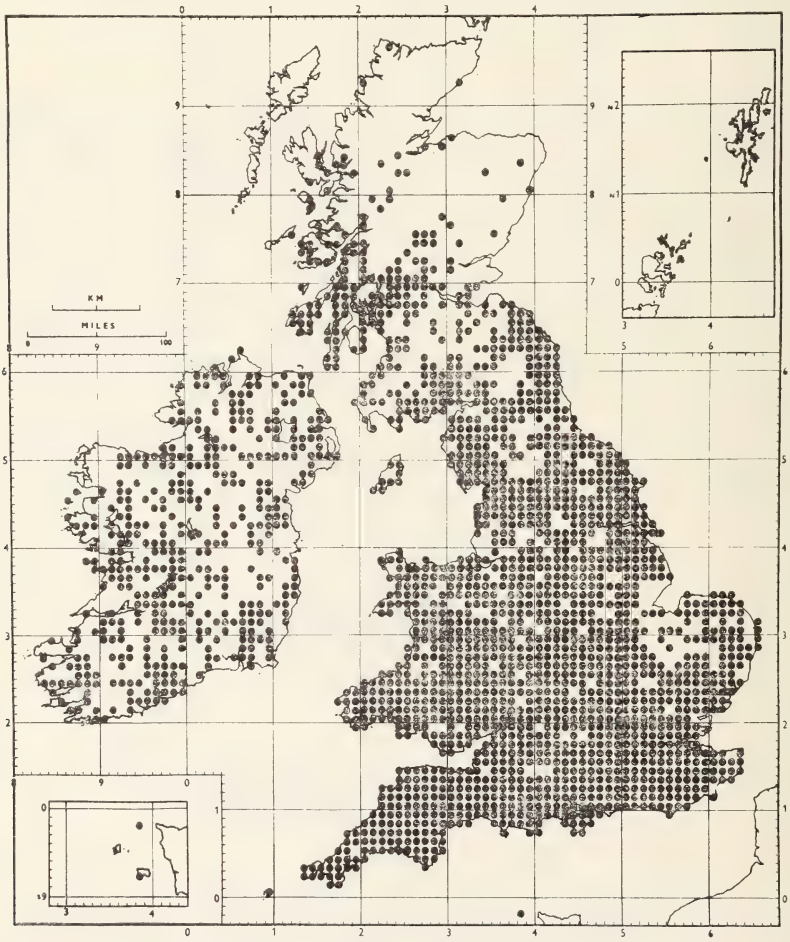


Fig. 3. Distribution of *Circaea lutetiana* L. in the British Isles.

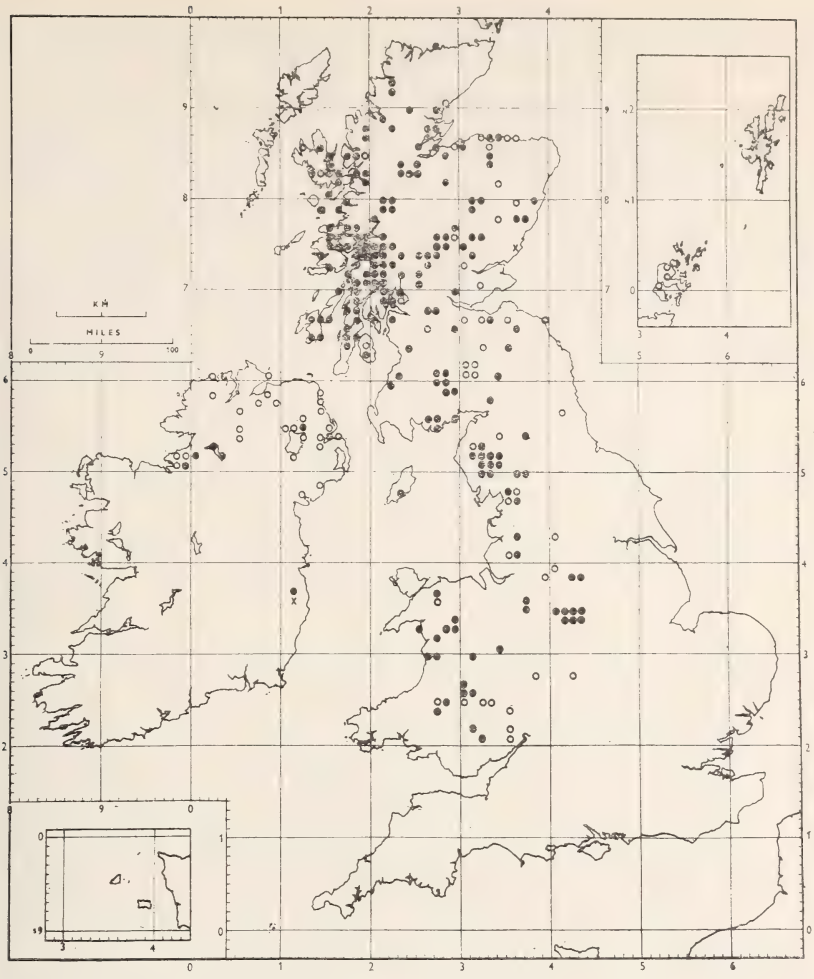


Fig. 4 Distribution of *Circaea* × *intermedia* Ehrh. in the British Isles.
Solid dots, 1930 onwards; open circles, before 1930; crosses, introductions.

with scattered localities in Wales and a single station in mainland Scotland (Westerness). Since the restriction of range proposed here for *C. alpina* is so striking, I will amplify my sources in greater detail.

All of the British material labelled *C. alpina* or *C.* × *intermedia* in the following institutions has been examined : Department of Botany, The University, Aberdeen (**ABD**); Department of Botany, The University, Birmingham (**BIRM**); Botany School, University of Cambridge (**CGE**); Department of Botany, National Museum of Wales (**NMW**); National Museum of Ireland (**DBN**); School of Botany, Trinity College, Dublin (**TCD**); The Royal Botanic Garden, Edinburgh (**E**); Department of Botany, University of Glasgow (**GL**); Royal Botanic Gardens, Kew (**K**), including herb. Watson; Department of Botany, British Museum (Natural History) (**BM**); The Manchester Museum, The University (**MANCH**); Druce Herbarium, Department of Botany, University of Oxford (**OXF**); Botanical Department, The University, St. Andrews (**STA**). In addition, material from the private herbaria of J. E. Lousley, R. H. Roberts, N. Y. Sandwith and E. C. Wallace has been examined by kind permission.

The resulting information has been used in drawing up the map of the distribution of *C. alpina* (Fig. 8). As now understood, the species is confined to only 10 vice-counties, all in Great Britain and Arran, instead of the 45 and 11 Irish vice-counties mentioned by

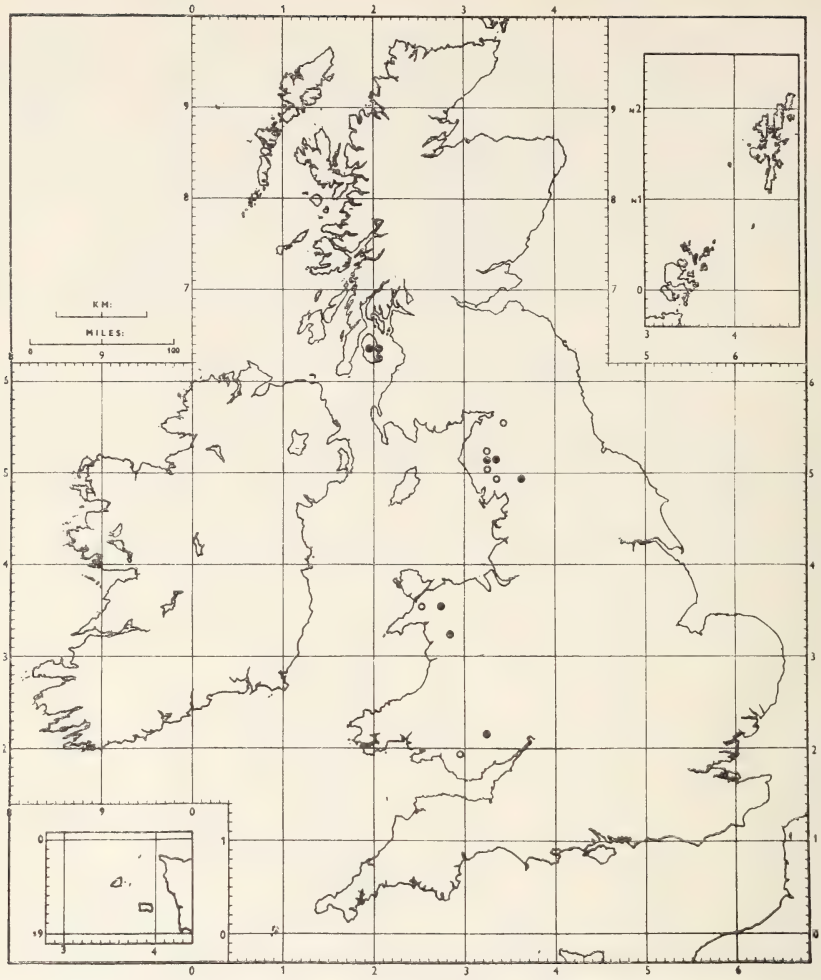


Fig. 5. Distribution of *Circaea alpina* L. in the British Isles. Solid dots, 1930 onwards; open circles, before 1930. Note the isolated Westerness record in grid square 27/07.

Clapham (1952, p. 614). The following list includes all British material of *C. alpina* that has been examined :

V.c. 41, Glamorgan: near a waterfall, west cliffs of the Rhondda Valley, 31 July 1890, *Ley* (**BIRM**; **BM**).

V.c. 42, Brecon: Craig-y-Cilau, 23 July 1952, *Guile* (**NMW**).

V.c. 48, Merioneth: Cliffs, Llaethnant, Pennant Dyfi, Llanymawddwy, 16 July 1955, *Condry & Richards* (**NMW**; herb. Sandwith); same, 6 July 1961, *Raven & Condry 16294* (**BM**).

V.c. 49, Caernarvon: wooded bank opposite the Dolbadarn Inn (shores of Llyn Peris), 3 July 1832, – (**CGE**); Cobdew Bridge to Capel Curig Lakes, Coed Bryn Engan, 22 July 1948, *E. Roberts 354* (**BM**); woods above Bryn Engan, Capel Curig area, *R. H. Roberts* (herb. R. H. Roberts).

V.c. 60, W. Lancs.: gravel margin of forest in oak wood between Wray Castle and Perry, Windermere, 10 Aug. 1920, *Adamson* (**BM**); gravel stream bank in oak wood, west side of Windermere, 5 Aug. 1920, *Adamson* (**BM**).

V.c. 65, N. W. Yorks.: above Rawthey Bridge near Sedbergh, 1938, *Sledge* (**BM**; **TCD**; herb. Lousley; herb. Wallace).

V.c. 69, Westm.: Glencoyne Dale, Ullswater, 30 July 1937, *Lousley* (**BM**; **K**; **NMW**; herb. Lousley; herb. Wallace); Glencoyne Wood, Ullswater, in large patches on stabilised scree in a good many places throughout the wood, 29 Aug. 1955, *Hervey H1828/1955* (**K**); same, 3 July 1961, *Raven 16222* (**BM**); same,

24 July 1937, *Carter* (**BM**; **K**); Ullswater, 12 June 1893, *Clarke 47531* (**K**); Stybarrow Crag, Ullswater, 19 Aug. 1880, *Slater* (**CGE**); Dungeon Ghyll, Aug. 1870, *Baker* (**BM**); abundant in Rough Crag, Riggindale, 30 July 1910, *Ley* (**BIRM**); rocks of Branstree, above Mardale Green, Aug. 1857, *Watson* (**K**-herb. Watson; **TCD**); Mardale, 1866, *Watson* (**CGE**); Swindale, Sept. 1856, *Watson* (**K**,herb. Watson).

V.c. 70, Cumb.: steep shady bank above Glencoyne Farm, Glencoyne Dale, Ullswater, 1937, *Lousley* (herb. Lousley); Thirlmere, June 1895, *Tennant* (**CGE**); west edge of Thirlmere, 29 Aug. 1881, *Ley* (**BIRM**); damp rocks, Fisher Ghyll between Armboth Fell and Thirlmere, July 1904, *Waterfall* (**K**, **MANCH**); Armboth Fell, July 1904, *Mason* (**OXF**); Lodore Wood, 20 July 1884, *Parsons* (**K**); Lodore Waterfall, Derwentwater, 1806, *Turner* (**K**); Derwentwater, 28 June 1842, *Wright* (**BM**); Troutdale, July 1904, *Waterfall* (**K**); in a moist place in Johnny's Wood, near Rosthwaite, Borrowdale, 8 Aug. 1946, *Whellan* (herb. Lousley; herb. Sandwith); Borrowdale, 31 July 1863, *Hind* (**TCD**); Borrowdale, Glaramara, at bottom of wet gully on north face in very deep shade under large boulder, 1200 feet, 14 June 1953, *Cannon & Herbert 2193* (**BM**); Glaramara, amongst dry overhanging boulders, 1300 feet, 7 July 1951, *Park 215* (**BM**); rocks above Seathwaite, 2000 feet, in wet *Sphagnum*, Aug. 1879,–(**OXF**); mountains, Keswick, July 1860, *Ward* (**MANCH**); plentiful about Stonethwaite, near Keswick, 13 July 1947, *Gerrans 73* (**BM**); Grange Fell, 7 July 1891, *Wolley-Dod* (**BM**).

V.c. 97, Westerness: steep slope of ravine, Coine, 30 June 1957, *McCallum Webster 1012* (**K**).

V.c. 100, Arran, among bracken, Benlester Glen, 300 feet, 3 Aug. 1937, *Mackechnie* (**BM**; herb. Wallace); same, 1000 feet, 8 Aug. 1937, *Mackechnie* (herb. Wallace); same, 1000 feet, 10 Aug. 1933, under *Pteris* (herb. Lousley; herb. Wallace); woodland, Monamore Glen, 300 feet, 23 July 1937, *Mackechnie* (**BM**; herb. Lousley herb. Wallace); Glen Cloy, Aug. 1872, *Craig-Christie 502* (**ABD**); Lamlash, July 1890, *Wilkie* (**GL**); same, Aug. 1928, *Mackechnie* (herb. Wallace); Arran, 29 Aug. 1888, *Thompson* (**BM**).

Not assigned to vice-county: 'North Wales,' *Weiss* (**MANCH**).

One of the more interesting facts that emerges from these maps and the listing of specimens is that *C. alpina* does not have a particularly northern or montane distribution in the British Isles. Rather, while conforming rather closely to the sort of distribution expected of a member of the "Continental Northern" pattern as outlined by Matthews (1955), it occupies a highly fragmented range along the western side of Great Britain. Its extreme rarity on the mainland of Scotland and apparent absence from the Hebrides and from Ireland were entirely unexpected, the more so since *C.* × *intermedia* is common over much of this area. Of equal interest is the occurrence of *C. alpina* in the Rhondda Valley at a locality which is south of the present range of *C.* × *intermedia;* it would be of importance to study this site ecologically if it could be re-located.

A few examples may be given of other species which have ranges in Britain similar to that of *C. alpina* (kindly suggested by Dr. F. H. Perring), but it should be noted that none of them is of the same geographical group when total range is considered. These are *Carum verticillatum* (W. Europe), *Vicia orobus* (W. Europe), *Centaurium littorale* (coasts of W. Europe and inland from Austria to S. Russia) and *Rhynchosinapis monensis* (endemic).

Origin and spread of Circaea × intermedia

On the continent of Europe, *C.* × *intermedia* occurs mostly in or near the zone of contact between *C. alpina* and *C. lutetiana*. In Scandinavia, for example, *C. alpina* is widespread, *C. lutetiana* is present only in the south, and *C.* × *intermedia* is nearly restricted to the area where its two parents overlap (Hultén 1950, maps 1293–1295). As can be seen from an inspection of Figs. 3, 4 and 5, however, the situation is quite different in Britain. *Circaea alpina* doubtless had a wider distribution in the British Isles in cooler times nearer to the last glacial period, but today it is restricted to relatively few localities. On the other hand, *C. lutetiana* is a woodland species that must have mostly expanded its area since the last glacial period. The morphological intermediacy and complete sterility of *C.* × *intermedia*, taken together with the lack of other possible parents, point to the fact that it must be regarded as being of hybrid origin between *C. alpina* and *C. lutetiana*. Despite this, *C. alpina* is now absent from many areas where *C.* × *intermedia* is common, such as Ireland, the Hebrides and much of mainland Scotland. Moreover, *C. lutetiana* also is absent from some of these areas, particularly northern Scotland and Orkney.

These apparent discrepancies may be explained in two ways. Either *C.* × *intermedia* has achieved its present wide distribution in the British Isles by means of its remarkably vigorous vegetative reproduction, or its distribution reflects the one-time area of *C. alpina* where it came into contact with *C. lutetiana*, or both factors may be important. Correlated with these considerations is the question as to whether *C.* × *intermedia* in Britain and Ireland originated from a single hybridisation, or whether it is produced with fair frequency whenever its parents come into contact. The latter question may be considered first. Arguing for the fairly frequent production of the hybrid is the sort of situation on which I made observations in Glencoyne Wood, Ullswater, Westmorland, on the 3 July 1961. Here all three species grew in a moist shaded area of woodland dominated by bracken and species of *Carex* and *Juncus*. *Circaea alpina* occurred in two small patches scarcely 3 m across, whereas *C. lutetiana* was more widespread both on this flat and in the neighbouring woods. The individuals of *C.* × *intermedia* formed a band approximately 2 m across, ringing the small patches of *C. alpina*, and they were in turn surrounded by the abundant *C. lutetiana*. It is extremely probable that these hybrids were produced *in situ*. Furthermore, *C.* × *intermedia*, as has been remarked by many writers of floras, is very variable in habit, pubescence, flower size, leaf margin and other characteristics. This sort of variability would be most unexpected if all the individuals concerned had been derived by vegetative reproduction following a single hybridisation. Finally, the range of *C.* × *intermedia*, from Britain to the Caucasus, argues against such an hypothesis. On the other hand, it would be a serious mistake to underestimate the capacity of *C.* × *intermedia* for vegetative spread, particularly when it is remembered that these plants are often serious garden weeds where they occur. Vegetative reproduction seems to have been important in the spread of certain other well-known plants that occur in gardens, such as *Aegopodium podagraria*, species of *Calystegia* and *Tussilago farfara; Circaea* × *intermedia* has obviously attained part of its present range in the same way. A particularly suggestive example of this, pointed out to me by Professor Webb, is its local occurrence in Co. Wicklow, Ireland, well south of its main area of distribution; here it is exclusively a garden weed and very probably introduced. Also in Merioneth, for example, it is mainly restricted to disturbed areas and man-made habitats, particularly in gardens and along roadsides, and is probably extending its range in connection with cultivation (Benoit & Richards 1961).

Thus, in summary, it does not appear likely that all of the present distribution of *C.* × *intermedia* in Britain and Ireland can be explained by its admittedly vigorous vegetative reproduction. A more probable hypothesis is that *C. alpina* was more widespread nearer the last glacial maximum. As it contracted from this wider range to the few stations it occupies at the present time, it was often in contact with *C. lutetiana*. Spreading as it must have done with the increase in wooded areas, *C. lutetiana* may eventually have come to occupy an area even more extensive than at present during the warm, dry period approximately 5,000 years ago (Matthews 1955). At the height of this warm, dry period, *C. alpina* may have been even more restricted in range than it is today, judging from the western, oceanic nature of its present range in Britain. As their ranges shifted, hybridisation between *C. alpina* and *C. lutetiana* probably occurred fairly frequently, producing numerous biotypes of *C.* × *intermedia* with intermediate morphology and ecological requirements. From these centres, the sterile *C.* × *intermedia* spread by means of its efficient vegetative reproduction and, in some instances, as a ruderal aided by man. It is important to note that the capacity for vegetative spread was already present in one of the parents, *C. lutetiana*, as gardeners will attest, and that it was this pre-determined capacity that allowed the sterile *C.* × *intermedia* to become established and spread; it is evidently even more vigorous in its spread than *C. lutetiana*. Progressive changes in climate finally led to the apparent extinction of *C. alpina* in Ireland and over much of Scotland and allowed its survival only in those few, particularly favourable localities where it persists to the present day. Its apparent absence from Ireland is particularly interesting in view of its present western oceanic distribution in Britain, which suggests that conditions in at least some

portions of Ireland may be suitable for it at the present time. It is possible that the shift to a cooler, more oceanic climate in the past 5,000 years has caused the restriction of *C. lutetiana* in the north and perhaps even allowed *C. alpina* to spread slightly in the Lake District and on Arran. Meanwhile, *C.* × *intermedia*, apparently well suited to the climatic conditions prevalent in northern Ireland, Scotland, northwest England, and portions of Wales, has flourished in those areas and become locally the commonest or even the only representative of the genus present in some of them, despite its complete dependence on vegetative propagation.

Thus *Circaea* × *intermedia* presents a truly remarkable example of a sterile hybrid better suited to a particular set of conditions than either parent, and consequently replacing them in certain areas. Two similar examples from the British flora that may be cited are *Nuphar* × *intermedia*, the apparently highly sterile diploid hybrid between *N. lutea* and *N. pumila* (Heslop-Harrison 1953) and *Rorippa* × *sterilis* (*R. nasturtium-aquaticum* × *R. microphylla*), a sterile triploid which occurs locally in the absence of both parents in much the same areas as *Circaea* × *intermedia*. Such patterns of variability are characterized by the ability of hybridisation to produce a large number of relatively uniform genotypes suited to a particular environment correlated with an apparent loss in evolutionary flexibility. Similar patterns occur frequently in the angiosperms but they are usually a product of the spread of fertile allopolyploids rather than of sterile, vegetatively propagated hybrids.

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VARIATION OF SOME DIAGNOSTIC CHARACTERS OF THE SESSILE AND PEDUNCULATE OAKS AND THEIR HYBRIDS IN SCOTLAND

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Abstract

A collection of Scottish oaks including nearly 1,000 fertile specimens has been analysed in respect of selected diagnostic characters. Pictorialized scatter-diagrams confirm that only two taxa are involved and that considerably more than half the fertile material cannot be diagnosed with confidence as belonging to either. The variation patterns within population samples are so exactly what would be expected from widespread and massive introgression that the objections to this interpretation are called into question. All the *robur*-dominated woods appear to be quite strongly introgressed but there are a few *petraea* woods which are relatively homogeneous and show no evidence of introgression. The latter are used to demonstrate the variation that may be expected from reasonably good *petraea* in Scotland.

Introduction

Q. robur L. and *Q. petraea* (Matt.) Liebl. have been described in varying detail many times since they were first distinguished. Jones (1959) has recently summarised the more important British and Continental contributions to our knowledge of the two species. The list below of some of the more reliable diagnostic characters is extracted from his account.

Character		*robur*	*petraea*
Leaves of spring shoots of the crown	Shape	obovate	ovate
	Lobing	deep, irregular, 3–5(–6) pairs	shallow, regular, 5–6(–8) pairs
	Petiole	short 2–3–7 mm	long 13–25 mm
	Leaf base	cordate with strong auricles	cordate to cuneate, weak auricles
	Abaxial surface	glabrous, occasional simple hairs	always some stellate hairs
Acorns	Colour	pale fawn	uniform dark brown
	Longitudinal stripes	olive green on fresh mature acorns	absent
Fruiting peduncle	Total length	2–9 cm	0–3(–4) cm
	Thickness	slender	stout
	Pubescence	glabrous	some pubescence
Buds	Size	small	large
	Apex	obtuse	acute

Two of these characters are reputedly qualitative : the striations on the maturing acorn of *robur* and the abaxial stellate pubescence on the leaf of *petraea*. The first is of little practical use in the field unless collecting is confined to the critical periods of good

fruiting years. The second is disputed : Jones follows Moss (1914) in accepting abaxial stellate hairs as a *petraea* character, but several Continental workers have described aff. *robur* forms as having them (*e.g.* Weimarck 1947). Of the remaining quantitative characters only petiole length has ranges for *robur* and *petraea* which do not overlap. Scottish collections however, do not conform to the specifications above; they show overlap in this as well.

Confident identifications of oaks in Scotland can therefore be made only when the individual exhibits most of the diagnostic characters in the extreme forms associated with one of the two species. A majority of individuals have to be classified as intermediate either because intermediate values for diagnostic characters predominate or because extreme *robur* and *petraea* characters occur on the same tree. Many Scottish woods have a very high proportion of such intermediate forms and for many years it was commonly assumed that they were of hybrid origin (*e.g.* Burtt Davy 1933, Tansley 1940). Opinion changed as the results of work by Pyatnitski and Dengler (refs. in Jones 1959) became known; they had demonstrated experimentally that the two species when crossed set on the average only 2% fertile seed. Jones expresses the new views when he defines the species more broadly than before and claims that hybrid forms, even in woods where both species are present, are unlikely to exceed 5%. While I agree that Jones' descriptions of the two species are a great improvement on former ones, they do not seem to clarify the position in Scotland (*cf.* attempts to apply earlier descriptions in Scotland by Greville (1841)).

The field botanist has neglected the oaks. The reasons are probably the obvious ones, the difficulty of collecting comparable material from mature trees and the long history of planting of these economically important species. If the field botanist has to accept the possibility of planting he can no longer place much ecological significance on the presence or absence of one or other species in a particular site.

Anderson (unpublished) has studied the history of oak planting in Scotland in great detail. There appear to be old planting records in all the areas where oak woodland occurs today and there are many records in what now seem the most unlikely places by reason of their remoteness or the roughness of the terrain. Tansley (1939) evades the problems of planting by classifying the older oak woodlands as semi-natural and saying that a plantation on an oak site would eventually become indistinguishable from a natural wood; but he makes no stipulations about the provenance of the planting stock used to form the plantation. There is considerable evidence, discussed by Jones (*ibid.* pp. 175 and 215), to show that *robur* was consistently preferred for planting irrespective of the species originally occupying the site.

A majority of the older oakwoods remaining in Scotland include many stems which have patently developed from coppice stools. Some areas, as in the Trossachs, are known to have been under intensive coppice management (or coppice with standards) for long periods. Between 1600 A.D. and 1900 A.D. coppice management spread throughout Scotland, at first for rural produce and later for tan-bark production and charcoal for smelting. The woodlands least intensively managed are likely to have been those least accessible from the sea and the main land-routes; the north-shore oakwoods of some of the inland lochs of the north-west may come in this category. The youngest coppice woods date from the First World War but many still obviously coppice woods are more than twice that age. Generally few standards remain though large stumps often show that they were present. On the better sites stools have usually been singled but very few stems show conspicuously good form. Woods derived from coppice have an unnaturally high stocking of oak; other woody species (except hazel) have presumably been eliminated deliberately. High oak stocking could conceivably have been attained with natural regeneration alone, but it seems more likely that planting was frequently necessary.

Objects

The original objective, which led to the work described in this paper, was the location of oakwoods of indigenous Scottish stock. The immediate objective was a practical defini-

tion of *robur* and *petraea* in terms of suitable diagnostic characters. As will be seen, the work carried out to this end has gone a long way towards the next objective – to discover whether there were distinctive variation patterns within oak populations which could be used to assess their status.

Collecting methods and choice of diagnostic characters

Variation on the tree is considerable and if comparisons between trees are to be meaningful an attempt must be made to minimise variation from this source. A preliminary study was therefore made of variation patterns on the tree and through the growing season with the aim of determining the most reliable diagnostic characters and the best general collecting procedure.

While the results of this study suggest that there may be significant differences in the variation patterns of *robur* and *petraea* it is the resemblances that are more important at this stage before the species have been defined. The pattern of leaf variation on the sun-shoot, for example, is remarkably consistent. There is a gradation from small basal leaves which are rather irregular, comparatively broad with deeper lobes, more ovate and have a more cordate base, through larger mid-shoot leaves to the apical leaves which are also smaller than average but are more regular, narrower with shallower lobes, more obovate and have a less cordate (or even cuneate) base. Mid-shoot leaves are most representative and also show the best auricle development. On horizontal shoots leaves arising from the under side are larger. A trial was made using two mid-shoot leaves for biometric measurements. A comparison of average figures for all leaves with those obtained from pairs of mid-shoot leaves can be made in Columns A and B of Table 1 below.

Table 1
Variation of leaf-length and petiole-length with position on the tree

Tree No.	*Part sampled*	*Leaf-length* (mm)		*Petiole-length* (mm)		*Petiole* %	
		A*	B	A	B	A	B
1. *petraea* (isolated)	Lower crown—W	80·2	92·0	9·4	10·3	11·7	11·2
	Lower crown—N	82·1	91·9	9·2	10·2	11·2	11·1
	Lower crown—E	76·3	88·4	9·9	12·2	13·0	13·8
	Lower crown—S	74·7	86·7	12·3	14·4	16·5	16·6
2. Hybrid (*robur* affinity)	Lower crown—W	90·4	107·1	6·3	7·5	7·0	7·0
	Lower crown—N	89·4	100·0	6·7	7·1	7·5	7·1
	Lower crown—E	97·0	106·3	8·0	8·5	8·2	8·0
	Lower crown—S	96·3	104·4	6·9	7·1	7·2	6·8
3. *robur* (isolated)	Lower crown—N	72·8	86·2	3·9	4·9	5·4	5·7
	Lower crown—S	86·3	102·9	4·6	6·2	5·3	6·0
4. *robur* (NW of a large gap)	Top of crown		76·8		2·6		3·3
	Upper crown—SSE		77·3		2·6		3·6
	Lower crown—SSE		85·0		2·4		2·8
	Inside crown (shade shoots)		101·8		3·5		3·4
	Epicormic shoots		99·8		3·0		3·0

*A – Averages for all leaves on 5 representative terminal shoots (sun-shoots except as indicated).
B – Averages for two mid-shoot leaves from each of the shoots (ten leaves).

These data show that there is marked variation with position on the tree; the collecting position should thus be standardised. The south-east aspect was eventually chosen because it appeared that the difference in petiole-length for *robur* and *petraea* would then be greatest. The figures also suggest a relationship between leaf dimensions and insolation or exposure.

For a study of variation through the growing season 12 trees were selected in Dalkeith Old Wood. This wood includes both *robur* and *petraea* with many intermediate types (see Table 3 below). Collections were made at the same point (SE of the accessible part of the crown) at increasing intervals from the time the buds began to swell. The pertinent observations from these data were :

(a) abaxial stellate pubescence remained substantially the same from the time the leaf was fully expanded till it fell in autumn even though scored from different leaves at each collection,

(b) buds of all specimens were small and obtuse at first – only towards autumn were *robur* and *petraea* types readily distinguishable,

(c) flowering peduncles reached their maximum length about mid-June but continued to increase in diameter for several weeks,

(d) after July the peduncle beyond the most distal developing acorn shrivelled and sometimes fell off; it follows that total length of fruiting peduncle must be an unreliable character for comparative purposes,

(e) during the same period the peduncle became more woody at the base and decreased in diameter roughly to the same extent as peduncles collected in July (after drying),

(f) peduncles of all specimens were densely pubescent at first; aff. *robur* forms were practically glabrous by mid-June; on aff. *petraea* forms the pubescence persisted at least on those parts protected from rubbing,

(g) peduncle length, particularly on aff. *robur* forms, could show considerable variation on the tree and sometimes on the shoot.

The period available each year for collecting ran from mid-June till early October. It was desirable therefore to select characters which would be comparable throughout this period. Leaf characters were suitable but buds and the acorn with its fruiting peduncle were not. In view of the importance attached to peduncle characters in diagnosis alternative biometric measurements were investigated. Length to the first flower locus proved very satisfactory; it does not change as the acorns develop and the flower bract persists even if the fruit does not develop; using this character the proportion of nominally fertile specimens is increased and better separation of typical *robur* and *petraea* is obtained. As both peduncle pubescence and peduncle diameter seemed promising diagnostic characters, collecting was planned to start not earlier than mid-July.

The following characters were eventually selected for recording : leaf length, petiole length, auricle type, abaxial stellate pubescence, lobe number, lobe depth, length of peduncle (total and to the first bract), peduncle diameter and peduncle pubescence.

Field collections were made with a pole-cutter reaching to twenty feet. A small branch was cut and a fertile (if present) terminal sun-shoot selected as typical of such shoots on it. Two representative mid-shoot leaves were detached and pressed and dried separately. After measurement shoots and leaves were mounted and retained for reference. Collection presented no problems in the open or scrub woods which predominate in Scotland. In woods with a closed high canopy samples had to be taken from the nearest gap at paced intervals or along roads and rides running roughly east-west. In a few woods sampling had to be done along the southern margin after checking that these marginal trees were similar to those inside the wood.

In practice it was some time before the importance of taking a satisfactory population sample was appreciated. Many of the earlier collections were rather small and some were selective. Collections have now been made in 127 different woods well distributed throughout Scotland (details appear in the *Forestry Commission Research Reports* for 1961 and

1962) and 55 of them include sufficient fertile specimens, systematically collected, for complete analysis as population samples on the lines described below.

Analysis

Of the characters recorded as continuous variables only petiole (as petiole % of leaf length) and peduncle length (to first bract) provided reasonable separation of typical examples of *robur* and *petraea;* leaf length, lobe number and lobe depth all provided minimal separation. Six characters were thus used, the two above (the primary characters) and four secondary characters – auricle type, stellate pubescence (abaxial), peduncle pubescence and peduncle diameter. The latter were first studied in some detail to determine which parts of their ranges were diagnostic of one or other species. Arbitrary limits were set and then each character was considered in turn, but only for those specimens for which all the other characters were positively diagnostic of *robur* or *petraea*. Each reappraisal was followed if necessary by reclassification and the process repeated until no further adjustment of limits was required. The definitions arrived at may be seen in Table 4. A specimen showing all four secondary characters within the diagnostic range for one species belongs to what is hereafter called the Theoretical Species Type (or TST). A specimen showing one character in the indeterminate range lies within the apparent normal range of the species but may not belong to it if the difference is actually due to hybridisation. The four characters each with a *robur*, indeterminate and *petraea* range provide 81 (3^4) possible combinations which can be classified according to their differences from either TST.

Table 2
Classification of Secondary Character Combinations

Character Combinations	*Secondary character combination classes*								
	I	II	III	IV	V	VI	VII	VIII	IX
	Theoretical *petraea* combination	Degrees of difference							Theoretical *robur* combination
		1	2	3	4				
					4	3	2	1	
Possible	1	4	10	16	19	16	10	4	1
Actual	1	4	10	13	18	14	10	4	1

The number of combinations which can appear in a population sample is determined by the variability of the population sampled and the sample size. However, quite a small sample (15-20 specimens) is likely to show the range of combination classes present in the population. A general picture of the variability in Scottish oakwoods is conveniently presented in terms of the range and frequency of these combination classes.

If obvious plantations are excluded a majority of the woods sampled fall into category A below; aff. *petraea* forms predominate, while aff. *robur* forms (Classes VIII & IX) are absent. Intermediate forms (Classes III-VII) dominated 15 woods (category B), two of them plantations. Only 8 woods fell in category C (*robur* woods) and 4 of these were obvious plantations; collectively they included a much higher proportion of intermediate classes than the *petraea* woods. The mixed woods (category D) totalled 7; they were distinctive in having both aff. *robur* and aff. *petraea* forms but without a complete series of linking intermediate classes. One of them (Knockman Wood, Galloway) was a rather poor plantation of *robur*

TABLE 3

Representative population samples classified on the range and frequency of their component secondary character combination classes

General category	*Wood sampled*	*O.S. Grid square*	*Combination classes – no. of specimens*									
			I	II	III	IV	V	VI	VII	VIII	IX	*Total*
A. *petraea*-dominated woods	Glentrool	NX	20	6								26
	Elgin	NJ	4	3	2							9
	Spean Bridge	NN	5	6	4	3						18
	Loch Sunart	NM	4	2	3	2	2					13
	Ptarmigan	NN	8	8	8	1	2	2	1			30
B. Dominated by intermediates	Kirkwood	NY			1	7	2	1	2	2		15
	Loch Katrine	NN		2	3	2	3	4	1	1		16
	Dalkeith	NT	1	1	3	9	6	12	9	7	2	50
C. *robur*-dominated woods	Erchless	NH				2	1	2	1	3	3	12
	Gourdie	NO					1	3	3	1	2	10
	Fearnoch	NM						2		3	1	6
D. Mixed woods	Aikieside	NT	9	2						1		12
	Tore of Troup	NJ	2	1		2		3	1	2	2	13
	Springkell	NY	3				1	5	5	2	4	20
Totals			56	31	24	28	18	34	23	22	14	250
Other population samples			122	103	58	57	66	37	58	49	21	571
All population samples			178	134	82	85	84	71	81	71	35	821

affinity bounded by a wall beyond which were a few remnant *petraea;* the few good *petraea* in the plantation may well have been natural seedlings. Another (Aikieside, Berwickshire) consisted mainly of good *petraea* derived from coppice, with scattered aff. *robur* trees which were probably planted in gaps at the same time as a neighbouring *robur* plantation was established.

The next step was the introduction of the primary characters, used as co-ordinates of scatter diagrams, to discover whether the TSTs themselves were discretely differentiated entities.

Fig. 1 shows that they are not; the distribution of values for each is strongly directional with a marked trend towards the concentration centre of values for the other TST and slight overlap. Classes II and VIII showed the same trend more strongly and the overlap was greater. There is in fact a fairly regular gradation right through from Class I (TST *petraea*) to Class IX (TST *robur*) when judged from the mean values for each class (see Fig. 1).

The combination classes are, of course, artificial aggregates of individuals drawn from many rather different types of population. It will only be possible to formulate 'normal' limits of variation for either species in Scotland if populations can be found which exhibit them. The final test therefore lies in analysis of variation within populations. For this purpose pictorialized scatter-diagrams were used; they allow simultaneous appraisal of all the variables and the population samples do not need to be large or identical in size. The secondary characters were represented by the symbols shown in Table 4 below.

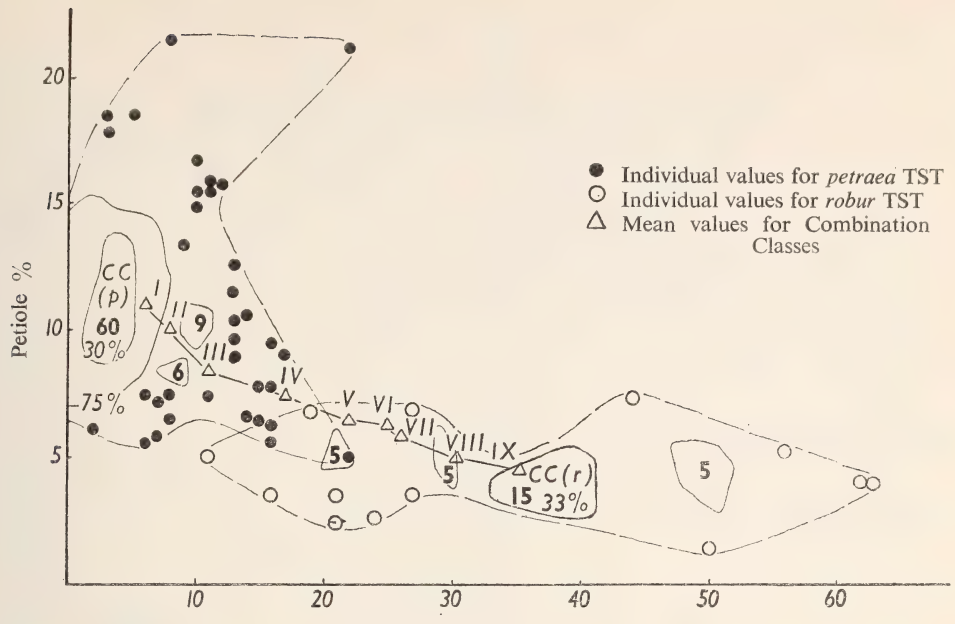


Fig. 1. Scatter diagram of combined petiole % and peduncle length values for all specimens classified as Theoretical Species Types (TSTs). Continuous lines enclose Concentration Centres (CC) for *petraea* (*p*) and *robur* (*r*). Broken lines outline the limits of variation of each TST.

Figures 2-7 show examples covering the range of woodland types. As might be expected from the analyses above, the greater the number of secondary character combinations in the sample, the wider is the scatter. The important observation here is that this principle applies also to the scatter of TST values. *If the TSTs from the more heterogeneous samples had been excluded in preparing Fig. 1 then they would have appeared as discretely differentiated entities.* The most homogeneous samples from *petraea*-dominated woods all include some individuals differing from the TST in one degree (Class II combinations) and all four possible variants occur. There are no equivalent samples from *robur*-dominated woods.

Discussion

These findings cannot be reconciled with the view Jones (1959) has expressed about the current status of *robur* and *petraea* in Britain. If they are acceptable taxa then these data show that the proportion of hybrids in Scotland is at least 50% and probably 75%. Alternatives which have not been seriously countenanced for a long time are (a) that the two taxa are not discrete entities and (b) that a third taxon, intermediate between *robur* and *petraea*, is involved. In spite of intensive collecting in reputed *robur* woods and plantations during 1961 the amount of *robur* material is only just adequate to demonstrate a concentration centre for combined petiole and peduncle values of the *robur* TST. Nevertheless it is fairly clear that two, and only two, taxa are involved in these data.

Introgressive hybridization (or simply ' introgression ') was defined by Anderson (1949) as a natural process of gene exchange arising from repeated back-crossing between hybrids and the parent species. ' Introgression ' is used here in the same sense, though the process is unnatural to the extent that it has been unintentionally accelerated by Man's activities. The variation described in Scottish oak populations is so exactly what would be

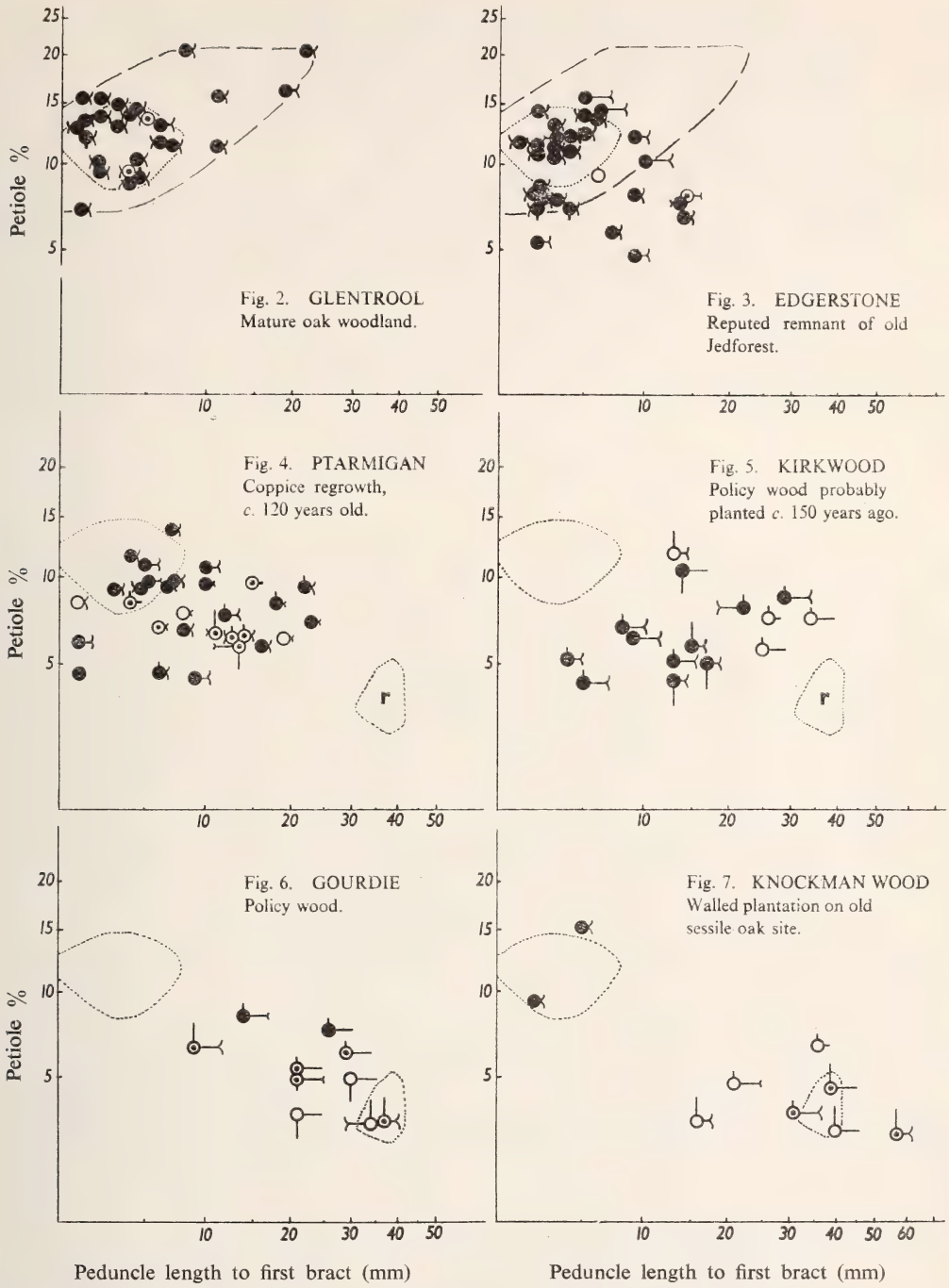
TABLE 4

The diagnostic ranges for secondary characters with symbols*

Character	*Diagnosis*		*Symbol*
1. ABAXIAL STELLATE PUBESCENCE Recorded separately for the small prostrate trichomes on the lamina and large erect trichomes beside the midrib.	Both types abundant	*petraea*	
	One type absent or one or both sparse	indeterminate	
	Both types absent	*robur*	
2. AURICLE TYPE Based on (a) the development of the basal lobes which in the extreme *robur* form overlap the petiole and (b) the sharpness of the reflexion of the lamina where it joins the petiole	Lobes weak (or nil); lamina not sharply reflexed	*petraea*	
	Medium lobes not reaching the petiole; lamina sharply reflexed	indeterminate	
	Lobes well developed reaching the petiole on at least one leaf; lamina sharply reflexed	*robur*	
3. PEDUNCLE DIAMETER Measured by gauge (cut to 1 mm, 1·5 mm and 2 mm) at the narrowest point below first bract	Stout 2 mm diam. or over	*petraea*	
	Intermediate *c.* 1·5 mm	indeterminate	
	Slender 1 mm diam. or less	*robur*	
4. PEDUNCLE PUBESCENCE Caducous pubescence lost by about mid-June. Persistent pubescence tending to rub off on all except very short peduncles	Very pubescent or pubescent at least on protected parts of peduncle	*petraea*	
	Trace of pubescence	indeterminate	
	Glabrous	*robur*	
Theoretical Species Combination		*petraea* TST	
Theoretical Species Combination		*robur* TST	

expected of two mutually introgressing species that conflicting evidence should be critically examined. The fertility barrier between the species demonstrated by Pyatnitski and Dengler is the only serious problem. This may be either not as important or not as generally applicable as workers in this field have assumed. Experimental crosses need to be made in other parts of the range of the two species and, possibly more important still, the success of back-crosses needs investigation.

* For a more detailed description of these characters with illustrations of auricle types see Cousens (1962)



Figs. 2-7. Scatter diagrams for six oak populations. Concentration Centres for *petraea* (from Fig. 10) and *robur* (from Fig. 1) are shown by dotted lines.

As Stebbins (1950) has pointed out oaks are long-lived and form more or less closed communities : interspecific hybrids becoming established in such communities will tend to be isolated among many individuals of the parent species and back-crosses rather than

interhybrid crosses will be the rule : furthermore one hybrid is potentially capable of producing an enormous number of back-cross progeny during its lifetime. The interspecific fertility barrier may be relatively unimportant if the hybrids are fully fertile with either parent. Numerous examples of introgession in American oakwoods have already been cited (see Tucker & Muller 1958, Cottam, Tucker & Drobnik 1959, Tucker 1960 and Tucker 1961 for some recent examples).

The historical facts point to widespread and extensive planting activity with a strong preference for *robur* planting stock. *Q. robur* must have been introduced in this way into many areas where *petraea* dominated the natural woodland and the chances of the cross *robur* ♀ × *petraea* ♂ appearing must have been very high. Collection of acorns from these *robur* nuclei would have given the hybrids very favourable chances of becoming established as crop trees in new plantings, particularly if a proportion of them exhibited hybrid vigour (refs. in Dengler 1941). Reasons will be put forward below for believing that the F1 hybrid bears a strong superficial resemblance to *robur;* collection of acorns from such hybrids may frequently have been made in the mistaken belief that they were good *robur*.

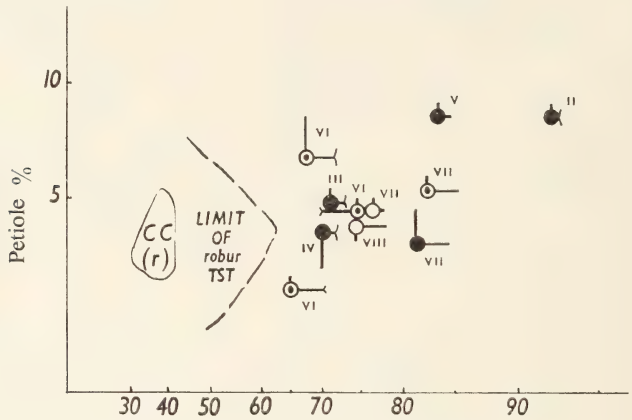


Fig. 8. Specimens with abnormally long peduncles.

The only suggestion of hybrid vigour in these data lies in eleven values for peduncle length to first bract beyond the range of the *robur* TST. They include 10 different secondary character combinations and every class from II to VIII is represented (Fig. 8).

The numbers of specimens recorded in the intermediate combination classes (III to VII) happen to be of similar magnitude (see Table 3). It seemed that analysis of the frequency with which *robur*, *petraea* and indeterminate characters appeared among these putative

Table 5
Frequency (%) of secondary characters in intermediate combinations

Character	*Auricle type*	*Abaxial pubescence*	*Peduncle diameter*	*Peduncle pubescence*
petraea	23	**40**	19	**48**
Indeterminate	**52**	31	28	36
robur	25	29	**53**	16

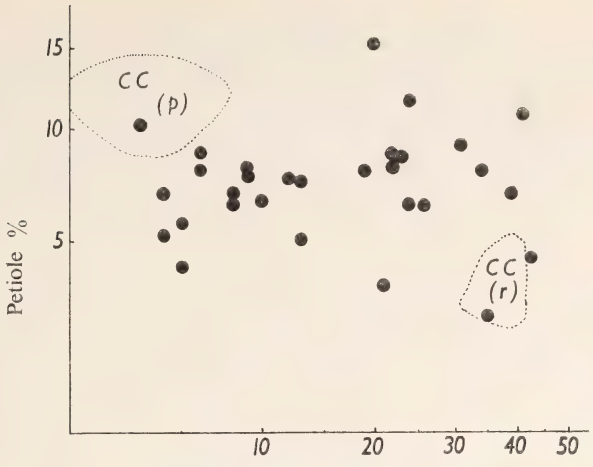


Fig. 9. All values for ⊢ ? an F.1. hybrid

hybrids might yield significant results. Only auricle type shows a maximum in the indeterminate range, the expectation if the character is under polygene control. The other three characters appear to exhibit partial dominance for *petraea* pubescence of leaf and peduncle and *robur* slenderness of peduncle. If these conclusions are valid the interspecific hybrid will consist mainly of forms with medium auricles, well-developed abaxial pubescence and slender pubescent peduncles. This combination is in fact the most frequent one in these combination classes and provides the only example of an intermediate combination dominating a population sample (*viz.* Kirkwood – see also Table 3 and Fig. 5). Figure 9 is a scatter-diagram for all specimens showing this combination : it will be seen that they show extremely wide scatter in the zone between the concentration centres for the TSTs. This combination is also found in a form described as *Q. robur* subsp. *puberula* (Lasch) Weim. by Weimarck (1947) who noted several ' aberrant forms ' – a f. *brevipedunculata* and a f. *petiolaris* (suggesting that petiole-peduncle values for the sub species would also show very wide scatter) and a f. *longipedunculata* (for which an equivalent did not occur in these data though it might correspond to the forms tentatively suggested above as due to hybrid vigour). *Q. robur* subsp. *puberula* is reported from Norway (Risdal 1955) and is said to become more and more frequent eastwards through Scandinavia; it is also reported as fully fertile (Weimarck 1947). It is interesting to note that Høeg (1929) described the most easily recognisable interspecific hybrid as resembling *robur* but with abaxial stellate pubescence on the leaves.

On the question of hybrid fertility the data offer a little evidence through a comparison of fertile and non-fertile specimens in certain collections. All are from *petraea*-dominated woods (category A of Table 3). The above collections were all made in 1961 when fertile material, particularly of aff. *robur* forms, was less plentiful than in the unusually good fruiting years 1959 and 1960. The proportion of possible hybrids in the collections rises from 42% (22/52) to 57% (49/86) if infertile material is included. Consideration of fertile material alone will lead to an underestimate of hybridity.

It is strange that none of the samples from plantations proved to consist of good *robur* forms, for many of them must have been established with stock raised from the many large consignments of acorns known to have been imported from England and the Continent. Could it be that all importations of acorns have included a high proportion of introgressed stock ? Or was the late Professor Anderson correct in his contention that *robur* is not native in Scotland and that hybrids thrive better here than good *robur* ? Maxwell (1900)

TABLE 6
Percentage fertility by combination classes of auricle type and abaxial pubescence

	Ptarmigan		*Ross Wood*		*Loch Ard*		*Combined*		
	Total	*Fertile*	*Total*	*Fertile*	*Total*	*Fertile*	*Total*	*Fertile*	%
TST (*petraea*)	19	16	13	9	5	5	37	30	81
1 difference	12	6	3	1	8	5	23	12	52
2 difference	12	6	2	—	2	1	16	7	44
3 difference	7	2	—	—	1	1	8	3	37
4 difference	—	—	1	—	1	—	2	—	—
Totals	50	30	19	10	17	12	86	52	60

claimed that both *petraea* and hybrids were much superior to *robur* for planting in Scotland. Only one observation can be offered in this context, namely, that several old *petraea* woods are growing on very heavy clays where *robur* might have been expected if it were native.

The wider implications of the introgression hypothesis extend into the realms of pure speculation. Widespread planting of oaks in the past would have accelerated any introgression that was in progress, but has there been enough time (perhaps nine centuries) for planting to be held completely responsible ? One of Tucker's examples of introgression (Cottam, Tucker & Drobnik 1959) is traced back to the Miocene era. In Scotland introgression could not date back much before the Climatic Optimum some 5,000 years ago. It is possible that *robur* reached Scotland naturally in the more favourable climate of those times.

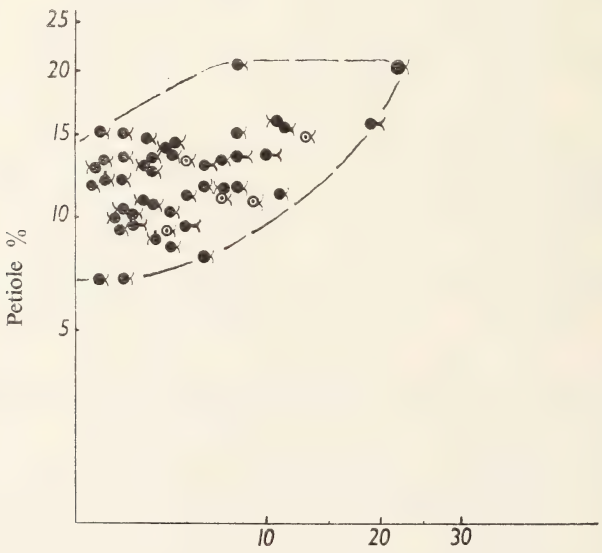


Fig. 10. Scatter diagram for the four most homogeneous *petraea* samples combined.

Conclusions

Q. robur and *Q. petraea* seem likely to be good taxa but they are very hard to define in Scotland, mainly because there are no obvious natural populations in which to assess the normal ranges of variation of the species. Striking variation patterns are found in Scottish oakwoods but practically all the variation can be completely accounted for by postulating (a) limited interspecific hybridization and (b) extensive introgression initiated or accelerated by Man's planting activities.

Table 7
Variation recorded in the most homogeneous samples from *petraea* woods in Scotland‡

		Glentrool SW Galloway	*Aikieside*† *SE Coastal*	*Cheviot SE Borders*	*Menstrie E. Central Ochils*	*Combined Totals*
Elevation		*c.* 250 ft (75 m)	*c.* 200 ft (60 m)	*c.* 600 ft (180 m)	*c.* 500 ft (150 m)	
No. of specimens		26	11	6	6	49
Leaf-length+ (cm)	range	8·5–15·2	7·5–14·7	7·4–11·3	8·4–10·4	7·4–15·2
	mean	11·4	10·6	9·6	9·9	10·8
Petiole-length+ (mm)	range	7·5–32·0	8·0–19·0	7·0–17·0	9·0–14·0	7·0–32·0
	mean	14·2	12·6	12·3	11·8	13·3
Petiole %+	range	7·0–21·5	7·0–16·0	9·5–15·2	9·7–13·8	7·0–21·5
	mean	12·6	11·5	12·3	11·8	12·2
Pairs of lobes+	range	4·3–7·0	4·3–5·8	4·0–6·0	4·0–7·0	4·0–7·0
	mean	5·5	5·0	5·2	5·4	5·3
Lobe depth %+	range	29–57	27–44	24–59	34–60	24–60
	mean	38	35	44	43	38·7
No. with deficient abaxial pubescence		2	2	1	—	5
Auricle type	nil	24	4	10	6	44
	weak	26	18	2	6	52
	medium	2	—	—	—	2
Peduncle× total length (mm)	range	3–48	6–34	9–34	2–21	2–48
	mean	14·4	17·5	21·0	9·7	15·3
Peduncle× length to first bract (mm)	range	1–22	3–11	2–13	1–10	1–22
	mean	5·3	5·8	5·7	4·3	5·3
No. with peduncle× diameter intermediate		2	—	1	3*	6
No. with only trace of peduncle pubescence		—	—	—	—	—

* a rather early collection

\+ mean for two mid-shoot leaves
†ignoring the one obviously non-*petraea* individual

× longest peduncle on specimens

‡ For illustrations showing the range of leaf variation in these samples see Cousens (1962)

Six homotypic characters have been tentatively defined. All are independent variables judging from the high proportion (93%) of the possible character combinations occurring. For each one normal variation in certain directions is indistinguishable from that due to introgression and all six characters appear to be needed to define the taxa. In terms of these characters there are a few woods for which the population samples are reasonably homogeneous and without an introgressive trend in their scatter-diagrams (Fig. 10). They are all *petraea* woods; variation in them is summarized in Table 7. They provide the best material available in these data on which to base a description of *petraea* in Scotland.

There seems little prospect of getting similar material in Scotland for *robur*.

Acknowledgments

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THE STATUS OF *ORCHIS LATIFOLIA* VAR. *EBORENSIS* GODFERY IN YORKSHIRE

By R. H. Roberts and O. L. Gilbert

Abstract

The Yorkshire dactylorchids formerly known as *Orchis traunsteinerioides* var. *eborensis* are shown to be referable to *Dactylorchis traunsteineri*, the separate populations showing extreme divergence in certain characters such as stature, leaf length, and the size and shape of the labellum. This is, apparently, the result of a high degree of genetic isolation, combined in some instances with the effect of the extremely small size of the populations.

Introduction

In his classic work on British Orchids, Godfery (1933) described plants from some Yorkshire and Durham localities as a new variety under the name '*Orchis latifolia* var. *eborensis*.' According to him their salient features were dwarf stature ($\pm$ 12 cm), very narrow, usually spotted leaves and a short, few-flowered spike. This new variety was also said to be early flowering, the only other orchid in flower at the same time being *Orchis mascula*.

Three years later Pugsley (1936) described two Irish marsh orchid forms as new subspecies of the Continental *Orchis majalis* Rchb. One of these, based on plants from Co. Wicklow, he named subsp. *Traunsteinerioides*, thereby recognizing its close resemblance to the Continental *Orchis traunsteineri* Saut. Despite this, however, he decided that these plants were more closely allied to *Orchis majalis* Rchb., under which the new subspecies was therefore placed.

The following year Pugsley (1939) examined a colony of Godfery's var. *eborensis* near Hellifield, Yorkshire, and decided to place this variety under his subsp. *Traunsteinerioides*, from which it was distinguished by its dwarf habit, and rather smaller flowers with a less distinctly deltoid labellum. Pugsley also recognized that in this latter feature these plants showed an approach to typical *O. majalis*.

Following the elevation by Wilmott (1938) of *O. majalis* subsp. *occidentalis* to the rank of full species as *Orchis occidentalis*, Pugsley (1940) raised the subsp. *Traunsteinerioides* also to species rank under the name *Orchis traunsteinerioides*. Subsequently, further colonies of it were discovered both in Ireland and in England (Pugsley 1946), and a biometric study of four of them by J. Heslop-Harrison (1953) showed beyond any doubt that all belong to the Continental species *Dactylorchis traunsteineri* (Saut.) Vermln. The var. *eborensis*, however, was not studied by Heslop-Harrison, who suggested that further field work on the Yorkshire and Durham plants was desirable.

Since the publication of Heslop-Harrison's paper, further finds of *D. traunsteineri* have been made in Wales, Ireland and eastern England (Lacey 1955; Heslop-Harrison 1956; Lacey & Roberts 1958; Roberts 1960; Bellamy and Rose, undated; Heslop-Harrison, *in litt.*). Subsequent studies of the Welsh populations have shown that in two of the Anglesey colonies a proportion of the plants have labella which are not sub-deltoid or obcordate, and have their lateral lobes angled and notched. In addition, the majority of the plants in these two colonies are very small. In both these features they strongly recalled the description of the var. *eborensis*.

Consequently in 1960 a search was made for the var. *eborensis* near Hellifield, and, with the help of information supplied by Miss C. M. Rob, at Rievaulx. The orchids were found at both places : at Hellifield a thorough search revealed about 22 plants in flower; at Rievaulx, where Miss Rob had informed us that the colony was a very small one, only 9 flowering individuals were found.

In order that a comparison of these plants might be made with *D. traunsteineri* elsewhere, and particularly with those in Anglesey, a biometric study of the two colonies was made in 1961. All measurements were made in the same manner as in previous studies of the dactylorchids, those of vegetative parts being made in the field. All differences between means were tested for significance by means of '*t*' tests.

Habitat

The close association of *D. traunsteineri* with areas in which *Schoenus nigricans* is locally dominant has been frequently remarked. The plants of the Hellifield colony are almost entirely restricted to the vicinity of the small patches of *Schoenus* which occur at a few places in the area. At the Rievaulx locality the orchids occupy a slightly wetter de-

Table 1

Species associated with *Dactylorchis traunsteineri* in Yorkshire and Anglesey

1, Hellifield; 2, Rievaulx; 3, Pentraeth.

	1	2	3		1	2	3
Selaginella selaginoides			*f*	D. incarnata			*o*
Equisetum fluviatile	*l*		*o*	D. purpurella			*o*
E. palustre	*f*	*r*	*f*	Crepis paludosa	*r*	*r*	
Trollius europaeus		*r*		Taraxacum officinale		*o*	
Ranunculus acris	*o*	*o*	*o*	Juncus subnodulosus	*o*		*la*
R. flammula			*o*	J. articulatus	*o*	*r*	*o*
Viola palustris		*o*		Eleocharis uniglumis			*l*
Polygala vulgaris		*o*	*o*	Eriophorum latifolium	*o*		
Hypericum tetrapterum		*r*	*r*	E. angustifolium	*f*		*f*
Linum catharticum	*o–f*	*o–f*	*o–f*	Schoenus nigricans	*ld*	*l*	*ld*
Genista anglica			*o*	Carex disticha	*o*		*o*
Lotus pedunculatus		*o*	*o*	C. diandra			*la*
Filipendula ulmaria		*r*	*o*	C. nigra	*a*	*o*	*a*
Potentilla erecta	*f*	*r*	*o*	C. elata			*o*
Parnassia palustris		*f*	*la*	C. dioica	*la*		*l*
Hydrocotyle vulgaris	*f*		*f*	C. flacca	*f*	*o*	*f*
Angelica sylvestris	*o*	*r*	*o*	C. panicea	*f*	*f*	*f*
Primula farinosa	*f*	*f*		C. pulicaris		*r*	*o*
Anagallis tenella		*r*	*o*	C. hostiana		*o*	*f–a*
Ajuga reptans		*r*	*r*	C. lepidocarpa	*f*	*o*	*f*
Plantago lanceolata		*o*	*o*	Molinia caerulea	*a*	*a*	*a*
Galium uliginosum	*o*			Briza media		*a*	*o*
Valeriana dioica	*a*	*o*		Festuca rubra	*f*	*a*	
Succisa pratensis	*f*	*o*	*f*	F. ovina		*a*	
Cirsium palustre	*o*	*o*	*o*				
Centaurea nigra		*r*	*o*				
Serratula tinctoria			*f*	Fissidens adianthoides	*o*	*o*	*o*
Leontodon hispidus		*o*		Thuidium tamariscinum	*f*	*a*	
Pedicularis palustris	*f*		*f*	Campylium stellatum	*f*	*f*	*f*
Pinguicula vulgaris	*f*	*f*	*f*	Drepanocladus revolvens	*f*	*o*	*f*
Prunella vulgaris	*o*	*o–f*	*o*	Scorpidium scorpioides			*o*
Listera ovata		*r*		Acrocladium giganteum			*l*
Ophrys insectifera			*r*	Acrocladium cuspidatum	*a*	*a*	*a*
Epipactis palustris	*o*	*f*	*f*	Ctenidium molluscum	*a*	*a*	*a*
Dactylorchis fuchsii	*f*	*r*	*o*				

pression in a damp meadow. Here again there are extensive *Schoenus* flushes. At both localities the community in which the orchids occur is very similar (Table 1), the soil being strongly flushed with calcareous ground water, and the habitat kept in a fairly open condition as a result of water-logging and trampling by cattle – conditions which are also met with in the Anglesey locality at Pentraeth.

Results

The sample data for vegetative characters in the Hellifield and Rievaulx colonies are given in Table 2, together with those from one of the Anglesey colonies with features recalling the description of var. *eborensis*. The sample numbers are small and may seem inadequate for a biometric comparison. It is, perhaps, relevant therefore to point out that they represent all that could be found in the course of one season. The colonies, particularly that at Rievaulx, are very small ones, so that even the small samples we have been able to examine embrace a high proportion of the total populations.

Stature

Basing his description mainly on plants from near Helmsley, Yorkshire, Godfery (1933) gave the stature of var. *eborensis* as ± 12 cm. However, five specimens from the Helmsley locality, collected by T. J. Foggitt (1455, 1456 (**BM**)), have statures from 19·5 cm to 25·5 cm. For the Hellifield plants Pugsley (1936) gave the range 15–25 cm, but the four plants gathered by him from this locality (**BM**) vary in stature from 16·0 to 31·5 cm.

Table 2

Sample data for vegetative characters

Locality	N	*Stature (cm)*		*Total number of leaves*		*Leaf length (cm)*		*Leaf width (cm)*		*Incidence of leaf marking* (%)
		mean	*s.e.m.*	*mean*	*s.e.m.*	*mean*	*s.e.m.*	*mean*	*s.e.m.*	
Hellifield	22	18·1	0·69	3·9	0·11	9·2	0·23	1·2	0·03	36
Rievaulx	9	9·5	0·41	2·7	0·18	6·7	0·54	1·0	0·08	67
Pentraeth	50	14·5	0·60	3·7	0·08	8·4	0·22	1·0	0·03	30

The data obtained from Hellifield and Rievaulx (Table 2) show that the mean stature in the two populations differs considerably, that of the Rievaulx plants being extremely small. Four specimens from the Rievaulx locality, gathered by Miss C. M. Rob in 1948 (**K**), show a similar range of stature. It can be seen that the mean stature of the Anglesey colony of *D. traunsteineri* quoted here is practically intermediate between those of the two Yorkshire colonies.

Leaf dimensions

Leaf-length, like stature, is a very variable character in *D. traunsteineri* and cannot be used to separate it from other species of marsh orchids. It is worth noting, however, that while the mean leaf-length of the Rievaulx colony is smaller than that of any other for which data are available, that of the Hellifield plants falls within the range of values found elsewhere in the British Isles for *D. traunsteineri*.

Leaf-width, on the other hand, has been shown to be one of the most important characters for discriminating *D. traunsteineri* from other tetraploid marsh orchid species (Heslop-Harrison 1953). Both the mean and range of leaf-width in the Hellifield and

Rievaulx colonies are in close agreement with those of the Anglesey colony (Tables 2 and 3) and with all the Britannic populations for which data are available (Heslop-Harrison 1953, Lacey and Roberts 1958). Moreover, examination of herbarium material of var. *eborensis* from other Yorkshire localities and of *D. traunsteineri* from several Continental ones, including the type locality, has shown a remarkable uniformity in this character among all of them (Table 3).

Leaf-number

It was shown by Heslop-Harrison that the vegetative characters of leaf-number and leaf-width, taken together, completely distinguish the colonies of *D. traunsteineri* from those of the other tetraploid marsh orchids; later studies have fully confirmed this. It can be seen that in both the mean and range of leaf-number the Hellifield colony agrees very closely with that at Pentraeth, and indeed with all the other colonies previously studied. In the Rievaulx sample the mean number of leaves per plant is even smaller, but the range falls within that of the Pentraeth colony.

TABLE 3

Ranges of variation of characters in populations of *D. traunsteineri*
(The numbers in brackets were found only in single instances)

Locality	*Total number of leaves*	*No. of non-sheathing leaves*	*Leaf width (cm)*	*No. of flowers in inflorescence*
Hellifield	3–5 (6)	0–1 (2)	0·8–1·5	5–14
Rievaulx	2–4	0–1	0·6–1·3	5–10
other Yorks. localities taken together*	3–5		0·6–1·3	
Pentraeth, Anglesey	2–5 (6)	0–1 (2)	0·7–1·5	2–14
Continental localities*	3–5		0·5–1·5	

* Data from herbarium specimens

Again, examination of herbarium specimens of var. *eborensis* from other localities in Yorkshire shows that the range of leaf-number in these also corresponds closely both with that in the Pentraeth colony and in all the herbarium material from Continental stations (Table 3).

Leaf marking and shape

The incidence of leaf marking in *D. traunsteineri* shows considerable variation from one locality to another and is completely lacking in some populations (Heslop-Harrison 1953, Lacey and Roberts 1958). In the Hellifield colony 36% of the plants have leaf marking either in the form of a few small dots or transverse bars in the apical half of the leaves; in the Rievaulx colony 67% of the plants had leaf marking consisting of a combination of narrow bars and dots. Both the form and incidence of leaf marking in these two populations agree well with those found elsewhere in colonies of *D. traunsteineri* (Heslop-Harrison 1953).

The leaves at both localities are narrowly lanceolate, in many cases linear-lanceolate, the lower leaves widest usually just below the middle, with an acute, slightly hooded tip.



a



b



c

Random samples of flower dissections from the three populations: (a) labella of 16 plants and spurs of 15 plants from the Hellifield colony; (b) labella and spurs of 9 plants from the Rievaulx colony; (c) labella of 60 plants from the Pentraeth, Anglesey, colony. All × 1.

Floral characters

According to Pugsley (1939) the plants of var. *eborensis* were distinguished from *O. traunsteinerioides* by their rather smaller flowers in which the labella were less distinctly deltoid.

A study of the Welsh colonies has shown that there is considerably greater variation in labellum and spur dimensions between separate populations of the species than was apparent from Heslop-Harrison's original study. Mean labellum-shape also varies from one colony to another. The sample data (Table 4) show that in both labellum and spur dimensions the differences between the Hellifield and Pentraeth populations are very small and statistically not significant. This is an unexpected and striking result.

TABLE 4

Sample data for labellum and spur dimensions

Locality	N	*Labellum length* (*cm*)		*Labellum width* (*cm*)		*Spur length* (*cm*)		*Spur width* (*cm*)	
		mean	*s.e.m.*	*mean*	*s.e.m.*	*mean*	*s.e.m.*	*mean*	*s.e.m.*
Hellifield	16	0·80	0·022	0·96	0·025	0·85	0·018	0·34	0·008
Rievaulx	9	0·66	0·028	0·73	0·046	0·81	0·033	0·30	0·010
Pentraeth	40	0·79	0·014	1·02	0·018	0·83	0·020	0·35	0·010

On the other hand the fact emerges that the Rievaulx population differs from the others in both labellum-length and labellum-width by large and statistically significant amounts. It also differs significantly from them in spur-width, but the small differences in spur-length fail to be significant.

The position with regard to labellum shape is rather different. By assuming that the Hellifield plants represented 'the normal condition of var. *eborensis*' Pugsley (1939) erroneously concluded that the labellum shapes found there are also those prevailing in the other colonies of var. *eborensis*. The present study has shown that this is not so. While it is true that, on the whole, the labella in all of the Yorkshire colonies are less deeply tri-lobed than in most other localities, these Yorkshire populations are evidently not homogeneous with respect to labellum shape. The Hellifield plants appear to deviate more from the typical labellum shape of *D. traunsteineri* than those at Rievaulx, where the labella, though small, clearly display the sub-deltoid shape more characteristic of this species (Plate 13).

As far as may be inferred from herbarium specimens the situation among the other Yorkshire colonies seems to be much the same : some, like the Helmsley plants, showing greater, and others, like those from Masham and Carperby, less deviation from the more typical labellum shapes (Fig. 1).



Fig. 1. Labellum shapes of 'var. *eborensis*' from other Yorkshire localities: (a) Masham; (b) Helmsley; (c) Carperby. All drawn from herbarium specimens.

The colour of the flowers in var. *eborensis* was described by Godfery as a dull red-violet. There is clearly some justification for this description, for in a large proportion of the plants of the two colonies examined flower colour is rather darker than in the Anglesey

and Caernarvonshire plants. But there is also a considerable overlap in this, a few individuals in all of the Welsh colonies having dull, deep red-purple flowers exactly matching the deeper shades in var. *eborensis*.

Another characteristic of var. *eborensis* mentioned by Godfery (1933) is that the lateral lobes of the labellum are reflexed, and this is very noticeable in these two populations. It is, of course, a character normally found in *D. traunsteineri*.

Inflorescence

The occurrence in *D. traunsteineri* of some plants with very few flowers in the spike has frequently been emphasized (Pugsley 1946, Heslop-Harrison 1953). In this there is a remarkably close agreement between the two Yorkshire colonies and the Anglesey one : in each of them the number of flowers in the inflorescence is consistently low (Table 3), the mode in all three lying from 9 to 11.

Flowering-time

In the British Isles *D. traunsteineri* is one of the earliest flowering marsh orchids, commencing in mid-May and extending into the middle of June (Heslop-Harrison 1953, Roberts 1961). In a particularly early season a few of the Anglesey plants have been in flower as early as 7 May.

As Godfery had observed, var. *eborensis* is also early flowering. In 1961 both the Hellifield and Rievaulx plants started flowering in the second half of May and reached a peak in the first week in June.

Discussion and conclusions

The results show that there are comparatively large and statistically significant differences between the Hellifield and Rievaulx colonies in both vegetative and floral dimensions. The mean expression of labellum shape also differs to a marked degree in the two populations.

On the other hand, between the Hellifield colony and that of undisputed *D. traunsteineri* at Pentraeth there is a remarkably close agreement in most of the morphological characters, the chief exceptions being stature and the overall expression of labellum shape.

The characters which, according to Pugsley, separated the var. *eborensis* from his *O. traunsteinerioides* are not uniformly represented among the Yorkshire colonies. Evidently the latter have diverged to a greater or lesser extent both from one another as well as from the other populations of *D. traunsteineri* in the British Isles. Despite this the results show conclusively that all these Yorkshire populations should be referred to *D. traunsteineri*.

In numbers of individuals these populations are very small : Pugsley estimated the Hellifield colony at just over fifty plants in 1937; in 1961 a careful search revealed about a half of this number. At Rievaulx only nine plants were found and this seems to be consistent with the numbers occurring in other seasons (Miss C. M. Rob, *in litt.*). Because of their restricted habitat requirements these populations are geographically isolated from one another, as well as from all other populations of the species in the British Isles. Between many of them gene exchange either does not take place, or does so at a very low rate. Under these conditions it is not surprising that some degree of morphological divergence has arisen among the Britannic populations, particularly so among those which, like these in Yorkshire, consist of very small numbers of individuals. In these the range of biotypes is necessarily restricted and the operation of genetic drift has probably been of far greater significance.

As has been shown, these population differences are most apparent in stature and in the size and shape of the labellum; and, it will be recalled, it is the diversity in these particular

characters which in the past has been the main obstacle to the correct identification of these northern colonies.

The recognition of these Yorkshire plants as *D. traunsteineri* considerably broadens our appreciation of the range of variation to be found within this species in the British Isles. This, however, is not unexpected. In Holland, as Vermeulen (1949) has shown, the species shows considerable variation in both stature and shape of labellum; in the Baltic states it displays even greater variation, the regional variants in some instances being sufficiently well-marked to have become the basis of several subspecies (Vermeulen 1947).

Localities

The known localities of *D. traunsteineri* in Yorkshire and the exsiccatae from them are listed below.

V.c. 62, North-east York. Beckdale, near Helmsley, 1905 and 1922, *T. J. Foggitt* (**BM**); Ashberry, near Rievaulx, 1937, *T. J. Foggitt* (**BM**); *ibid.*, 1948, *Miss C. M. Rob* (**K**).

V.c. 64, Mid-west York. Near Hellifield, 1937, *H.W.P. & W.A.S.* (**BM**).

V.c. 65, North-west York. Carperby, Wensleydale, 1885, *F. Arnold Lees* (**BM**); Masham, 1893, *A. B. Sampson* (**K**); Tanfield, 1906, *T. J. Foggitt* (**BM**).

The var. *eborensis* was also stated by Godfery to occur in Durham, but there appear to be no herbarium specimens of it from that vice-county. Nevertheless, further exploration may well prove the occurrence of *D. traunsteineri* not only there but in other fen areas in the north of England and in Scotland.

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STUDIES IN *RANUNCULUS* SUBGENUS *BATRACHIUM* (DC.) A. GRAY
II. GENERAL MORPHOLOGICAL CONSIDERATIONS IN THE TAXONOMY OF THE SUBGENUS

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Abstract

An account is given of the characters that are taxonomically important in separating subgenus *Batrachium* from *Ranunculus*. The morphology of the stipules and achenes is discussed in some detail as they have been largely overlooked. Although of no direct taxonomic importance, embryology, teratology and chromosome size are described.

Introduction

Batrachium was first described by De Candolle (1818) as a section of *Ranunculus*. S. F. Gray (1821) gave it generic status and A. Gray (1886) designated it a subgenus of *Ranunculus*. Some recent authors such as Kreczetovicz in Komarov (1937), Janchen (1958), Rostrup (1958) and Löve (1961) have chosen to give *Batrachium* generic rank, while most other workers include it within *Ranunculus;* the infrageneric rank is frequently not designated, but Ascherson & Graebner (1935), Benson (1948) and Clapham (1952) have recognised it as a subgenus.

The full description of De Candolle's section *Batrachium* is as follows :

Pericarpia ovata mutica rugulis transversis striata. Flores albi ungue flavo foveola ad basin nectarifera exsquamulata. Plantae aquaticae; folia glaberrima, emersa dentato-sublobata, immersa capillaceo-multifida; radices fibrosae; pedunculi uniflori oppositifolii.

Clapham adds that the species are annual or perennial and that they have stipules. In most Floras it is a combination of these characters that is normally used to delimit this group. There are, however, some exceptional species which will be discussed later.

The batrachian group contains about eighteen morphologically recognisable species, found in climatically temperate regions throughout the Northern Hemisphere and in limited areas of South America, South Africa, Australia, Tasmania and New Zealand. Atlantic Europe is the region containing the greatest species density (Fig. 1a) and the greatest morphological diversity (Fig. 1b). The distributions shown on Figs. 1a and 1b are semi-diagrammatic and the species boundaries are not as smooth as illustrated. It is hoped to publish detailed distribution maps of each species later. Except in South America the species that are heterophyllous or entirely laminate-leaved are always found in areas also occupied by species that develop only capillary leaves.

Most of the species are annuals or short-lived perennials but *R. fluitans* Lam., *R. pseudofluitans* (Syme) Baker & Foggitt ex Newbould and *R. circinatus* Sibth. are long-lived perennials. Some species such as *R. tripartitus* DC., *R. peltatus* Schrank, *R. aquatilis* L. and *R. trichophyllus* Chaix may be annuals or perennials. They are often found in temporarily aquatic habitats; if the habitat dries out in summer they behave as annuals, but if the water remains throughout the year they may perennate. If cultivated in an aquatic habitat these species usually die in the third year, but this varies in different races of each species. For example, two morphologically distinguishable races of *R. peltatus*, one from Portugal and the other from southern France, are obligate annuals in cultivation in England.



1 species
2 species
4 species
6 species
9 species

(a)

(b)

plants with only laminate leaves
plants with only capillary leaves
plants with both laminate and capillary leaves



Fig. 1. Distribution of (*a*) species density, and (*b*) morphological diversity in *Ranunculus* subgen. *Batrachium*.

R. hederaceus L. and *R. omiophyllus* Ten. (*R. lenormandii* F. Schultz) are primarily terrestrial plants of wet places but all the other species are aquatic, completely or partly submerged in water. All the aquatic species cultivated (*R. tripartitus*, *R. ololeucos* Lloyd, *R. baudotii* Godr., *R. peltatus*, *R. aquatilis*, *R. trichophyllus*, *R. rionii* Lagger, *R. sphaerosphermus* Boiss. & Blanche, *R. pseudofluitans*, *R. fluitans* and *R. circinatus*) can be grown as terrestrial plants during the summer in water-logged soil.

Discussion of characters

Hairiness

Almost all descriptions of *Batrachium* state that all the species are glabrous. This is not the case. All the specimens that I have seen bear unicellular hairs on the stem, leaves and stipules. Even the submerged capillary leaves have hairs surrounding the hydathodes.

Heterophylly

At all times of the year, in or out of water, *R. hederaceus* and *R. omiophyllus* produce only laminate leaves, while *R. trichophyllus*, *R. rionii*, *R. sphaerospermus*, *R. circinatus* and some races of *R. aquatilis*, *R. pseudofluitans* and *R. fluitans* bear only capillary leaves. The other species, *R. lobbii* (Hiern) A. Gray, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus* and some races of *R. aquatilis*, *R. pseudofluitans* and *R. fluitans* show heterophylly with capillary and laminate leaves. This type of heterophylly is not confined to *Batrachium* but is found in some other aquatic species of *Ranunculus* such as *R. polyphyllus* Waldst. & Kit. ex Willd., *R. gmelinii* DC. and *R. flabellaris* Raf.

In most aquatic plants that have both capillary and laminate leaves the change from one type to the other is gradual with the formation of sequential intermediates and is largely controlled by the presence or absence of water. In *R. lobbii*, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus* and *R. aquatilis* the change from one type of leaf to the other type is abrupt. In *R. peltatus* and *R. aquatilis* the initiation of the laminate leaf must take place underwater and if the apex is lifted above the water a capillary leaf of the terrestrial type develops. Intermediate types of leaves are occasionally found but they are not sequential intermediates but more of a mixture of the two types. The presence of these intermediate leaves can be correlated with pollen sterility, and they are found in high polyploids and hybrids. I have only just started studies on heterophylly but it appears that, in the presence of water, the form of the leaf is primarily controlled by temperature and day-length.

Stipules

In taxonomic accounts the Ranunculaceae are usually described as being exstipulate, but occasionally, for example Lawrence (1951), an exception is made in the case of *Thalictrum*, and Clapham (1952) describes both *Thalictrum* and *Batrachium* as stipulate. Hiern (1871), Freyn (1890), Glück (1919, 1924), Salisbury (1934) and Drew (1936) in monographic accounts have all described stipules in *Batrachium* and have used them as taxonomic characters within the subgenus. Morphologists, however, have been more reluctant to call them stipules and Goffart (1901) called them *auricules*, while Weberling (1956) called them *Scheidenlappen* or lobes of the leaf-sheath.

To define stipules it is necessary to look at the development of the leaf. The first visible sign of leaf formation is a swelling below and to the side of the apical meristem. This swelling is usually called the leaf primordium and it may remain small and localised on one side of the stem apex or it may grow, occasionally forming a ring around the apex. The leaf proper (petiole and lamina) develops from a localised area of this primordium so the whole primordium contributes cells to the axis and the leaf proper. Eichler (1861)

proposed two terms : *Unterblatt* and *Oberblatt*. The *Oberblatt* is the area in the primordium that gives rise to the leaf proper and the *Unterblatt* is that which is left. He then defines stipules as being a product of the *Unterblatt*. Sinnott & Bailey (1914) carried out more detailed anatomical investigations of leaf development and found themselves in agreement with Eichler; they suggested ' leaf-base of the primordial leaf ' as a translation of *Unterblatt*.

Colomb (1887) defined the stipule as ' an appendage inserted on the stem at the base of the leaf all the bundles of which are derived entirely from corresponding foliar bundles.' Sinnott & Bailey stated that this definition would fit Eichler's but they found that it was often hard to apply and could not be adopted as stipules occasionally lack bundles.

Sinnott & Bailey pointed out that leaf-sheaths, stipules, ligules and some other appendages at the base of the petiole arise from the *Unterblatt* and are morphologically homologous. Nobody has doubted that the leaf-sheaths found in the Ranunculaceae originate from the *Unterblatt*. It has been noted that these leaf-sheaths are occasionally lobed, so the problem is one of terminology. When should the lobe on a leaf-sheath be called a stipule ? Weberling suggested that if the lobes show proleptic growth, that is, if they anticipate growth of the leaf proper (*Oberblatt*), then they should be called stipules. The lobes in *Batrachium* do anticipate growth of the leaf proper and therefore should be called stipules. It is perhaps worth mentioning that *Trollius* and *Caltha* also show well-developed stipules but the stipule ruptures as the next leaf develops.

Petals

Comparative studies on the floral parts of the Ranunculaceae (Eichler 1878, Prantl 1888) have shown that the so-called petals of *Ranunculus* are strictly speaking homologous to nectaries and are occasionally called *Nektarblätter* (usually translated into English as honey-leaves). It is proposed to call the *Nektarblätter* petals as this usage is generally accepted in *Ranunculus* and does not cause confusion.

The petals in *Batrachium* are usually described as being white with a yellow claw. This is true for the majority of species but in races of *R. ololeucos* they are entirely white and in *R. flavidus* (Hand.-Mazz.) C. D. K. Cook* they are uniformly pale yellow. This species seems to be allied to *R. aquatilis* and is confined to the Himalayas.

The petals have a matt surface (Parkin 1928) and do not contain starch. This appears to be a good distinction between subgenus *Batrachium* and section *Hecatonia* of subgenus *Ranunculus* which contains the most batrachian-like species. This character is not of much practical use as it requires microscopical examination of living petals.

The nectary pit is highly reduced (Benson 1940). It may be lunate, circular or pyriform. Nectary characters are useful taxonomically within the subgenus but cannot be used to separate *Batrachium* from the rest of *Ranunculus*.

Achenes

The presence of transverse ridges on the achene is perhaps the most important diagnostic character of *Batrachium*, but it must be used with caution. *R. rivularis* Banks & Sol., *R. undosus* Melville, *R. papulentus* Melville and *R. inundatus* R. Br. ex DC., semi-aquatic species from Australasia, have transverse ridges on the achene. The ridges, however, are somewhat irregular and ill-defined. Anatomically the pericarp of *R. rivularis* consists of an inner layer of regular, almost symmetrical sclereids five to eight cells deep and an outer layer of loose parenchyma five to eight cells deep. The pattern is the same in longitudinal and transverse sections.

The pericarp of *Batrachium* has a much more complicated structure and consists of three well defined layers. The innermost consists of a single layer of fibres forming a continuous sheath arranged tangentially around the achene at right angles to the longitu-

*Ranunculus flavidus (Hand.-Mazz.) C. D. K. Cook, *comb. nov.* *Batrachium flavidum* Hand.-Mazz., *Acta Hort. Gotob.* **13**, 168 (1939)

dinal axis. The fibres are as much as twenty times as long as broad and have thick walls with numerous simple pits. The next layer consists of a layer of elongated sclereids, three to four cells deep and from five to ten times as long as broad with thick walls and many simple pits. The sclereids lie at right angles to the fibres, parallel to the longitudinal axis. Each cell lies directly on top of the one below. The ends are slightly swollen and tend to turn away from the longitudinal axis. As these cells are in simple ranks the upturned ends form quite large ridges between 0·4 and 0·1 mm apart. The ridges lie at right angles to the longitudinal axis and are found on the lateral walls of the achene.

The outer layer consists of between four and eight layers of loose parenchymatous cells which wither and die as the achene matures. The outermost layer may or may not bear unicellular hair cells. Fig. 2a shows a median transverse section and Fig. 2b a median longitudinal section. The ends of the sclereids swell and turn outwards before fertilization and, to a large extent, subsequent development is not dependent on fertilization. Normally, the walls of the sclereids start to lignify just as the endosperm starts laying down cell walls. Lignin is first laid down at the ends of each cell while the middle is still elongating. The fibres of the inner layer do not become lignified until the embryo is almost mature.

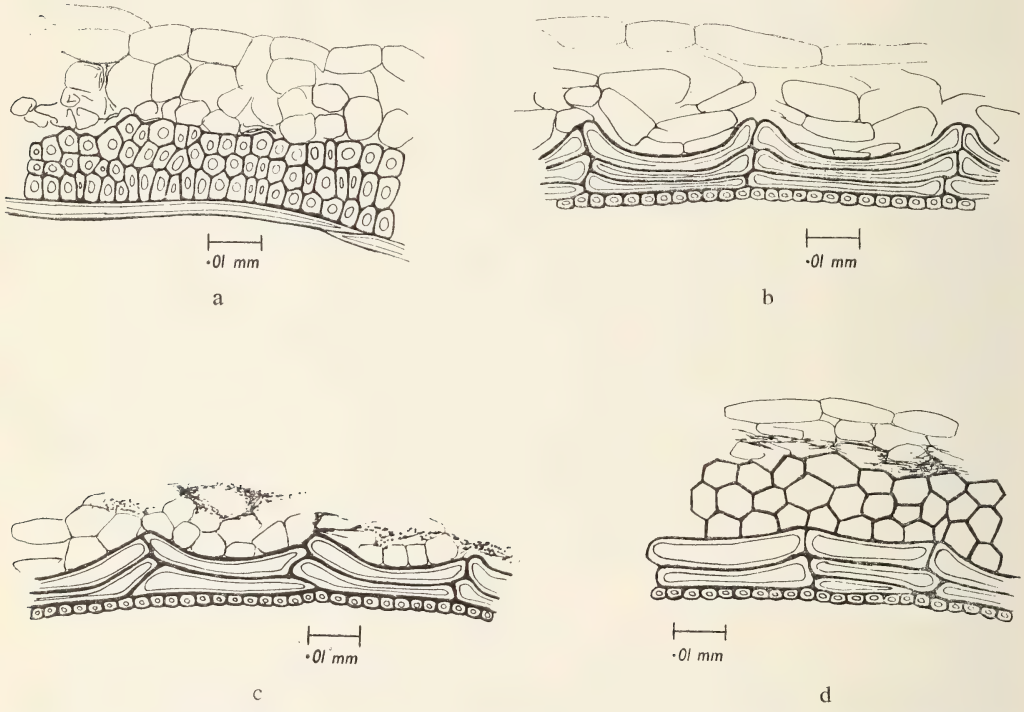


Fig. 2. Sections of the lateral wall of achenes of *Ranunculus* spp., *c.* half-way from base to apex. (*a*) *R. tripartitus* 175/57, T.S.; (*b*) *ibid.*, L.S.; (*c*) *R. sceleratus*, Bács-Bodrog, nr. Zombor, Hungary, J. Proden May 1912 (achenes ridged), L.S.; (*d*) *R. sceleratus* (achenes non-ridged), L.S.

The important property of these ridges on the batrachian achene is that they are areas of weakness. When the achenes are roughly handled they break along the ridges. During germination the pericarp ruptures along the ad- and abaxial crests which are areas of upturned sclereids. Although there is no direct evidence it is tempting to regard the ridges as possible passages of water through the periderm when the seeds are wetted after being dried.

Some races of *R. sceleratus* L. have transverse ridges on the lateral walls of the achene that look similar to those found in *Batrachium*. Plants with ridged achenes are sympatric with non-ridged ones.

Anatomically the periderm of *R. sceleratus* is similar to that found in *Batrachium* (Fig. 2c). The ends of the sclereids, however, are not markedly swollen and it appears that the ridges are largely formed by a collapse of the central part of the cell. The unridged race has a layer of symmetrical sclerenchyma cells, three deep, between the sclereids and the outer parenchyma (Fig. 2d). When the sclerenchyma is present the sclereids do not collapse and no ridges are formed. Lonay (1901, 1907) examined the structure of the achenes of many species of *Ranunculus* and it would appear that these elongated, ranked, sclereids may well be confined to *Batrachium* and *R. sceleratus*.

Chute (1930) stated that the achene of *Batrachium* represented the most reduced type of any known. She said ' so complete is this reduction that the ventrals, as distinct bundles, have completely disappeared; hence the ovule trace appears to come from the dorsals.' The vascular anatomy of so few species of *Ranunculus* has been studied that it is not known if it is possible to use the lack of ventral bundles as a diagnostic character.

Embryology

Each achene contains a single anatropous ovule. The nucellus is monosporic, 8-nucleate, of the *Polygonum*-type with early fusion of the endosperm nuclei. Most pollen tubes reach the nucellus by travelling down the funicle, none have been seen ascending the micropyle. After fertilization the endosperm nucleus divides rapidly and cell walls are not laid down until the embryo has reached a sixteen- or thirty-two-celled stage. The embryo of *R. tripartitus* has the same development as the *Myosurus* variation of the Onagrad type (terminology after Johansen 1950). A limited number of embryological stages have been seen in *R. hederaceus*, *R. omiophyllus* and *R. aquatilis;* they all appear similar to *R. tripartitus*.

No self-incompatibility, pseudogamy or agamospermous processes have been discovered.

The synergid cells disappear before or just after fertilization; their disappearance does not appear to be correlated with pollination. The antipodal cells do not disappear until late in embryo development. They become enlarged and show considerable activity and are often borne on a short well-differentiated stalk. Enlargement of the antipodal cells has been seen in several species within the Ranunculaceae, Fumariaceae and Papaveraceae (Coulter 1898, Osterwalder 1898, Grafl 1941, Tschermak-Woess 1956). Not only do the antipodal cells become enlarged, they show giant chromosomes which continually divide forming highly polyploid cells; Hasitschka-Jenshke (1959) estimated cells up to 64-ploid for *Eranthis hyemalis* (L.) Salisb. An interesting feature that has not, I believe, been noted before is that the activity and growth of these cells is increased if pollination is withheld. Conversely, if pollination is carried out as soon as the nucellus is mature, there is very little development of the antipodal cells. In *Batrachium* the antipodal cells have never been seen to divide.

Teratological variants

Although teratological variants can hardly be used in taxonomy, it is, perhaps, worth mentioning the commonest types found. Occasionally one sepal is partly petaloid; sometimes it is laterally asymmetrical with one half petaloid and sometimes it is the distal end that is petaloid. Petaloid sepals are without nectary pits. Intermediates between petals and stamens are more common; one extreme is an almost perfect stamen with a flattened filament and the other extreme is an almost perfect petal bearing one or two functional anther loculi. In the latter case the anther may occur laterally or centrally on the petal

but if it is central it usually replaces the nectary pit; sometimes this type of anther is so reduced that it looks like a pollen-producing nectary.

Supernumerary petals (more than five) are quite common in *R. fluitans*, *R. pseudofluitans*, *R. peltatus* and *R. aquatilis*. They appear to be formed at the expense of stamens and in one population of *R. pseudofluitans* in the River Wye in Derbyshire plants have up to fifteen petals and no stamens. The plants examined in this population were sterile pentaploids. This ' double-flowered ' character has been seen to breed true in cultivation in plants of *R. peltatus* collected from Slayley in Derbyshire.

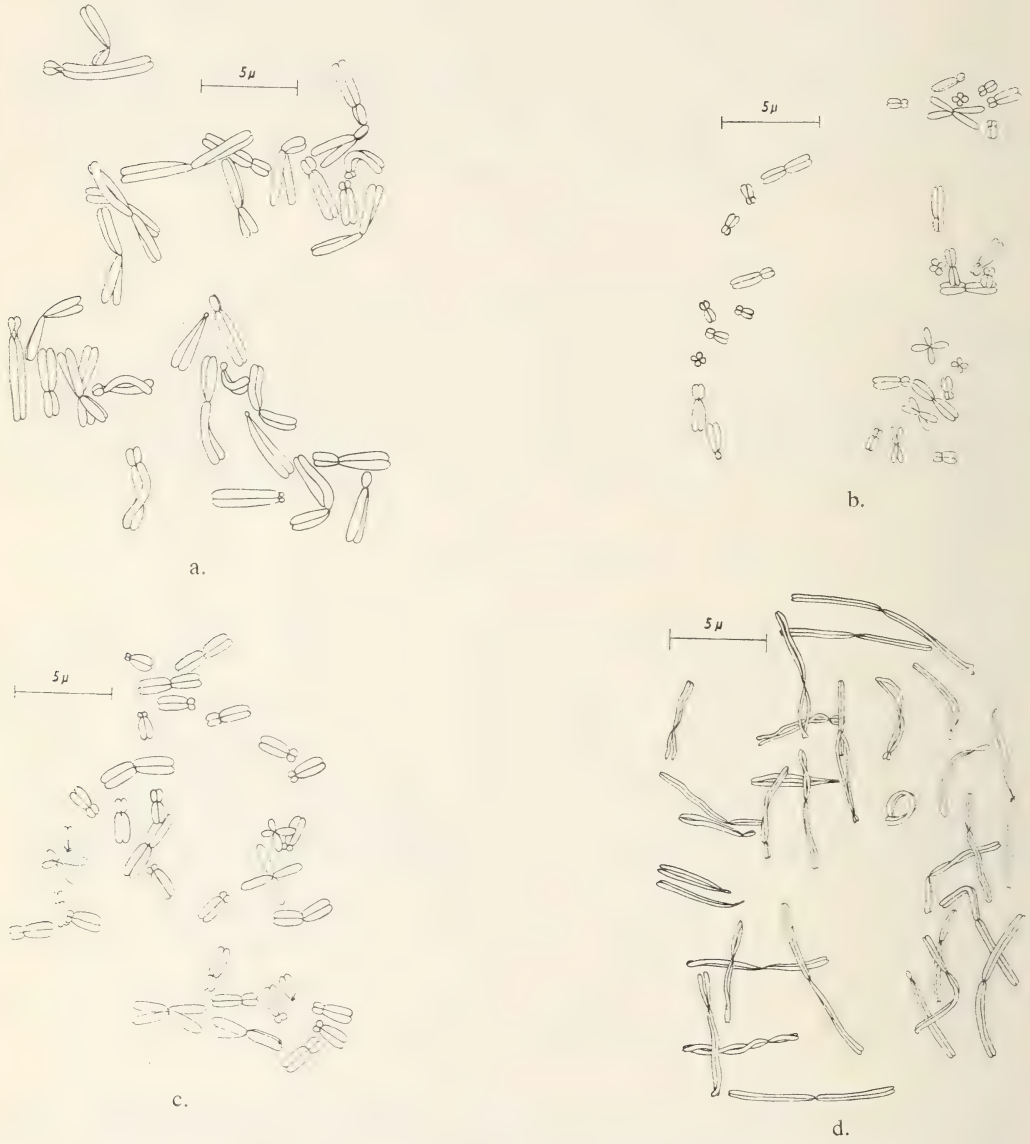


Fig. 3. Chromosomes of *Ranunculus* spp. from root-tip squashes, × 2500; Feulgen staining, all except (*d*) pre-treated for 3 hrs with α-bromonaphthalene. (*a*) *R. ficaria*, under *Hippophae rhamnoides* by pond, Botanic Garden, Munich, Germany, $2n = 32$; (*b*) *R. sceleratus*, from collection of aquatic plants, Botanic Garden, Munich, $2n = 32$; (*c*) and (*d*) *R. trichophyllus*, collected wild from pool by R. Stillach, S of Möserbrücke, 1·5 km SW of Oberstdorf, S Germany (specimens deposited in M).

Chromosome size

It has been suggested that *Batrachium* could be delimited from the rest of *Ranunculus* on chromosome size, but no really significant difference has been found. Larter (1932) reported that the chromosomes of *R. peltatus* were less than one sixth the bulk of those of *R. acris* L. and considerably smaller than those of the other species illustrated in his paper, (*R. constantinopolitanus* (DC.) d'Urv., *R. trilobus* Desf., *R. serbicus* Vis., *R. parviflorus* L., *R. arvensis* L., *R. repens* L., *R. ficaria* L., *R. chius* DC., *R. nelsonii* A. Gray, *R. sprunerianus* Boiss., *R. oxyspermus* Bieb., and *R. ophioglossifolius* Vill.). From the work of Skalińska *et al.* (1959) it can be seen that the chromosomes of *R. circinatus* are approximately the same size as those of *R. flammula* but smaller than those of *R. montanus* and much larger than those of *Isopyrum thalictroides* L. and *Thalictrum aquilegiifolium* L.

Langlet (1927) doubted that *Batrachium* was a distinct genus on the basis of chromosome size and number and in his later work (1932) on the relationships within the Ranunculaceae he included *Batrachium* within the same category as *Ranunculus*. Other workers on cytological variation in the Ranunculaceae (Coonen 1939, Gregory 1941, Kurita 1958) have also included *Batrachium* within *Ranunculus*.

It is difficult to compare chromosome sizes from data given by different publications as there are either variations in size within a single species or inaccuracies in the scales quoted. Fig. 3a shows chromosome preparations from root-tip squashes, with Feulgen staining (12 min. hydrolysis in normal hydrochloric acid at 60°C), all prepared within a week and all drawn with the same microscope and camera lucida. Except for Fig. 3b, the roots were given a three hour pre-treatment in saturated α-bromo-naphthalene solution. This pre-treatment is necessary as the chromosomes of *Ranunculus* are rather long and somewhat sticky at metaphase and it is seldom that one gets a late prophase preparation with a good chromosome spread such as that shown in Fig. 3d.

It can be seen that the chromosomes of *R. ficaria* illustrated are larger than those of *R. trichophyllus* while those of *R. sceleratus* are smaller. In *Batrachium* there is a certain amount of variation in chromosome size; none has chromosomes as large as those of *R. ficaria* but in *R. tripartitus* they are as small as those of *R. sceleratus*. In many genera there are species with different chromosome sizes; *Anemone*, also within the Ranunculaceae, is a good example (Langlet 1932, fig. 2; Gregory 1941, plate 2.)

Conclusion

In the introduction it was pointed out that the status of *Batrachium* has varied from section to genus. The group shows most affinities to *Ranunculus* and it cannot be confused with any other genera in the Ranunculaceae. However, it can only be separated from *Ranunculus* by the combination of the minimum of two characters (transversley-ridged achenes and matt-surfaced petals). Sectional status is inappropriate so the choice lies between genus and subgenus, but it is felt that the level of differentiation is insufficient to merit generic status so *Batrachium* is given subgeneric rank.

A suggested description of *Ranunculus* subgenus *Batrachium* is as follows :

Aquatic or semi-terrestrial annuals or perennials. Leaves mostly cauline, laminate or finely dissected; stipules membranous, partly fused to the petiole. Sepals usually five, not petaloid, caducous. Petals five or more, with matt surface; nectary-pit lunate, circular or pyriform. Achenes not strongly compressed, with regular transverse ridges from 0·4 to 1 mm apart on the lateral walls.

The lectotype of subgenus *Batrachium* is *Ranunculus hederaceus*, sheet number 74 (Savage 1945) in the Linnaean Herbarium, Linnean Society, London (**LINN**), selected by Britton and Brown, 1913, *Ill. Fl. N.U.S. ed.* 2, **2**, 115.

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STUDIES ON *ALCHEMILLA FILICAULIS* BUS., *SENSU LATO*, AND *A. MINIMA* WALTERS.

INTRODUCTION, AND I. MORPHOLOGICAL VARIATION IN *A. FILICAULIS.*, *SENSU LATO*

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Abstract

Alchemilla filicaulis Bus., *A. vestita* (Bus.) Raunk. and *A. minima* Walters form a critical group within the *A. vulgaris* L. aggregate. The results of a biosystematic study of variation in morphology, habit and cytology are presented in a series of papers. These indicate that *A. vestita* should be treated as a subspecies of *A. filicaulis* but *A. minima* should be maintained as a species.

In paper I morphology and habit are considered. Density of the indumentum of the flower-stem and leaves is genetically determined but greater variation occurs in the more hairy plants, subsp. *vestita*, than in the less hairy subsp. *filicaulis*. Plants of intermediate hairiness may be genotypes or environmentally-induced variants. Colour of the stipules and leaf shape are genetically determined but can be modified by environmental factors. Lowland, meadow and rock-ledge plants are tall with few shoots; a dwarf much branched genodeme occurs in close-grazed upland grassland. Such ecogenodemes are analogous to the ecotypes of sexual species and important in the evolution of apomicts.

Introduction

In recent years a number of papers have been published on the taxonomy and distribution of the British species of the apomictic *Alchemilla vulgaris* L. aggregate by Walters (1949, 1952), Bradshaw (1957), Bradshaw & Walters (1961) and Bradshaw (1963). In Britain there are twelve named taxa and a critical group temporarily referred to as the Lawers '*acutidens*' (see Clapham, Tutin, & Warburg, 1962). Several species of the *Alchemilla vulgaris* aggregate were shown to be obligate apomicts by Strasburger (1905) and Murbeck (1901). All the British taxa are thought to be obligate apomicts. Walters' paper (1949) illuminated some of the difficulties associated with the group formed by *A. filicaulis* Bus., *A. vestita* (Bus.) Raunk. and *A. minima* Walters. Of the first two, Walters wrote ' The morphological difference is very slight – the only " good " character appears to be the hairiness of the inflorescence – nevertheless, the two can with rare exceptions be satisfactorily separated in the field, and exhibit somewhat different geographical ranges.' Exactly how ' good ' needed to be ascertained, as field collections made between 1951 and 1954 contained several plants of intermediate hairiness not readily assignable to either taxon. Furthermore dwarf plants of these two taxa from closely grazed habitats are very similar to *A. minima*. In the field, the latter proved not so easy to separate from the former as suggested by Walters (1949), so that further study of the dwarf populations was needed to ascertain the proportions of genotypic and environmentally induced dwarfs.

The present work is based on a biosystematic study of these taxa with particular reference to variation in morphology, habit and cytology. As a result of these investigations certain changes of status are recommended.

The new designations and reasons for the changes are briefly given here in order that these names can be used throughout the papers in which fuller explanations will appear.

Satisfactory separation of *A. filicaulis* and *A. vestita* by morphological characteristics is not possible because of intermediates. The two taxa do exhibit somewhat different ecological and geographical distributions; and it is accordingly proposed that they be ranked as subspecies of *A. filicaulis* Bus., viz :

(1) subsp. *filicaulis*

(2) subsp. *vestita* (Bus.) M. E. Bradshaw stat. nov. (*A. filicaulis* Bus. forma *vestita* Bus., Bull. Herb. Boiss. **1**, app. 2, 23 (1893).

A. minima Walters is retained at specific rank.*

I. MORPHOLOGICAL VARIATION IN *A. FILICAULIS* BUS., *SENSU LATO*

A. filicaulis, *sensu stricto*, was first described by Buser (1893). From it he separated ' Une f. *vestita*.' As his description is rather long and not easily accessible the following shortened translation is given :

Plant small to medium sized, rhizome medium thick. Lower part of stem and petioles usually with spreading hairs; upper part of stem and pedicels glabrous. Leaves variously clothed with spreading hairs often only on the veins below and folds above. Earliest petioles and leaves often ± glabrous, later petioles with spreading hairs. Base of the petioles and stipules usually wine-red. Leaves medium (3–9 cm wide, 2·5–8 cm long), ± reniform in outline, with wide basal sinus, somewhat blue-green, paler below, lobes 7 or incompletely 9, round or ± triangular, toothed all round; teeth (9–) 11–13 (–15), subacute, somewhat connivent, all ± equal except the small terminal tooth. Stems (5–) 20–30 (–40) cm, ascending, slender. Inflorescence medium, flowers large, 3–4 mm, clusters not very dense.

Of the forma *vestita* Buser continued ' (la plante entière plus ou moins velue) a été constaté en outre dans les Cevennes, en Normandie, au Jura (Reculet). Dans ces localités la forme semble se présenter comme une race indépendante, à l'exclusion du type, tandis qu'au Salève on ne la rencontre qu'en individus égrenés et rares parmi la forme normale fréquente.' Raunkiaer (1906) raised this forma to specific rank, no doubt impressed by its frequency in Denmark.

1. Variation in hairiness

(*a*) *The flowering stem*

It has already been indicated that the hair cover on plants of *A. filicaulis*, *sensu lato*, varies from dense to slightly hairy. A measure of this hairiness is most conveniently made on the flowering stem, where the density of the indumentum usually decreases from the base upwards. This change, however, may be slight, in which case the plant will be either densely hairy throughout, or with all but the basal internodes glabrous. The hairiness of the flower-stems was measured by direct visual comparison of the density of the indumentum on the internodes with a set of six standards. This method was of sufficient accuracy, and easier to apply than an analysis based on the number of hairs per unit length of stem, which would have wasted too much time obtaining a degree of exactitude which was not necessary.

(*i*) *Method*

The flower-stems were classified in the following way. Standards were set up to provide six *classes* of degree of hairiness of the stem in Fig. 1.

* In his latest paper, Rothmaler (1962) treats these three taxa as varieties of *A. filicaulis*.

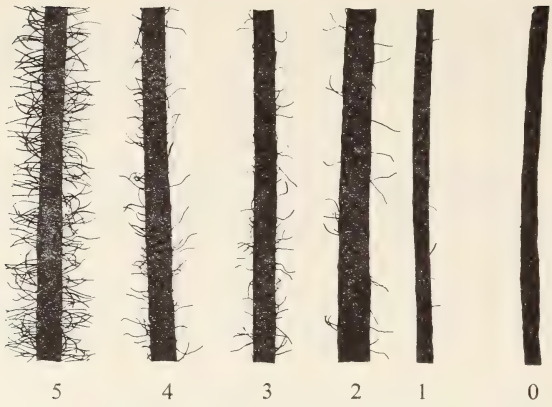


Fig. 1. Classes of hair density on internodes of the flower-stem. Drawing based on a photograph ($\times$ 4).

Internodes II, IV, VI and VIII were thus scored for hairiness according to this scale, other internodes being scored where necessary. Since some flower-stems have more internodes than others comparison was made over the lower six internodes only. The *grade* of hairiness of the flower-stem corresponds to the decrease in hairiness of the internodes of the flower-stem, and since internode II is usually densely hairy, it was assumed to be class 5 in all cases. Therefore, the *grade* for each flower-stem was calculated as the difference between the class of the VIth internode and class 5. In Fig. 2, in grade 5 the VIth internode is glabrous, the difference between this class (0) and the most hairy state (5) is 5; in grade 0, all internodes are class 5, so that there is no difference between the class of internode VI and the most hairy state (5). This gives seven grades of hairiness of the flower-stem (0–6). It should be noted that in grades 0–4 the internodes above the sixth (VI) may be hairy; in grade 6, internode V as well as VI is glabrous, internodes below the fifth (V) may be glabrous; also, in some cases the most hairy internode may be less hairy than class 5.

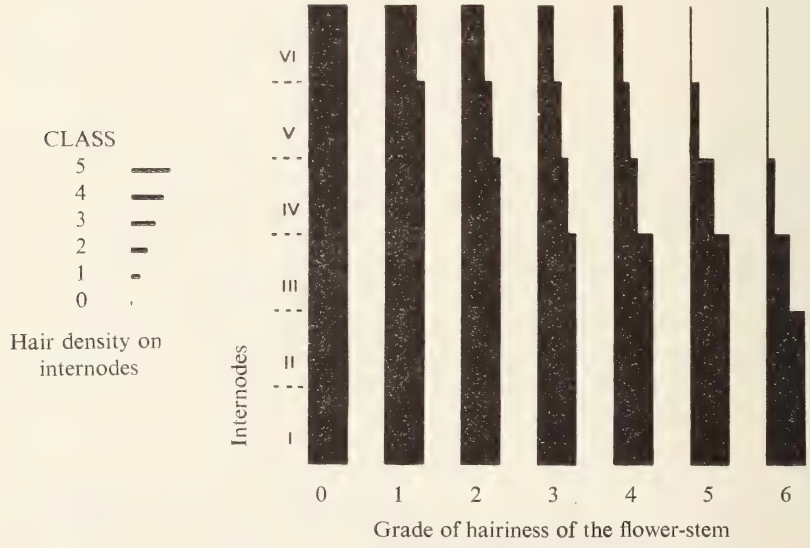


Fig. 2. Diagrammatic representation of the seven grades of hairiness of the flower-stems.

(*ii*) *Variation in the grade of hairiness of the flower-stem of individual plants* (*i.e. variation within a plant*)

Preliminary studies showed that a slight variation may occur in the grade of hairiness of two or more flower-stems on the same plant. For example, the grade of hairiness may be 0 and 1, or 3, 4 and 3, in both plants the variation is one grade; those plants with 0, 1, 2 or 1, 1, 3 show a variation of 2 grades, etc. Analyses of 353 plants are shown in Fig. 3. In the whole sample, 83% showed either no variation or a difference of only one grade between the two or three flower-stems which were scored. When the more glabrous (Grade 6) and more hairy (Grade 0–3) plants were plotted separately, it was clear that most variation occurred in the more hairy plants.

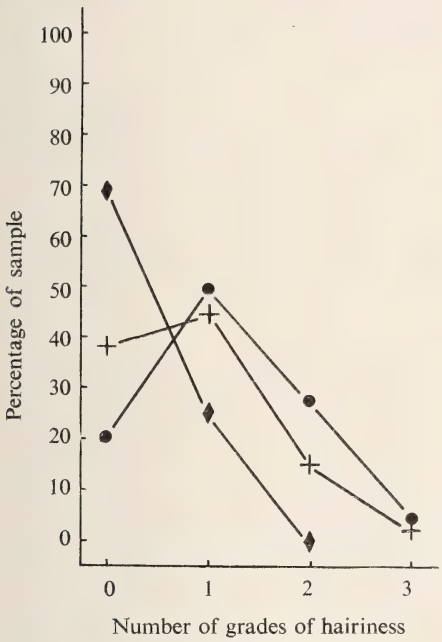


Fig. 3. Variation in grade of hairiness of two or more flower-stems on the same plant. Crosses, *A. filicaulis, sensu lato* (353 plants); dots, grades 0–3 (163 plants); diamonds, grade 6 (72 plants).

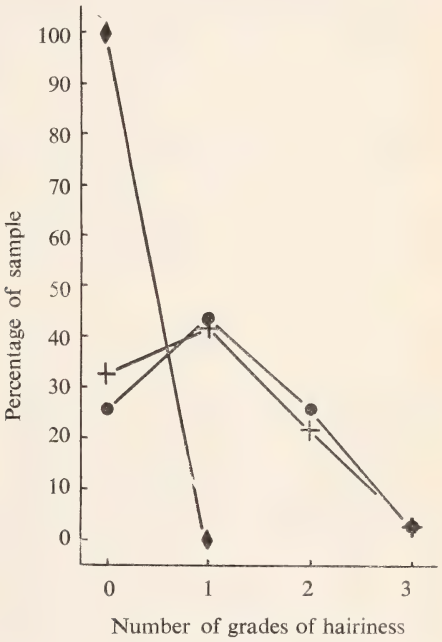


Fig. 4. Variation in grade of hairiness of the flower-stems on the same plant from year to year. Crosses, *A. filicaulis, sensu lato* (102 plants); dots, grades 0–3 (82 plants); diamonds, grade 6 (8 plants).

(*iii*) *Variation from year to year*

This analysis was made on 102 plants grown in the garden for three (in some cases two) years. In most cases it is based on the mean of three flower-stems per plant in the final year, and one flower-stem per plant in the other year(s). (Fig. 4).

Whilst 74% show variation of no more than 1 grade, 26% have greater variation; this is somewhat higher than was found within the plants and no doubt is in part due to the analysis being based on a single flower-stem from each plant in the earlier years, thus giving an over-estimation of the difference.

In both of these analyses the more hairy plants, grades 0–3, show greater variability than the less hairy grade 6.

From the above observations on plants grown under similar conditions in the garden, it is clear that there is some fluctuation in the density of the indumentum between the several flower-stems of each plant and on the same plant from year to year. The less hairy plants are least variable, but even in the more variable hairy plants the oscillation is over only a portion of the total range of hairiness. Thus this method of analysis does provide a means of discriminating between the various degrees of hairiness of the flower-stem found in *A. filicaulis, sensu lato.*

(*iv*) *Variation within families*

Offspring of plants of different hair density were raised from seed. As far as possible, 20 plants of each family were grown in boxes of John Innes Compost No. 1 containing 10 plants each. Three mature flower-stems were collected from each plant and scored for hairiness by the method described. Results are given below (Table 1).

TABLE 1

Variation in hairiness of the flower-stems within families. (grade mean, usually of three flower-stems per plant)

Code number	*Hairiness grade*		*Frequency of each grade of hairiness in each family*						
	Parent	*Family*							
			0	1	2	3	4	5	6
4/38/371	0	0·65	7	13					
4/28/326	2	0·8	4	18	1				
4/11/116	2	1·1	3	11	6				
4/9/101	2	1·2	2	13	44				
4/3/45	2	1·4	1	10	7	1			
4/30/318	3	1·7	1	7	10	2			
4/39/269	1	1·85		5	13	2			
H	1	2·0		5	8	6			
4/30/316	3	2·25		2	11	7			
4/39/272	5	4·8					4	16	
4/8/84	6	5·8						4	16
4/15/216	6	5·9						2	37
4/16/207	6	6·0							10
Sc. 8	6	6·0							13
4/10/109	6	6·0							5
52/1		1·0	5	11	4				

In line with the earlier observations, least variation occurred in the more glabrous families with means of 5·8, 5·9 and 4·8 (families 4/8/84; 4/15/216 and 4/39/272). In addition three small families of 5, 10 and 13 plants respectively and means of grade 6 showed no variation. Other nearly uniform families are at the other end of the scale with means of 0·5 and 0·65 (families 4/11 and 4/38/371). The families with means between 0·8 and 2·25 were much more variable, even containing plants of three or four grades of hairiness. One would have liked more examples of families with the grade mean of 0, 4 or 5. The range of variation found in all these families is of the same order of magnitude as that found within individual members of the families; in no case does it exceed the maximum range found in individuals.

(*v*) *Variation in hair character of parents and offspring*

In the same families, comparison was made between the hairiness of the parent (the mean over a number of years) and the variation found in the families (as above). As before the greatest similarity was found in the more glabrous families (4/8/84; 4/15/216 and 4/39/272). The one family of a grade 0 parent showed a shift of the mean towards grade 1, but other families of parental grade 0–3 are those with a wide range in the offspring. This spreads over 2–4 grades usually ranging about the mean of the parent, but rarely is the mean of the offspring the same as that of the parent.

Care must be taken when drawing conclusions from these breeding experiments because the most hairy (0) and intermediate grades (4–5) are represented by only one family each. It is clear that determination of the hairiness of the flower-stem in *A. filicaulis, sensu lato* is largely genetical. In the least hairy plants this is within quite narrow limits. Family 4/39/272 is of particular interest; this is a plant of the dubious intermediate grade. Here the hair character is maintained in the offspring with little variation and shows very well that the intermediate character is not improbably genetically determined. Results of breeding from grades (0–) 1–3 suggest that these grades should be grouped together; the method of analysis reveals an amount of variation which may be genotypic but is more probably environmental in origin. This is supported by the evidence of wide variation within single plants and the fluctuation above or below the grade of the parent.

At this stage it is convenient to correlate the grades used in classification of the flower-stem with the taxonomic treatment recommended at the beginning of this paper. Grades 0–3 may be regarded as subsp. *vestita* and grade 6 as subsp. *filicaulis;* grades 4–5 are intermediate in character.

(*vi*) *Variation in plants grown under field and garden conditions*

The preceding observations have been made on plants grown under garden conditions. Investigations were also made on the hairiness of plants as collected in the field and after a period of cultivation in the garden for one or more years. These 30 plants gave 57% showing no variation and 33% with variation of 1 grade; the remaining 10% varied 2 or 3 grades; this suggests that on the whole variation with change of growing conditions is within the range found in individual plants. Certain rather sparsely hairy plants do require special mention; some of these with glabrous or nearly glabrous flower stems in the field produced more normal, grade 6 flower stems after cultivation. These were all plants of high altitudes and will be discussed fully after variation in hairiness of the leaf has been considered.

(*b*) *Other parts of the flower-stem*

Variation in hair density is not limited to the main branches of the flower-stem only. On the pedicels (ultimate inflorescence branches) hairiness is of the same nature as the rest of the branches, being absent in the more glabrous grades. Hairiness of the urceole shows a similar series. Urceoles in the more hairy grades are usually also densely hairy. In other grades the density decreases, but rarely are all the urceoles on the flower-stem without hairs, though in grade 6 there may be no more than one or two hairs on a few urceoles only.

(*c*) *The leaves*

Variation occurs in the hairiness of the petiole and of the upper and lower leaf surfaces. No detailed analysis was made on the hair density of the petiole but a series from densely hairy in the grade 0–3 plants to sparsely hairy or almost glabrous in grade 6 does occur.

More detailed work was done on the lamina of the leaf. Mature summer leaves were compared. Only in the most densely hairy plants are the hairs apparently evenly distributed over the surfaces of the leaf; in less hairy leaves decrease of hair cover is localised so that

hairs persist on the folds and ends of the lobes of the upper surface and the veins and basal lobes of the lower. Such a distribution of hairs cannot be measured quantitatively, so a series of standards had to be used. These were chosen for upper and lower surfaces of the leaf as in Fig. 5.

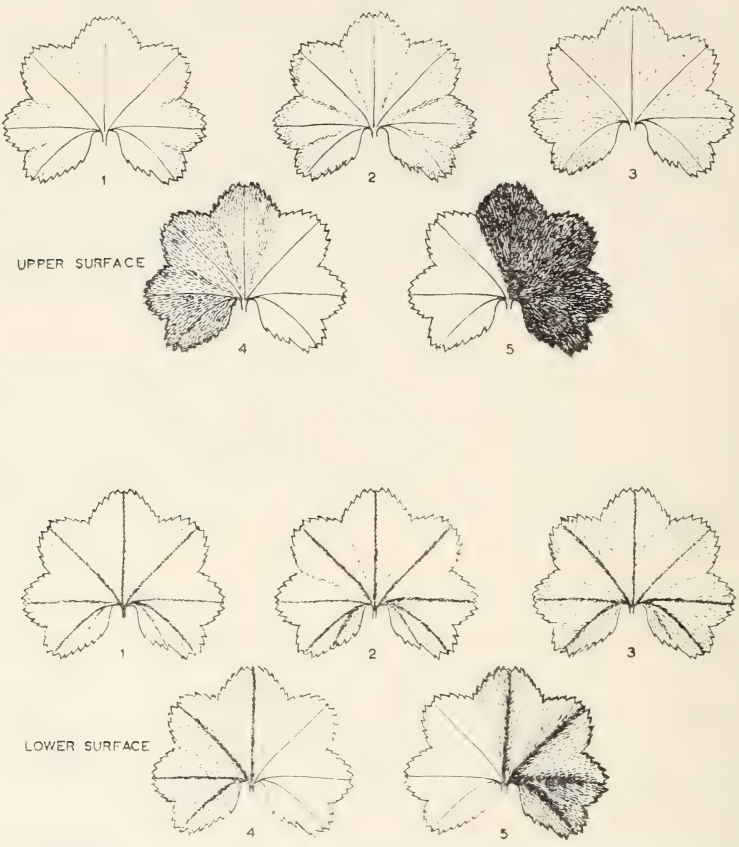


Fig. 5. Classes of hairiness of upper and lower leaf surfaces. In classes 4 and 5 hairs are shown on a portion of the leaf only.

Preliminary investigations of the hairiness of both leaf surfaces of plants of different grades of hairiness of the flower-stem showed a close correlation between the lower surface and the flower-stem grade (Table 2).

TABLE 2

Correlation of flower-stem hairiness. Mean values for class of leaf hairiness of several plants with flower-stems with the same grade of hairiness.

Flower-stem grade	*Leaf*	
	Lower surface	*Upper surface*
0	4·4	4·4
1	3·0	3·4
2	2·7	2·75
3	2·7	3·3
4	1·75	2·75
5	1·3	2·7
6	1·1	3·1

Further comparisons between flower-stem and leaf hairiness (lower surface) were made on cultivated plants. Observations on three leaves per plant showed very little variation within the plant, even in the hairy ones. Means of these supported the preliminary findings of correlation between the hairiness of the flower-stem and the leaf, e.g. in family 4/38/371 of flower-stem hairiness 0–1, leaf class was consistently 4; i.e. maximum flower-stem hairiness with near maximum leaf hairiness. In Sc. 8 and 4/15/216, both of grade 6 flower-stem, leaf hairiness is of minimum density.

Results of scoring 218 garden and field plants assessed on one flower-stem and one leaf are given in Table 3.

These results support those from the families at both ends of the series and, as with the hairiness of the flower-stem, greater variability was found in the intermediate grades.

TABLE 3

Correlation of flower-stem hairiness and hairiness of the lower surface of the leaf.

Class of hairiness of the lower surface of a leaf.	*Grade of hairiness of the flower-stem* 0	1	2	3	4	5	6
1						5	41
2			3	3	2	9	16
3	1	9	14	12	8	12	6
4	12	16	10	5	5	4	
5	6	13	4	2			
Total	19	38	31	22	15	30	63

Certain almost glabrous plants can now be considered. These formed a very small proportion (16) of all the plants collected in the field. In most cases the lower surfaces of the leaves were hairy only on the nerves; the flower-stems were glabrous, including all or most of the urceoles. All were very dwarfed when collected and of high montane habitats, including very wet flushes. After cultivation for 2–3 years they increased in size and all but one developed the hairs typical of the more glabrous variants of *A. filicaulis, sensu stricto*. In plant 6/28/201 the petioles and leaves became hairy as in *A. filicaulis, sensu stricto*, but the flower-stem remained glabrous. This was the only plant in which the absence of hairs appeared to be genetically determined. Details of variation in five plants are given in Table 4.

2. VARIATION IN LEAF SHAPE

From the beginning of these investigations it was apparent that there was considerable variation in the shape of the leaf, especially in that of the lobes; but this was difficult to measure and too variable to assess qualitatively. Only when leaves of families were available did the genotypic nature of the variation become clear.

Three mature leaves were collected from samples of twenty plants of different families. Though the general shape of the leaf in *A. filicaulis, sensu lato*, is reniform, the angle of the basal sinus does vary a little; of greater significance is the variation in the length of the lobes, most obviously in the median lobe. This may be broad and shallow or long and narrow or even with a truncate end. Leaves of five representative plants from four samples of twenty raised from different parent plants are shown in Fig. 6. The relative length of the lobe decreases in the order 4/9/101, 4/11/116, 2/1, 4/30/316. The great similarity within each family clearly shows the genotypic nature of this character. This range is shown in plants of the grade 0–3 hairiness range; from general observations it is known

TABLE 4
Hairiness of five dwarf montane plants when collected and in cultivation

Code no.	Date	Leaf hairiness: Petiole	Leaf hairiness: Lamina, lower	Leaf hairiness: Lamina, upper	Flower-stem hairiness: Internodes	I	II	III	IV	V	VI	Urceoles
6/22/172	1956 f	class 1	class 1, distal 2/3 nerve	class 2	class	0	1	0	0	0		few on most
	1957 g	class 2–3*	class 1, distal 2/3 nerve	class 2	class	.	1	.	0	.	0	few
	1958 g	—	—	—	class	0	4	3	0	.	0	—
6/28/201	1956 f	class 1	class 1, distal 2/3 nerve	class 2	class	.	0	.	0	.		most hairy
	1957 g	class 2–3*	class 1, distal 2/3 nerve	class 2	class	.	0	.	0	.	0	few on most
	1958 g	—	—	—	class	0	2	0	0	0	0	
					class	.	0	.	0	.	0	—
					class	.	0	.	0	.	0	
6/28/202	1956 f	class 1	class 1, distal 1/2 nerve	1/few	class	.	0	.	0	.	0	few on most
	1957 g	class 2–4*	class 1, distal 2/3 nerve	class 2	class	.	1	.	0	.	0	very few
	1958 g	class 4	class 1, distal 2/3 nerve	—	class	.	3	.	2	.	0	
					class	.	3	.	3	.	1	—
					class	.	3	.	0	.	0	
6/28/203	1956 f	0 hairs	class 1, distal 1/4 nerve	1/few	class	.	0	.	0	.	0	0
	1957 g	class 3–5*	class 1, distal 3/4 nerve	class 2	class	.	4	1	0	.	0	few on some
	1958 g	hairy	class 1, distal 3/4 nerve	—	class	.	4	.	4	.	2 1	—
					class	.	4	.	2	1	0	
6/26/181	1956 f	class 2	class 1, distal 3/4 nerve	class 3	class	.	0	.	0	.		? 0
	1957 g	class 5	class 2, distal 3/4 nerve	class 3	class	.	1	2	0	.	0	few on most

f = field, g = garden, * = 3 leaves

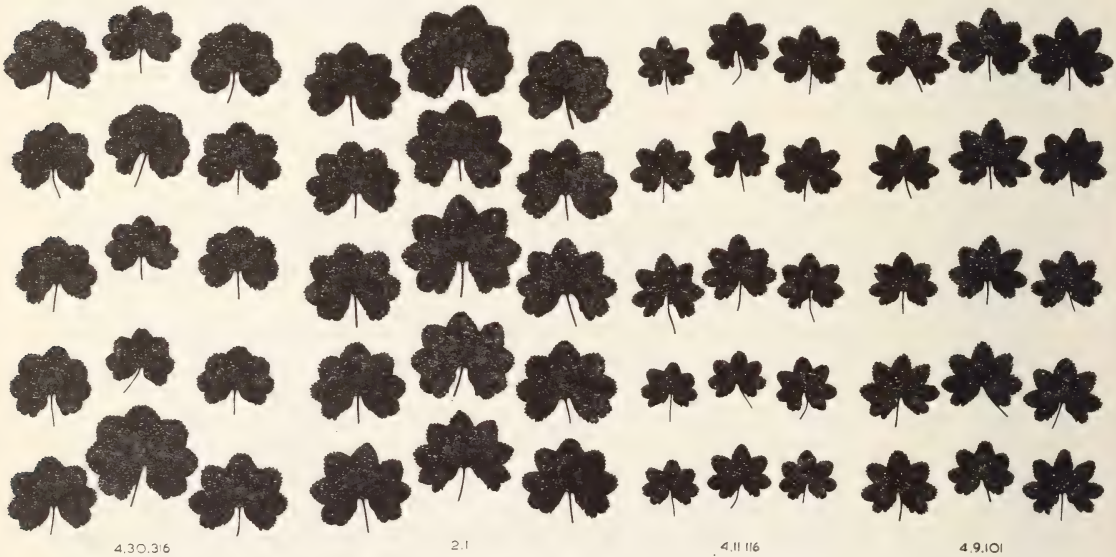


Fig. 6. Variation in leaf-lobe shape between families. Three leaves from each of five plants in each family.

that a range of leaf shapes is also found in plants of the other hair groups. It would appear that this variation is quite independent of the variation in hairiness.

A preliminary analysis of the variation in the shape of the leaf-lobe has been made. Measurements were made of the median lobe of a well grown leaf; though the ratio length/($\frac{1}{2}$ greatest breadth) makes no allowance for the degree of curvature of the sides of the lobes, it does differentiate between the long and narrow, and short and broad lobes. Analysis of *c.* 100 herbarium specimens showed that there is considerable variation in lobe shape; the values obtained were between 0·58 and 3·26 with a mean of 1·36. Although the sample was not random, it showed there is considerable variation in the lobe size throughout Britain, without local concentrations of any one size.

TABLE 5

Variation in shape of the median lobe of the leaf in several populations.

Population code no.		*No. of plants*	*Length of lobe / ½ breadth.*	
			mean	*s. d.*
	4/39	6	0·77	0·11
mixed	4/44-52	9	0·9	0·04
	4/9-11	10	1·03	0·07
	4/22	7	1·1	0·16
	4/3	9	1·1	0·20
	4/8	9	1·1	0·21
	5/48	10	1·18	0·06
	5/45	12	1·2	0·13

Values for some populations of uneven size from different habitats but grown under the same garden conditions for one or two years are given in Table 5. The range of variation within the populations is usually wide (e.g. 0·7–1·7), but some populations are less variable and centre about different means : e.g. the mixed collection with 0·9 ± 0·04 and 5/48 with 1·18 ± 0·06. Whilst the first two samples (Table 5) are from long rough grass at 1300 ft and *c.* 350 ft the last two are from high altitude pasture at *c.* 2000 ft. Further investigation may show that leaf-lobe shape is associated with habitats.

3. VARIATION IN STIPULE COLOUR

In *A. filicaulis, sensu lato*, the base of the petiole is usually wine-red due to anthocyanin; the colour may extend along the stipules and usually occurs on the rhizome. Occasionally concolourous forms without the pigment are found.

Cultivation and breeding have shown that the presence or absence of anthocyanin is genetically determined. All the offspring of three concoloured plants, (60, 20, 20 plants respectively) were without the pigment. Offspring of pigmented plants were coloured but the intensity varied considerably. This variation is found in both subspecies in *A. filicaulis, sensu lato*. It was noticeable in wild material that the deeply coloured plants were most frequently found in long grass, whilst plants of open or grazed habitats were more variable and usually less deeply coloured. Experiments have supported these observations. Samples of seedlings from several plants were grown under the following conditions :

(a) in grass which was allowed to grow tall (meadow).
(b) in grass which was kept short with a lawn mower.
(c) open soil in the garden.
(d) boxes (see page 308).
(e) as (d), these plants were kept short (2·5 cm above soil level) by cutting throughout the summer.

Results are given in Table 6.

Table 6
Variation in colour of the base of the petiole

Code number	*Garden plot*			*Boxes*	
subsp. *vestita*	a (20 pl.)	b (20 pl.)	c (20 pl.)	d (40 pl.)	e (20 pl.)
4/3/45	3	2 −, 2	2, 2 +	3	2 − —
4/12/173	2 +, 3	1, 2 −	2 −, 2		
4/39/270				3 (20 pl.)	2 −, 2
4/30/318				2, 3	2 −, 2
4/9/101				2 +, 3	2
subsp. *filicaulis*					
4/15/216	3	2 − —, 2		2, 3	2 + (10 pl.)

a tall grass
b short grass
c open soil
d open soil
e short grass
pl. = plant
1 = no wine colour
2 = intermediate
3 = deep wine-red

This shows that the wide variation in the intensity of the wine colour is correlated with the conditions in which the plants are grown. In the shade produced by closely associated plants (a and d) the bases of the plants are deep wine-red (3). Under simulated grazed conditions (b and e) the colouring is slight – maybe only a very little on the rhizome or stipules, rarely is it completely absent. Widely spaced plants grown in open soil (c) were intermediate in colour. It seems probable that the quantity of pigment present is correlated with the amount of light which reaches the base of the plants.

Concolourous plants are readily recognised in rough grass, meadow and woodland habitats; they are difficult to determine in open or grazed habitats, since genetically determined coloured plants may be so lacking in colour that only careful examination, preferably followed by cultivation, will separate the concoloured genotypes. They are very difficult to determine in herbarium material. Only a few concoloured plants have been confirmed during these studies, and then occurrence is sporadic.

		Map reference No.
Nr. Malham, Yorks.	several plants	34/68
Scarborough, Yorks.	1 plant	54/08
Upper Teesdale	1 plant	35/83
S. Scottish Uplands	3 plants	36/0612
Central Highlands	1 plant	27/6544
W. Pennines	2 plants	35/7131

Only around Malham is this form known to be at all frequent. Further cultivation experiments on grazed plants will undoubtedly show that the concoloured plant is more widespread.

4. Morphological delimitation of subsp. filicaulis, subsp. vestita and the intermediate

The subsp. *filicaulis* and subsp. *vestita* have been separated by the single character of hair density, in particular that of the inflorescence. This hair density has been shown in the preceding observations and cultivation experiments to be genetically determined; but it is subject to variation which is most marked in the more hairy plants. On the basis of these data it is now possible to define more exactly the limitations in the morphological characters of the two taxa and their intermediate. This, of course, is based on the hair character only, since there is no evidence that the observed variation in leaf shape is in any way correlated with the variation in hair density.

Subsp. *filicaulis* usually has flower-stems with hairiness grade 6 and the lower surface of the leaf class 1 or 2. Thirty plants in cultivation and 92% (of 203 plants) of the offspring of type 6 parents had this grade of hairiness of the flower-stem, i.e. with internode V glabrous. The remaining 8% of the offspring of type 6 parents had some hairs (class 1) on internode V. It is not yet known if the hairiness of these plants is environmentally induced or genetically determined. Internode IV is often glabrous or with a low hairiness value (class 1 or 2). Usually internodes II and III are densely hairy and so the abrupt change between III and IV is very noticeable; at first, it was thought that this was characteristic of subsp. *filicaulis* but this is not so, as these internodes may be less hairy. No attempt has been made to subdivide the less hairy forms within subsp. *filicaulis* as in most cases these appear to be environmentally-induced states (p. 311). The leaves are very uniform in hairiness of the lower surface, which is hairy only on the nerves or also on the lowest lobes; a very small proportion are thinly hairy all over.

From the preceding data over 90% of the plants referable to subsp. *filicaulis* are separable from other plants of *A. filicaulis, sensu lato*, on the basis of flower-stem hairiness supported by leaf hairiness.

Subsp. *vestita* forms the other end of the hairiness scale. All observations have shown a large amount of variation of an environmentally determined nature but it is not possible to say whether the wide variation seen in the families is mainly the same or partly genotypic. It seems best to include in subsp. *vestita* all those plants with flower-stems of hairiness grades 0–3; this includes plants densely hairy throughout, and those moderately hairy (class 2) on internode VI and maybe glabrous in the upper branches. Though it is apparent in the breeding experiment that the most hairy plants are a little less variable than the others, there is no reason why these plants should be considered to be anything more than equivalent to the most glabrous members of subsp. *filicaulis*. As in the flower-stem the leaves show a greater range of variability than in subsp. *filicaulis;* in 110 plants hairiness of the lower surface of the leaf was :

class 5 in 25 plants
class 4 in 43 plants
class 3 in 36 plants
class 2 in 6 plants

Thus 95% were within the more hairy half of the scale (classes 3–5) class only 5% were of the most glabrous classes (1 and 2).

The intermediates between the lower limit of hairiness of subsp. *vestita* and the upper limit of subsp. *filicaulis* are those plants with flower-stems of hairiness grade 4 and 5. These are not so frequent as the other genodemes. In cultivation the grade of hairiness of the flower stem was maintained over several years with slight variations between grades 4 and 6. It was only possible to raise offspring of one plant of grade 5; all these were of grade 4 and 5. Although so near to subsp. *filicaulis*, no plant had a mean of grade 6 though single flower-stems on some plants were this grade. (The leaves are also intermediate in the class of hairiness of the lower surface).

5. Variation in the habit of A. filicaulis, sensu lato

Considerable variation in the size of plants of *A. filicaulis, sensu lato*, was very obvious in field samples collected from grazed pasture, meadow and wood over a wide altitudinal range. Walters' recognition (1949) of *A. minima* as a dwarf species opened up the question of whether in fact these other assumed dwarf variants of more ' normal ' species were environmental dwarfs or not.

A preliminary experiment to test this was set up. Habitat samples were obtained mainly from close-grazed pasture, but also from long grass and woodland, from nine sites between 450 ft (138 m) in East Durham and 2,500 ft (723 m) on the Pennine escarpment

near Cross Fell to the west, all about latitude 54° 40′N; and from 2,000 ft (610 m) on Ingleborough where *A. minima* grows. As far as possible equivalent-sized pieces of unbranched rhizome of ten plants from each habitat were planted in boxes of John Innes Compost No. 1 in March, 1957. The plants were grown under similar conditions until August and then scored for the following characters :

1. number of rhizome branches.
2. number of flower-stems.
3. length of the petioles of three well-developed leaves.
4. breadth of the lamina of three well-developed leaves.
5. length of the three longest flower-stems.

In 3, 4 and 5 the mean value of three measurements per plant was used. Results are shown as graphs in Figs. 7 and 8.

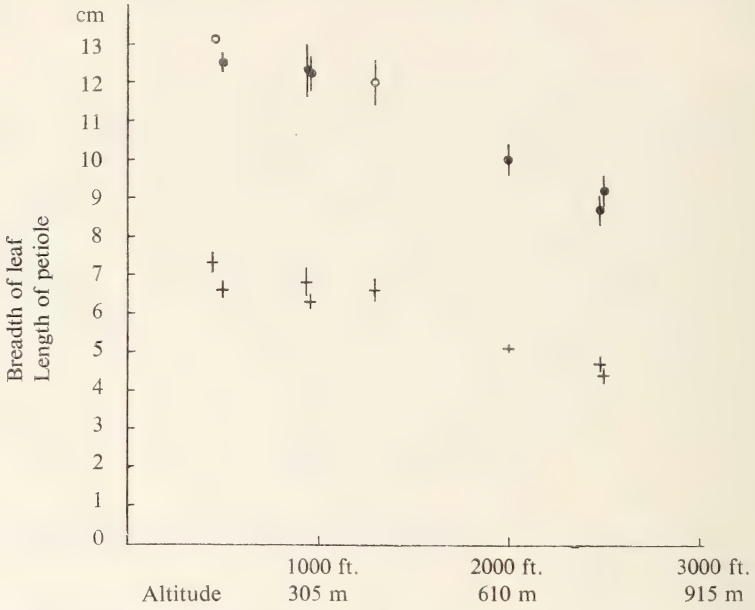


Fig. 7. Variation in breadth of leaf and length of petiole of population samples from various altitudes after cultivation. Leaf measurements, plain crosses; petiole measurements, solid dots (pasture) and open circles (meadow). (Standard deviation is given as a vertical line above and below the mean).

The sample from Ingleborough differed greatly from the others in the high number of flower stems (15·7) and short petioles, which are characteristics of *A. minima*. It was surprising that all the plants in this sample were of this kind; and, since no *A. filicaulis, sensu lato*, plants were present, this sample will be considered no further here, but will be included in a later paper on *A. minima*. In the other samples, although the dwarf plants attained a greater size in cultivation than in the field, a correlation between size of plant (as measured by petiole length and leaf size) and altitude was revealed. Fig. 7 shows the steady decrease in size found in the pasture plants as the altitude increases; the absence of pasture samples between 1,350 ft (411 m) and 2,000 ft (610 m) emphasises the difference between the lowland and montane populations. Additional correlation exists between the numbers of shoots produced per plant and altitude (Fig. 8). This is positive, the plants of high altitudes producing more shoots than those of low altitudes; variation within samples was greater here but significant differences were found between high and low samples.

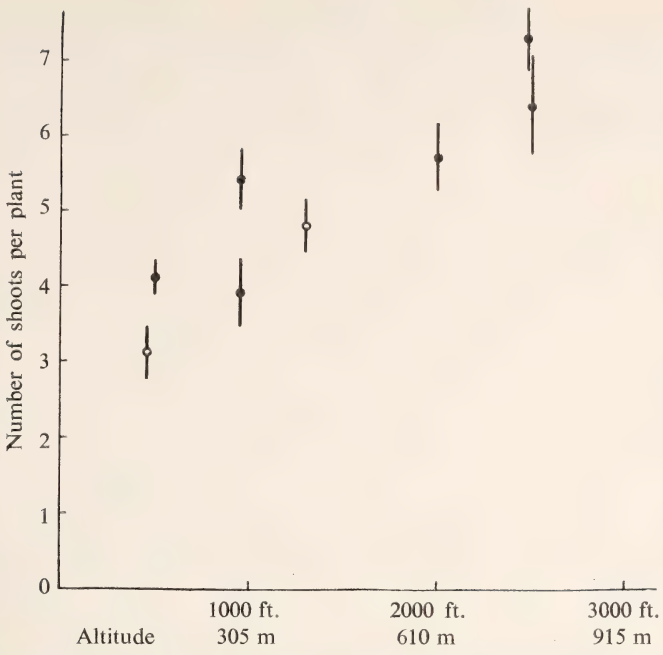


Fig. 8. Variation in the number of shoots produced per plant after cultivation of population samples from various altitudes; solid dots, pasture, open circles, meadow. (Standard deviation is given as a vertical line above and below the mean).

The two samples from meadows show the same correlation with altitude, and somewhat surprisingly fit with little distortion into the curve of the pasture plants. A single woodland sample was not included in the graphs because of the greater difference in the nature of the habitat. The number of shoots and breadth of the leaves are very similar to those of samples from the other habitats at 950 ft (290 m); the petioles are slightly but not significantly longer. The number of the flower-stems per plant has not been considered any further because there did not appear to be any obvious correlation with any of the other factors.

The combined effect of these variables is that the montane plants form shorter, more dense clumps, whilst the more lowland plants are taller, less branched and hence less compact.

Two of these pasture samples from 2,500 ft (723 m) and 950 ft (290 m) have been grown in a garden plot for several years. The low, dense growth habit has been maintained by seven of the ten plants from 2,500 ft (723 m); the other three became taller and of lowland habit. This was revealed in the first year in the plot and has been maintained. Subsequent inspection of the data used in Figs. 7 and 8 did, in fact, show that these plants had leaf measurements slightly greater than the means of the samples. All plants in the 950 ft (290 m) sample maintained the lowland type of growth.

Seed progeny samples have been grown, and were analysed in a similar way in their second year. Table 7 shows that the characteristics of the parents are maintained in the families. Families 1, 2 and 3 from the highest altitudes show the characteristic low dense habit. Those from 2,000 ft (610 m) and 1,350 ft (411 m) have maintained the same low growth for four years but had produced fewer shoots per plant than families 1–3 in two years. The number of shoots was not recorded in later years. Although family 6 is from 1,800 ft (549 m) it is of more lowland form and taller in cultivation. The lowest pasture family (7) from 1,200 ft (366 m) is of lowland stature. Four families from a lower pasture and other habitats maintained the lowland form of their parents. These results confirm that the habit characters are genetically determined.

TABLE 7
Analysis of the number of shoots per plant and leaf size in several families

No.	Code no.	Alt. (ft.)	Habitat	No. of plants	Shoot no.	Petiole length (cm)		Leaf breadth (cm)		Height after 4 years
						*Parent 1957	Offspring 1959	*Parent 1957	Offspring 1959	
1	5/47/267	2,400	pasture	20	9·8 ± 0·41	3·1	7·4 ± 0·28	3·5	3·9 ± 0·29	short
2	5/46/261	2,400	pasture	10	10·2 ± 0·76	3·5	5·5 ± 0·40	3·6	3·9 ± 0·15	short
3	5/6/46	2,000	pasture	20	12·3 ± 0·34	2·8	6·8 ± 0·48	3·8	4·0 ± 0·07	short
4	5/45/247	2,000	pasture	10	3·5 ± 0·45	1·6	6·7 ± 0·34	2·7	5·4 ± 0·43	short
5	5/1/13	1,350	pasture	20	5·4 ± 0·30	2·3	6·9 ± 0·32	3·4	4·5 ± 0·21	short
6	5/4/29	1,800	pasture	20	4·8 ± 0·34	5·8	7·5 ± 0·33	4·9	5·4 ± 0·21	medium
7	4/33e	1,200	pasture	20	6·3 ± 0·53	10·0	11·1 ± 0·50	5·4	6·1 ± 0·12	tall
8	4/15/216	950	grass	20	3·9 ± 0·32	11·5	10·3 ± 0·34	7·3	6·7 ± 0·40	tall
9	4/39/272	1,300	meadow	10	3·7 ± 0·42	10·0	10·1 ± 0·34	7·2	7·4 ± 0·13	tall
10	4/30/318	950	meadow	20	4·7 ± 0·44	not available				tall
11	4/8/89	950	wood	20	4·9 ± 0·22	12·2	11·0 ± 0·88	7·4	6·8 ± 0·56	tall

*The measurements were made in different years, therefore comparative values between the parents and between the families should be considered, not the direct parent-family value.

This variation in size and habit is closely connected with environmental factors; as is to be expected the *A. filicaulis, sensu lato*, plants are small in closely grazed habitats; so far, in all lowland samples, this character appears to be only environmentally induced, but at the higher altitudes probably the majority of the dwarf *A. filicaulis, sensu lato* plants of the close grazed montane habitats (above 1,500 ft, 458 m) are the dwarf, much-branched variant. The cline in size and habit shown in Figs. 7 and 8 and Table 7 is most obviously correlated with altitude and hence, the associated factors of climate, temperature, exposure and their effects on the soil. In the pasture habitats the grazing pressure is very important. All the montane habitats are very much more closely grazed by sheep than the lowland pastures, and may have been subject to this close grazing for a long time, probably several centuries.

It is difficult to assess the relative importance of the biotic and altitudinal factors in the evolution of this variant. The low-growing, much-branched variant is so obviously well adapted for survival under high grazing pressure that it appears to be axiomatic that grazing pressure has been of great importance. This is confirmed by field observations on rock-ledge plants protected from grazing which are similar in size and habit to the more lowland plants. It seems reasonable to assume that altitudinal factors also have been of some importance in the development of the cline, since variation is continuous over the whole altitudinal range of samples from the long grass habitats as well as those from the grazed habitats.

The gradual variations found in these two characters, size and shoot number, form clines similar to those known in sexual species; for instance the well known example of *Achillea lanulosa*, investigated by Clausen, Keck & Hiesey (1948), which shows a similar correlation between plant height and altitude, forming several ecotypes in isolated localities between *c.* 4,000 ft (1,220 m) and 10,000 ft (3,050 m); or *Plantago maritima* where Gregor (1939) recognised ecoclines related to ecological gradients. In *A. lanulosa* the ecotypes are geographically and morphologically isolated but in *P. maritima* where variation is continuous, separation is difficult, and each end of the cline may be regarded as an ecotype. In *Alchemilla filicaulis, sensu lato*, the evidence so far obtained suggests a parallel with the ecoclines found in *P. maritima*, with the possibility of a separation into a dwarf montane and a tall ecotypic variant or ecogenodeme.

The existence of genodemes within the species in *Alchemilla vulgaris* agg., similar to the ecotypes in sexual species, was first demonstrated by Turesson (1943). The initial work, based on eleven species, was qualitative and showed variation in morphological and physiological characters in several species, from widely spaced localities in Sweden; those within *A. filicaulis* differed in habit, time of flowering and mildew resistance as follows:

Type	*Habitat*	*Flowering*	*Mildew*
Lapland	small low tussock	earliest	very severely damaged
Scania	compact well formed tussock	latest	severely damaged
Uppland	,,	intermediate	,,
Småland	loose spreading tussock	,,	less attacked
Gotenburg	large, loose spreading	late	slight

Photographs of two types were given. Turesson regarded this species as the most variable of those which he studied.

Later work on seed progenies of some species has confirmed the genotypic nature of some of these characters (Turesson 1956). In the earlier work Turesson introduced the term ' agamotype ' for the different genodemes, which he regarded as equivalent to the ecotypes of the sexual species. This work revealed the genetic heterogeneity of species, which had been regarded as uniform and monotypic apomicts. Recently, Grun (1955) has shown that morphological variation also occurs in the obligate apomict *Poa nervosa*.

Acknowledgments

I am pleased to record my thanks to Professor D. H. Valentine and Dr. S. Max Walters for encouragement and their interest in the work presented in this and the subsequent papers in this series. I wish to thank the Nature Conservancy and Research Fund Committee of the Durham Colleges for financial assistance while this work was being done, Professor Valentine for providing working space in the Department of Botany, and the Laboratory staff for technical assistance.

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Appendix—Localities

Key to code numbers, a/b/c, where, a = year b = population and locality, and c = number of the individual plant.

Code No.	*Year*	*Locality*	*O.S. Nat. Grid. ref.*
2/1/	1952	Craven	34/720780
4/3/	1954	Weardale	35/964392
4/8/	1954	Teesdale	35/922274
4/9/	1954	Teesdale	35/921273
4/10/	1954	Teesdale	35/861303
4/11	1954	Craven	34/910633
4/11/	1954	Teesdale	35/921273
4/12/	1954	Teesdale	35/930258
4/15/	1954	Teesdale	35/922274
4/16/	1954	Teesdale	35/926270
4/22/	1954	Teesdale	35/866313
4/28/	1954	Weardale	35/875388
4/30/	1954	Weardale	35/900378
4/38/	1954	Bishop Auckland	45/214294
4/39/	1954	Teesdale	35/865309
4/45/	1954	E. Durham	45/338384
5/1/	1955	Teesdale	35/855284
5/4/	1955	Teesdale	35/833273
5/6/	1955	Teesdale	35/837264
5/44 and 45/	1955	Mickle Fell	35/815247
5/46-52/	1955	Knock Fell	35/7130
6/22/	1956	Ben Lawers	27/658444
6/26/	1956	Ben Lawers	27/635405
6/28/	1956	Ben Lawers	27/6443
H	1946	Scarborough	54/08
Sc. 8		Borghamn, Sweden	

STUDIES ON *ALCHEMILLA FILICAULIS* BUSER, *SENSU LATO* AND *A. MINIMA* WALTERS.

II. CYTOLOGY OF *A. FILICAULIS, SENSU LATO*

By Margaret E. Bradshaw
Department of Extra-Mural Studies, University of Durham.

Abstract

All chromosome counts of segregates in the *Alchemilla vulgaris* L. aggregate are listed. Cytological preparations of root-tips, grown in water-culture, and pollen-mother-cells of *A. filicaulis, sensu lato*, were examined with a phase-contrast microscope. It was difficult to obtain exact counts; in both subspecies $2n = c.$ 101–110, and one count of a dwarf montane plant (see p. 323) gave $2n = c.$ 105 ± 2. P.M.C.'s stained more easily, but the small and variable number of probable bivalents made interpretation difficult. One plant of *A. filicaulis* had $2n = c.$ 150.

Introduction

Cytological studies of the segregates in the *Alchemilla vulgaris* L. aggregate have proved very difficult. Although the chromosomes are small it was difficult to spread the large number sufficiently well to obtain accurate counts. Löve & Löve (1961) list the counts obtained so far within the *A. vulgaris* aggregate. All are high polyploids and apomicts. The particular type of embryology will be described in the third paper of this series.

Turesson's counts (1957) of the *A. vulgaris* L. agg. appear to be the most accurate, but he was not able to give absolutely exact figures, each value being within range of the figures given. However, the accuracy is sufficient to show that some species have a number of $2n = c.$ 105–106; these are : *A. cymatophylla* Juz., *A. sarmatica* Juz. and *A. xanthochlora* Rothm. Most of the others probably have several numbers between $2n = 100$ and 110; these are : *A. glaucescens* Wallr. (*A. minor* Huds.), *A. acutiloba* Opiz, *A. subcrenata* Bus., *A. gracilis* Opiz., *A. subglobosa* C. G. West, *A. vestita* (Bus.) Raunk., *A. filicaulis* Bus., *A. monticola* Opiz., *A. glabra* Neyg., *A. obtusa* Bus., *A. wichurae* (Bus.) Stef., *A. murbeckiana* Bus. and *A. glomerulans* Bus. The lower values of $2n = 93$ and 96 are undoubtedly counts of insufficiently spread plates, the latter an obvious multiple of 8 which has been considered to be the basic number.

A higher range of numbers is found in *A. oxyodonta* Bus. ($2n = c.$ 165-168), *A. oskarssonii* Löve (= *A. glacialis* Oskarss.) ($2n = c.$ 144) and *A. transpolaris* Juz. (= *A. borealis* Sam.) ($2n = c.$ 130–152).

In addition to the chromosome numbers given for *A. wichurae*, *A. murbeckiana*, *A. oxyodonta* and *A. glomerulans*, the value $2n = c.$ 64 is reported by Löve & Löve (1956) and for the last by Bøcher (1938) also. Differences of this magnitude are unlikely to be errors in counting, so that if the material has been identified correctly they imply the existence of intraspecific chromosome races. There may be some significance in the fact that

Turesson's material was of Scandinavian origin whilst Bøcher's was from Greenland and Löve & Löve's was from Iceland; though the material of Jørgensen *et al.*, was also from Greenland. Obviously some rechecking is needed here.

Cytology of A. filicaulis, sensu lato

Method

Preparations of root-tips and pollen-mother-cells were made, and both had their special difficulties. Cells of the root-tips seemed to divide rarely; the chromosomes were difficult to spread and stained poorly. The pollen-mother-cells were easier to handle and stained better, but were more difficult to interpret than the root-tip preparations.

The best results were obtained from roots grown by a simple water-culture method. All except the young roots were stripped from the rhizome of a healthy shoot before it was suspended in a beaker of water. When new adventitious roots had grown, after a few weeks, several millimetres of the yellow-tipped roots were cut off and pre-treated with 0·002 M 8-hydroxyquinoline. The tubes were immersed in running water (*c.*15°C) for 4 hours. Root-tips were fixed in acetic-alcohol, placed in a domestic refrigerator (*c.* 4°C) for 3-6 days to increase the spread of the chromosomes (Walker 1956), and then stored in a deep-freeze refrigerator. It proved difficult to get well spread, deeply stained chromosomes; best results were obtained with aceto-carmine stain using a modification of the combined staining and maceration technique of Proctor (1955). The root-tip was heated in about 1 cc of an aceto-carmine – N HCl mixture in the proportions 9:1 in a test-tube in a boiling water-bath for 5-7 min. Iron was introduced by standing a cleaned needle in the test-tube or earlier as a few drops of ferric acetate in the fixative. The hydrochloric acid aided maceration and hence helped to increase the spread of the chromosomes but had the disadvantage of reducing the stain uptake by the chromatin material. However, better definition was obtained by the use of a phase-contrast microscope.

For meiosis flower buds were fixed when the inflorescences were still very compact, preferably in April, though flowering continues until September or even later. The flower-buds were separated and fixed in acetic-alcohol and chloroform (1 : 3 : 1) for at least 24 hr, then stored in 70% alcohol in a deep-freeze.

Meiosis takes place when the flower buds are about 2 mm long. The four anthers were dissected out into a drop of aceto-carmine, split, and as much of the wall as possible removed. At the correct stage for metaphase plates the pollen-mother-cells float out as separate round cells. These were stained in the usual way. Only a small drop of aceto-carmine must be used or the PMC will float to the edge of the cover-slip and be lost; more stain can be added from the edge of the cover-slip if air gaps remain.

Suitable preparations were made permanent in Euparal. All the chromosome numbers were high ($2n = c.$ 100). To obtain accurate counts, an enlarged photographic print was used as a base on which to ink-in the chromosomes as each was observed under the microscope. In this way, no chromosome is missed or duplicated, and any uncertainty about the exact number is due to inability to interpret the preparation. This method is described by Manton (1950).

Results

The high number of chromosomes, and the difficulty of getting them well spread, made it almost impossible to obtain exact counts; somatic counts from the root-tips are given below.

(*a*) *Mitotic counts*

Subspecies	*Code No.*	*Locality and grid ref.*		*2n*	
vestita	4/9/101	Teesdale	35/921273	105 ± 2	
				105 ± 2	
				104 ± 2	
vestita	4/24/300a	Teesdale	35/861296	104 ± 1	
				105 ± 2	
				106 ± 1	(Plate 14a)
				101 ± 1	
				106 ± 1	
vestita	4/39/269a	Teesdale	35/865309	104 ± 2	
				104 ± 1	
				105 ± 1	
				104 ± 1	
vestita	4/30/318b	Weardale	35/900378	106 exact	(Fig. 1a)
vestita (montane)	5/45/250a	Mickle Fell	35/815247	105 ± 2	
filicaulis	3(60) n	Meall nan	27/5838	152 ± 3	
	„ m	Tarmachan	„	150 ± 2	(Fig. 1d)

The probable margin of error is given in each case.

The count for 4/30/318b is thought to be exact.

(*b*) *Meiotic counts*

Preparation of pollen-mother-cell squashes was relatively easier than the root-tips and stain differentiation was better, but the interpretation was much more difficult. In all cases there were many univalents, and it was not easy to determine which were bivalents or even if multivalents were present; no certain cases of the latter were found. Certain closely associated pairs of chromosomes have been queried as probable bivalents; whether they are interpreted as such or regarded as univalents makes no difference to the total chromosome number. All interpretations are made in the light of somatic counts obtained from the root-tips. In general, when the larger chromatin bodies were regarded as bivalents and the smaller as univalents, the total chromosome number obtained was near the somatic value of the species; thus this interpretation seems justified and does give some idea of the number of bivalents which usually occur. It is essential to know the somatic value when studying meiotic figures as other interpretations could easily be made; because of this all chromosome numbers are approximate only.

Subspecies	*Code No.*	*Locality and grid ref.*		*2n*
vestita	4/2/31	Weardale	35/963392	109?
	4/45/414b	E. Durham	35/338384	*c.* 108
filicaulis	4/3/55a	Weardale	35/964392	*c.* 103
				c. 103
filicaulis	3(60)b	Meall nan Tarmachan	27/5838	*c.* 150

Each plate will be considered separately. In the explanatory diagrams, the univalents are outlined, the bivalents and closely associated chromosomes are blacked in.

subsp. *vestita* 4/2/31 (Fig. 1c). This was very well squashed and is probably a late anaphase, though it could be regarded as a metaphase II. All the chromatin bodies are much the same size and if interpreted as single chromosomes give $2n = 109$ or 110; which is near the number obtained for the somatic counts in the species and the same as that given for *A. vestita* by Turesson.

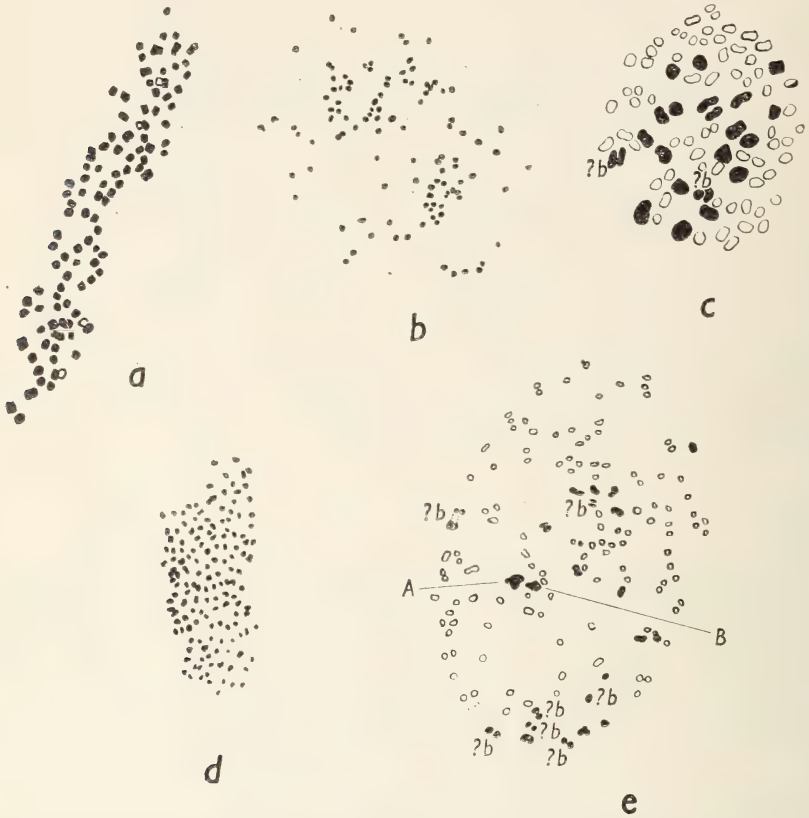


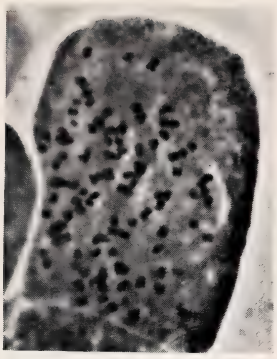
Fig. 1. Chromosomes of *Alchemilla filicaulis, sensu lato.* (a) subsp. *vestita,* Weardale (RT, $2n = 106$, $\times$ 770); (b) subsp. *filicaulis,* Weardale (PMC, $2n = 103$, $\times$ 530); (c) subsp. *vestita,* Weardale (PMC, $2n = 109$ or 110, $\times$ 1070) (d) subsp. *filicaulis,* Meall nan Tarmachan (RT, $2n = 150 \pm 2$, $\times$ 760); (e) subsp. *filicaulis,* Meall nan Tarmachan (PMC, $2n = c.\ 150$, $\times$ 1000). Doubtful bivalents are marked ?b. For further explanation see text.

subsp. *vestita* 4/45/414b (Plate 14b). This is a metaphase plate with 21 II and 66 I giving $2n = 108$.

subsp. *filicaulis.* The only somatic count of British material is of somewhat atypical material 3(60) which is considered separately below. Turesson has published values $2n = 101$ to 110 for Scandinavian plants. Interpretation of the meiotic figures of British material has been based on the assumption that this has approximately the same range of numbers.

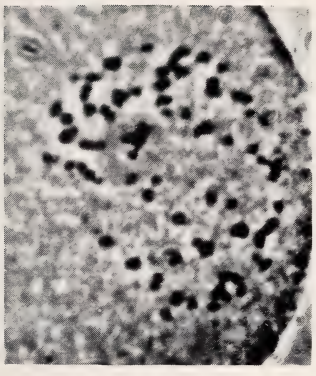
subsp. *filicaulis* 4/3/55a (Plate 14c). A fairly straight forward metaphase I with 20 II and 63 I giving $2n = 103$. Same plant (Fig. 1b) also a metaphase I plate with $2n = 103$: 18 II and 67 I. Although the number of bivalents varies the total number of chromosomes is $2n = 103$; it is of particular interest to know if the somatic count is the same, but a countable preparation was not obtained.

PLATE 14



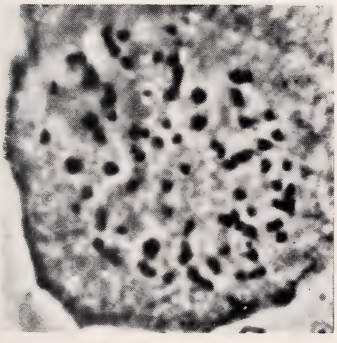
a





b





c



Chromosome plates and explanatory diagrams of *Alchemilla filicaulis, sensu lato*. (a) subsp. *vestita*, Teesdale (RT, $2n = 106 \pm 1$, $\times$ 1340); (b) subsp. *vestita*, E. Durham (PMC, $2n = c.$ 108, $\times$ 1310); (c) subsp. *filicaulis*, Weardale (PMC, $2n = c.$ 103, $\times$ 1020). Doubtful bivalents are marked ?b. For further explanation see text.

subsp. *filicaulis* 3(60)b (Fig. 1e). The presence of the nucleolus and indication of an outer membrane suggest that this is at diakinesis or maybe metaphase I. The diffuse nature of the chromatin bodies makes their interpretation as univalents or bivalents difficult and hence the total number uncertain. Two clusters A and B probably consist of a total of 6 or 7 chromosomes. Of the other bodies, if the larger are interpreted as bivalents, the probable values are 20 II and 117 I giving a total of 159; if all are considered as univalents the total is 144, one above and the other below the somatic value of $2n = c.\ 150$.

(*c*) *Cytology of subsp.* vestita.

The mean values obtained for lowland plants of subsp. *vestita* were :

Somatic counts $2n = 104, 105, 105, 106$.

Meiotic counts $2n = c.\ 108, c.\ 109$.

In spite of the closeness of the somatic numbers and the difficulty of getting exact counts, it is very probable that several chromosome numbers do occur in the species. Turesson (1957) obtained a range of numbers between 101 and 110 for several species of *A. vulgaris* agg. He gave $2n = 110$ for the only two plants of ssp. *vestita* which he examined.

A count was obtained for only one of the dwarf montane plants; this gave $2n = 105$, which is within the range of the lowland plants.

(*d*) *Cytology of subsp.* filicaulis

The only count obtained of a British lowland plant was from a pollen-mother-cell, $2n = c.\ 103$. Turesson (1957) found a range of numbers :

$2n$ =	102	103	104	105	106	107	108	109	110
No. of plants	2	6	1	7	5	1	3	4	2

This overlaps the range found in subsp. *vestita*.

Most interesting and surprising is the value $2n = 150$–152 obtained for a subsp. *filicaulis* plant, 3(60), which represents a Scottish mountain population. These plants have the usual subsp. *filicaulis* hair character and wine-red base, but the leaves have very short broad lobes and sharply pointed, somewhat connivent teeth, rather similar to *A. wichurae;* the leaves tend also to be more shiny and crisp than in other subsp. *filicaulis* plants. They could easily be recognised in the field from amongst plants of *A. vulgaris* agg. Whether or not this plant should be classified as subsp. *filicaulis* will be considered later.

The chromosome numbers obtained by Turesson (1957) and myself for subsp. *vestita* and subsp. *filicaulis* agree well and show no major differences in the cytology of the two taxa except in the case already mentioned. Both have a range of numbers which are similar to those found in several distinct morphological species in *A. vulgaris* agg. (Turesson 1957). The difference in hair density which separates subsp. *filicaulis* from subsp. *vestita* is not correlated with any constant difference in the chromosome numbers of these taxa.

So far no counts are available for the genodeme of intermediate hairiness.

(*e*) *Cytology of the ecogenodemes*

A chromosome count of one example of the dwarf montane ecogenodeme (Bradshaw 1963, p.) is clearly an insufficient basis for any conclusions on the correlation between chromosome numbers and ' ecotypic ' variation. If it is representative of the dwarf ecogenodeme then there would appear to be no major cytological differences between the ecogenodemes. Further data on the same kind of variation are provided by Turesson (1956). He worked with six species (but not *A. filicaulis*), and also found statistically significant differences in stem and petiole length and leaf size between genodemes. Later (1957) he published chromosome counts of many species but it is not clear if the numbers are those of the plants used in the earlier work or not. Turesson did not give the chromosome numbers of his morphological genodemes individually; neither is it known if the plants used in his experiment

all came from the same or different types of habitat. Turesson concluded ' Our Alchemillas apparently do not adapt themselves to different habitats by any change in chromosome numbers.' Difference in habitat is implied by the wide latitudinal range of the original samples. Only by obtaining exact counts of several plants of each genodeme will it be possible to determine if this kind of variation is correlated with differences in the chromosome numbers.

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BOOK REVIEW

A Handbook to Plants in Victoria. Vol. 1. *Ferns, Conifers and Monocotyledons.* J. H. Willis. Melbourne University Press, 1962. Price 45s. 0d. net.

With the steadily increasing interest of Australians in their native flora the provision of up-to-date Floras covering different parts of the country is becoming an urgent necessity. Floras of most of the States of the Commonwealth have been published in the past but the great majority of them are now out of date and out of print. This is true of Victoria, Ewart's Flora having appeared over 30 years ago. There is therefore a great need for a new Flora embodying the research carried out during these intervening years and correcting the errors in the previous account. The work here reviewed is designed to fill this gap. It will be published in two volumes, the first one of which deals with the Ferns, Gymnosperms and Monocotyledons. The Dicotyledons will occupy a second larger volume.

The present work is intended to be more of a pocket handbook for use in the field than Ewart's account. The author, who is a member of the staff at the Melbourne Herbarium, has an extensive knowledge of Victorian plants, both in the field and in the herbarium. He has also been able to examine many important historical specimens in this country while acting as liaison officer at the Royal Botanic Gardens, Kew. The Flora is in the form of a key, separate descriptions of the species being furnished only for species of genera which are monotypic in the State. In addition to synonymy, references to illustrations are included with each species and the distribution within Victoria and other parts of Australia is given.

Many British and European plants have been introduced into Australia, a large proportion of which have become quite naturalised, sometimes locally even replacing the native flora. The English botanist will encounter many old friends in the pages of this Flora; he will also find species which he has seen as introductions in this country but which are native in Australia, for example, *Juncus pallidus.*

Altogether Mr. Willis has provided a very useful book for the field worker in Victoria and adjacent parts of the neighbouring States, and its publication will no doubt stimulate further work on Victorian plants. It can be recommended to any plant lover visiting this State and wishing to name the plants which he encounters. The appearance of volume 2 will be looked forward to with interest.

V. S. Summerhayes

Flora of the British Isles

A. R. CLAPHAM, T. G. TUTIN & E. F. WARBURG

The first edition of the standard British Flora appeared in 1952, and has been reprinted several times. This new edition, largely rewritten and completely reset, embodies the results of research in the last eight years. Most of the larger keys have been modified for easier use, and accounts of introduced plants have been extensively altered. As the *Excursion Flora* (1959) now satisfies the need for a pocket edition, the page size has been increased. SECOND EDITION. 70*s. net*

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ELEOCHARIS AUSTRIACA HAYEK, A SPECIES NEW TO THE BRITISH ISLES

By S. M. Walters

Botany School, University of Cambridge

Abstract

Eleocharis austriaca Hayek, discovered in 1947 in Yorkshire by N. Y. Sandwith, but not identified until 1960, is described and illustrated. It is an easily recognised species of the *E. palustris* group, and is now known to be widespread mainly in the mountains of Continental Europe from the Pyrenees to the Urals, occurring also in Norway. Six British localities are now known, in vice-counties 64, 67 and 70. Some information is given on the habitat in three of these localities, all of which are by upland rivers.

The group of species to which the common *Eleocharis palustris* belongs presents some difficulties of identification, and the critical taxonomy of the European representatives of the *E. palustris* group needs further elucidation. It is not, therefore, surprising that one of these species has only recently been detected as a member of the British flora. This is *E. austriaca* Hayek, originally described from Central Europe, but now known to be quite widespread in the European mountains.

Material of *Eleocharis austriaca* was first collected in Britain by Mr. N. Y. Sandwith in July 1947 ' in a marshy ox-bow of the R. Wharfe below Buckden,' Upper Wharfedale, v.c. 64. Sandwith was obviously impressed by the differences between this plant and normal *E. palustris*, and submitted part of the material to me in 1948. At that time my own work on the European species allied to *E. palustris* was only just beginning, and I did not know *E. austriaca*; it was not until 1953 that I was able to publish a short paper on the species in question (Walters 1953). In 1960 I refound the sheet of Sandwith's original collection, and realised what the plant was. In the following season, Sandwith and others revisited the locality, and found the plant still growing there in some quantity. The detailed account of the plant, and the illustrations accompanying this description, are based upon fresh material from the original locality. I am most grateful to Mr. Sandwith for the material, and for notes on the habitat (Table 1a).

Very recently, during the preparation of this paper, Dr. G. A. Swan has found four new localities for *Eleocharis austriaca* in Northumberland (v.c. 67) and one in Cumberland (v.c. 70), and was good enough to show me one of these in the North Tyne Valley. Dr. Swan and Dr. M. E. Bradshaw have kindly supplied further information about the other North Tyne locality by the Kielder Burn, which they visited on the same day. (See Appendix and Table 1 for details of these localities.)

In habit, *Eleocharis austriaca* resembles the other British *Palustres* (i.e. *E. palustris* and *E. uniglumis*) in the possession of a vigorous rhizome system, from which arise leafless stems terminating in simple flowering spikes (Fig. 1A). The spikes (Fig. 1B) are characteristically compact and bluntly conical, however, contrasting with the typically longer, more cylindrical spikes of *E. palustris* or *E. uniglumis*. (The difference between *E. austriaca* and the rather rarer subsp. *microcarpa* of *E. palustris*, in respect of spike-size and -shape, and glume-size, is rather less than that between it and *E. palustris* subsp. *vulgaris*. As, however, subsp. *microcarpa* is not known in N. England, recognition of *E. austriaca* by general appearance is relatively easy.)*

* Strandhede (1960) considers that subsp. *microcarpa*, not subsp. *vulgaris*, must be the type subspecies, *i.e.*, *E. palustris* subsp. *palustris*, according to the current International Code of Botanical Nomenclature. To avoid confusion, I have here used the names as originally published (Walters 1949).

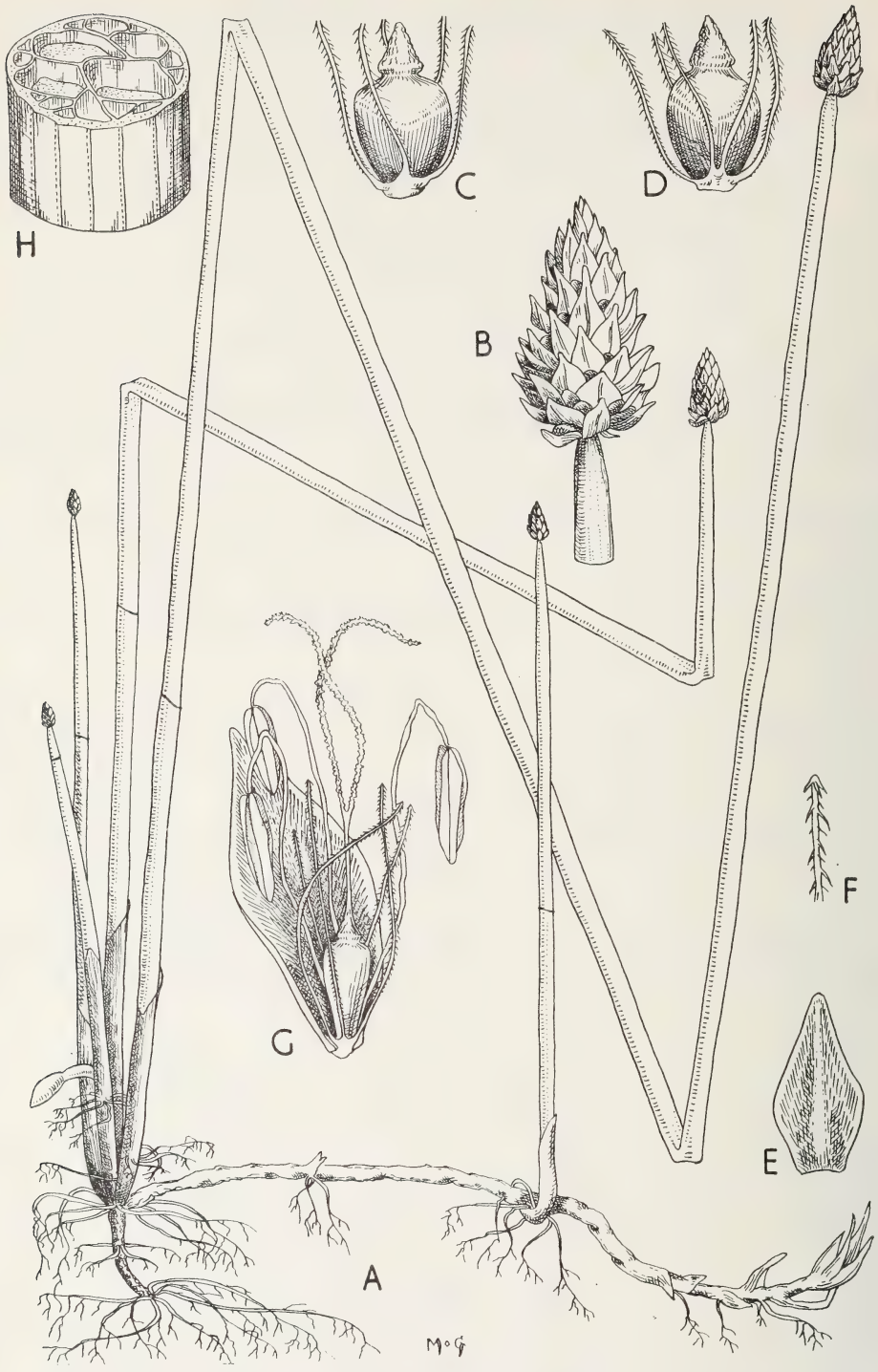


Fig. 1 *Eleocharis austriaca.*

A. Habit × 1 B. Fruiting Spike × 3 C, D. Fruit × 12 E. Glume × 6 F. Tip of bristle × 40
G. Single Flower × 14 H. Section of stem × 8

Two other characters which were rather obvious in the North Tyne population, but which may not apply generally, were the dark brown colour of the spikes, and the extremely high proportion of fertile stems borne rather close together on a relatively short rhizome. When the plant is dug up, another character is obvious – the absence or very poor development of the reddish-purple colour so characteristic of the base of the stem in both *E. palustris* and *E. uniglumis*. This colour character seems reliable on both British and Continental material, and can be used to some extent on dried specimens.

Field recognition of *Eleocharis austriaca* is therefore relatively easy – at least in Britain where, so far as we know, a fourth species, *E. mamillata*, does not occur. Detailed characters of the stem anatomy, and particularly of the ripe fruit, however, provide the precise qualitative differences by which the species can be certainly recognised.

The differences in stem anatomy can be described in several ways, but can perhaps be most easily shown by the epidermal pattern of strips of tissue (readily prepared by scraping off lightly the internal tissues from a strip of stem; Fig. 2A). There is a very obvious difference between *E. austriaca* and *E. palustris* (Fig. 2B) which can be described as follows. The vascular bundles, with which are associated the stomatal rows, are widely-spaced in *E. austriaca*, and much more closely packed in *E. palustris*. Between the stomatal rows can be seen the rows of elongated fibre-cells; in *E. austriaca* there are up to 5 rows of ordinary epidermal cells between these fibre-rows, whereas in *E. palustris* only 1–3 rows are found between the fibre-rows. These differences are clearly seen in Figs. 2A and B. (*E. uniglumis* resembles *E. palustris* in these characters, whilst the Scandinavian *E. mamillata* is closely similar to *E. austriaca* in all vegetative characters). These anatomical differences are responsible for a difference readily observable in fresh material, namely that *E. austriaca* stems (Fig. 1H) are weak and readily cracked, in contrast to the more pliant stems of *E. palustris*. In fresh material, and even more in dried specimens, it is relatively easy to count the number of vascular bundles; stems of *E. austriaca* have 10–16 main bundles, which show as ridges in dried material, whilst those of *E. palustris* have 20 or more, which are far less conspicuous in the dried state.

The ripe fruit of *E. austriaca* differs from that of *E. palustris* in two main features. Firstly, the perianth-bristles are rather well-developed, always exceeding the fruit, and they are often 5 in number, by the bifurcation of the abaxial bristle (Figs. 1C and D, 2C). In contrast, the bristles of *E. palustris* are not infrequently relatively short and always 4 in number (Fig. 2B). In practice, this means that if three or four ripe fruits of the two species are examined, at least one of the *austriaca* fruits will be found to have either a divided bristle or a pair in the abaxial position. Secondly, the style-base is typically long and narrow, with only a small constriction at the junction with the nut. This contrasts with the more broadly triangular style-base, typical of *E. palustris*. There is, however, a good deal of variation in style-base shape, and the character cannot be used reliably on single fruits. Its value is greater in distinguishing *E. austriaca* from *E. mamillata*, which has the low broad style-base indicated by the name. The differences between *E. austriaca* and *E. mamillata* in style-base and in other characters are discussed and illustrated by Walters (1953) and Strandhede (1962).

The European distribution of *E. austriaca* is as yet very incompletely known, but it seems to occur mainly by mountain lakes and streams from the Pyrenees to the Urals; in Scandinavia, where *E. mamillata* is widespread, *E. austriaca* seems to be rare (Strandhede 1962). Its occurrence in N. England therefore fits well with the distribution of species such as *Primula farinosa*, a widespread European mountain plant not occurring in the Arctic. A complete list of localities is given in Appendix B.

There is a general similarity between all the British habitats of *E. austriaca*. All the habitats are relatively impermanent ones by rivers, and the plant seems to form vigorous stands where there is rather open alluvial gravel or sand.

The Wharfedale locality was re-visited by Mr. N. Y. Sandwith on 9 July, 1961, when the species-list (a) in Table 1 was compiled. The plant is growing in an old ox-bow of

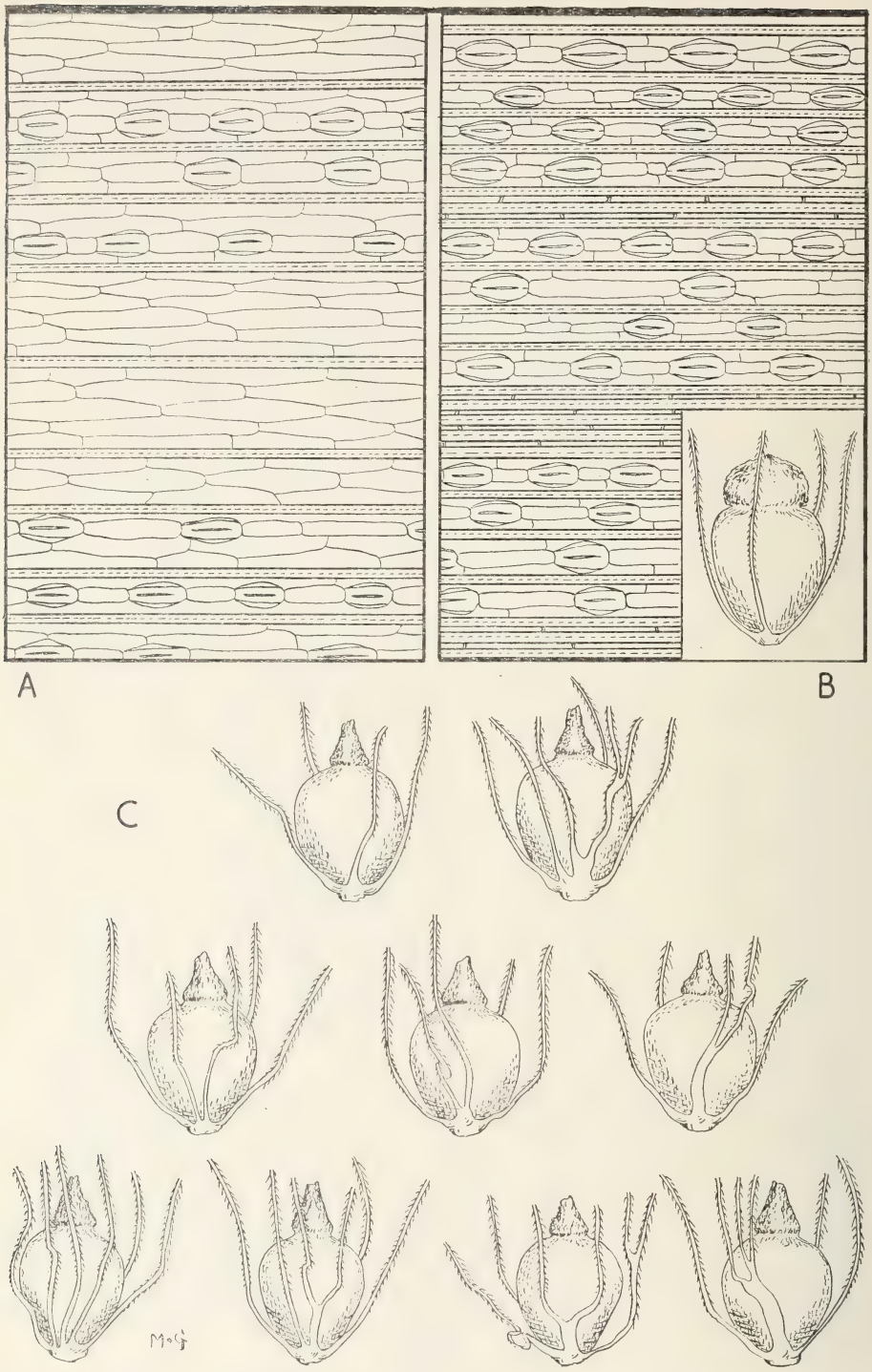


Fig. 2

A. *Eleocharis austriaca*: Epidermis of stem × 100

B. *Eleocharis palustris* subsp. *microcarpa*: Epidermis of stem × 150 and (inset) fruit × 12 (Material from Aldenham Reservoir, Herts, v.c. 20, coll. M. A. Grierson, 1961 (K)).

C. Fruits of *E. austriaca*, showing range of bristle-number and -form, × 12

the River Wharfe, rooted in silty mud. A sample of the mud gave on analysis 33·1% of organic matter, and a pH of 6·8.

TABLE 1.

Localities of *E. austriaca*—lists of associated species

	(*a*)	(*b*)	(*c*)		(*a*)	(*b*)	(*c*)
Achillea millefolium			+	Leontodon autumnalis		+	+
A. ptarmica			+	Linum catharticum			+
Agrostis stolonifera	+	+	+	Lotus corniculatus			+
Alnus glutinosa	+		+*	Lysimachia nemorum			+
Angelica sylvestris			+	Mentha aquatica	+		
Anthoxanthum odoratum			+	Myosotis caespitosa			+
Bellis perennis			+	M. scorpioides	+		
Callitriche sp.	+			Parnassia palustris			+
Caltha palustris	+		+	Pedicularis palustris			+
Cardamine flexuosa			+	Phalaris arundinacea	+		
C. pratensis	+			Plantago lanceolata		+	
Carex demissa			+	P. major		+	
Centaurea nigra			+	Poa trivialis			+
Cynosurus cristatus			+	Potamogeton natans	+		
Deschampsia cespitosa			+	P. polygonifolius			+
Eleocharis palustris	+			Potentilla anserina		+	
Epilobium palustre			+	Prunella vulgaris		+	+
E. nerterioides			+	Ranunculus flammula	+	+	+
Equisetum arvense		+	+	R. repens	+	+	+
E. fluviatile			+	Rhinanthus minor *sens lat.*			+
Euphrasia brevipila		+		Rumex obtusifolius		+	
E. nemorosa			+	Sagina procumbens			+
Festuca arundinacea		+	+	Salix sp.*			+
Filipendula ulmaria	+		+	S. triandra	+		
Galium palustre	+	+	+	S. viminalis	+		
Galium uliginosum			+	Sparganium erectum	+		
Glyceria fluitans	+			Succisa pratensis			+
Holcus lanatus			+	Trifolium pratense			+
Juncus acutiflorus		+	+	T. repens			+
J. articulatus		+	+	Triglochin palustris			+
J. bufonius			+	Tussilago farfara		+	+
J. effusus	+	+	+	Veronica beccabunga	+	+	+
Lathyrus pratensis			+	V. chamaedrys			+

(*a*) Original locality in Wharfedale, 9 July, 1961
(*b*) North Tyne near Otterstone Lee, 23 Aug. 1962
(*c*) Kielder Burn, 23 Aug. 1962
* Seedlings.

The locality in the North Tyne Valley near Otterstone Lee, discovered by Dr. G. A. Swan, was shown by him to Dr. M. E. Bradshaw and myself on 23 August, 1962. It is very similar to the Wharfedale habitat; the plant is growing in a silted backwater by the side of the river, in a community containing six species common to both localities (see Table 1b). A sample of the mud from the rhizomes of the plant here showed an organic content of 6% and a pH of 7·1. Dr. Swan and Dr. Bradshaw visited the Kielder Burn locality on the same day, and furnished a description and species list (Table 1c). Here *Eleocharis austriaca* grows in a gravelly and silty backwater by the stream in an open community with much bare gravel. The soil sample gave a very low organic content (2·7%) and a pH of 7·0.

The significant difference in organic content between the Wharfedale locality and the other two emphasises the only obvious difference, namely that the Northumberland habitats were less stable and more obviously subject to flooding. One could, however, reasonably assume that there had been an earlier seral stage in the Wharfedale habitat, before the ox-bow was cut off from the parent river at its upstream end, when the community would have been much more open.

Detailed information on Continental habitats of *E. austriaca* for comparison with these British ones is not yet available, but Strandhede (1962) indicates that the Norwegian

localities by upland rivers, at any rate, are very similar, and also points out that *E. austriaca* differs in its ecological requirements from the closely similar *E. mamillata*, which is characteristic of peaty ground, often of acid reaction. Some Continental habitats are by upland lakes (*e.g.* the *locus classicus* of *E. benedicta*, *cf.* Appendix); it would be interesting to have further information about such localities.

I am greatly indebted to Miss M. A. Grierson, of the Herbarium, Royal Botanic Gardens, Kew, for the line-drawings reproduced in Figs. 1 and 2, and to Mr. P. Freeman, of the Botany School, Cambridge, for the soil analyses.

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Zinserling, G. (1935). in V. L. Komarov (ed.) *Flora U.R.S.S.* **3,** 75–6 and 581.

Appendix

A. *Nomenclature and Synonymy*

Eleocharis austriaca Hayek, *Flora Stiriaca Exsiccata*, Lieferung 19/20 (1910).

E. benedicta Beauverd, *Bull. Soc. Bot. Genève*, *sér. II* (2) **13**, 245 (1921).

E. leptostylopodiata G. Zinserling in Komarov (ed.), *Flora U.R.S.S.* **3** (Addenda), 581 (1935).

B. *List of Localities*

(i) *Britain*

V.c. 64, Mid-West Yorks: marshy ox-bow of the R. Wharfe below Buckden (Grid ref. 34/945760), N.Y. Sandwith, July 1947 (ref. no. 3185); July 1961 (ref. no. 5906).

V.c. 67, S. Northumberland: by R. Rede near Byrness (Grid ref. 36/770022) 22 July 1962; by R. North Tyne near Otterstone Lee (Grid ref. 35/670879) 6 Aug. 1962 (see details on p. 333); by Kielder Burn (Grid ref. 35/651957) 6 Aug. 1962 (see details on p. 333); in silted-up pond by R. North Tyne near Plashetts (Grid ref. 35/664897) 29 Sept. 1962.

V.c. 70, Cumberland: by R. Irthing near Gowk Banks (Grid ref. 35/682737) 16 Sept. 1962.

(Localities in V.c.'s 67 and 70 were discovered by G. A. and M. Swan).

(ii) *Continental Europe*

Austria

Steiermark: ' Stiria media in stagno exsiccato ad pagum St. Peter prope urbem Graz, 370 m. Juni 1906, K. Fritsch,' lectotype in (**H**); *cf.* Walters (1953) p. 284).

Tirol: ' in paludibus prope Lienz (?) Pichler, Juni 1865 ' (mixed sheet with *E. palustris*) **(BM).**

Czechoslovakia

Beskydy and Tatra (Holub, 1960).

France

Haute-Savoie: Plage du lac Bénit, 1580 m, massif des Vergys, 15 Aug. 1922, G. Beauverd, Ch. Duffour Exsicc. 4277 (*E. benedicta* Beauv., type locality) (**G**); Servoz, Lac Vert, 3 Sept 1934, M. E. Edmonds No. 9 (**K**); Chalets de Méri, 1910, de Palézieux (**G**).

Jura: Bords du lac des Rousses 17 July 1869, Herb. Manceau (**P**).

Hautes-Pyrénées: Vallée supérieure du lac de Gaube, 31 Aug. 1836, E. Doassans (as *E. uniglumis*) (**K**); Cautarets, le Cayan—alt. 1630 m, fin août, Mouillard, Ch. Duffour Exsicc. 1104 (**P**).

Germany

Several localities are given for Bavaria by Podlech (1960) (**M**).

ITALY

Prov. Belluno: Shore of Lago Alleghe, Caprile, 29 Aug. 1862, Herb. Churchill (K).

JUGOSLAVIA

Flora Bosnae: ' ad Koran prope Pale,' (near Sarajevo), *c.* 860 m, 21 July 1929, leg. Maly (K).

NORWAY

Three localities (2 in Saltdal, Norrland, and one in Sör Tröndelag) are given by Strandhede (1962).

POLAND

Three localities in the Tatra (W. Carpathians) (KRA) (Walters 1959).

SWITZERLAND

Apparently widespread; add to the 27 Swiss localities listed in Walters (1953) (mostly in ZT):
Fribourg: Commune de Charmey, rive du lac de Montsalvans, 803 m, 19 July 1849, H. Brunner, Soc. Franc. Éch. Pl. Vasc. Exsicc, B. de Retz, fasc. 3, No. 819 (K),
Engadine: Près Bevers 7. 1867. L. Favrat & W. Barbey (K).

U.S.S.R.

The distribution given by Zinserling in Komarov (1935) for *Heleocharis leptostylopodiata* is European Russia to Middle Volga region, Ural Mountains and adjacent territories, Siberia (Kusnetskij Alatau), Amur region and the Caucasus. The disjunct nature of the distribution is stressed. The type material (LE) is from ' Baschkiria, Canton Zalaia,' and is in excellent fruiting condition. There can be no doubt as to the identity of Zinserling's species with *E. austriaca*.

In their account of *Heleocharis* in *Flora R.S.S. Ucr.* (1940), Krečetovič & Zoz do not give the species from the Ukraine. It does, however, grow within the present boundaries of the Ukraine, as I have seen the following specimen:

Orelac, near Šniatyn, on R. Prut (Podolia, W. Ukraine) 17 Sept. 1880. A. Sleňdiňski (KRA).

[The Herbaria in which material is to be seen are indicated by the standard abbreviations as given in ed. 4 of *Index Herbariorum* (*Regnum Vegetabile* **15**, 1959). I am grateful to the authorities in these institutions for facilities to consult and borrow material.]

VARIATION IN *MELAMPYRUM PRATENSE* L.

By A. J. E. Smith

*Department of Botany, University College, Swansea**

Abstract

Melampyrum pratense is morphologically extremely variable in Britain and this variability has been found to occur at three levels. There is geographical variation brought about by climatic selection from a basic pattern. Superimposed upon this geographical variation is ecological variation caused by selection in different habitats. The third level of variation is brought about by the random isolation of particular genotypes in individual populations leading to minor but detectable differences between populations in similar ecological habitats.

It was found that there are two morphologically separable groups within *M. pratense* which differ also ecologically in Great Britain and these have been given subspecific rank: subsp. *commutatum* is restricted to base-rich habitats in southern England; the remaining British populations belong to subsp. *pratense*.

Introduction

Melampyrum pratense is an annual hemiparasitic member of the subfamily Rhinanthoideae of the Scrophulariaceae. The plant is found throughout most of Great Britain and Ireland, and in Britain usually occurs as small isolated populations of up to about two hundred plants. In this account only British plants are dealt with, as insufficient material from Ireland was seen.

Parasitology

Melampyrum pratense, in common with other members of the Rhinanthoideae, parasitises host plants by means of root haustoria. This parasitic habit appears first to have been noted by Decaisne (1847) and the nature of the parasitic attachment has been studied in considerable detail by subsequent authors.

Little is known of the physiology of the parasitism of the Rhinanthoideae but from field observations of *M. pratense* it is possible to suggest what some of these physiological requirements might be. In Britain, the seeds of *M. pratense* germinate about December and develop an extensive root system, but little vegetative growth takes place beyond the production of cotyledons until March. If the roots become attached to a suitable host during this period rapid growth commences towards the end of March and flowering begins within six to eight weeks. If no contact with a host is made the cotyledons expand and two or three pairs of very diminutive stem leaves are produced, after which growth ceases. During May and June these undeveloped plants gradually wither away. Plants of *M. pratense* do not appear to be able to parasitise one another, unlike species of *Euphrasia* (Yeo 1961).

Plants of *M. pratense* are able to thrive on soils which are exceedingly low in nutrients. Growth of other vascular plants in such habitats is extremely slow in comparison with *M. pratense* which reaches its full size in a matter of a few weeks. It seems that this can only be by the acquisition of nutrients from the host plants and it is evident that, in nutrient-deficient habitats at least, the species obtains a considerable proportion of its nutrients from the host.

It has been suggested by J. L. Harper (personal communication) that the requirement is for growth substances and that these are responsible for the rapid burst of growth mentioned above. It is difficult to conceive of this occurring without the acquisition of nutrients

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from a host, particularly on poor soils, so that whilst it may be possible that growth substances are necessary, these are not the sole requirement.

The ability to parasitise also appears to be important in connection with water relations. During a dry period in the summer of 1959 a perfectly healthy population of *M. pratense* was seen in a wood on Keston Common, Kent, in which other herbaceous plants were dead or severely wilted. In this locality *Melampyrum* was presumably growing on the roots of tree species. A similar situation was noted in an experimental plot at Oxford when, after a period of drought during which weeds were dead or dying, young plants of *M. pratense* parasitic on *Betula* and *Calluna* were growing vigorously. *M. pratense* is a shallow rooted species but is evidently able to obtain a fully adequate water supply from the host species and is thus independent of soil water.

Host plants

It is frequently assumed that *M. pratense* parasitises herbaceous plants but all the evidence suggests that the hosts are woody plants. Although it is rare for populations to occur without any associated herbaceous species, *M. pratense* is never found away from trees or shrubs and, in parts of northern Britain where large woody plants are absent, it is associated with *Calluna*, *Erica*, *Myrica* or combinations of the three.

It is extremely difficult in the field to trace root connections and it has not been possible to determine whether *M. pratense* parasitises herbaceous plants, but from the fact that it never occurs solely with these plants, this is unlikely. In several populations examined, connections have been traced between *M. pratense* roots and those of *Quercus robur*, *Corylus avellana* and *Betula pubescens*. In cultivation experiments the plant has been successfully grown on *Betula pubescens*, *Calluna vulgaris* and *Rubus fruticosus*, but not on herbaceous plants. From field observations it is clear that *Fagus sylvatica*, *Sorbus aucuparia*, *Quercus petraea*, *Vaccinium myrtillus*, *V. oxycoccus*, *Erica tetralix* and *Myrica gale* are also host plants.

Whilst it is evident that *M. pratense* can parasitise a number of woody species—it is not clear whether particular populations are host-specific. Bog populations in northern Scotland do not spread to neighbouring birch woods where the plant might be expected to grow. In the New Forest, Hampshire, it is always associated with trees, although in certain other parts of the country it grows on *Calluna*, *Erica* or *Myrica*, all three of which occur in the New Forest.

Ecology

M. pratense shows considerable ecological diversity and populations from different types of habitats tend to be morphologically different. The three main types of habitat in Britain are (i) calcareous scrub and woodland, (ii) acid woodlands and (iii) bogs. These habitats are subdivisible as follows:

(i) *A.* chalk and limestone habitats.
(ii) *B.* acid woodland in the New Forest, Hampshire.
C. other acid woodland habitats in southern England (neogenic region).
D. acid woodland habitats in south-west England (palaeogenic region)
E. acid woodland habitats in northern England
F. acid woodland habitats in Scotland
(iii) *G.* bogs in northern Scotland
H. bogs in northern England

The most commonly associated species in each habitat are listed in Table 1. Those of types *E* and *F* are so similar that they are listed together. The acid woodland habitats were grouped into four types because of geographical differences and likewise the two bog types. Neogenic and palaeogenic regions of southern England were considered separately as it was thought that plants from these areas of different origin might differ morphologically.

TABLE 1. Commonly associated species from the different ecological types

Ecological type	A	B	C	D	E & F	G	H
Acer campestre	+	—	—	—	—	—	—
Anthoxanthum odoratum	—	—	—	—	+	—	—
Betula spp.	—	—	+	+	+	—	—
Calluna vulgaris	—	—	—	—	—	+	—
Corylus avellana	+	—	+	—	—	—	—
Crataegus monogyna	+	—	+	—	—	—	—
Deschampsia flexuosa	—	—	—	—	+	—	—
Drosera spp.	—	—	—	—	—	+	—
Erica tetralix	—	—	—	—	—	+	+
Eriophorum spp.	—	—	—	—	—	+	+
Hedera helix	+	+	—	—	—	—	—
Holcus lanatus	—	—	+	—	—	—	—
Ilex aquifolium	—	+	+	+	—	—	—
Myrica gale	—	—	—	—	—	+	+
Molina caerulea	—	—	—	—	—	+	—
Narthecium ossifragum	—	—	—	—	—	+	—
Potentilla erecta	—	—	—	—	+	+	—
Potentilla palustris	—	—	—	—	—	—	+
Pteridium aquilinum	—	+	+	+	+	—	—
Quercus robur	+	+	+	+	+	—	—
Quercus petraea	—	+	—	—	—	—	—
Rubus fruticosus	+	+	+	—	—	—	—
Solidago virgaurea	—	+	—	—	—	—	—
Teucrium scorodonia	—	+	—	—	—	—	—
Thelycrania sanguinea	+	—	—	—	—	—	—
Trichophorum caespitosum	—	—	—	—	—	+	—
Vaccinium myrtillus	—	+	—	+	+	—	—
Vaccinium oxycoccus	—	—	—	—	—	—	+
Viburnum lantana	+	—	—	—	—	—	—

In southern England, populations occupy two very different habitats; chalky or limestone soils with a pH of 6·8 or more, and acidic soils with pH values of up to about 5·5.

On the chalk of Kent, Surrey, Hampshire and Oxfordshire, *M. pratense* usually occurs on the edge of scrub and chalk grassland or as a hedgerow plant. Populations of *M. pratense* are also found in similar habitats on the oolitic limestone of the Cotswolds and the carboniferous limestone of the Wye Valley and associated species are much the same.

On acid soils in southern England *M. pratense* usually occurs at the edges of rides, paths or roads through woods, or in clearings, and in common with populations from calcareous habitats only thrives in light shade or in the open. Where shading becomes heavy the number and vigour of the plants is reduced.

Populations from woodland in the New Forest are quite characteristic in appearance and differ very much from other southern forms but are sometimes indistinguishable from plants from Scottish bogs. They differ from these, however, in always being associated with trees. As will be mentioned later, the New Forest populations of *M. pratense* form a disjunct feature in an otherwise more or less continuous picture of variation in southern England.

In south-west England and Wales *M. pratense* grows in habitats very similar to the acidic woodlands of southern England but populations also occur on shallow soils and on steep and often rocky banks. This type of habitat is the one most commonly found in northern England and parts of Scotland and plants from such habitats are morphologically similar. As *M. pratense* is an annual it is clear that in these places where the soil is so shallow and nutrient-deficient the ability to thrive is closely correlated with the parasitic habit.

All the habitats so far described are usually well drained, but there are two types of habitat where this is not so. These are blanket bogs in northern Scotland and bogs or mosses in northern England. In Ross, Sutherland and Caithness *M. pratense* was found growing in considerable quantity in boggy flushes and waterlogged peat.

In the only two known bog habitats visited in England, at Wybunbury Moss, Cheshire, and Brigham Moss, Cumberland, the associated species differ somewhat from the Scottish bogs and the plants of *M. pratense* are rooted in *Sphagnum* rather than in peat.

From an investigation of *M. pratense* in the field the following points were apparent:

(i) Plants from ecologically different habitats are frequently morphologically distinct.

(ii) Plants from habitats with a low nutrient status are generally smaller than those from richer soils.

(iii) The host plants from various habitats are not necessarily the same.

From these points two questions arise. First, whether morphological differences are phenotypic or genotypic, and secondly, whether the apparently different morphological races are host-specific. A series of cultivation experiments were carried out in an attempt to answer these questions.

Cultivation experiments

Although up to 50% of the seeds sown (with or without a host) germinated, only about 0·5% reached maturity and because of this the value of the results obtained from the cultivation experiments was much reduced.

Samples, each of twenty seeds all from one population, were sown in pots with forty-three of the most commonly associated species, but only two plants matured, one on *Betula pubescens* and one on *Rubus fruticosus*, and it was not possible to come to any conclusion concerning host range.

In another experiment seeds were collected from seventy-five wild populations as follows:—

Acid woods	50 samples
Scottish bogs	15 samples
Calcareous habitats	9 samples
Wybunbury Moss, Cheshire	1 sample

Twenty seeds were sown from each sample under the following conditions:

(i) Acid ground (pH 4·5) with *Betula pubescens* as host in a forestry nursery bed at Bagley Wood, Berkshire.

(ii) As (i) but with *Calluna vulgaris* as host.

(iii) Calcareous ground (pH 8–8·2) with *Betula pubescens* as host at the Botany School, Oxford.

Of the seeds sown on *Betula pubescens* one or more plants from five samples reached maturity as follows:

Four plants of sample 90 from an acid woodland from which *Betula pubescens* was absent. Although the soil in Bagley Wood was much richer than that from which the seed had been collected, morphologically the plants were indistinguishable from the wild population.

One plant from sample 80 and two from sample 84, both from Scottish bogs. Again *Betula pubescens* was not present in the original locality, and soil conditions were very different. The plants were morphologically indistinguishable from those of the populations from which the seeds were collected, apart from the plant from sample 80 which was shorter.

Two plants from sample 100 and one from 103, both from calcareous habitats. The plants from sample 100 were very stunted and died as soon as flowering started, but the plant from sample 103 was normal although growing in acid soil.

Only three of the seeds sown on *Calluna* reached maturity. Two of these came from and were indistinguishable from the sample collected from Wybunbury Moss, Cheshire, despite the very different habitat.

The other plant was from sample 107 and grew perfectly satisfactorily on *Calluna vulgaris* which was absent from the original calcareous habitat.

It is evident from these experiments that whilst seeds of *M. pratense* germinate freely,

even in the absence of a host, establishment on a host appears difficult. In a wild population examined near Oxford in May, a number of undeveloped seedlings like those described previously were found, although not in the great proportions (about 99%) found in cultivation. It is evident that the plant is difficult to grow successfully but the reasons for this are not apparent as plants that did grow had come from a variety of very different habitats.

Although the cultivation experiments were not successful as a whole, certain conclusions can be drawn from them in combination with field observations.

M. pratense does not necessarily appear to be host-specific beyond being confined to woody species. That there is a lack of specificity for any particular woody species, in some populations at least, is shown by the ability to grow on *Betula* or on *Calluna* when not previously associated with these species. However, as mentioned earlier, *M. pratense* does not appear to be able to spread from one habitat with certain associated woody species to a neighbouring habitat in which different species are present.

Plants grown in cultivation under very different conditions from those appertaining in the wild did not differ morphologically (with the exception of height in sample 80 and the stunted plants of sample 100) from the populations from which they originally came. It would seem, therefore, that for these populations at least, population differences are genotypic rather than phenotypic.

Morphological characters

A large number of morphological characters have been used by previous authors for the discrimination of various subspecific taxa. Attempts to name forms using descriptions of Ronniger (1914), Beauverd (1916), Soó (1928), Britton (1943) and Jasiewicz (1958) frequently failed, either because of the inadequacy of the descriptions, or because the plants in question did not fit any prescribed taxon. Many of the taxa are based on different numbers of parts or ranges of size and when a large number of specimens are examined it is often found that variation in the particular characters is continuous. Some of the subspecies and varieties are based on minor morphological variants and two or more can often be found in the same population.

The most recent account dealing with British forms is that of Britton (1943) in which some eleven subspecies, seventeen varieties and ten forms of *M. pratense* are described.

From examination of herbarium material it was evident that morphological variation in *M. pratense* is to some extent correlated with geographical distribution and, in order to investigate this further, 140 random samples of 25 plants each were collected from four main areas of Britain (southern and northern England, and central and northern Scotland). These areas were selected as being those in which the species is most abundant.

On attempting to group the populations objectively by eye it was found that there were several morphological groups, linked by intermediates which had an ecological basis. It was also clear that the ecological groups corresponded with those described earlier. Similar results were obtained using scatter diagrams. As it was not possible to separate all the samples into discrete groups, either by eye or by the use of diagrammatic methods, it was decided to classify populations on the basis of geographical distribution and habitat in order to analyse the variability biometrically.

The characters selected for examination are listed below and were selected either because they had been regarded as important by previous authors or because they were considered to be amenable to statistical analysis.

1. Length of hypocotyl.
2. Height.
3. Number of sterile nodes and total number of nodes
4. Number of pairs of cauline and intercalary leaves.
5. Branching habit.

6. Number of sterile and fertile branches.
7. Presence or absence of cotyledons at maturity.
8. Shape and size of cauline leaves.
9. Number of pairs of entire and toothed bracts.
10. Degree of toothing of bracts.
11. Calyx length.
12. Corolla length and colour.
13. Anther and anther-appendage length.
14. Pollen size.

For conciseness the ecological types are referred as *A*, *B*, *C*, etc., as described on page 337. Type *H* has been omitted as there were only two samples of this type.

Statistical analysis of morphological characters

A biometric analysis of certain of the listed characters was carried out to obtain comparative information on the morphology and also on the degree of genetic variability in the different ecological types and to see if any of the morphological differences were of taxonomic significance. Twelve selected populations were also compared. Seven of these populations were from bogs in Sutherland and five from chalk habitats in Kent. These were selected in order to compare two groups of populations differing widely ecologically and geographically from the point of view of morphology and genetical variability.

Morphological differences and genetic variability in plant populations can be investigated by means of analyses of variance of means and standard deviations. The method used for *M. pratense* was based on that described by Day & Fisher (1937) for the analysis of populations of *Plantago maritima*.

In the analysis of genetic variability it is necessary to make an allowance for the wide diversity of some of the mean values (Day & Fisher 1937), e.g. mean heights vary from about 6 to 37 cm. Differences in means might be expected to be accompanied by similar differences in the standard deviations. If this were so, analysis of variance of the standard deviations would supply little further information than the analysis of the means.

It is possible to compare variabilities by dividing the standard deviation by the mean and obtaining a ' coefficient of variation.' This method would be satisfactory if an increase in the mean carried with it a proportional increase in the standard deviation. In biological material this is not always so (Day & Fisher 1937).

To eliminate the effect of widely differing means when comparing variabilities, an analysis of covariance of the means and the standard deviations of the populations must be carried out.

An analysis of covariance of means and standard deviations was carried out on characters 2, 8, 11, 12 and 13 and an analysis of variance on 3, 4, 9 and 10.

Where differences among types or populations are significant, the least significant difference is estimated using the Student-Newman-Keuls' test (Steel & Torrie 1960). This method is used because the estimation of the least significant difference using the usual *t*-test is suitable only for independent comparisons involving two means. When more than two means are compared the comparisons are non-independent and the *t*-test is not a truly valid criterion. The Student-Newman-Keuls' procedure takes into account the number of means.

As the number of populations from each ecological type was not equal (numbers varying from six to twenty), the least significant difference was estimated using the following formula:

$$q\ \alpha(p,n)\ s\ /\ \tfrac{1}{2}\left(\frac{1}{r_i}+\frac{1}{r_j}\right)$$

where q α is a value read from a table (Table A8, Steele & Torrie 1960) and

p = number of means
n = number of degrees of freedom of the error variance
α = 5% or 1% level of significance
s = error variance
r_i, r_j = number of observations in means for desired comparison.

Tables 2, 3, 4 and 5 show the significant differences between means and variabilities of the ecological types and selected populations.

Taxonomic value of morphological characters

(i) *Length of hypocotyl*

Hypocotyl length was not treated statistically as from field observations it was clear that length varies very much with density of surrounding vegetation. Length also varies with the depth of burial of the seed and this is important in view of the seeds being dispersed by ants. Although hypocotyl length has been used by Britton (1943) as a taxonomic character it cannot be regarded as having any value.

(ii) *Height*

All measurements of height refer to the length of the main axis from the cotyledonary node to the stem apex. Total height is unsatisfactory because of the variable length of the hypocotyl. Height decreases markedly northwards (Fig. 1), but as can be seen from

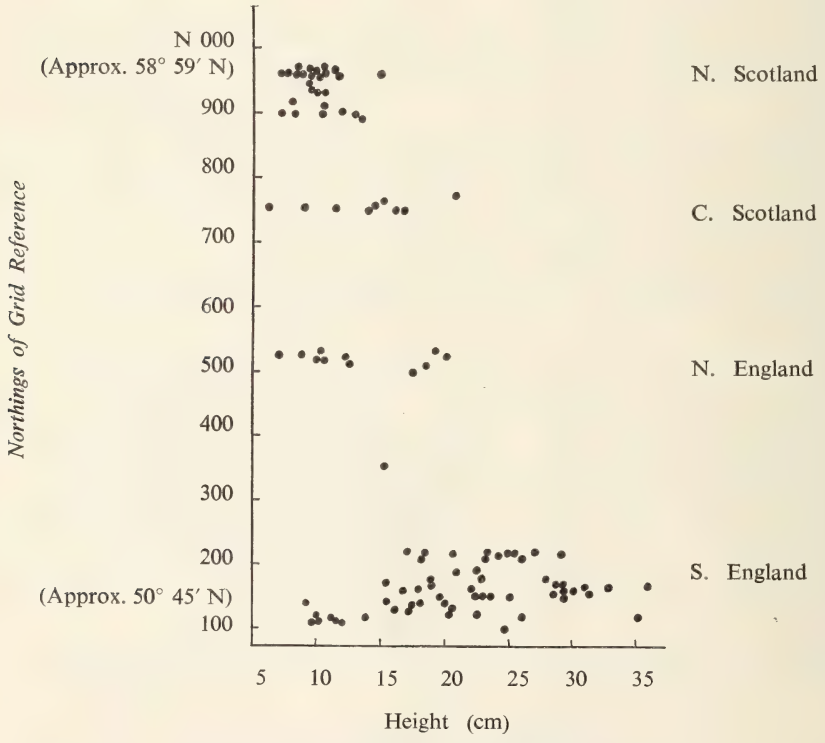


Fig. 1. Geographical scatter diagram of height showing diminution of height of populations northwards.

Fig. 2, variation is almost continuous so that there are no clear groupings based on height alone, although in combination with characters such as leaf shape, ecological types *A* and *G* form two groups only partially merging with other populations. Height has been widely used in the delimitation of subspecies and varieties but its unsuitability is seen from the description of the subsp. *vulgatum* (Pers.) Ronn. in which height is said to vary from 10 to 50 cm. This covers almost the whole range of heights of all other forms of *M. pratense*.

(iii) and (iv) *Number of nodes and sterile nodes on the main axis and pairs of cauline and intercalary leaves*

These characters are taken together because the sum of pairs of cauline and intercalary leaves is equal to the number of sterile nodes. Considerable importance has been attached by previous authors to the node at which the inflorescence commences (*i.e.* sterile

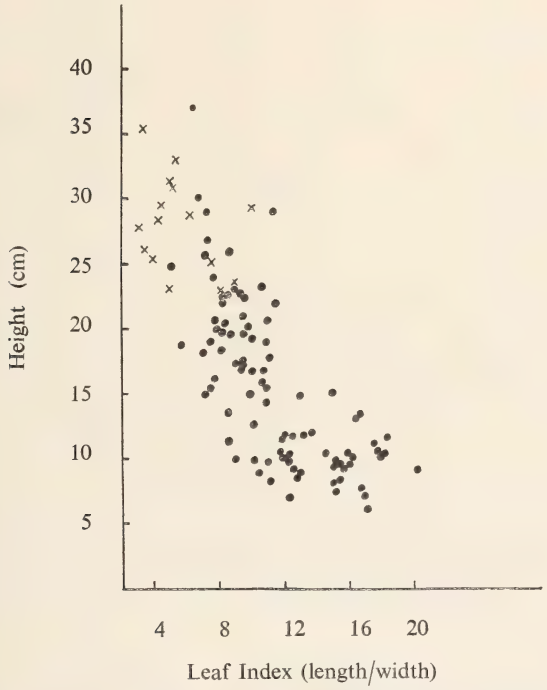


Fig. 2. Height plotted against leaf index. Crosses, populations from calcareous habitats; solid dots, all other populations.

node number plus one) and the relative numbers of cauline and intercalary leaves. Cauline leaves are those leaves with axillary branches, and intercalary leaves the leaves without axillary branches between the cauline leaves and bracts.

It is not always possible to distinguish between intercalary leaves and bracts as the lowest flower buds, in the axils of untoothed bracts, sometimes abort and fall off, especially if the plant is growing in deep shade. Further, in old plants dehisced fruits are also lost so that the number of intercalary leaves is not a satisfactory character. It is of interest to note, however, that populations of type *A* and type *G* do not differ significantly with

regard to intercalary leaf number but differ from all other populations. As type *A* is found in southern England and type *G* in northern Scotland, this upsets the south-north geographical cline in this character (see Fig. 3.).

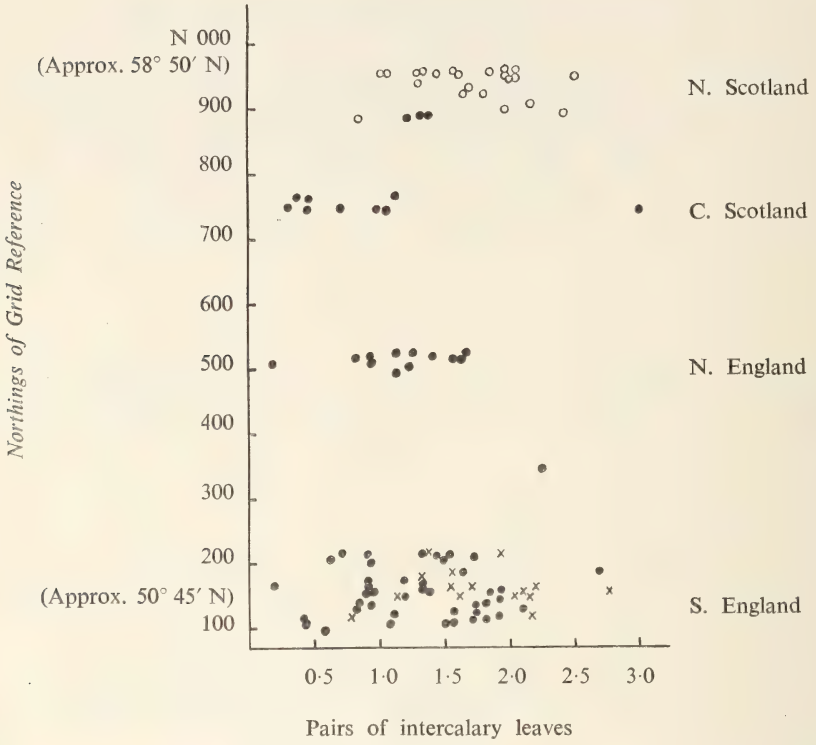


Fig. 3. Geographical scatter diagram of number of pairs of intercalary leaves showing similarity of northern bog populations (open circles) and populations from calcareous habitats (crosses).

Britton (1943) separates six of his subspecies into two groups on the basis of cauline leaf number and the position of the inflorescence. Four subspecies are defined as having one pair of cauline leaves and the inflorescence commencing at nodes 2-3-(4). The other two are said to have 1–3 pairs of cauline leaves and the inflorescence commencing at nodes 4–5. Identification of forms so described is frequently impossible as there is considerable variation in the number of sterile nodes, cauline and intercalary leaves both within and between populations. There appears to be no correlation between number of parts and habitat in Britton's taxa and hence these taxa appear to be of little significance.

(v) *Branching habit*

The angle of branching varies from horizontal to almost vertical and from cultivation experiments appears to be genetically controlled. The character was not analysed for two

reasons. Firstly, in pressed specimens the branches were distorted. Secondly populations where the main axis was prostrate had branches which were likewise horizontal but rose vertically at the tips and these were difficult to compare with other populations. The character might have proved of interest if analysed in the field.

(vi) *Number of sterile and fertile branches*

Although this character has been used taxonomically it is of little use, as the proportion of sterile to fertile branches decreases with age and unless all populations are sampled at the same time comparisons are not valid.

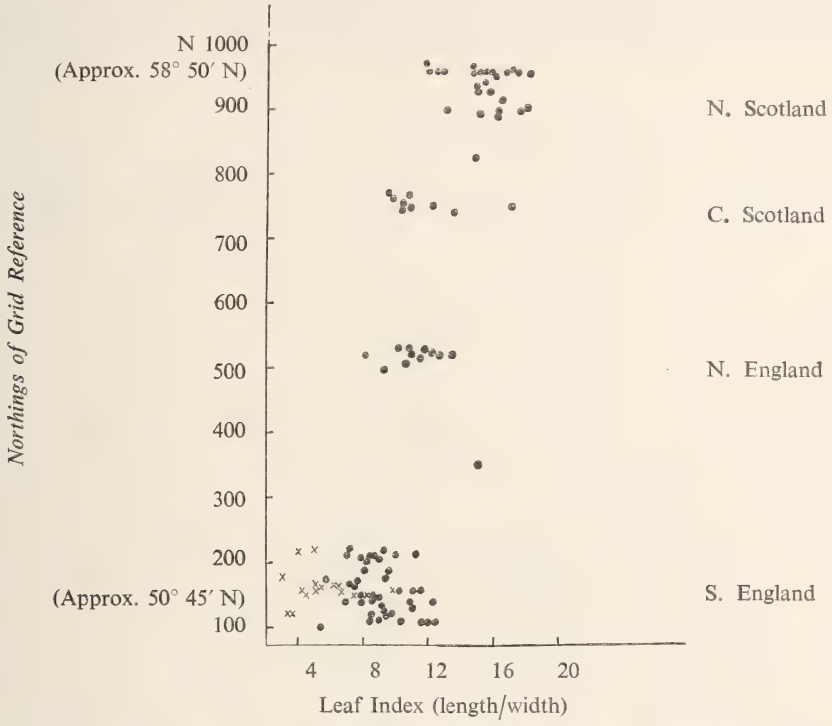


Fig. 4. Geographical scatter diagram of leaf index (length/width) showing narrowing of leaves northwards. Solid dots, populations from acid habitats; crosses, populations from calcareous habitats.

(vii) *Presence or absence of cotyledons at maturity*

This character is again affected by age, although in populations of small plants the cotyledons are frequently still present when flowering commences. With large plants the stems become woody at the base and the cotyledons are lost. As with the number of sterile and fertile branches, all populations would have to be sampled at the same time and allowance would have to be made for the effect of climatic differences on the rate of growth due to geographical distribution and altitude.

(viii) *Cauline leaves*

Leaf shape is one of the most conspicuously variable characters of *M. pratense* and a number of infraspecific taxa have been largely based on leaf shape. One of these, subsp. *commutatum* (Tausch) C. E. Britton (1943), is defined as having lanceolate to ovate leaves, all other forms having narrower leaves. From field observations, examination of herbarium

specimens and statistical analysis, this subspecies, corresponding with ecological type *A*, appears to be more distinct than any others described.

Leaf shape is closely correlated with geographical distribution and height, as can be seen from Figs. 4 and 2. A measurement of leaf shape is obtained from the length/breadth ratio of one of the uppermost pair of cauline leaves of each plant. Length is total length of the leaf and width is measured across the widest portion. In Fig. 5, where leaf length is plotted against leaf width, it is clear that there are two patterns of variation, one made by plants from calcareous habitats and the other from the remaining populations.

Plants from calcareous habitats, with the exception of some populations from Kent, are quite distinct with regard to leaf shape from all other populations, the leaves being ovate to ovate-lanceolate instead of lanceolate to linear-lanceolate. Despite some of the Kentish populations inter-grading in leaf shape with populations on non-calcareous soils in the same area, type *A* populations are significantly different from all other populations in leaf shape.

(ix) *Number of entire and toothed bracts*

This character does not appear to be of much use taxonomically, as the number of entire bracts is correlated with height, short plants having more entire bracts than tall plants.

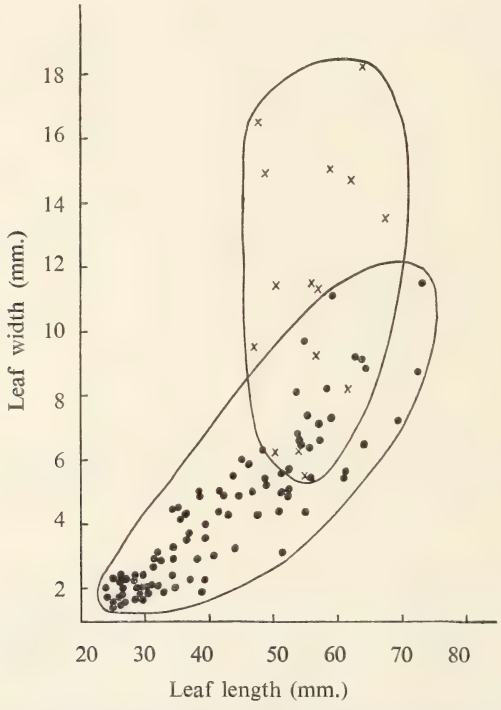


Fig. 5. Leaf width plotted against leaf length showing difference between plants from calcareous habitats (crosses) and other populations (solid dots).

(x) *Degree of toothing of bracts*

The number of teeth per bract varies very greatly from population to population. The various British taxa are described as having few to many teeth per bract, with teeth small and blunt to long and acuminate. Usually the number and size of bracts and the extent of toothing is correlated. If the bracts are few in number they tend to be small with

blunt teeth and, if numerous, are larger with long acute teeth. Because of the great variability in toothing of bracts, both within and between populations, and because the nature of the teeth depends upon the number of bracts, the toothing of bracts is not a good character.

(xi) *Calyx length*

The calyx of *M. pratense* is four-lobed, with the two upper lobes frequently longer than the lower. The calyx becomes enlarged in fruit and all measurements were made on the oldest flower of a stem or branch. The length of the calyx tube is relatively constant throughout the country but total calyx length, measured from the base of the calyx to the apex of the longest tooth, was found to be very variable.

The mean calyx length of populations examined varies from about 3·5 mm to 7·8 mm, and there is a higher proportion of populations with long calyces in the north of Britain than in the south.

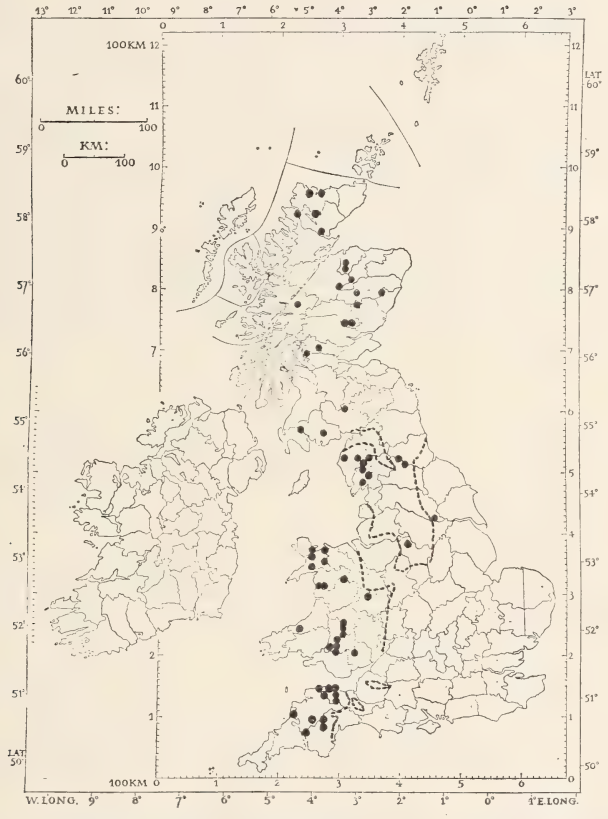


Fig. 6. Distribution map of the golden-yellow flowered form of *M. pratense* (var. *hians* Druce). The dotted line roughly divides the western palaeogenic regions of Britain from the south-eastern neogenic regions.

(xii) *Corolla length and colour*

Variation in corolla colour is a conspicuous character and there are three distinct colour forms which do not merge. The first type has a whitish or pale-yellow corolla tube with a pale-yellow mouth. This is widespread throughout Britain. The second type of flower is uniformly golden-yellow, sometimes verging on orange. This occurs as pure populations and apart from an unconfirmed record from Sussex appears to be restricted to palaeogenic regions of Britain (Fig. 6). It also occurs in Ireland but there are insufficient

data to gain an adequate idea of its distribution. It appears to be very rare or absent on the Continent. The golden-yellow form was first described by Druce (1884) as var. *hians* and was raised later to subspecific rank but, apart from flower colour and geographical distribution, there is nothing to distinguish it from other forms of *M. pratense*.

The third colour form which is limited to northern Britain has a pale-yellow or whitish corolla tipped with crimson and usually occurs mixed with plants with pale corollas. It is found in Scandinavia and in mountainous areas of other parts of Europe. It does not normally occur in pure populations in Britain and does not show any particular geographical distribution other than tending to be northern and montane.

In the first important monograph on the genus *Melampyrum* (Beauverd 1916) great stress is laid on the colour of the corolla after anthesis in *M. pratense* and the two subspecies are based on this. In subsp. *eu-pratense* Beauv. the corolla is said to become purple to pale red after anthesis and in subsp. *vulgatum* Pers. the corolla becomes blackish. Britton (1943) follows Beauverd and, although he recognises more subspecies, these are in two groups corresponding to the original two subspecies of Beauverd. It is not clear either from Beauverd or from Britton whether anthesis means (correctly) opening of the flower or (incorrectly) shedding of pollen.

In many of the populations examined, the flowers became slightly to markedly pinkish as they began to wither. The anthers usually burst just after the flowers open but there is no change in colour until the flowers begin to wither. No blackish corollas were seen other than decaying ones that had not fallen off. From vegetative characters a number of the populations could be allocated to varieties of either of Beauverd's subspecies when flower colour was ignored. If, however, flower colour was taken into consideration it was impossible to name many of the populations simply because none had blackish corollas. It is impossible to identify pressed specimens using either Beauverd's or Britton's descriptions as corolla colour is lost on drying and identification can only be made by comparison with specimens named by Beauverd or Britton. It is considered that corolla colour either

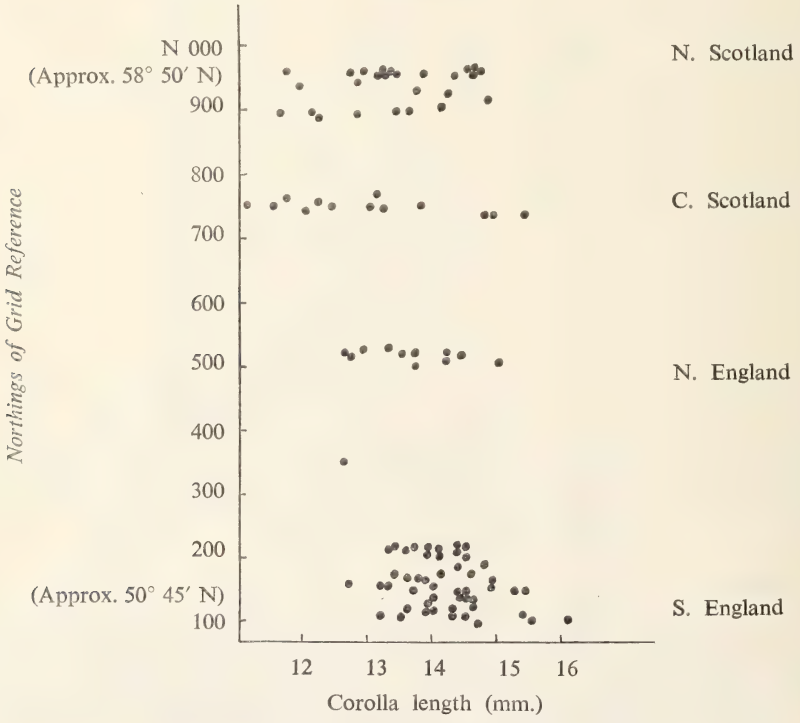


Fig. 7. Geographical scatter diagram of corolla length.

after anthesis or pollen shedding is a useless character and Beauverd's two subspecies are worthless and that Britton's identifications are based on invalid criteria.

Corolla length is variable, population means varying from 11·1 to 16·1 mm and individual corollas from 11 to 18 mm, and there are literature records of corollas up to 20 mm. There is a higher proportion of populations with short corollas in the north of Britain than in the south (see Fig. 7). There is no correlation between corolla and calyx length.

(xiii) *Anther and anther-appendage length*

Until recently anther length has not been used as a taxonomic character, although Beauverd (1916) used the relative length of the basal hairs of the anthers and the length of the anther appendages. The uselessness of this is seen in that different 'taxa' distinguished on this character sometimes occur in the same population and even on one plant.

Whilst attempting to find a character to separate badly pressed specimens of *M. sylvaticum* from depauperate forms of *M. pratense* it was found that there was great variation in the anther length of *M. pratense* and that anther length was of no use in separating the two species.

Anther length (length of loculus plus appendage) varies in Britain from about 2 to 3·5 mm. Populations with anthers 2·5 to 3·5 mm are widespread throughout the country but those with anthers less than 2·5 mm long are limited to northern and montane areas (see Fig. 8). There is no correlation between anther, corolla and calyx lengths. Observations on Continental material revealed that average anther length decreases northwards and Jasiewicz (1958) remarks that plants with small anthers are montane in Poland.

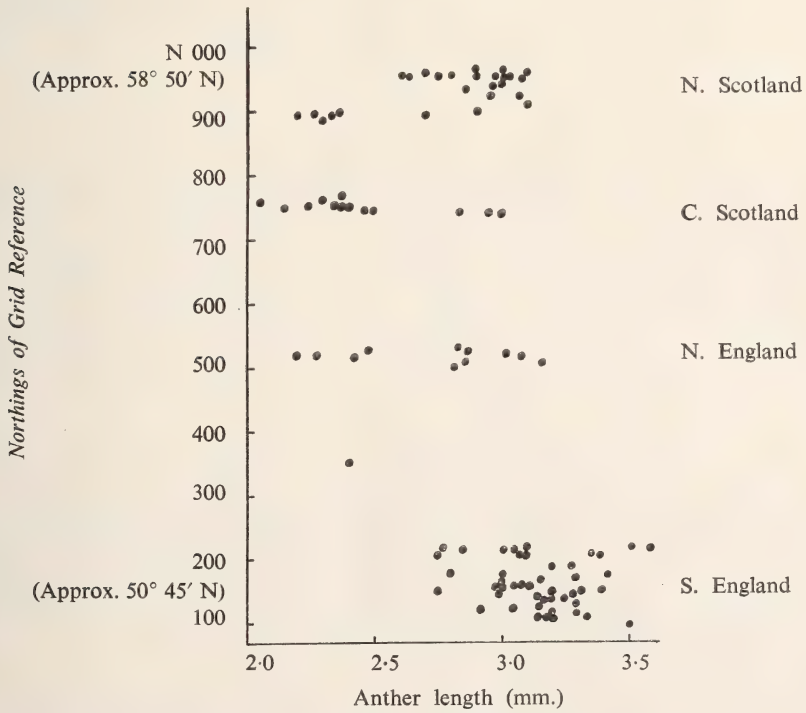


Fig. 8. Geographical scatter diagram of anther length.

Jasiewicz (1958) divides *M. pratense* into two groups, the first mainly lowland with anther loculi (2·2–) 2·4 – 2·7 (–3·2) mm long and appendages (0·2–) 0·3 – 0·5 (–0·6) mm long and the second mainly montane with anther loculi (1·6–) 1·8 – 2·2 (–2·7) mm long and appendages (0·5–) 0·6 – 0·8 (–1·0) long. It is clear that the proportions between loculus length and appendage length are different in the two groups and are of importance in separating them.

Measurements of loculus length and appendage length of the anterior pair of anthers in flowers from each population sampled were carried out and it was found that appendage length was directly proportional to loculus length and that there were not two groups. The same was found of Continental material throughout the range of the species. Hence it seems unlikely that there are two types of anthers, as suggested by Jasiewicz, unless they are restricted only to Poland. Insufficient Polish material was seen to come to any conclusion about this.

(xiv) *Pollen*

For each sample, twenty-five pollen grains were measured from each of three plants, making seventy-five pollen grains per sample.

In most of the samples the pollen was 95–100% good, but about 2% of the plants examined had up to 50% of the pollen grains empty.

Pollen varied in diameter (18–) 19 – 22 (–24)μ. In some populations pollen grains were elliptical, measuring approximately 18 × 21μ, but in most the pollen grains were spherical. In a few populations there were occasional larger pollen grains, up to 27μ, these presumably being unreduced. Whilst the average diameter in populations was mostly 20 to 21μ, two samples had mean diameters of 23μ and 23·6μ and one had 18·5μ. It does not seem that variation in pollen size can be put down to differences in chromosome number as in all the samples on which chromosome counts were made, including the population with small pollen grains, the diploid chromosome number was eighteen.

Pollen of *M. sylvaticum* varies from 21–27μ in diameter and, hence, pollen size cannot be regarded as a reliable character for separating the two species.

Geographical variation

From Fig. 1 it is clear that height diminishes northwards and from Fig. 4 it can be seen that there is a decrease in leaf width in relation to leaf length northwards. In southern Britain there is also a slight decrease in height from east to west. There is an increase in calyx length northwards, brought about by the occurrence of some populations with longer calyces than those of the south. Similarly there is a slight decrease in corolla and anther lengths northwards, but the cline in these two characters is not smooth, as populations from central Scotland have shorter corollas and anthers than populations elsewhere in Britain. This is seen in Figs. 7 and 8.

Variation in Continental M. pratense

As British material of *M. pratense* showed distinct geographical trends in certain characters it was thought that it might be informative to study the geographical variation of *M. pratense* on the Continent. To obtain a comparison with British material, British and Continental specimens were divided into the following groups which are designated by the prefixed letter or figures in the geographical scatter diagrams (Figs 9 to 11.).

i S. England (v.c. 1–35, 51° N)
ii N. England (v.c. 60–70, 54° 15′ N)
iii Central Scotland (v.c. 88–89, 56° 20′ N)
iv N. Scotland (v.c. 105–108, 58° N)

NN	N Norway (68° 30′ N)	P	Poland (52° N)
SN	S Norway (61° 30′ N)	C	Czechoslovakia (50° N)
NS	N Sweden (62° N)	Ba	Bavaria (49° N)
SS	S Sweden (58° N)	T	Thuringia (51° N)
F	Finland (62° N)	LA	Lower Austria (48° 15′ N)
D	Denmark (56° N)	G	Geneva (46° 15′ N)
H	Holland (53° N)	I	Italy (northern) (45° N)
B	Belgium (51° N)	J	Jugoslavia (45° N)

Only areas from which more than twenty-five specimens were seen have been used in plotting the scatter diagrams. The countries or districts used do not represent the distribution of the plant but merely the areas in which it has most frequently been collected, or from which a sufficient quantity of material was seen. The herbarium at Geneva contains a collection of *M. pratense* from neighbouring French and Swiss provinces and hence the name of the city has been used to designate a geographical area.

Height

Whilst height decreases northwards the diminution is much more rapid in Britain than in north-west Europe. Plants from Scotland are markedly smaller than those from similar latitudes in Norway and Sweden and, even in the extreme north of Norway, the plants hardly approach the small stature of those of northern Scotland (see Fig. 9).

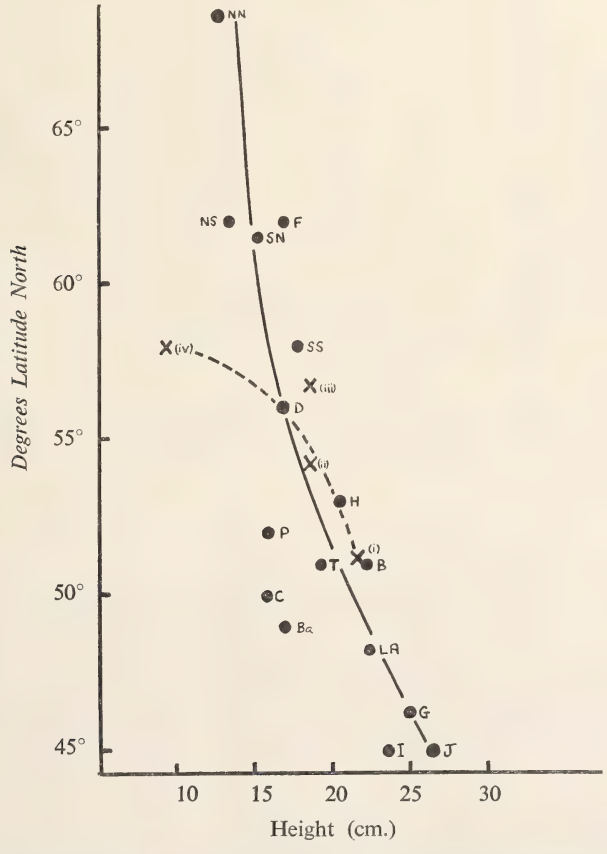


Fig. 9. Geographical scatter diagram of height showing differences between British material (crosses) and Continental material (solid dots). For interpretation of lettering see text.

Leaf index

The slight increase in leaf index from latitudes 45° N to 70° N on the Continent contrasts markedly with pronounced increase in that of British material, as can be seen from Fig. 10.

Number of branches

The number of pairs of branches of British plants does not differ noticeably from that of northern European plants although from the different trends in height this is unexpected.

Calyx length

In Britain there is a northward increase in calyx length and the trend appears more extreme than on the Continent.

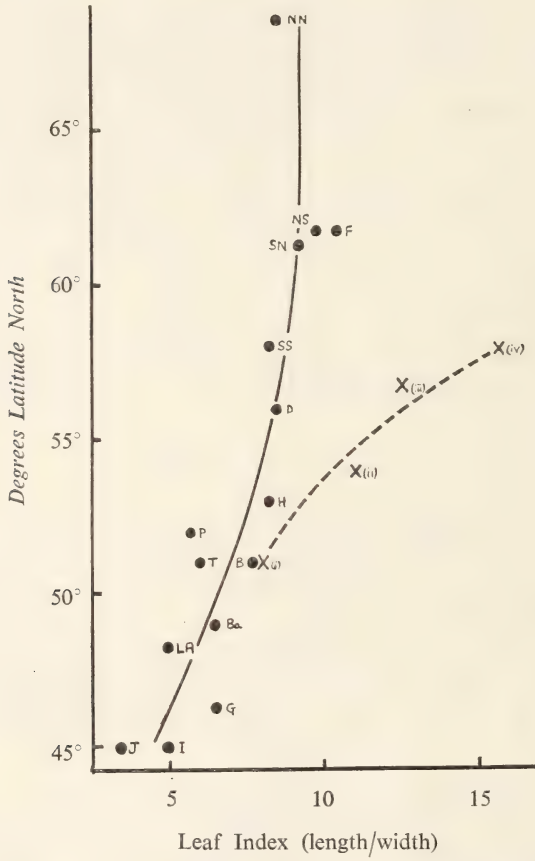


Fig. 10. Geographical scatter diagram of leaf index (length/width) showing differences between British material (crosses) and Continental material (solid dots). For interpretation of lettering see text.

Corolla length

Whilst there is a slight decrease in corolla length northwards in British plants, the variation in Continental material does not reveal any noticeable northerly trend.

Anther length

Except in central Scotland the anthers of British plants tend to be longer than those of Continental plants from similar latitudes and in Europe as a whole there is a steady decrease in length from south to north (Fig. 11).

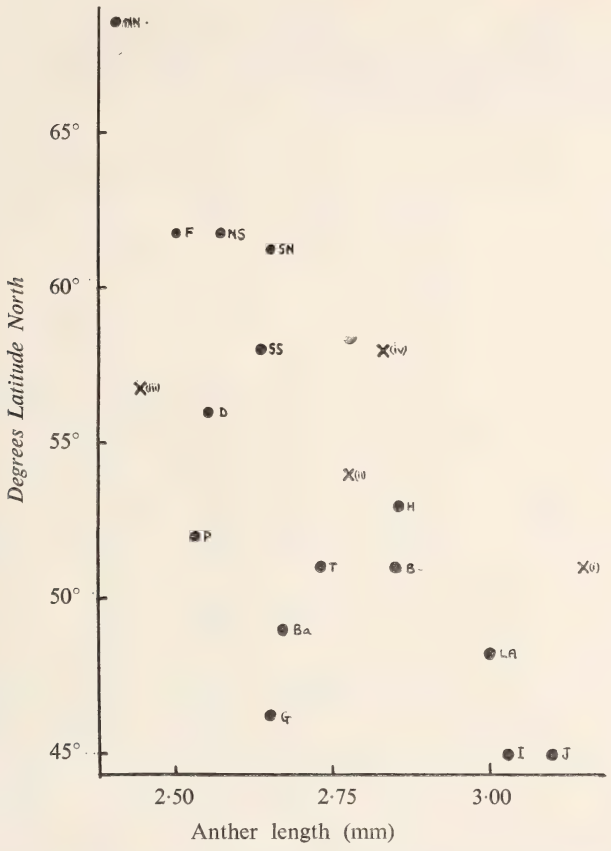


Fig. 11. Geographical scatter diagram of anther length. Crosses, British material; solid dots, Continental material. For interpretation of lettering see text.

General comments

It might be expected that plants of *M. pratense* from west and north Scandinavia would resemble plants from northern Scotland, but this is not so. Northern Scandinavian plants are taller, have markedly broader leaves, slightly longer corollas and the same number of pairs of branches (or cauline leaves.) This gives the plants from these two areas a strikingly different appearance. These differences may be due to climatic and day-length differences in the two areas. Woodland plants from other parts of Scandinavia resemble more closely British plants though few are as small as those of many populations found in some parts of Britain. Plants collected from limestone areas in various parts of Europe from Gotland southwards closely resemble the forms from chalk and limestone in Britain. All plants from Belgium and Holland are very similar to plants of south and east acid-woodlands in Britain.

Results of statistical analyses

In Tables 2 and 4 the means of particular characters for the populations of each ecological type are arranged in ascending order of magnitude. In Table 3 the means of variabilities (obtained by taking the logarithm of the standard deviations) are likewise arranged. In Table 5 again the means of variabilities (obtained by squaring the standard

Table 2

Significance of differences between means (in brackets) of ecological types *A* to *G*. Any two means *not* underscored by the same line are significantly different. Any two means underscored by the same line are *not* significantly different using the SNK test.

Character and level of significance	*Ecological type and mean*						
Height (*cm*) 5%	*A* (27·8)	*C* (22·4)	*D* (16·5)	*E* (12·8)	*F* (11·8)	*B* (11·2)	*G* (10·4)
1%	*A*	*C*	*D*	*E*	*F*	*B*	*G*
No. sterile nodes 5%	*A* (5·7)	*C* (4·67)	*G* (4·53)	*D* (3·79)	*B* (3·73)	*E* (3·63)	*F* (3·59)
1%	*A*	*C*	*G*	*D*	*B*	*E*	*F*
Total No. nodes 5% and 1%	*A* (11·6)	*C* (10·1)	*G* (8·18)	*D* (8·14)	*B* (8·01)	*E* (7·89)	*F* (6·91)
No. intercalary leaves 5% and 1%	*A* (1·79)	*G* (1·77)	*C* (1·24)	*B* (1·18)	*D* (1·06)	*E* (0·99)	*F* (0·93)
Leaf shape (*l*/*b*) 5% and 1%	*A* (5·53)	*C* (8·29)	*D* (9·44)	*B* (10·29)	*E* (11·11)	*F* (12·95)	*G* (15·67)
No. of entire bracts 5%	*A* (1·26)	*C* (1·73)	*F* (2·23)	*D* (2·28)	*E* (2·36)	*G* (2·56)	*B* (2·73)
1%	*A*	*C*	*F*	*D*	*E*	*G*	*B*
No. of teeth per bract 5% and 1%	*A* (6·52)	*C* (5·48)	*E* (3·41)	*D* (3·25)	*B* (2·81)	*G* 2·42()	*F* (1·85)
Calyx length (*mm*) 5%	*C* (5·1)	*D* (5·2)	*A* (5·25)	*E* (5·45)	*F* (5·5)	*B* (5·7)	*G* (6·35)
1%	*C*	*D*	*A*	*E*	*F*	*B*	*G*
Corolla length (*mm*) 5% and 1%	*D* (14·8)	*A* (14·4)	*C* (14·1)	*B* (14·1)	*E* (13·6)	*G* (13·6)	*F* (12·8)
Anther length (*mm*) 5%	*B* (3·25)	*D* (3·17)	*C* (3·16)	*A* (3·08)	*G* (2·88)	*E* (2·70)	*F* (2·42)
1%	*B*	*D*	*C*	*A*	*G*	*E*	*F*

deviations) are treated similarly. Although the variabilities in Tables 3 and 5 were obtained by different methods used in the original research, they are essentially similar since the log. of the square of the standard deviation (variance) is equal to twice the logarithm of the standard deviation. These variabilities represent the degree of genetic variability. The significance of differences between the means and variabilities have been analysed statistically as described on p. 341 at the 5% and 1% levels. Means or variabilities that are

TABLE 3

Significance of differences between variabilities of ecological types *A* to *G*

Character and level of significance	*Type and variability mean*						
Height 5% *and* 1%	Not significant						
Leaf shape 5%	*F* (1238)	*C* (1244)	*A* (1260)	*E* (1263)	*B* (1296)	*D* (1336)	*G* (1361)
1%	Not significant						
Calyx length 5% *and* 1%	Not significant						
Corolla length 5% *and* 1%	*F* (625)	*E* (701)	*A* (708)	*B* (710)	*C* (712)	*D* (783)	*G* (821)
Anther length 5% *and* 1%	Not significant						

not significantly different are underscored by the same line. Where differences are significant the means or variabilities are not underscored by the same line. This provides a pictorial method of comparing ecological types in any one of the characters analysed.

From Table 2 the following points can be seen: Type *A* is significantly different from all other types in five characters at the 5% level and four characters at 1%.

Types *C* and *F* are significantly different from all other types in two characters at the 5% and 1% levels.

Types *B* and *G* are significantly different from all other types in one character at the 5% level.

The morphological differences between type *A* and other types are greater than those between any of the other types. In view of the marked ecological difference as well, type *A* forms a distinct unit as will be mentioned later. It is evident that the various ecological types differ from one another to a greater or lesser extent. It is also clear, however, that the characters in which the differences occur are not necessarily the same for any two types.

From Table 4 it can be seen that there are significant differences between populations from Scottish bogs (type *G*, samples 70–80) with respect to the number of nodes and calyx and corolla length, and similarly with populations from calcareous habitats (type *A*, samples 101–109) in Kent. This suggests that, whilst there is selection for particular morphological forms in particular habitats, there are distinct genetical differences between closely sited populations in any one ecological type.

Tables 3 and 5 both indicate that there is relatively little difference in genetical variability between individual populations and between ecological types. The significance of this will be discussed later.

CYTOLOGY

Root-tips of pot-grown seedlings from fifteen samples were stained with feulgen and squashed in aceto-carmine. All had a diploid chromosome number of 18 and all except four had the chromosome morphology illustrated in Fig. 12a. In four samples there were additional pairs of satellites as illustrated in Figs. 12b to 12e.

The constrictions forming the satellites mark the position of nucleolar organisers and it has been suggested (K. Lewis, personal communication) that where chromosomes are

TABLE 4. Significance of difference between means of 15 populations
(pops. 70 to 80 from northern Scottish bogs, type G; pop. 101 to 109 from calcareous habitats in Kent, type *A*)

Character and level of significance	*Population and mean*														
Height (cm) 5%	71 (7·8)	75 (9·2)	76 (9·5)	77 (9·8)	73 (10·1)	80 (10·3)	74 (10·4)	72 (10·4)	78 (14·9)	101 (23)	106 (23·6)	107 (25·3)	108 (28·4)	109 (29·5)	103 (31·3)
1%	71	75	76	77	73	80	74	72	78	101	106	107	108	109	1·3
No. of nodes 5%	70 (7·6)	75 (7·7)	71 (7·8)	76 (8·1)	77 (8·4)	80 (8·5)	73 (8·5)	106 (8·6)	72 (8·8)	109 (9·7)	101 (10·7)	78 (10·8)	108 (11·5)	107 (11·8)	103 (12·6)
1%	70	75	71	76	77	80	73	106	72	109	101	78	108	107	103
Leaf shape 5% *and* 1%	70 (18·2)	80 (17·7)	71 (16·7)	77 (16·1)	76 (16·0)	72 (15·9)	75 (15·6)	73 (15·1)	78 (12·8)	106 (8·7)	101 (8·1)	107 (7·3)	103 (5·0)	109 (4·4)	108 (4·2)
Calyx length (mm) 5%	77 (7·8)	72 (6·97)	71 (6·95)	80 (6·56)	101 (6·50)	78 (6·48)	70 (6·40)	76 (6·07)	75 (5·99)	73 (5·96)	107 (5·64)	106 (5·48)	109 (5·15)	103 (4·98)	108 (4·97)
1%															
Corolla length 5%	80 (11·7)	75 (12·8)	76 (13·2)	73 (13·6)	77 (13·7)	101 (13·7)	108 (14·0)	70 (14·1)	72 (14·2)	106 (14·4)	107 (14·5)	78 (14·6)	71 (14·8)	103 (14·9)	109 (15·4)
1%	80	75	76	73	77	101	108	70	72	106	107	78	71	103	109

Watsonia **5** (6), 1963.

TABLE 5. Significance of difference between variabilities of fifteen populations (as in Table 4)

Character and level of significance	*Population and variability mean*														
Height	101	103	109	77	73	80	106	75	76	72	107	78	71	70	108
	(1·4)	(6·6)	(7·4)	(9·2)	(10·7)	(10·8)	(10·9)	(11·3)	(11·6)	(11·7)	(11·9)	(12·4)	(13·7)	(16·3)	(24·0)
5%															
1%	Not significant														
No. of nodes	Not significant														
Leaf shape	Not significant														
Calyx length	72	80	76	78	107	70	75	106	101	73	109	103	108	71	77
	(9·2)	(11·9)	(43)	(48)	(66)	(71)	(80)	(82)	(86)	(92)	(94)	(98)	(100)	(105)	(172)
5% *and* 1%															
Corolla length	72	108	106	70	101	80	77	76	71	109	103	107	73	78	75
	(13·8)	(15·1)	(15·9)	(21·0)	(31·6)	(32·0)	(32·2)	(37·0)	(41·9)	(42·8)	(44·5)	(45·2)	(46·1)	(55·9)	(91·3)
5%															
1%	Not significant														



Fig. 12. Camera lucida drawings of root-tip chromosomes of *M. pratense*; (a), normal chromosome complement (sample 96); (b)—(e), abnormal chromosome complements with additional satellites and/or non-homologous chromosomes (samples 99, 26, 100 and 97 respectively).

non-homologous this might be due to the suppression of some of the nucleolar organisers by those remaining. The chromosomes are very heterochromatic and, because of staining in the resting nuclei, it is not possible to count the number of nucleoli.

Staining of the root tip chromosomes with feulgen and aceto-carmine was very satisfactory, but great difficulty was had in staining meiotic chromosomes in pollen-mother-cells. Aceto-carmine and aceto-orceine produced poor results with fresh material although the former stain was satisfactory with material fixed in 1:3 acetic alcohol. Best results were obtained by warming fresh anthers for about five minutes in a mixture of five drops each of aceto-orceine and aceto-lacmoid and three drops of normal hydrochloric acid. Examination of fresh material was desirable as in fixed material the chromosomes become very woolly in appearance.

It proved difficult to find dividing pollen-mother-cells but sucessful preparations were made from material from ten populations. In all these the results were identical and the chromosomes always showed the same pattern of behaviour.

At metaphase eight bivalents became arranged around the ninth on the metaphase plate as in Fig. 13a. At anaphase the eight bivalents appear to move to the wall of the pollen-mother-cell and fuse with each other at the ends to form a ring (Fig. 13b). That they fuse is suggested by the fact that when heavily squashed the dispersed chromosomes remain joined by bridges (Fig. 13d). The central bivalent becomes attached at its ends to the inside of the ring. In fresh material, however treated, the pollen-mother-cells always become orientated so that there appears to be only a single ring of chromosomes at anaphase. In fixed material orientation of the pollen-mother-cells is at random and it is clear in such preparations that there are two rings. At telophase (Fig. 13d) the chromosomes become separated but still have the same arrangement as at metaphase and this is retained until the later stages of the second division.

In *M. sylvaticum* there is the same phenomenon at anaphase but metaphase was not seen and the chromosomes were too woolly to count in the preparations made.



Fig. 13. (a)—(c), stages in meiosis of pollen mother cells of *M. pratense* ((a), metaphase; (b) anaphase; (c), telophase); (d) heavily squashed cells showing apparent bridges between chromosomes at anaphase.

The chromosomes of *M. pratense* are relatively large when compared with those of related genera such as *Rhinanthus* and *Euphrasia* and it may be that their peculiar behaviour is only a mechanical effect dictated by the lack of space for random orientation in the pollen-mother-cells. The bivalents are not sufficiently different morphologically to determine whether the same chromosomes always occupy the same position at anaphase.

Resting nuclei of both root-tips and pollen-mother-cells are very heterochromatic and the same situation is reported in *M. cristatum* (Hambler 1954). *Melampyrum* differs in this respect from *Rhinanthus*, the species of which have varying numbers of heteochromatic *B* chromosomes (Hambler 1954) which form stainable blobs in resting nuclei.

Discussion

It is evident from the foregoing account that there are three types of variation in *M. pratense*, (i) geographical variation, (ii) ecological variation and (iii) variation from population to population.

(i) *Geographical variation*

In Britain there is a marked south-north cline in such characters as height and leaf shape. These clines can be explained on the basis of natural selection acting through climate. Such clines have been shown in *Alnus glutinosa* (McVean 1953).

With calyx, corolla and anther lengths the pattern differs. There is not a gradual change in size, but there is a change in the proportion of populations with floral parts of particular dimensions. It is difficult to conceive of a reason for this. If, for example, short anthers and long calyces are of selective advantage in the north then it might be expected that they would have been selected for in all populations in such areas. In northern Scandinavia there is a higher proportion of such populations than in Scotland and it may be that short anthers and long calyces (which are not necessarily selected for together in any one population) have a slight advantage under more extreme climatic conditions. This being so, selection for them would increase in a northerly direction and they might even be selected against in the south. In Britain this particularly applies to anther lengths, there being no populations with short anthers in the south. Similarly with calyx length there are very few specimens with long calyces from southern Europe.

Corolla colour is also a puzzling feature. Taking first the golden-yellow form, this occurs in pure populations in palaeogenic regions of Britain and with the possible exception of a record from Wurttemburg is apparently absent elsewhere except in Ireland. That it occurs in pure populations indicates that it is of selective advantage and when a mutation to this colour form occurs it spreads through the whole population. If it was a normal mutant it would be expected to occur throughout the whole geographical range. It is possible that the selective advantage of golden-yellow flowers is connected with a particular pollinator in certain areas.

The plants with crimson-tipped corollas are northern and montane and in Britain they mainly occur mixed with the normal form. The situation on the Continent is unknown. As will be mentioned later *M. pratense* is usually self-pollinated so that these mixed populations are unlikely to be instances of balanced polymorphism, and the fact that pure populations of the crimson-flowered form are rare suggests that it is of no particular selective advantage. As with the golden-yellow form its absence from a considerable part of the species' range is inexplicable.

(ii) *Ecological variation*

Whilst some characters show an almost continuous geographical cline, others, for a considerable part of their distribution, show a similar cline, but there are certain anomalies which appear to have an ecological basis. The most conspicuous irregularity is in the cline of intercalary leaf number and is caused by the northern bog populations (see Fig. 3) which have a larger number of intercalary leaves than any other populations except those of type *A*. Evidently plants with numerous intercalary leaves have been selected for in Scottish blanket bogs.

Plants from calcareous habitats might also be said to cause discontinuities in the leaf-shape cline (Fig. 4) though, as they all occur in southern Britain where leaves are broader than elsewhere, this is not obvious. Leaf shape of the calcicolous forms is significantly different from all other forms, but otherwise the northerly change in leaf shape is more or less continuous. It seems that the broad-leaf character has been strongly selected for in nearly all basic habitats, both in Britain and on the Continent. Whether or not broad leaves are of selective advantage in calcareous habitats is not clear, but they may be an external manifestation of a physiological difference.

It was mentioned earlier that some chalk populations in Kent were indistinguishable from populations occuring in acid pockets in the same area. There are two possible explantions for this.

The first is that there may originally have been two types of population, one calcifuge and narrow-leaved and the other calcicole and broad-leaved. In Kent conditions on the chalk, where there are acid pockets of soil, would provide adjacent habitats for the two types. Since they would be close together hybridisation and introgression would be possible. None of the populations from chalk soils in Kent have such broad leaves as those from calcareous soils in Hampshire, Somerset and Gloucestershire where the populations appear to be more isolated. This suggests that the narrower leaves of some Kent populations may be due to introgression.

The second possibility is that originally there was only one taxon composed of narrow-leaved plants and that there was selection for broad-leaved forms where populations developed on calcareous soils. This selection would presumably be relatively slow and it might be that in Kent populations from acid soils might still be spreading to calcareous soils, giving forms with a variety of leaf shapes.

From each of the ecological types mentioned (i.e. *A* to *H*) plants of characteristic appearance have been collected (Fig. 14–19), although with the partial exception of type *A*, these various types intergrade to form a continuous series of morphological forms, i.e. they are a series of ill-defined ecotypes. This ecotypic differentiation has been super-

imposed upon continuous geographical variation so that discontinuities in clines of certain morphological characters have been produced. One very marked exception to the pattern of variation in southern Britain, other than the calcareous plants, is the form found in the New Forest. The reason for this exception can be dealt with in considering variation in *M. pratense* in Britain as a whole.

It is possible that at the end of the last Ice Age the form of *M. pratense* found in southern Britain was like the form now found in northern Scottish bogs. As the ice retreated this form would have migrated northwards. As climatic and vegetation changes occurred it is possible that, beginning in the south, this bog form became more variable because of less rigorous climatic selection and diversification of habitats. In any one type of habitat particular gene combinations were probably selected for, resulting in the phenotypes characteristic of the particular habitats. The anomalous New Forest populations (type *B*) could be relicts of an earlier phase in the post-glacial period, as they much more resemble northern plants, especially those from blanket bogs, than other forms. This does, however, raise the question why this form of *M. pratense* has persisted in the New Forest whilst elsewhere in southern England there appears to have been selection for different and more vigorous forms. Furthermore this suggestion implies the existence of wet acid peat in southern Britain in the late-glacial and early Post-glacial periods. All the evidence suggests that the only boggy areas were base-rich shallow valley mires and fens, totally different types of habitats from the wet acid peat of northern Scotland and the dry acid podsols of the New Forest.



Fig. 14. Plant of type A (subsp. *commutatum*) from an oolitic limestone bank, Wotton-under-Edge, Gloucestershire (grid ref. ST 954940), $\times \frac{1}{4}$.

There is an alternative and more likely explanation which will account for geographical variation of the species in Britain and also for the existence of the New Forest populations.

The New Forest plants and those from northern Scottish bogs differ markedly from Continental plants, but other forms of *M. pratense* in Britain, expecially those from southern England, resemble closely those forms from similar latitudes in western Europe.

It is suggested that *M. pratense* migrated from southern Britain northwards after the last Ice Age, either as a periglacial survival or as an immigrant. As the migrant forms spread northwards there was a diminution in size, possibly because of a more rigorous climate, and a diversification of forms resulting from the colonisation of new habitats.



Fig. 15. Plants of type *B* (New Forest form) from Warwick Slade, near Lyndhurst, Hampshire (grid ref. SU 268065), $\times \frac{1}{4}$. *Cf.* Fig. 18.

If, as is suggested by McVean & Ratcliffe (1962), northern Scotland was until recent times wooded, suitable habitats for *M. pratense* would have been present. When the woods were destroyed *M. pratense* could have survived on the subsequent blanket bog as a woodland relict. This may also account for the absence of the species from raised bogs in England and Wales, since these may never have been wooded (*e.g.* Tregaron Bog, Borth Bog). Plants on nutrient deficient soils, such as the acid peats of northern Scotland and the podsols of the New Forest, tend to be small and the similarity between New Forest plants of *M. pratense* and those from Scottish blanket bog may be entirely accidental.

Status of ecological variants of M. pratense

From Table 2 it can be seen that in types *E*, *F* and *G* for certain (and not necessarily the same) morphological features any one of the types is significantly different from the

others, indicating that there has been selection for a particular expression of a morphological character in a particular habitat. In none of these types, however, has selection proceeded sufficiently far to delimit well-defined ecotypes. From a taxonomic point of view all the types from northern Britain (*i.e.* *E*, *F* and *G*) can be regarded as a single taxon. Type *H* which was not dealt with statistically, can, from its morphology, be regarded as falling within this taxon.

In southern Britain the situation is different. Again referring to Table 2 it is evident that, ignoring type *B*, types *C* and *D* are indistinguishable except in the degree of toothing of the bracts and can be included in one taxonomic unit.

Type *A* differs considerably from all other types, in five characters at 5% level and in four at the 1% level. The situation here seems to be either that ecological selection has proceeded further than in other ecological types, or, as was suggested earlier, there were two distinct types of plant to start with. In Europe plants of *M. pratense* from calcareous habitats are usually distinct although in a few areas, e.g. Pas de Calais (F. Rose, personal communication), plants with narrower leaves like those from Kent are found in such habitats.



Fig. 16. Plants of type *C* from Fence Wood, near Newbury, Berkshire (grid ref. SU 511717), × ¼.

Even when the intermediate Kentish populations are included, the calcicolous forms are sufficiently well-defined to be regarded as a taxon distinct from that containing types *C* and *D*. Types *C* and *D* differ significantly from all of types *E*, *F* and *G* only in the number of nodes and toothing of bracts. Although types *C* and *D* tend to be larger in number and size of parts than the northern types there is a completely intergrading series, so that type *C* cannot be considered as distinct from the northern forms. There are a few New Forest populations tending towards the plants of type *C* and it is considered best to regard

the New Forest plants as a form of type *C*. Thus there are two taxa, one consisting only of type *A* and the other of types *B* to *H*. For convenience, nomenclature being dealt with later, these will be referred to as subsp. *commutatum* (plants from calcareous habitats) and subsp. *pratense* (plants from acid habitats).

Plants like those of type *C* are widespread throughout the geographical range of *M. pratense*. On the Continent there is a multiplicity of variant forms but from examination of herbarium specimens it seems that many of the Continental forms are of restricted distribution and that selection has produced different forms in similar types of habitat. The exact status of many of these forms is not clear as insufficient material has been seen, but it is suspected that the situation is as in Britain, i.e. that these forms are ill-defined.

With the exception of type *A* plants, all material seen from the Continent comes within the range of subsp. *pratense*.

Plants of subsp. *commutatum* are widespread being found in many of the areas where there is base-rich rock. It is clear that subsp. *commutatum* and subsp. *pratense* are ecologically and to a considerable extent morphologically distinct and hence the most suitable taxonomic status for them is that of subspecies.



Fig. 17. Plants resembling types *E* and *F* from Struan, Perthshire (grid ref. NN 806655), $\times \frac{1}{4}$.

(iii) *Variation at the population level*

That there is variation between individual populations is evident from Table 4, but before considering this it is necessary to deal with the genetics of the species.

In Britain *M. pratense* usually occurs in small isolated populations. According to Knuth (1906–9), the plant is pollinated by bumble bees and failing this, it selfs. No observations were made of insect visitors, but in several samples when pollen grains were being



Fig. 18. Plants of type *G* from blanket bog near Meall Tuirslighe, Sutherland (grid ref. NC 654599), × ¾



Fig. 19. Extreme form of plants of type *H* from Wybunbury Moss, Cheshire (grid ref. SJ 695502), × ¼.

measured it was found that the anthers dehisced before the flowers opened. During the course of cultivation experiments at Bagley Wood, where *M. pratense* does not occur naturally, a solitary plant flowered about three weeks before any others and set seed, again suggesting that there is no self-incompatibility mechanism. Further, in Britain, many of the populations of *M. pratense* are so isolated as to form small inbreeding units and such populations could be expected to be more or less homozygous.

If the populations are homozygous it would be expected that the level of genetic variability both from population to population and from ecological type to ecological type would be relatively uniform. That this is so is indicated in Tables 3 and 5.

It was suggested earlier that *M. pratense* spread across Britain after the last Ice Age and it is probable that populations became isolated, either by fragmentation of large populations or the distribution of solitary or small numbers of seeds. Random assortments of genes would become fixed in individual isolated populations. This would account for the many minor but noticeable differences between individual populations in similar ecological habitats.

From the point of view of general inter-population variability *M. pratense* is morphologically much more diverse in southern Britain than in the north. This may be due to greater ecological diversity or to the less extreme climatic conditions of the south or a combination of both.

At present *M. pratense* is decreasing in wooded parts of Britain because of felling of some woods and the overgrowth of others. In northern Scotland it appears to be limited to waterlogged areas that do not get burnt in the periodical firing of heather that is carried out in connection with grazing.

Taxonomy of M. pratense

In past investigations of *M. pratense* solitary plants or small numbers of plants have been collected in different parts of Britain and the Continent. Because of geographical, ecological and population differentiation these plants have appeared to be distinct from one another and this has led to the description of many subspecies, varieties, subvarieties, forms and subforms, which do not have any validity when a large number of plants collected continuously over a geographical region are examined.

It has, however, been found that plants fall into two morphological groups that are sufficiently distinct to be considered as subspecies i.e. the subsp. *commutatum* and subsp. *pratense* mentioned earlier.

The specimen of *M. pratense* in the Linnean herbarium comes within the range of those plants which have for convenience been called subsp. *pratense* and which should therefore be called *M. pratense* L. subsp. *pratense*.

The plants with golden-yellow flowers belong to subsp. *pratense*. This form was first recognised as var. *hians* by Druce (1884) and later regarded as a subspecies by Beauverd (1914). The taxon is probably best regarded as a variety, being characterised by flower colour and a distinct geographical distribution. The correct name is therefore *M. pratense* L. subsp. *pratense* var. *hians* Druce.

The plants with crimson-tipped corollas cannot be regarded as having any taxonomic status since they do not occur in pure populations and have no distinct distribution, but can for convenience be called f. *purpureum*.

Plants resembling subsp. *commutatum* were distributed as *M. commutatum* Tausch by Tausch in 1832 but with no description. The original specimens distributed by Tausch have not been seen but from later-named specimens and descriptions it is clear that Tausch's plant was the one that for convenience has been called subsp. *commutatum*. Tausch's plant was described by Kerner in 1870 who said it should be regarded as a variety of *M. pratense*, and the correct citation would be *M. pratense* var. *commutatum* Tausch ex Kerner. The plant was raised to a subspecies by Britton in 1943 and, as this appears to be the correct taxonomic status, the valid name of the plant is *M. pratense* L. subsp. *commutatum* (Tausch ex Kerner) C. E. Britton.

Descriptions of the subspecies

M. PRATENSE L. subsp. PRATENSE: Plants (3–)9–25(–60) cm high (excluding hypocotyl). Uppermost cauline leaves (10–)20–80(–110) mm long, (1–)2–10(–20) mm wide, leaf length/

breadth ratio (5–)7–15(–20). Calyx 3.5–7(–12) mm long. Corolla tube whitish or pale yellow, mouth pale yellow, usually darker than the tube; or mouth crimson-streaked; or whole corolla golden yellow (var. *hians* Druce); (11–)12–14(–18) mm long. Anthers (2.0–)2.4–3.2(–3.8) mm. Plants of acid soils in woodlands, hedgerows and bogs, widely distributed but rare in East Anglia, the Midlands and southern Scotland.

M. PRATENSE L. subsp. COMMUTATUM (Tausch ex Kerner) C. E. Britton: Plants (20–)25–45(–60) cm high (excluding hypocotyl). Uppermost cauline leaves (30–)40–70(–100) mm long, (4–)8–20(–27) mm wide, leaf length/breadth ratio (2–)3–8(–12). Calyx (3.5–)4.0–5.5(–6.0) mm long, corolla 13–15.5 mm, anthers 2.5–3.5 mm. Restricted to calcareous or base-rich habitats, usually a scrub or hedgerow plant, common in south-east England, rare in the south-west. Also recorded from Oxfordshire, Somerset and Lancashire but probably extinct in these counties.

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FERTILE SEED PRODUCTION AND SELF-INCOMPATIBILITY OF *HYPERICUM CALYCINUM* IN ENGLAND

By E. J. Salisbury

Abstract

Hypericum calycinum is shown to produce, in England, a small number of viable seeds which, in well-grown capsules, approximates to a constant proportion. Ovaries contain an average of some 800 or more ovules which, following self-pollination, exhibit a wide range of development. Well developed seeds yield a far higher percentage germination if sown when immature and it is suggested that self-incompatibility manifests itself not only through the first male gamete by degrees of failure in embryo development but also, through the second male gamete by inefficient endospermic nutrition during the attainment of the resting stage in this exalbuminous species. Germination, which extends over a period of months, is of the intermittent type, whether at normal or higher temperatures, and appears to be photoperiodically indifferent. Seedlings have not, however, been observed near colonies and possible reasons for this are discussed.

The Rose-of-Sharon (*Hypericum calycinum*) is found growing wild in south-eastern Europe and was introduced into this country in 1676 by Sir George Wheeler who had collected the plants from the neighbourhood of Constantinople (*Bot. Mag.* t. 146 (1796)). It has thus been with us not far short of three centuries and is more or less naturalised in many localities throughout Great Britain and Ireland, especially in the southern counties of England (Perring & Walters 1962, p. 57). More than sixty years ago, however, Hanbury & Marshall (1899) commented upon the fact that, although then well established in a few places in Kent, the Rose-of-Sharon apparently never spread in this country ' except by root extension '. So too, that excellent field botanist, James White, stated that ' this species is believed not to ripen seed anywhere in this country but to spread and maintain itself by root-extension only '(White 1912). Most gardeners and field botanists would probably subscribe to this generalisation although the phrase ' root-extension ' is liable to mislead, since the vegetative spread of *H. calycinum* is mainly, if not exclusively, by means of axillary underground stems. The distinction is significant since in other members of this genus, for example *H. perforatum* and *H. pulchrum* (see Salisbury 1942, Fig. 32), it is actually the roots which are responsible for the vegetative extension, since adventitious shoots arise from them. The production of such root-shoots can be greatly stimulated in *H. perforatum* by cutting down the erect stems but I have observed no such response in *H. calycinum*. Vegetative extension takes place slowly. The stoloniferous shoots (Fig. 3) grow obliquely upwards from the underground portion of the previous year's leafy shoots. The number arising from each is usually two to four, commonly paired and involving from one to three nodes. Each stolon bears some 8 to 15 pairs of small brown scale leaves below the soil and develops normal foliage leaves on reaching the light. The internodes do not usually attain a length of more than 1–2 cm so that the radial extension in a season rarely exceeds 15 to 20 cm. The very large areas, as along the cutting between Leatherhead and Dorking, that are often occupied exclusively by the Rose-of-Sharon are visual evidence both of the efficacy of its stoloniferous spread and its stability.

A similar generalisation concerning the absence of reproduction by seed in Britain has been made with respect to the two Periwinkles (*Vinca major* and *Vinca minor*) likewise characterised by conspicuous vegetative vigour. Both these species I recorded as having fruited successfully in this country in 1961 (see Salisbury 1961). In the warm late autumn of 1961, examination of capsules of *H. calycinum* revealed a small number of, apparently, fully developed seeds and this discovery, as also my experience with the species

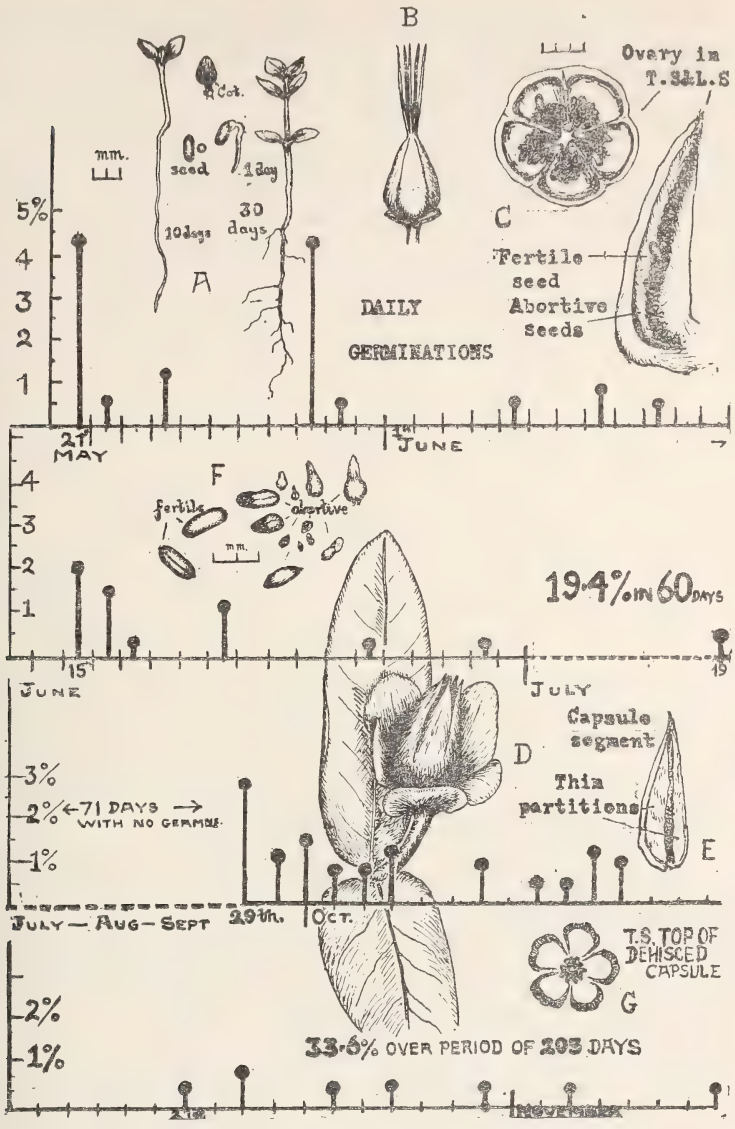


Fig. 1. Intermittent germination of 300 apparently fertile seeds of *H. calycinum*, with (inset) details of the fruit, seeds and seedlings. Magnifications as shown by millimetre scales.

of *Vinca*, led me to look carefully at diverse colonies of *H. calycinum*, both in 1961 and subsequently, from which it would appear that some seed production, though very sparse, is not uncommon, at least in southern England.

Normally the Rose-of-Sharon is probably self-incompatible and, again as with the Periwinkles, this would tend to be accentuated by the large colonies formed by the vegetative spread of a single individual, since the attentions of pollinating insects might be confined to the flowers on only one plant, even if another individual were in the neighbourhood. Moreover it is quite likely that the entire population of *Hypericum calycinum* in this country may have been derived from a single stock. However that may be, the five styles that surmount the ovary are relatively long (see Fig. 1 *B*) so that perhaps only exceptionally favourable weather conditions when pollination occurs, especially with regard to temperature, can enable the pollen-tubes from the plant's own pollen to traverse this distance and

grow sufficiently rapidly to effect fertilisation. Eight large capsules obtained in October 1961, and eight more in November 1962, were dissected carefully and the numbers of apparently fertile seeds, abortive seeds and ovules alike counted with the following results.

Fully-developed apparently 'fertile' seeds	*Percentage 'fertile' seeds*	*Obviously abortive seeds*	*Total number of seeds in capsule*
11	1·8	581	592
18	2·9	597	615
22	3·4	629	651
7	1·0	647	654
13	2·0	647	660
37	5·1	678	715
36	4·7	721	757
24	3·2	767	791
18	2·1	828	846
14	1·6	840	854
15	1·5	966	981
27	2·7	964	991
19	1·8	1040	1059
11	1·0	1071	1082
35	3·2	1058	1093
12	1·0	1155	1167
Average number of fertile seeds 20 [s. d. 9·6: s.e.m. = 2·4]	Average % 2·4	Average number of abortive seeds 824	Average total number of seeds in capsule 844 [s.d. 261: s.e.m. = 65]

Those sixteen capsules were deliberately selected because of their exceptional size and might therefore be expected to contain the highest proportion of fertile seeds and thus provide an indication of maximum fertility. In these the observed range was from seven to thirty-seven with an average of twenty. A random sample, of a number of other 1961 capsules, was also examined, in which the apparently fertile seeds were alone counted, and these provided an average of only 6·2 per capsule.

The apparently fertile seeds were 1·5 to 2 mm in length and from 0·7 to 0·9 mm in width. Almost cylindrical in shape, with rounded ends and a slight ridge along one side, the symmetry of the seeds, as well as their size, usually distinguishes the viable from the abortive ones. The colour is dark brown and the average weight of a seed is 0·00058 gm (the largest from 0·0006 to 0·0007 gm). This is about five or six times the weight of the seeds of the herbaceous species (see Salisbury 1942); they are, nevertheless, sufficiently small and light for gusts of wind to disperse them readily (Fig. 1, C & F).

Subsequently, three hundred of the 'apparently fertile' seeds, harvested in late autumn, were sown on 1 May following. The outcome is presented in the accompanying histogram (Fig. 1) from which it will be seen that germination began within three weeks and was then intermittent through May and June, with a total of only 19% in the first forty days followed by a pause of seventy-one days and then a further surge of germinations bringing the total to 33% in about 5½ months with only two more (0·6%) on 15 December, after 205 days. It should be emphasised that, in order to obtain a sufficiency for a representative test the seeds were collected from various plants at different times. More seeds were collected in 1962. Of these some were harvested from a number of capsules, produced by a single colony and all obtained and sown on the same day, 4 November. There was a total of 183 apparently good seeds but whereas 106 were deep-brown and presumably mature, the remaining 77 ranged in colour from cream to pale-brown and were clearly immature. Both batches were sown side-by-side in the same seed-pan and placed where the temperatures during the daytime attained about 20° C and the minimum night temperatures were about 5° C.

It was anticipated that the immature seeds might yield a low germination but, in fact, their percentage was the highest observed for the species, namely 92%, and the much lower percentage germination of the riper seeds from the same capsules, namely 62·2%,

would strongly suggest inadequate nutrition by the endosperm during the later stages of maturation, a point to which I shall revert. The pattern of germination, in both batches, was again intermittent but, as might be expected from the temperatures being appreciably higher than those in which the 1961 seeds were germinated, it was far less protracted (Fig. 2) occupying about ninety-nine days instead of two-hundred and five. A point that may be of significance is that although the number of viable seeds was almost the same in both the 1962 groups, germinations of the immature seeds took place on only twenty-three separate days compared with germinations on thirty-three days for the mature seeds.

When considering self-incompatibility attention has, hitherto, been almost exclusively focussed upon the normal embryo which, in endospermic seeds, has achieved its resting stage *before* the transfer of food from the endosperm. In an exalbuminous seed such as that of *H. calycinum*, the resting stage is not attained till *after* the endospermic nutrition has been transferred.

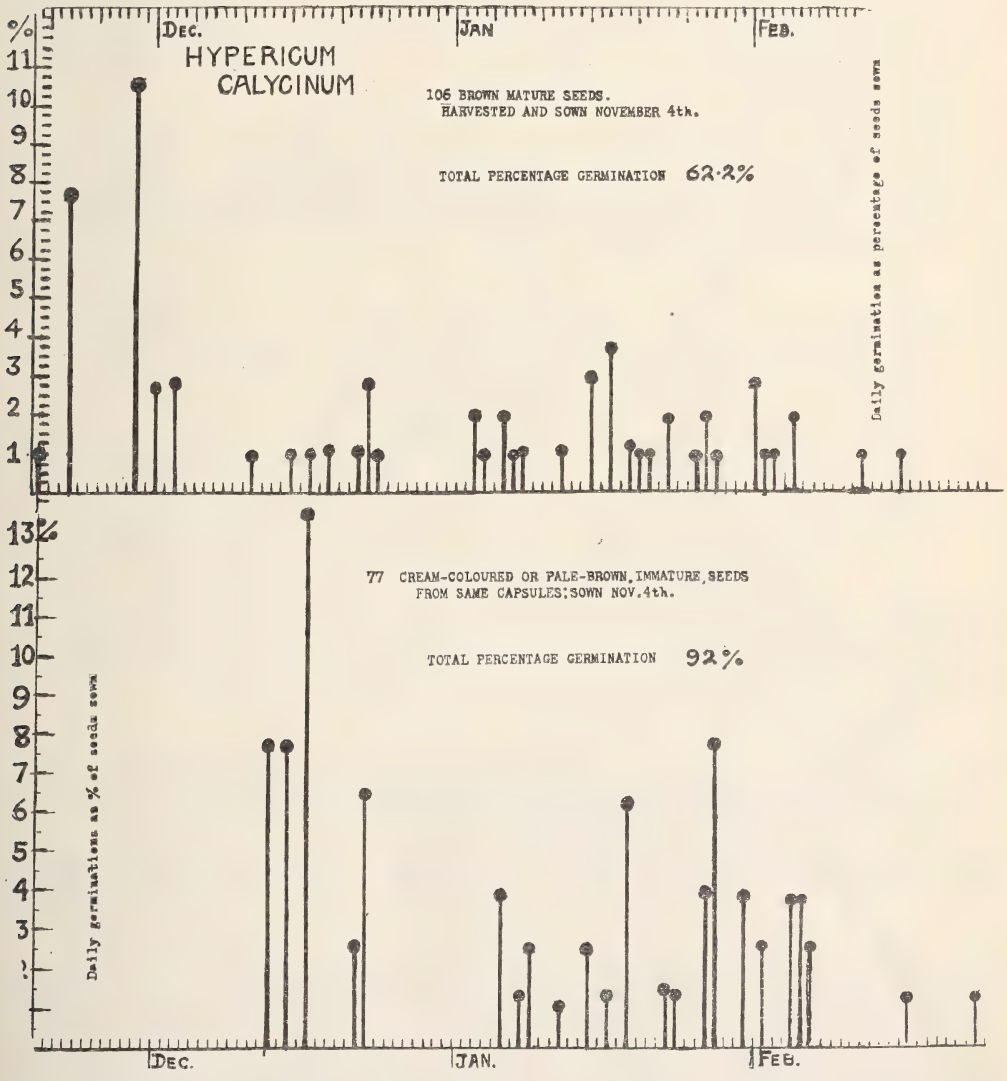


Fig. 2. Germination of fully formed mature and immature seeds from the same capsules sown immediately after harvesting, showing much higher percentage germination of latter.

Having regard to the fact that partially developed embryos were found in some of the seeds regarded as abortive and which a green coloration suggested were present in an appreciable proportion, 1,800 of the better-developed of these were sown (at the same time as the 'good' seeds and under like conditions), to check the validity of one's assessment of their abortive character.

Of these seeds which, from their size and shape, were deemed to be abortive, two germinated after 68 days and ten more between the 83rd and 116th day after sowing. The error, in judging the abortive seeds visually, would then appear to be almost negligible and, since those tested consisted of the most promising only, the error of assessment was certainly much less than 6 in 1000. It is, moreover, not unlikely that this small fraction proved viable only because they were sown immediately and should be considered in the

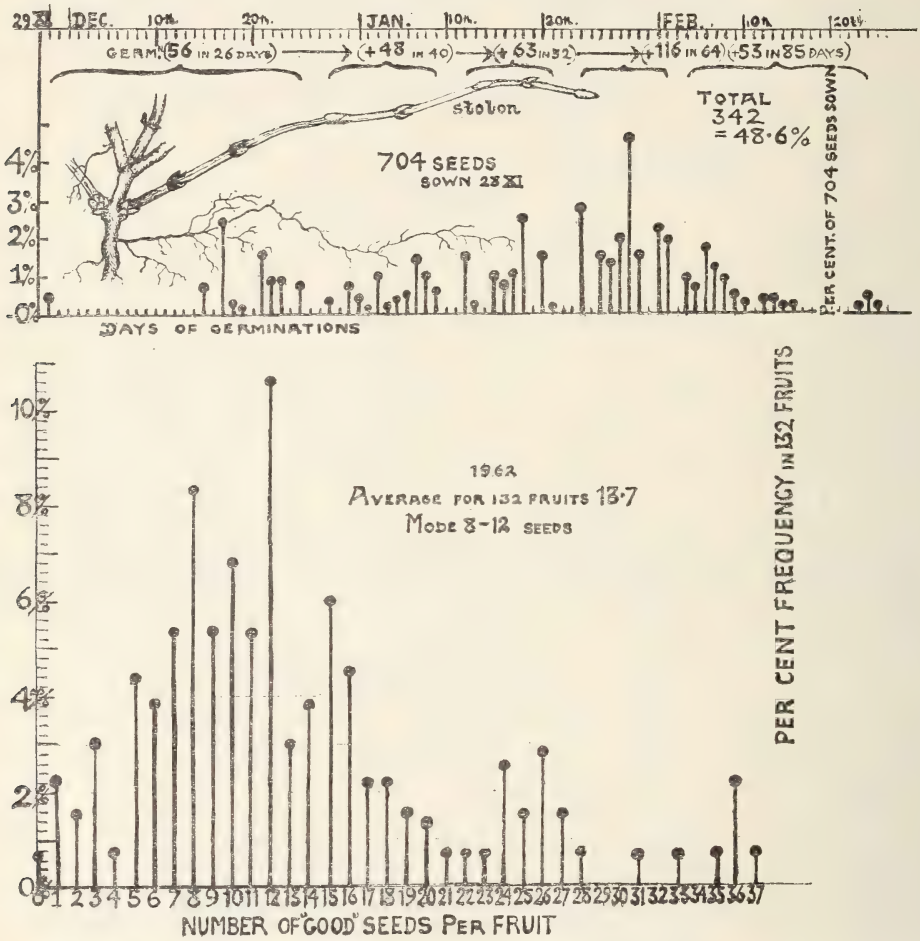


Fig. 3. Upper diagram, shows daily germination of 704 freshly-ripened and apparently good seeds over period of 85 days. Inset, drawing of stolon half natural size. Lower diagram shows number and frequency of 'good' seeds in 132 fruits.

light of the enhanced percentage germination of immature seeds. However, the noteworthy feature that these germination tests collectively reveal is that there is obviously no abrupt transition from the viable to the non-viable but the distinction between them is one of degree rather than of kind. Most of the fruits examined were from Sussex plants growing at approximately 49° 48′ N. Fruit collected near Wendover (c. 51° 45′ N) contained some apparently fertile seeds and it would be of interest to know how far northwards the ability

to produce fertile seeds can extend[1]. It should be noted that there is no obvious negative correlation between seed production and the formation of stolons (cf. Fig. 3), and that the emphasis here on vegetative spread, rather than seed development, is not, as in so many species, a concomitant of polyploidy since the Rose-of-Sharon is a diploid species with twenty chromosomes (Darlington & Wylie 1955 p.114).

From various localities 132 fruits were collected in October 1962, before they were quite mature, but beginning to change colour. As the seeds at this stage are not yet fully pigmented, one is able not merely to distinguish between the possibly viable seeds and the apparently abortive ones but also in some degree to assess, in many of the latter, the amount of development before abortion. Even the collapsed and withered ovules were still distinguishable, somewhat resembling microscopic autumn leaves. The well-developed symmetrical seeds, that germination tests indicate as including almost all the only viable ones, ranged in number from one to thirty-seven in a capsule and the frequencies of occurrence are represented in the accompanying graph (Fig. 4). The arithmetic mean was 13·8, compared with 6·2 in 1961, but it will be seen that the mode is between 8 and 12 (the average for the capsules represented in Fig. 4 was 18 but these were not a random sample, having been selected for range of size).

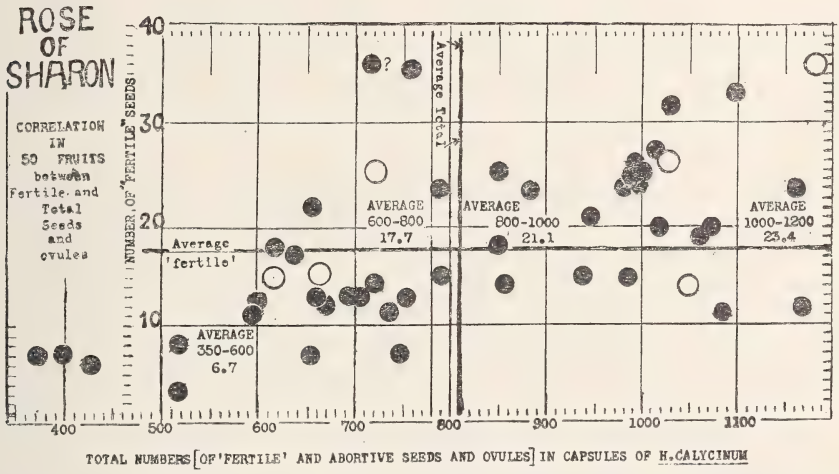


Fig. 4. Each spot represents one capsule; its position in the vertical direction corresponds to the number of apparently fertile seeds which it contained and its horizontal position to the total content of ovules whether fertilised or abortive. O=Capsules from 'Highdown'

It may, I think, be assumed that the usual percentage of those that would germinate is unlikely to exceed the average for the 1187 actually tested, namely 48%. If so, and if the average total of ovules in the fruit be taken as about 800, this would imply an effective development of not more than about eight per thousand of the ovules present. This may represent the normal incidence of compatibility and effective fertilisation in this species when self-pollinated.

One can thus envisage that, in a normally self-incompatible species, the triple fusion which produces the endosperm and involves the second male nucleus may similarly exhibit partial or complete failure with correspondingly variable effect upon the development of the embryo. Precocious planting of seeds with ineffective endosperms, might however provide substitutional nutrition and so account for the enhanced percentage germination of the immature seeds of a capsule.

[1]From information provided by Professor Pichi Sermolli, it would seem that in Northen Italy, at Genoa, seed production of this species is as sparse and unreliable as with us.

Another collection of 704 mature seeds was obtained, about three weeks later in 1962, from several widely separated colonies, growing in various situations and soils. These also were sown at once, under the same conditions as those just considered. This composite sample yielded only 48·4% seedlings, a reduction perhaps associated with the seeds having ripened in the less favourable temperatures of mid-November. These 704 seeds, having been culled from capsules produced in distinctive environments, the intermittence, as might have been anticipated, is obscured but is nevertheless manifest as repeated surges in the germinations (cf. Fig. 3). Elsewhere evidence has been furnished (Salisbury 1962 p. 394 et seq.) to indicate that the potentiality for intermittence is genetically determined but that its manifestation is probably dependent upon developmental conditions. If this be accepted we should not expect the intermittent germination of seeds from distinctive individuals and habitats to exhibit contemporaneity.

Since the 1961 seeds were sown in May and all the 1962 seeds late in autumn, it would appear that the difference in photoperiodic environment (short nights for the one: long nights for the others) had little, if any, effect. No replication was possible since all available seeds have been utilised for the experiments here described.

The lower percentage germination of the 300 seeds of 1961 (a decrease of 15%, as compared with that of the 704 seeds of 1962) is to be attributed not merely to seasonal differences but to the the former having been kept for several months whereas the latter were sown immediately. The decrease of germination with increasing age is a familiar feature accompanying the passage of years, or even months, but here, as we have seen, this decline appears to go back to the period within the capsule and a gradual diminution in the proportion of viable seeds would seem to be indicated *from the time of their formation onwards.*

Although the number of ovules to be fertilised in an ovary is so large and, as mentioned later, may be over 1400, it seems unlikely that inadequate pollination plays any part in bringing about the poor seed production, since there is a multitude of stamens (350 or more in a flower) each of which perhaps produces some 900, or more, pollen-grains; a ratio of pollen-grains to ovules of the order of 300 to 1! Moreover the greater the number of ovules present in an ovary the more would appear to be fertilised (cf. Fig. 4), a relationship that could scarcely obtain were quantity, and not quality, the limiting condition.

Investigators, using a diversity of types, have provided evidence that the incompatibility between individuals of a species depends on a series of alternative genetic characteristics. These determine the biochemical relations between the germinating pollen-grain and the tissues of the pollinated plant, a subtle disparity between them being necessary for effective growth and fertilisation. External conditions, as Professor D. Lewis demonstrated with respect to temperature (Lewis 1942), can modify their interaction. It is scarcely surprising therefore that some pollen tubes do, in fact, reach the egg cell and effect fertilisation. Even for the markedly self-incompatible sweet cherries, Crane & Lawrence (1938) obtained about 0·1% fertility when selfed. Thus, the occurrence of a small proportion of viable seeds in self-pollinated *H. calycinum* is not unexpected. Why, in the race against time to the ovules, some pollen-tubes achieve success may be an outcome of the shuffling of the genes that takes place during the formation of the sexual cells. Theoretical considerations lead us to recognise that the nuclei of both pollen-grains and egg cells, though derived from the same parent, may yet have individual differences that could influence their effective union. So we may postulate that successful self-fertilisation could depend upon the chance mating of such male and female nuclei as exhibit compatible constitutions. If this hypothesis be correct then with an increased number of matings the number of successes should augment although the *proportion* of these might be expected to remain roughly constant. Both these conditions are, in fact, apparently fulfilled.

Owing to the fortunate circumstances that the successes and failures in the fruit can alike be determined with a fair degree of accuracy, it is possible to check these features although such determinations, owing to their laborious and time-consuming character, could only be made upon a limited number of fruits, actually fifty-one, selected for the

range of size they presented. The data for fifty of these are displayed in Fig. 4. By grouping these capsules, according to increments of about 200 in their ovular content, the rise in the average numbers of ' fertile seeds ', accompanying the total increase, is made evident.

The examination included some large capsules from a colony, established for more than half-a-century, growing on an exceptionally sheltered, south-aspect slope in Sir Frederick Stern's garden at ' Highdown'. One of these (not included in Fig. 4) was quite outstanding, with no less than 58 apparently fertile seeds out of a total content of 1458; a proportion still barely achieving 4%, of which not more than a third would probably germinate. If all the fifty-one fruits in which the contents were determined be grouped, we find that the *proportion* of apparently fertile seeds is strikingly similar, in all but the lowest category of contents, namely 370 to 600, 1·4%; 600 to 800, 2·6%; 800 to 1,000, 2·2% and 1000, to 1,458, 2·3%. The facts then would appear to correspond with our hypothetical presentation, the more so that the discrepancy in the class-interval representing the smallest capsules could be due to nutritional stresses inoperative for the larger fruits.

A very noteworthy feature of the incompatibility in this species is that various stages of abortion appear to have occurred subsequent to nuclear fusion. The green colour of many of the abortive seeds is indicative of the presence of embryos arrested in their development at different stages. The pollen tubes of incompatibles may often grow in the style to different degrees and any which reach the egg-cell may effect fertilisation. The genetic barriers thus act by affecting the temporal aspects of growth and perhaps this extends further, beyond the fertilisation of the egg, to affect also mating of the second male nucleus with the fused polar nuclei to provide the endospermic nourishment for the developing embryo. If in *H. calycinum* this second fusion is similarly retarded it might explain the arrest of the embryo at various stages. The much higher % germination of immature seeds is in harmony with such an interpretation.

It would not appear likely that nutrition materially influences the number of ' good ' seeds produced since, although the shoots of the Rose-of-Sharon are normally single-flowered, I have found paired fruits not infrequently and very rarely a shoot bearing three fruits. On three-fruited and two-fruited shoots alike, the capsules did not exhibit any diminution below the average in numbers of ' good ' seeds.

Although flowering may begin in July, I have rarely found ripe fruit before the end of October and frequently not till late November. This retarded maturation may be the result of the different climatic conditions that prevail here, compared with those of S.E. Europe. Dehiscence takes place from the apex towards the base into five segments (Fig. 1, D & G) surrounding a central, conical column formed by the placentas. Frequently, however, the capsules do not appear to split open sufficiently widely for the larger seeds to escape readily. Though sometimes erect, the fruits are usually inclined so that, when the segments spread at the apex, the contained seeds should be shaken out by the gusts of wind. Two circumstances appear to militate against the successful operation of this ' censer ' device. Firstly, owing to the high proportion of seeds which abort, the capsule is largely empty and as it dries and contracts may do so without creating the tensions that, with a well-filled capsule, would more readily ensure the effective rupture and gaping apart of the segments towards the top of the fruit. To test this aspect, ten capsules were selected which had pronounced dehiscence slits and these were each in turn held by the stalk and violently shaken and jarred, to simulate wind movement in an exaggerated form. The result was that 54% of the total of fully-developed seeds escaped. However the 46% that were still retained included, not unnaturally, the larger ones, and if only 22% of the total were actually viable might well account for all of these.

The second circumstance is that since the fruits ripen so late in the year the chance of a thorough sun-baking in these latitudes is meagre. Capsules, which had dehisced but in which the slits were too narrow to permit the escape of any but the abortive seeds, were placed in a warm room to simulate sun-drying. Only after several days was it that the segments separated sufficiently to permit the ready escape of the fully-developed seeds. This would seem to indicate that lack of adequate insolation probably impairs seed-dispersal

under the climatic conditions that normally prevail here in late autumn. Obviously, with decay of the capsules, all seeds would eventually be released but, during the intervening period, they would have been subjected to great fluctuations of temperature and probably also to recurrent changes from dryness to saturation, conditions known to be the reverse of those conducive to the retention of viability.

Towards the end of February a random collection of 62 fruits was obtained from an exposed habitat and their contents examined. All the capsules were dehisced and had been subjected to severe winds that had attained gale force on several occasions. Nevertheless although just under one third contained no seeds, 43 of the capsules contained apparently good seeds the number of which ranged from 1 to 32, the average being 4·2 (s.d. = 6), so that even under these extreme conditions, so favourable to dispersal, an average of only about eight 'good' seeds would be liberated from a capsule and this would imply an average seedling potential for the escaping seeds of not more than four. In an actual test of 210 of these retained 'good' seeds germination attained 37·6% and was completed in 13 days, which suggests the leaching out or inactivation of an inhibitor. Ineffective dispersal would then seem to be an important contributing factor, but not a complete explanation, for the apparent absence of seedlings.

From the foregoing considerations it is not unlikely that an appreciable proportion of the potentially viable seeds may not reach the ground until after their germinative capacity has become impaired. Further, the scanty seeds and even scantier seedlings might perhaps be largely, or even entirely, accounted for by predators. It will be obvious from the data presented in Figs. 1 and 3 that germination takes place in a discontinuous manner which implies that the number of seedlings at any one time could, at best, only be small and so might readily be overlooked. However, I have in fact searched the fringes of colonies, in various localities and on various soils, for seedlings, so far without success. Furthermore, there does not seem to be that degree of discontinuity in occurrence, near the borders of colonies, that might be expected if the species had spread from seedlings.

Although we now know, with certainty, that some viable seeds are produced by the species in southern England, it still remains to be ascertained whether, in the open, seedlings do actually develop and, if so, when. Are conditions normally adverse to germination or, if not, what are the circumstances responsible for the non-survival of seedlings? Only further observations can resolve these questions.

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THE EXPECTATION OF PLANT RECORDS FROM PRESCRIBED AREAS

By J. G. Dony

The success of the Distribution Maps Scheme of the Botanical Society of the British Isles has caused a number of workers on local floras to adopt divisions of 10-kilometre grid squares of the National Grid as a basis for their recording. In 1954 the Birmingham Natural History and Philosophical Society started to use a one-kilometre grid for collecting records for a revision of the flora of Warwickshire. This was, however, slightly amended at a later stage. Two years later, in 1956, E. S. Edees began to use a two-kilometre grid (i.e. four square kilometres) for a survey of the Staffordshire flora. In 1955 the author started work on a revision of the flora of Hertfordshire and in 1957 decided to collect records as Edees had done on the basis of a two-kilometre square, referred to below as a tetrad. Few records were made on this basis until 1959 and the results summarised here are mainly those of four years' field work.

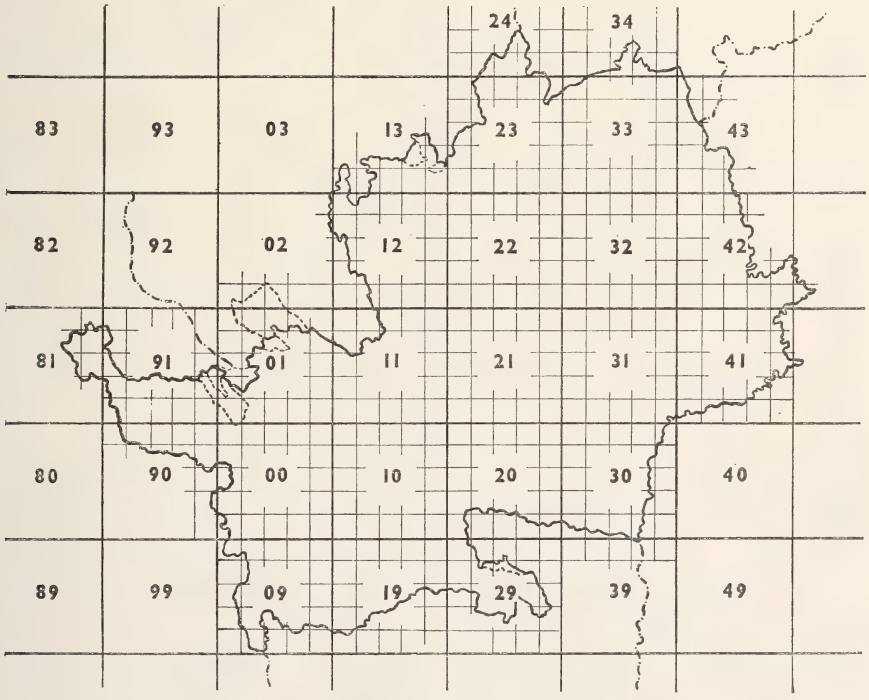


Fig. 1. Hertfordshire. The boundary of Watsonian vice-county 20, Hertford, is shown with a dotted line where it differs from that of the present (1963) administrative county. The prefixing numbers of the 10-kilometre grid squares are omitted but they are given in Table 1.

The area of survey (see Fig. 1) is the present administrative county of Hertfordshire with those parts of the Watsonian vice-county 20, Hertford, which now lie in neighbouring administrative counties. This has a total area of about 1,631 square kilometres and is very irregular in shape. It includes only four complete 10-kilometre grid squares and parts

of twenty-five others, making a total of 336 complete tetrads and parts of 131. The object of this paper is to try to determine the average number of plant species that could be expected to be found in a tetrad or in any other given area in Hertfordshire.

After eight years' intensive field work and the contribution of records from fellow workers the total number of species to be found in the county is reasonably well known and it is unlikely that in the next few years many more will be found other than aliens and casuals. Almost complete records have also been obtained for the full 10-kilometre grid squares and for those the greater part of which is included in the county. From these records it is possible to determine the number of species now known to occur in parts of the county larger than a 10-kilometre grid square.

The species considered for the purpose of this exercise are those given in the *List of British Vascular Plants* (Dandy 1958). Aliens, casuals and garden escapes are not included unless they are in the List, and are neither microspecies nor hybrids. Records made before

TABLE 1.

Summary of records of species made in Hertfordshire (1955–1962).

10-kilometre grid square	*Approximate area in Herts. (sq. km.)*	*Total species recorded*	*Total area (sq. km.)*	*Total Species recorded*
52/24	10	225	19 (A)	282
52/34	9	230		
53/13	12	421		
52/23	85	544	220 (B)	651
52/33	98	521		
52/43	25	415		
52/02	6	303		
52/12	87	499		
52/22	100	604	364 (C)	712
52/32	100	588		
52/42	68	579		
52/52	3	117		
42/81	12	265		
42/91	37	560		
52/01	84	488		
52/11	87	528	493 (D)	834
52/21	100	640		
52/31	99	688		
52/41	73	579		
42/90	25	451		
52/00	96	597		
52/10	100	594	377 (E)	758
52/20	84	561		
52/30	72	591		
51/09	66	647		
51/19	62	554	158 (F)	724
51/29	30	461		
A+B+C (52/24–34, 52/03–13, 52/02–42)			603 (G)	798
E+F (42/90–30, 51/09–29)			635 (H)	836
D (see above)			493 (D)	834
G+D			1096 (I)	899
G+H			1138 (J)	908
D+H			1038 (K)	911
Total			1631	956

The totals of species given above are not totals of the columns from which they are derived, as a species recorded from more than one ten-kilometre grid square is counted only once and so on for the larger areas. A very common species included in the grand total may well have been recorded in all the twenty-seven ten-kilometre grid squares from which the totals have been made.

1955, when the survey began, are also excluded. The results of the work done until the end of 1963 are summarised in Table 1.

These figures enable one to show by means of a simple graph (Fig. 2) the average number of species that one might expect to find in any given part of the county. This emphasises the fact, seen less readily from the figures themselves, that some parts of the county are floristically richer than others. If the whole county were as productive as these the total number of species found in the county would probably be greater. On the other hand, if all the county were as unrewarding as other portions are, the total number of species would be fewer. The gradient of the line drawn to show the probable average of number of species in a given area is, however, too great in the region of the smaller areas to be of any use in determining the average number of species one would expect to find in an area as small as a tetrad.

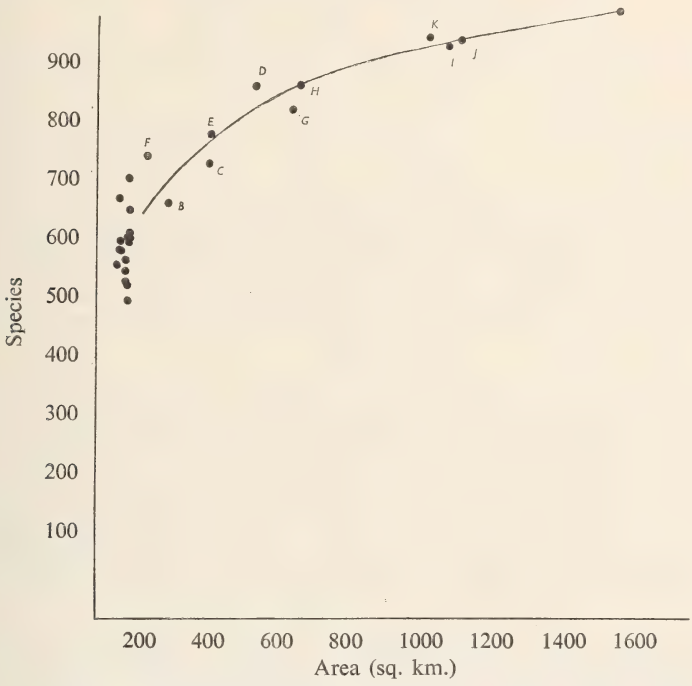


Fig. 2. Distribution of records of species by area in Hertfordshire.

A different result is obtained if a logarithmic scale is used for both the area and the number of species. The curve now approximates to a straight line. Indeed it can in the areas being considered here be assumed to be a straight line. This is shown in Fig. 3 for records from a considerable area of the county, i.e. from 60 square kilometres to the whole of the area. The line drawn shows the expectation of records based on the assumption that as the survey proceeds very few additional species will be found in the whole county or in the larger parts (I, J and K) which are each approximately two-thirds of the county. It is certain, however, that more species already known to appear elsewhere in the county are awaiting record in the smaller areas such as a 10-kilometre square. The present average of species recorded from the complete or almost complete 10-kilometre grid squares (52/33, 52/22, 52/32, 52/21, 52/31, 52/00, 52/10) is 608 and the linear relationship suggests that it should be 623. If additions are made at the rate they have been hitherto in the survey it will probably reach this figure by the time the task is completed.

If this method is to be useful for the purpose in hand it is necessary to consider records from both larger and smaller areas. The species considered are those in Dandy's list, that is 2,137 for the whole of the British Isles (area 310,600 square kilometres) and this

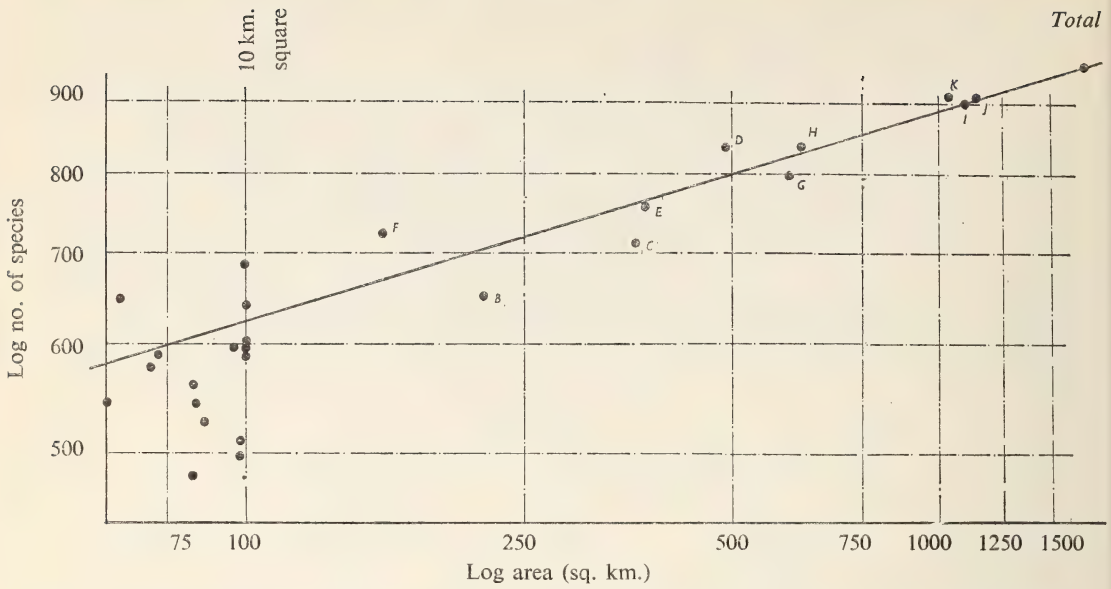


Fig. 3. The expectation of records of species from the larger areas in Hertfordshire. The records shown in Fig. 2 are now shown on logarithmic scales for both area and the number of species recorded for the respective areas. The line drawn to show the average expectation of records is based on the assumption that few additional records will be made for the whole of the county or for the areas shown as I, J and K, each representing about two-thirds of the county. Additional records may, however, be expected from the smaller areas.

gives a maximum reference point. During 1962 close studies were made of 106 small habitats having floras representative of that of the county as a whole. Each study was made in a measured area of five yards radius (65·7 square metres) which was visited twice in the year and the frequencies of the various species noted. The number of species recorded for the studies varied from 82 to 13 with a median of 45. Samples taken from small areas will show a great range in the number of species present as they will include both rich and comparatively barren plant communities. The full results are given in Table 2. Also in

TABLE 2.

Numbers of species recorded in 106 studies in an area of five yards radius (1962).

82, 82, 79, 78, 77, 77, 76, 76, 72, 65, 64, 63, 62, 62, 61, 60, 59, 59, 57, 57, 57, 56, 55, 55, 53, 53, 53, 52, 52, 52, 51, 50, 50, 50, 49, 49, 49, 49, 49, 48, 48, 47, 47, 47, 46, 46, 46, 46, 46, 46, 46, 45, 45, 45, 44, 44, 44, 43, 43, 42, 41, 40, 40, 39, 39, 38, 38, 38, 38, 37, 37, 36, 36, 36, 36, 36, 36, 34, 34, 33, 33, 32, 32, 32, 32, 32, 31, 31, 30, 26, 26, 26, 24, 24, 23, 23, 22, 21, 20, 18, 17, 15, 15, 15, 13, 13.

1962 a town garden with an area, including the house, of 297 square metres, yielded 84 species of wild plants and it is probable that urban sites generally have floras comparable with this.

These figures allow an extension of the line of average expectation (Fig. 4). The change in gradient at 100 square kilometres arises from the fact that Hertfordshire being a lowland county is more floristically rich and varied than the British Isles as a whole. The results show that the average expectation of species in a tetrad is 335 and in a square kilometre 275. It also allows an estimate to be made, with less accuracy, of the maximum and minimum expectation. For a 10-kilometre grid square these are 708 and 500 and the present records for these areas in Hertfordshire range from 688 to 521. The maxima and minima to be expected from a tetrad are 446 and 224 and from a square kilometre 402 and 155.

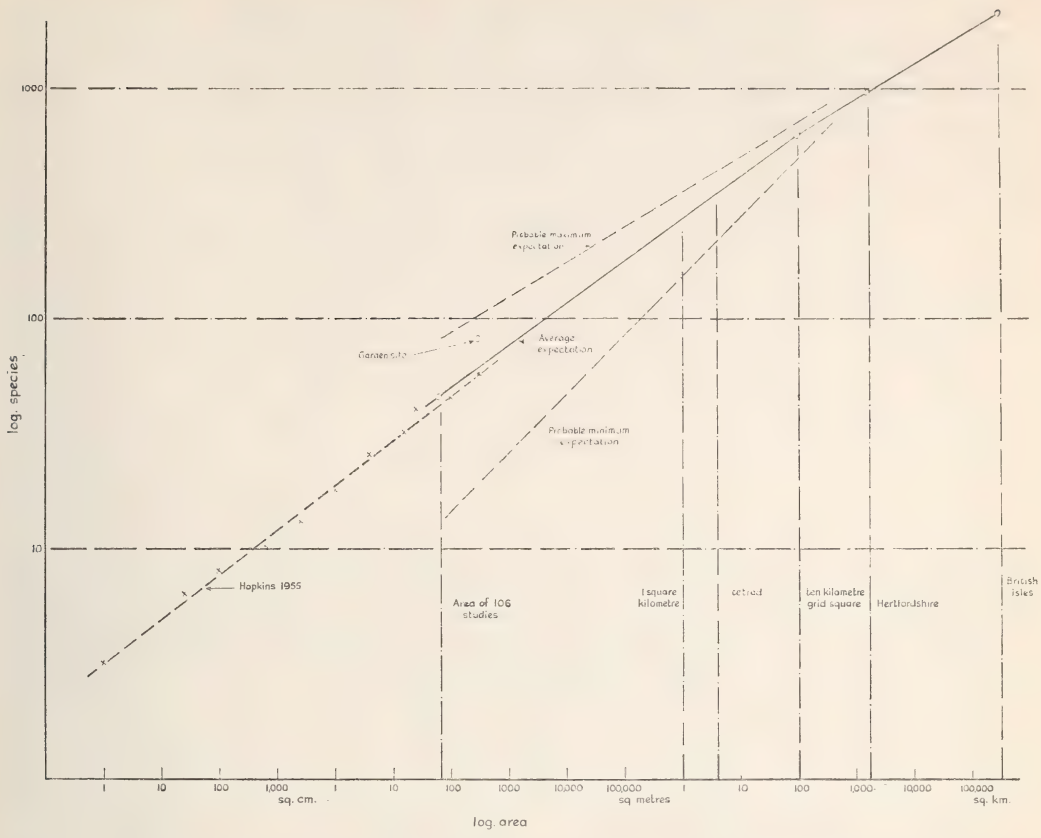


Fig. 4. The average expectation of records of species in Hertfordshire. The dotted line at the lower end of the line of average expectation shows the number of species estimated by Hopkins to occur in various areas in one plant community which he studied. This was not in Hertfordshire and was the community, among the twelve he examined, with the largest number of species. The line drawn to show the average expectation of species is based on two assumptions: the first that the median of the number of species recorded for the 106 studies made of small areas is the average expectation of the number of species that would be found in Hertfordshire in areas of the same size as the areas of the studies: the second that the total number of species to be found in the whole of Hertfordshire is known as this consists of a large number of kinds of habitats each type of which has been studied. The lines of probable maximum and minimum expectation are based on the assumption that the greatest and smallest numbers of species recorded for the 106 studies represent the range of floristic diversity of areas throughout Hertfordshire comparable with the areas of these studies. It is further assumed that this range will diminish as the area is increased to a point somewhat larger than the county.

Records between the average and maximum expectation for tetrads have been obtained as the result of long and thorough search in the field in widely separated parts of the county. The method I have used for enumerating the tetrads is shown in Fig. 5.

31.A. 395* species were recorded by Mr A. G. Brown and Mr H. Williams of the John Innes Horticultural Institution who spent many lunch hours accounting for all the plants that could be found on the Bayfordbury Estate.

31.R. 376 species were recorded largely as the result of a concentrated effort by a number of members of the Wild Flower Society on a one-day field meeting.

32.V. 342 species were found by Dr and Mrs Lloyd-Evans during a number of visits in one season.

Large totals have also been made in some marginal tetrads:

*The number of species given for tetrads from this point in the paper includes some casuals, garden escapes, etc. not included in Dandy's list as I have no easy means of excluding them. They are few and do not affect materially the main conclusions reached

23.B. (area 3·5 square kilometres, expected average 320). 312 species recorded by Mr Harry and Miss Doris Meyer in a semi-urban area they know intimately.

09.R. (area 3·75 square kilometres, expected average 322). 309 species recorded by Mr G. Day who has listed all the plants he could find in Moor Park.

09.J. (area 2·7 square kilometres, expected average 317). 320 species recorded.

E	J	P	U	Z
D	I	N	T	Y
C	H	M	S	X
B	G	L	R	W
A	F	K	Q	V

Fig. 5. The enumeration of tetrads within a 10-kilometre square. Each 10-kilometre grid square (e.g. 52/31) is divided into 25 tetrads which are lettered from A to Z (omitting O to avoid confusion with Q) following the sequence used in the numbering of the 10-kilometre squares themselves in the National Grid. The prefixing numbers, i.e. 42, 51, 52, are omitted as there is no duplication of the second numbers in an area as small as a county. The tetrads thus follow a sequence of 31.A., 31.B., 31.C., etc., beginning at the bottom left-hand corner of the 10-kilometre square.

The average expectation of the number of species to be found in a tetrad may be used as a basis for determining the thoroughness with which an area has been studied. The total number of records made for the 336 full tetrads in Hertfordshire, by the end of 1962, was 72,594, an average of 216 per tetrad. As the expected average is 335 this gives a 61% cover. It would not be possible except by wearisome calculations to determine the cover for marginal tetrads but it is probably at least as high. A summary of the records is given in Table 3.

The peculiar distribution of records in Table 3 arises from targets of 150 and 200 records having been set during the field work. When 200 species had been listed from a tetrad and the rate of recording had slowed down there was a great temptation to move on

Table 3.

Summary of records of species made in individual tetrads in Hertfordshire (1955–1962).

Full Tetrads

395, 376, 342, 307, 297, 295, 294, 293, 292, 290, 289, 286, 281, 280, 278, 276, 274(2), 271, 269(2), 268, 265, 264, 262, 256(2), 255(2), 254, 253, 252, 248(2), 247, 245, 242(4), 241(2), 240(2), 239(2), 238, 237(2), 236(2), 235(2), 234, 233, 232(3), 231, 230(3), 229(4), 228(4), 227(3), 226(3), 225, 224(4), 223(2), 222(6), 221(8), 220(3), 219(4), 218(4), 217(6), 216(3), 215(3), 214(7), 213(4), 212(15), 211(9), 210(13), 209(8), 208(2), 207(13), 206(14), 205(21), 204(15), 203(18), 202(16), 201(29), 193, 185, 183(2), 176, 175, 172, 170, 167, 165, 162, 160(3), 159, 158, 157, 155(2), 154, 153(2), 152(2), 151(2). Total: 72,594.

Marginal Tetrads

320, 312, 309, 289, 283, 280, 265, 254, 252(2), 237, 235, 234, 233(2), 230, 229, 226, 223, 220, 219, 218, 217(4), 216(2), 215, 214(3), 213(4), 212, 211, 209(2), 207(6), 206(4), 205(6), 204(4), 203(10), 202(4), 201(6), 196, 187, 185(2), 172(2), 175, 172, 171, 168, 167, 166, 164, 157(2), 154(2), 153(2), 152, 143, 133, 128, 127, 123, 119(2), 117, 115, 114, 105, 102, 97, 91, 80, 67, 55, 54, 33, 27, 5. Total: 22,911.

and begin work in virgin country. As 200 species is 89% of the probable minimum expectation it has proved to be an exceedingly well-chosen target. In some cases it has been very difficult to find this number. It has, however, resulted in the more intensive

search of the less rewarding country to the neglect of the better areas.

After four years of field work and with records made for complete or almost complete tetrads ranging from 143 to 395 there is no species recorded for all. Thirteen are awaiting record from fewer than five tetrads and another twenty-four from fewer than twenty. The records made so far indicate that between seventy and one hundred species may be in all tetrads. It is obvious that a great deal of work could still be done. It must be left to each worker using tetrads as a basis for recording to decide for himself when a satisfactory cover has been made. I have been able to make some very useful maps with a cover of 61% and to pursue the study much further would occupy a long period of time.

The concept of an average expectation has its limitations. If a cricketer has a batting average of sixty it does not follow that he scored this number of runs in his last innings or will score it in the next, neither does it mean that if one's expectation of life is established as eleven years one will indeed live that time. If the average expectation of species from a tetrad is 335 it does not help the worker in the field to know what to expect from any particular tetrad. I recognise in Hertfordshire twenty different types of habitats and the various tetrads may contain one or more of these. A tetrad with only one or two different habitat types would with effort probably yield only 225 species but one with as many as ten habitat types could well give 400.*

The relationship between species and area in very small areas can be solved only by the very close study of plant communities. This I have not done but it has attracted much attention from ecologists (Arrhenius 1921, 1922, Greig-Smith 1957, Gleason 1922, 1925, Hopkins 1955, 1957, Williams 1943, 1944, 1947, etc.). One of the most thorough studies of this kind was the investigation of twelve very different communities by Hopkins (1955). The number of species he recorded was surprisingly small especially as he included bryophytes and lichens as well as vascular plants. On the other hand his studies were limited to one short period and there were 'additional species' in most of his communities which

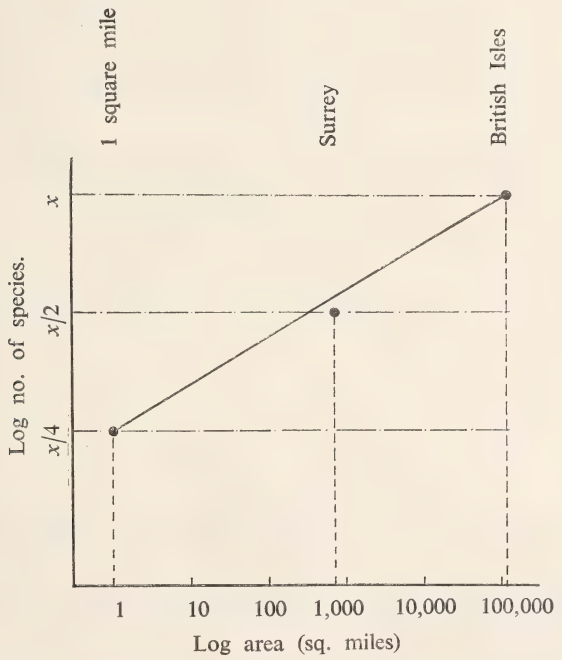


Fig. 6. Watson's Hypothesis. It is obvious from *Cybele Britannica* that Surrey was the county he had in mind.

*This was an experience well known to workers for the Distribution Maps Scheme. One lady returned exhausted after a mapping meeting with the information, amusing to the rest, that she had had a 'big square'. She had only meant that her square contained a large number of plant communities that needed to be visited before the day's work could be said to be done.

did not enter into his samples. I have chosen one of Hopkins' communities with species closely comparable with the lower ranges of my line of expectation and using a log area—log species scale it fits my conclusions perfectly. (Fig. 4.)

Much has been written on the species-area relationship but H. C. Watson was as near the truth as anyone has been or is likely to be when he observed as early as 1835 that 'on the average a single county appears to contain nearly one half the total number of species in Britain; and it would, perhaps, not be a very erroneous guess to say that a single mile contains half the species of a county'. Watson is making in simple language a relationship which, by the use of a logarithmic scale, may be made a linear one (Fig. 6). The matter appears to have rested there until ecologists became interested in the build-up of species in plant communities. It was claimed by Arrhenius (1921) that 'the number of species increases continuously as the area increases' and that this increase could be expressed by the simple formula $\frac{y}{y_1} = \left(\frac{x}{x_1}\right)^n$ when y = the number of species and x = the area containing these species. This gives a linear relationship when log species and log area scales are used as has been demonstrated in this paper.*

The relationship demonstrated by Arrhenius was challenged by Gleason (1922) who suggested that a linear relationship could only be arived at by plotting the number of species against the logarithm of the area. Ecologists have tended ever since to accept this and much work has been done to establish the exact nature of the species—log area curve and the limits of its linear distance. It must be stressed that the problem of the ecologists is different from mine and their attentions have been limited to uniform plant

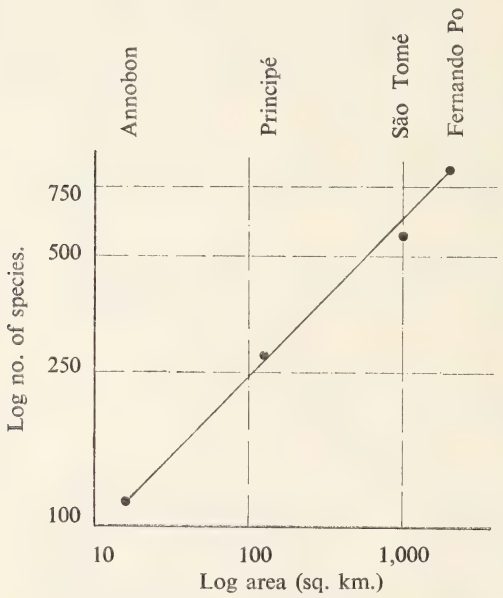


Fig. 7. A comparison of Island Floras, based on the list of 'significant species' given in Exell's *Flora of São Tomé*.

*The above formula can be expressed more simply as $y = ax^n$ where y is the number of species, a is a constant and x is the area. It would appear from the method demonstrated here that the average number of species included in Dandy's list that could be found in any given area of the British Isles can be expressed as

$y = 237\ x^{0\cdot1738}$

given x as the area in square kilometres

or $y = 21.8\ x^{0\cdot1738}$

given x as the area in square metres.

This would give an average expectation of species for a ten-kilometre grid square of 527 which would agree with most botanists' experience in the field.

The corresponding relationship for Hertfordshire and probably most lowland English counties could be expressed as

$y = 275\ x^{0\cdot1772}$

given x as the area in square kilometres

or $y = 21.8\ x^{0\cdot1772}$

given x as the area in square metres.

communities and they have always assumed that the situation changes when the sample areas extend into other communities.

The method outlined here needs to be tested further by making comparisons of the number of species known to occur in the various parts of the British Isles, e.g. England and Wales, Scotland, Ireland and the Isle of Man and also for the separate islands of the Channel Islands group. I give (Fig. 7) its application to some closely grouped islands off the African coast taken from Exell's *Flora of São Tomé*. If the method were confirmed by further data it would be possible to calculate the degree of cover obtained for the Distribution Maps Scheme.

I wish to thank Dr C. B. Williams for suggesting to me the use of the logarithmic scale and helping me to apply it to the Hertfordshire problem; Dr M. C. F. Proctor for drawing my attention to the work done by ecologists with a similar problem; Dr B. Hopkins for allowing me to use the data quoted in his paper; Mr E. S. Edees for helping me to confirm my conclusions by providing me with details of his work in Staffordshire; and my many co-workers who have carried out the wearisome task of providing records from such small areas. Amongst the latter I thank especially Mr and Mrs P. C. Hall who made themselves responsible for collecting records from about 20% of the county in a part which it would have been difficult for me to visit frequently.

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THE TAXONOMY OF *POLYGONUM LAPATHIFOLIUM* L., *P. NODOSUM* PERS., AND *P. TOMENTOSUM* SCHRANK

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Abstract

An account is given of the variation in *Polygonum lapathifolium* L., and of its previous taxonomic treatment. The taxonomic value of various characters is examined. Herbarium, field, and cultivation studies are described. It is suggested that *P. nodosum* Pers, and *P. tomentosum* Schrank are in fact merely parts of the range of variation found within *P. lapathifolium* L. and that they should no longer be regarded as distinct species.

1. Historical introduction

Polygonum lapathifolium L. is a species which exhibits considerable intraspecific variation and is frequently regarded as 'plastic' or 'critical'. There are two main sources of confusion:

(a) From at least the time of Linnaeus many botanists have regarded *P. lapathifolium* as a pale form of *P. persicaria*. Chromosome counts have shown that *P. lapathifolium* has $2n = 22$; while *P. persicaria* has $2n = 44$, and there are constant morphological differences between the species. Identification, however, has often still been made on the basis of perianth colour, and herbarium material of the white form of *P. persicaria* is often incorrectly labelled. *P. persicaria* may easily be distinguished from *P. lapathifolium* since the former has eglandular perianths, peduncles and leaves.

(b) Two other names, *P. nodosum* Pers. (1805) and *P. tomentosum* Schrank (1789) have been described and published as species. Unfortunately, the characters given in the literature for the delimitation of these from *P. lapathifolium* vary from author to author and sometimes they are regarded as synonyms or subspecies, etc.

Britton (1933) states that the only reliable character is the fruits of *P. nodosum* which are 'smaller on the whole, less roundish and with a more ovate outline' than those of *P. lapathifolium*. In fact the size of the fruits, which is discussed later, is largely dependent on the environment of the parent plant. Britton also states that the glands of the peduncles and perianths are less numerous in *P. nodosum*. There is certainly some variation in the density of glands in different populations but there is no agreement in the literature with regard to this character. Tutin (1952) uses 'peduncles sparsely glandular' against 'peduncles densely glandular' to separate *P. lapathifolium* from *P. nodosum* respectively. Tutin also states that *P. lapathifolium* has 'leaves with sunk pellucid glands beneath' while *P. nodosum* has 'leaves with golden glands beneath'. Moss (1914) and Davey (1909) regard the presence of red spots on the stem as characteristic of *P. nodosum*, and Persoon in his original description gives the stem as spotted.

P. tomentosum is a name rarely used in Britain but commonly used by authors on the Continent. Schrank in his original description states that the leaves are tomentose beneath, and it is interesting to note that he does not give a description for *P. lapathifolium*. Plants which correspond to his description of *P. tomentosum* are not uncommon in Britain where they are usually regarded as *P. lapathifolium* or *P. nodosum*.

Schuster (1906) erected an elaborate hierarchy of taxa which he believed to be an approach to a natural system of classification for *P. lapathifolium*. The first division in his key uses the leaf glands character to divide subsp. *verum* which has pellucid glands, from subsp. *punctatum* which has yellow glands. Each of these subspecies is further divided

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into varieties and some of the latter are subdivided into several forms. Most of the characters used for the varietal and form divisions are phenotypically variable, *e.g.* degree of branching, length of internodes, etc. Some of the forms seem rather improbable; in particular f. *natans* Schröter (*Veg. d. Bodensees* **2**, 1902), which is described as inhabiting lakes as a free-floating form with internodes 15 cm long, and with many adventitious roots on the greatly swollen nodes.

Danser (1921) carried out cultivation experiments and found that the variation due to the environment was less than had been previously thought. He lists the following characters as being affected by the environment: plant height and habit, the abundance of branching, the swelling of the nodes and the splitting of the ochreae, the size of the leaves and whether they are tomentose or not. He regards the following characters as constant: the shape of the leaves, the colour of the perianth and other organs, the presence or absence of red spots on the stem, and the shape and the presence or absence of the leaf blotches. On the basis of this work Danser erects a classification in which the shape of the leaves and of the leaf blotches is important. The data presented here agree with Danser's conclusions with the following exceptions:

1. The tomentose leaves were only found during the cultivation experiments on plants raised from the fruits of tomentose plants.

2. The leaf blotches vary even on a single plant and there is even more variation within a population which is otherwise uniform.

Leaves corresponding to two of Danser's taxa have been found more than once on a single plant.

2. Taxonomic characters studied

(*a*) *Vegetative characters*

Habit

The habit and size of the plant have been used by various authors to delimit taxa below the species level, e.g. Fernald (1950). Habit varies with the immediate environment of the plant, and fruits from prostrate plants will produce erect plants in suitable habitats. There appears to be only one taxon in which habit is important. This is subsp. *danubiale* Kern. (= *brittingeri* Opiz) which von Koch (1935) showed retained a prostrate habit in cultivation. This plant does not appear to occur in Britain. With living material the habit has been scored as E = erect or D = decumbent.

Stems

The stem is clearly divided into nodes and internodes and the amount of swelling of the nodes has been used as a diagnostic character. Danser (1921) showed that this swelling was largely the result of moist conditions. Anatomical examination showed that the nodes contained many starch grains and appear to function as storage organs. It is not surprising, therefore, that larger plants growing in favourable habitats with a fairly high water content should have swollen nodes. The stems are sometimes glabrous but are more usually very slightly pubescent; they are never very pubescent. Stem pubescence is, therefore, not suitable for biometrical treatment and has been scored as P = present or A = absent.

The anthocyanin pigment of the stems, which appears as the stem matures, may be in the form of a diffuse, unlocalised, light red colouration, or in the form of discrete, more intensely red spots. The former occurs mainly on the south-facing sides of the stems and is not formed on the ventral side of prostrate stems. It is clearly correlated with the environment and probably with light incidence. The red spots are found on the entire stem surface including the ventral part of prostrate stems although the colour is darker on the parts with the highest light incidence. Both characters were scored as 'present' or 'absent'.

Leaves

The leaves of *P. lapathifolium* are lanceolate to linear-lanceolate and vary in size with

the environment. The length of the leaves was measured in centimetres from the apex to the point of fusion with the petiole. The maximum breadth was also measured in centimetres. An index was then obtained by dividing the length by the breadth. The presence or absence of a leaf blotch, and of hairs on both surfaces was recorded. Where the tomentose condition was found this was recorded as T. Yellow glands on the lower surface were recorded as P if present; the A, recording absence of yellow glands, indicates that the glands were in fact pellucid.

Ochreae and ochreolae

The fused membranous stipules known as ochreae which are characteristic of the family Polygonaceae are of little taxonomic value in section *Persicaria* in which *P. lapathifolium* is placed. The cilia of the ochreae are often said to be longer in *P. persicaria* than in *P. lapathifolium*, and some authors regard the latter as eciliate. This is rarely if ever quite true as it is usually possible to find at least a few short cilia. The difference in length is an indifferent character for separating the species.

The ochreolae or floral ochreae are found in the inflorescence and like the ochreae may be ciliate or eciliate, glabrous or pubescent, and glandular or eglandular.

Peduncles

The peduncles of *P. lapathifolium* are glandular with stalked glands. Those of *P. persicaria* are usually regarded as eglandular. Schotsman (1950), however, records the presence of 'sometimes a few stalked glands' on the peduncle of *P. persicaria.* It is not impossible that this plant was an anthocyanin-containing specimen of *P. lapathifolium.* The peduncles are also occasionally pubescent.

(*b*) *Flower and fruit characters*

Flowers

The flowers of *P. lapathifolium* are hermaphrodite, and the perianth segments, which are free, are not divided into sepals and petals. They are not large, seldom reaching 4·0 mm in length and they remain attached to the fruit when it is shed. The perianth segments of *P. lapathifolium* are glandular and those of *P. persicaria* are usually regarded as being eglandular. References to microscopic perianth glands on *P. persicaria* have been found on herbarium sheets in the British Museum and Schotsman (1950) records 'pluricellular yellowish glands on some flowers' of this species. I have not seen these; they are in any case of a different order of magnitude from the perianth glands in *P. lapathifolium* which can be clearly seen with a hand lens. There are usually 4 perianth segments (occasionally 5) in *P. lapathifolium* and 6 (5) stamens with 2 (3) styles. The styles of *P. lapathifolium*, unlike those of *P. persicaria*, are separate to below the middle.

The perianth glands were scored as present or absent, and the number of perianth segments was recorded on fresh material. The colour of the perianth was scored as Pk = pink (i.e. with anthocyanin) or W = white (i.e. without anthocyanin). The number of stamens and styles was also recorded.

Fruit

The 'seeds' of *P. lapathifolium* are in fact nuts which fall from the parent plant with the dead perianth still attached. The length of the perianth relative to the fruits has been used by some authors with but little success. Moss (1914) records all species in section *Persicaria* as having nuts 'as long as the persistent perianth' except for *P. nodosum* which had nuts 'scarcely as long as the perianth'. Styles (1962) found this relationship of use in section *Polygonum* but it appears to be of little value in section *Persicaria.* The length and maximum breadth of the nuts (without perianth) were measured in millimetres to the nearest 0·1 mm, each set of measurements being on a sample of mature nuts usually fifty or more in number. An index was obtained by dividing the length by the breadth. The arithmetic mean, standard deviation and the range of these measurements were calculated.

TABLE 1

Data from herbarium material.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*
Leaf length	13·3	12·3	13·4	10·0	13·7	6·8	6·5	14·3	10·2	7·3
Leaf breadth	3·2	3·8	3·9	2·5	4·1	1·3	1·3	4·1	2·3	2·4
Leaf index	4·2	3·3	3·4	4·0	3·4	5·2	5·0	4·5	4·4	3·0
Leaf blotch	P	P	P	A	A	P	P	P	P	P
Leaf hairs above	P	P	P	P	P	P	A	P	P	P
Leaf hairs beneath	P	P	P	P	P	T	P	P	P	T
Leaf yellow glands	P	P	P	A	A	P	P	P	P	A
Ochrea cilia	A	A	A	A	A	A	P	P	P	P
Ochrea hairs	P	P	P	A	A	P	P	P	A	P
Perianth colour	Pk	Pk	Pk	?	W	W	W	Pk	W	Pk
Perianth glands	P	P	P	P	P	P	P	P	P	P
Peduncle glands	P	P	P	P	P	P	P	P	P	P
Peduncle hairs	P	P	A	A	A	A	A	A	A	A
Ochreola cilia	A	A	A	A	P	A	P	P	P	P
Ochreola hairs	A	A	A	A	A	A	P	P	A	A
Stem hairs	P	P	P	P	P	P	A	P	A	P
Stem red spots	A	A	P	A	A	A	P	P	A	A

Origin :

1. European Russia, 1908 (**BM**, No. 95/6/8/2848).
2. Tepelen, Albania, 1935 (**BM**, No. 95/6/8/2420).
3. Athens, Greece, undated (**BM**, No. 95/6/8/789).
4. Valais, Switzerland, 1895 *R. Murry* (**BM**, No. 95/6/8).
5. Barcelonia, Spain, 1923 *F. Jenner* (**BM**, No. 95/6/8a/4857).
6. Surrey, 1959 *B. A. Kneller* (Herb. Univ. Leicester).
7. Scotland, 1959 *U. K. Duncan* (Herb. Univ. Leicester).
8. Tlemcen, Algeria, 1929 (**MANCH**).
9. Osses, France, 1961 *E. K. Horwood* (Herb. Univ. Leicester).
10. Thraki, Greece, 1961 *P. W. Ball* (Herb. Univ. Leicester).

The nuts of *P. lapathifolium* are usually ovate, biconcave to planoconcave, brown and shiny; a few trigonous nuts also occur.

(*c*) *Results*

Herbarium data

More than 500 herbarium specimens have been seen and about 150 (well-preserved specimens selected to cover a wide geographical area) have been scored. Some typical scoring data are presented in Table 1. It will be seen that the length and breadth of the leaves varies considerably but that there is much less variation in the leaf index. The leaf blotch is usually present and has been found in most cases but it is not always easy to see on preserved material and is, therefore, an uncertain character to score on herbarium material. The perianth colour usually preserves well enough for scoring purposes but in the case of specimen No. 4 it was no longer possible to see it, perhaps because of the age of this specimen.

Data from field material

About 40 natural populations were scored and the data from some typical populations are given in Table 2.* In the case of measurements, the entries in the table are means. Where there was variation in quantitative (scored) characters, as in numbers of flower parts, within a population, the less common type is given in brackets. Although the leaf blotch was present in all the populations the amount of pigment present in each leaf varied widely within each population. It appeared that the plants growing in less exposed situations had less pigment.

*Small populations are usually quite uniform and this becomes evident quite rapidly. With larger populations, e.g. No. 1 in Table 2, about 100 specimens selected at random were scored.

TABLE 2
Data from natural populations

	1	*2*	*3*	*4*
Habit	E	E	E	E
Stem pigment	P	P	P	A
Stem red spots	P	P	P	A
Stem hairs	P	P	P	A
Leaf length	12·9	7·0	15·1	9·4
Leaf breadth	3·2	1·5	4·6	2·5
Leaf index	4·1	4·6	3·3	3·8
Leaf hairs above	P	P	P	P
Leaf hairs beneath	T	T	P	T
Leaf yellow glands	P	P	P	A
Leaf blotch	P	P	P	P
Ochrea cilia	P	P	P	P
Ochrea hairs	P	P	P	P
Peduncle glands	P	P	P	P
Peduncle hairs	A	A	A	A
Perianth glands	P	P	P	P
Perianth colour	Pk/W	W	Pk	Pk
Perianth segments	4 (5)	4	4	4
Stamens	6	6	6	6
Styles	2 (3)	2	2	2
Ochreola cilia	P	P	P	P
Ochreola hairs	P	A	A	A
Ochreola glands	P	P	P	P

The habitats: 1. Borough-on-the-hill v.c. 55. 19 July, 1959. A large population of c. 2–3,000 plants in wheat and barley fields.
2. Skeffington, v. c. 55. 31 July, 1960. Hollow by roadside containing water.
3. Billesdon, v.c. 55. 18 Sept., 1960. Damp ground by side of road.
4. Burton Overy, v.c. 55. 24 July, 1961. Roadside, bare patch of ground with few other plants.

TABLE 3
Data from cultivated plants.

	1	*2*	*3*	*4*	*5*	*6*
Habit	E(D)	E(D)	E(D)	E	D	E
Stem pigment	P	P	P	P	P	P
Stem red spots	A	P	P	P	P	A
Stem hairs	A(P)	P	P	P	P	P
Leaf length	3·7	6·7	5·5	7·8	9·2	8·2
Leaf breadth	0·7	1·6	1·3	1·9	1·9	2·0
Leaf index	5·3	4·3	4·2	4·1	4·6	4·1
Leaf hairs above	P	P	P	P	P	P
Leaf hairs beneath	P	T	T	T	T	T
Leaf yellow glands	P	P	P	P	P	P
Leaf blotch	P	P	P	P	P	P
Ochrea cilia	P	P	P	P	P	P
Ochrea hairs	P	P	P	P	P	P
Peduncle glands	P	P	P	P	P	P
Peduncle hairs	A	A	A	A	A	A
Perianth glands	P	P	P	P	P	P
Perianth colour	W	Pk	W	W	W	Pk
Perianth segments	4(5)	4	4	4(5)	5	4
Stamens	6	5	6	6	6	6
Styles	2(3)	2	2	2	2	2
Ochreola cilia	A	A	P	P	P	A
Ochreola hairs	A	A	A	A	P	A
Ochreola glands	A	A	P	P	P	P

Origin of nuts: 1. Cambridge Botanic Garden; collected Ryston, Norfolk.
2. Botanical Garden, Lund, Sweden, as *P. lapathifolium* subsp. *nodosum*.
3. as 1. Collected West Dereham, Norfolk, as *P. nodosum*. Grown 1959.
4. as 3. Grown 1960.
5. Habitat 1 in Table 2. Plant with no anthocyanin in perianth.
6. Hortus Botanicus Bergianus, Stockholm, as *P. lapathifolium* subsp. *nodosum*.

PLATE 15a

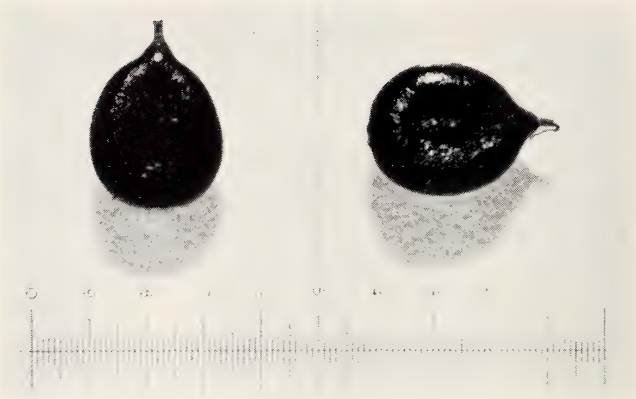


PLATE 15b



(a) Fruits of *Polygonum lapathifolium* and (b) fruits of '*P. nodosum*.' The scale is 1 cm divided into 10mm.

Data from cultivation experiments

Many plants have been grown both in the greenhouse and in the University Botanic Garden at Leicester. Some typical results from these cultivated plants (usually grown in populations of not less than ten individuals) are presented in Table 3. They have been scored in the same way as the natural populations and show the same kind of intraspecific variation. The population (No. 2) which was grown from Swedish nuts had five stamens instead of the more usual six. Careful observation of the plants grown from the fruits of scored plants showed that the Critical Characters (see later) were stable in cultivation and did not vary qualitatively with the environment.

Fruit Data

The averages of the data for all the nuts measured are given in Table 4. From this it is clear that the British and foreign material is essentially similar. In Table 5 data for *P. lapathifolium* (No. 1 in Table 3), *P. nodosum* (No. 3 in Table 3), and *P. persicaria* (from the same source as the other specimens), grown under uniform conditions are given. From these data it is clear that, while there is no significant difference between *P. lapathifolium* and *P. nodosum*, *P. persicaria* has narrower nuts in relation to the length and this produces a significant difference in the index obtained. Typical nuts from these samples of *P. lapathifolium* and *P. nodosum* are shown in Plate 15 and it can be seen that they are extremely similar.

TABLE 4

Combined data for all fruits measured in the *P. lapathifolium* complex

		British	*Foreign*	*Total*
Length	mean	2·67	2·61	2·64
	s. d.	0·14	0·12	0·13
	range	2·0–3·3	2·2–3·0	2·0–3·3
Breadth	mean	2·38	2·15	2·27
	s. d.	0·14	0·12	0·13
	range	1·7–2·9	1·8–2·5	1·7–2·9
Index	mean	1·12	1·22	1·17
	s. d.	0·04	0·05	0·045
	range	1·0–1·3	1·1–1·5	1·0–1·5
Shape	% *biconcave*	99·4	99·0	99·2
	% *trigonous*	0·6	1·0	0·8
Average weight (mg)		2·94	2·19	2·57

In all cases the surface was shiny and the colour brown to brown-black.

TABLE 5

Fruit data. Plants grown under uniform conditions in greenhouse 1959.

		P. lapathifolium	*P. nodosum*	*P. persicaria*
Length	mean	2·47	2·54	2·62
	s. d.	0·13	0·15	0·14
	range	2·2–2·7	2·3–2·9	2·3–2·9
Breadth	mean	2·32	2·33	2·07
	s. d.	0·16	0·15	0·15
	range	2·0–2·6	2·0–2·7	1·7–2·4
Index	mean	1·05	1·08	1·27
	s. d.	0·07	0·01	0·04
	range	1·0–1·2	1·0–1·2	1·1–1·4
Shape	% *biconcave*	100	100	57
	% *trigonous*	0	0	43

Styles (1962) found that fruit length was very stable in section *Polygonum* and useful in the delimitation of species in that section. The data presented here, however, indicate that this is not so in section *Persicaria*. Not only do different species have much the same length of nut but there is also some variation with environment, *e.g.* in the *P. nodosum* of Table 5, the nuts of the original wild material had a mean length of 2·95 mm; the maximum breadth mean was 2·68 mm, and thus the mean index of 1·11 was the most stable character.

3. The breeding system

The relatively slight variation within the populations and the similarity of plants in cultivation to their parent plant, together with the much greater variation between the populations, suggests either apomixis or a high frequency of inbreeding. No evidence has been obtained of apomixis but inbreeding is apparently the rule. The anthers appear to dehisce before the flower buds open and pollen has been found on the stigmas of quite immature flowers. The pollen produced is sticky and there are relatively few grains; there are no regular insect visitors apart from aphids and these are usually found on the leaves and peduncles. It appears, therefore, that there is no mechanism for outbreeding and that *P. lapathifolium* consists of a number of pure breeding lines separated by the barrier of autogamy.

4. The critical characters

The various attempts to systematise the wealth of variation, both genotypic and phenotypic, found in *P. lapathifolium*, described in outline in the introduction, are unsatisfactory. Four characters were, therefore, chosen for investigation and named for convenience the Critical Characters. They were the presence or absence of:

1. red spots on the stem
2. yellow glands in the leaf
3. tomentose leaves
4. anthocyanin in the perianth.

These were chosen because:

1. they do not vary from one part of the plant to another
2. they were found to be constant in cultivation
3. the three taxa considered here have been distinguished by several authors using various combinations of these characters
4. they have been used by previous authors to define taxa below the species level.

There are theoretically sixteen possible combinations of these four characters. Of these combinations herbarium specimens have been found for twelve. The four not found are not correlated in any way and in the absence of contrary evidence may be presumed to exist. The possible combinations, together with the scoring of other characters on the specimens found, are given in Table 6. From this it seems clear that:

(a) these Critical Characters account for a large part of the variation within the species.

(b) there is no other character, at least amongst those scored, which is correlated with them.

5. Discussion and conclusions

Polygonum lapathifolium is a species which exhibits a wide range of variation and may reasonably be described as critical. The previous attempts to classify this variation either into a number of species or into taxa below the level of species fail, largely because of the large number of specimens which do not readily fall into any of the suggested groups. The species appears to consist of several distinct autogamous pure lines which differ from each other usually by only one or two characters. Over the whole range of variation, however, the canonical extremes appear to be quite different and an author with two of these extremes and no knowledge of the whole situation and the intermediate forms will naturally describe two species. If an intermediate form is later found it will probably be regarded as a hybrid. The most important variable characters appear to be those referred

TABLE 6
The Critical Characters

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*
Stem red spots	P	P	P	P	P	P	P	P	A	A	A	A	A	A	A	A
Leaf yellow glands	P	P	P	P	A	A	A	A	P	P	P	P	A	A	A	A
Leaf, tomentose	P	P	A	A	P	P	A	A	P	P	A	A	P	P	A	A
Perianth colour	Pk	W	Pk	W	Pk	W	Pk	W	Pk	W	Pk	W	Pk	W	Pk	W
Leaf length	5·2	–	19·5	14·7	6·1	5·6	–	–	4·5	9·2	14·7	15·1	9·3	–	6·1	6·0
Leaf breadth	1·3	–	4·2	3·8	1·3	1·1	–	–	1·2	2·8	3·9	4·7	2·0	–	1·3	1·1
Leaf index	4·0	–	4·7	3·9	4·7	4·8	–	–	3·8	3·3	3·8	3·2	4·6	–	4·7	5·4
Leaf blotch	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Leaf hairs above	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Leaf hairs beneath	T	–	P	P	T	T	–	–	T	T	P	P	T	–	P	P
Ochrea cilia	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Ochrea hairs	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Ochreola cilia	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Ochreola hairs	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Stem hairs	P	–	P	P	P	P	–	–	P	P	P	P	P	–	P	P
Number found*	21	0	7	15	10	1	0	0	1	2	4	5	2	0	5	5

* Among herbarium specimens that could be scored with certainty for perianth colour.

to above as the Critical Characters, but there are other less discrete variations which may also be important. Only controlled cultivation on a large scale would reveal the limits of genetical variation. Since all the pure lines will continue to exist and will not blend or segregate because of the autogamous breeding system, it is clear that *P. lapathifolium* will continue to consist of a number of distinct pure lines—at least twelve and probably more—and to name all these lines would only add to the existing confusion. It would probably be possible to give names to many combinations of characters so that a *Rubus*-like situation on a smaller scale would result. For a taxonomist taking a special interest in *P. lapathifolium* the 16 combinations of the Critical Characters could form the basis of a classification but for less specialised use, e.g. in floras, I suggest that the species *P. lapathifolium* should not be subdivided.

6. Taxonomic Revision

P. LAPATHIFOLIUM L. Spec. Pl. ed 1; 360 (1753).
Principal synonyms:
P. tomentosum Schrank, Baiersche Flora (1789)
P. nodosum Pers., Synopsis **1** (1805).
P. brittingeri Opiz, Natural. **8**: 74 (1824).
P. danubiale Kern., Oesterr. Botan. Zeitschr. **25**: 255 (1875).
P. petecticale Druce, Fl. Bucks. 287 (1926); *Rep. Bot. (Soc.) Exch. Cl.*, (1926).

Annual. Plant erect, decumbent or nearly prostrate. Stem green often becoming red from the base in the autumn, slightly pubescent, with or without discrete red spots. Leaves 3·7—15·1 × 0·7—4·6 cm, 3·0—5·3 times as long as broad, lanceolate, usually with dark central blotch, usually pubescent on both surfaces, with or without tomentose hairs beneath, glandular beneath with either pellucid or golden-yellow glands. Ochreae not or very shortly ciliate, pubescent, occasionally glandular. Peduncle glandular, with or without a few short hairs. Inflorescences dense-flowered, one or many, terminal. Perianth glandular, with or without pink anthocyanin, with 4 (5) segments. Stamens (5) 6; styles 2 (3). Ochreolae not or shortly ciliate, glabrous or slightly pubescent, sometimes glandular. Fruits biconcave, rarely trigonous, *c.* 2·5 × 2·25 mm, brown to dark brown, shiny.

Holotype. The specimen in the Linnean Herbarium (**LINN**) London is clearly not *P. lapathifolium* and does not appear to be a herb at all but to be a branch of a shrub. Fortunately Linnaeus refers in *Species Plantarum* to the specimen in *Hortus Cliffortianus*, and this specimen, which is in the British Museum Herbarium (**BM**) (No. 42/2), agrees with Linnaeus's description and with the generally accepted concept of *P. lapathifolium*.

Geographical Distribution

P. lapathifolium is a widespread weed in Britain and it is probably present in all vice-counties. Simmonds (1945) suggests that it may be more common in the south than in the north of Britain but there is no evidence that this is more than a reflection of the more intensive agriculture in the south. It is found as a weed throughout Europe to 65° N in Iceland (Moss 1914), 68° N in Lapland (Lindman 1926), 70° N in Norway (Blytt 1906), and in Russia to 70° 20′ N (Komarov 1936). It is also recorded from north India (Hooker 1890), South Africa (Moss), North, Central and South America and the West Indies (Small 1913). It is regarded as native in Europe and Asia and as a naturalised alien in America and Australasia. Specimens very similar to the British and European material have been seen in the British Museum Herbarium from the United States, Canada, Japan, China, and Tibet ('marshy places near Lhasa'). It is a weed of arable land, disturbed ground, and river banks and appears to be relatively intolerant of competition. It probably, therefore, does not extend far beyond the limits of cultivation.

Acknowledgements

My grateful thanks are due to Professor T. G. Tutin, under whose supervision this work was carried out, for his advice and encouragement.

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Atlas of the British Flora. Edited by F. H. Perring and S. M. Walters. Pp. xxiv + 432. Botanical Society of the British Isles and Thomas Nelson and Sons Ltd., London and Edinburgh, 1962. Price £5 5s. 0d.

The proposal for mapping the distribution of British plants made by Professor A. R. Clapham at the B.S.B.I. Conference in 1950 has been most faithfully and ably implemented under the editorship of Drs. Perring and Walters. Between 1954 and 1960 over 1,500,000 field records, contributed by some 1,500 amateur and professional botanists, as well as a vast accumulation of data from literature and herbaria, were sorted and, by ultra-modern mechanical methods, tabulated on to maps.

The superlative volume which was the end product of this activity was made possible only by the support of the Nuffield Foundation and the Nature Conservancy, who generously financed the scheme from its inauguration.

The *Atlas* contains over 1,600 maps, preceded by a 15-page introduction covering the history of the mapping of plant distribution, an account of the origin and history of the B.S.B.I. Maps Scheme and details of the production of the *Atlas*. The maps are arranged, in most cases, four to a page, and on them are depicted the distributions of about 1,700 species of flowering plants and vascular cryptograms which are found in Great Britain and Ireland. The basic recording unit is the 10 × 10-km. square of the Ordnance Survey National Grid, and each map contains approximately 3,500 of these. It is indeed an achievement that all but 7 of the 3,500 squares were visited by botanists during the course of the survey and floristic lists compiled from each of them.

A brief study of some of the maps quickly reveals a number of interesting facts – the truly southern distribution of such species as *Euonymus europaeus*, *Tamus communis*, *Rosa arvensis*, *Viburnum lantana* and *Euphorbia amygdaloides*. The typical northern distribution as shown by *Polygonum viviparum*, *Betula nana* and *Juncus trifidus*. The western distribution of *Lotus hispidus* and *Rubia peregrina*, and the eastern distribution of *Chenopodium botryodes*, *Trifolium ochroleucon*, *Verbascum pulverulentum* and *Sonchus palustris*. The scarcity in Scotland, and in Ireland, of such common lowland English weeds as *Aethusa cynapium*, *Euphorbia peplus*, *Convolvulus arvensis*, *Tragopogon pratensis* subsp. *minor* and *Hordeum murinum*. The paucity in western England of common southern plants like *Silaum silaus*, *Bryonia dioica*, *Lysimachia nummularia*, *Primula veris*, *Galium verum* and *Carex hirta*, and the very restricted distribution of *Oenanthe crocata* in East Anglia. A more detailed study of the maps shows that the rarer species have been very well documented, but that, in southern England at least, many common species have been under-recorded.

The 10 × 10-km. square is undoubtedly a much more adequate recording unit than the vice-county, though, unfortunately, the placing of a single dot within a square still does not indicate the frequency of a species within that square. Thus, for *Clematis vitalba*, the dot in 51/28 represents isolated occurrences about Willesden, Kingsbury, Highgate and Hampstead, where the plant is an introduction, while the dot in 51/09 represents the species as abundant and native. Many other instances come readily to mind. It is, however, very difficult to see how this problem may be overcome without introducing a mass of symbols indicating different degrees of frequency or rarity.

The selection of species to be mapped must have been a complex one for the eminent committee appointed for the task, and so far as native species are concerned there appears to be little to criticise. The choice of alien species is less satisfactory, and too many well-established species have been excluded – to name but a few – *Sisymbrium loeselii*, *Rosa rugosa*, *Astrantia major* (perhaps native in Salop?), *Falcaria vulgaris*, *Erica lusitanica*, *Trachystemon orientalis*, *Campanula medium*, *Cicerbita macrophylla*, *Lagarosiphon majus* and *Lilium pyrenaicum*. Was it lack of data, or space, that compelled their exclusion? If not, I feel that they have as great a claim to inclusion as *Fagopyrum esculentum*, *Rorippa austriaca*, *Coronilla varia*, *Laburnum anagyroides*, *Cerastium tomentosum*, *Sedum spurium*, *Tilia* × *europaea* and *Phalaris canariensis* – the latter, in particular, does little more than plot the distribution of pet-birds and rubbish-tips.

Hybrids are mostly excluded, though a map is given of the distribution of *Apium nodiflorum* × *repens*. I should like to have seen maps of *Equisetum* × *litorale*, *Geum* × *intermedium* and *Senecio* × *ostenfeldii* but it is likely that these will appear with others in the critical supplement to the *Atlas* now in the course of preparation.

Subspecies are also omitted with the exception of those of *Arenaria norvegica*, *Armeria maritima* and *Asparagus officinalis*. It would have been useful if others had been given, particularly *Fumaria muralis*

subsp. *boraei*, which has a very different distribution from *F. muralis* subsp. *muralis*. We are, however, promised a further selection of subspecies in the critical supplement.

Looking through the maps a number of random points come to mind – is not *Clematis vitalba* native on the Magnesian Limestone of Yorks. and Durham? How many of the dots on the map of *Ranunculus aquatilis* refer to *R. peltatus* which is best regarded as a distinct species? The 'introductions' shown for *Aconitum anglicum* may well refer to hortal forms of *A. napellus*. Are many of the old records of *Chenopodium urbicum* valid – or were they merely forms of *C. rubrum? Herniaria glabra* is shown as a casual in 51/18, yet it has persisted as an introduction in the 'square' for at least 20 years. *Silene nutans* could be found in its Surrey (51/17) station well after 1930. May not *Euphorbia lathyrus* be native in some woods in southern England – particularly in Surrey and Sussex? *Anthriscus caucalis* is often only casual in some of its inland localities.

The method of using different symbols on a single map to show pre- and post-1930 records is a very good one that could have been usefully extended to many other diminishing species, e.g. *Berberis vulgaris*, *Erophila verna*, *Viola palustris*, *Geranium lucidum*, *Saxifraga tridactylites*, various species of *Potamogeton* and *Orchis simia*. It is helpful also in showing the spread of a number of adventive species, e.g. *Impatiens capensis*, *Heracleum mantegazzianum*, *Buddleja davidii* and *Veronica filiformis*, since 1930. Curiously, *Impatiens glandulifera* is not included under this method.

Yet another useful idea is the system of showing inland records on railway ballast of certain coastal species. e.g. *Cochlearia danica*, *Cerastium atrovirens* and *Corrigiola litoralis*.

A major feature of the work is the inclusion of a series of transparent overlay maps which nestle neatly in a pocket at the end of the volume. These show rivers, vice-counties, altitude, location of chalk and limestone, average temperatures, humidity and rainfall. It is by the combined use of the overlays and the maps that the correlations between plant distribution, climate, altitude and soil are revealed and a veritable mine of information made readily available. This is the vital purpose for which the *Atlas* was created, and for which contributors and editors alike may take the greatest credit.

An appendix lists vice-county records excluded from the maps, usually because of the absence of localized records.

Lastly, there is a short bibliography, which in my opinion is quite inadequate for a work of this importance; and it is an important work – one of the most significant books published on the flora of our islands. It will remain for ever a monument to the enthusiasts who created it.

D. H. KENT

Native Wild Plants of Eastern Canada and the adjacent northeastern United States. F. H. Montgomery. Pp. xxxvi + 193, with 24 small coloured plates and 298 line drawings in the text. Toronto: Ryerson Press. (Agents: Bailey Bros. and Swinfen Ltd.), 1963. Price £2 2s.

California Desert Wild Flowers. Phillip A. Munz. Pp. 122, with 96 colour photographs and 172 line drawings in the text, 2 maps. Berkeley and Los Angeles: University of California Press (Agents: Cambridge University Press), 1963. Price £1 4s.

Here are two more little flower-books, both written *con amore* by professors for amateurs in opposite corners of the North American Continent. Professor Montgomery's book, illustrated with his own drawings, will be appreciated by those who swear by our Collins 'Pocket Guide to Wild Flowers' but, as it deals with only about 400 native and mostly herbaceous wild flowers of eastern Canada, and excludes the grasses, sedges and ferns, it is perhaps more for the beginner on the spot than for the visitor from Britain. Prof. Munz's Californian desert book will have a wider appeal because it deals with a single, and most remarkable, vegetation type. I suppose that less than half a dozen of the strange and beautiful plants shown and described here will ever be found in Britain, even in gardens, but very many of us will visit southern California and, with vivid memories of Walt Disney's film or the Sherman Hoyt Cactus House at Kew, will want to brave the heat and the rattlesnakes. Prof. Munz tells us in less than three pages most of what we need to know about plant life in the Mojave and Colorado Deserts. His selected shrubs and herbs – with such fascinating common names – are placed in five sections, the first devoted to ferns and cone-bearers while the remaining four are based on flower-colour.

N. Y. SANDWITH

Skånes Flora. Henning Weimarck. Bokförlaget Corona AB, Lund, 1963. Price 45 Swedish Kronor

Skåne, the southernmost province of Sweden, has a rich and interesting flora. Professor Weimarck's new account of it (in Swedish) will be welcomed by botanists interested in phytogeography and taxonomy as well as by those who live in or visit the region covered.

To the English reader this book contains some features which will be unfamiliar in local floras. Most important of these is that it really is a flora in the fullest sense of the word. It contains clear but concise descriptions of families, genera and species, as well as keys for identification, so that it forms a complete field guide to the vascular plants of Skåne. Chromosome numbers are also given, those determined from native material being distinguished by asterisks; these provide impressive evidence of the activity of Swedish cytologists.

Ecological and distributional data, including the presence or absence of species in the neighbouring provinces and in Denmark, are also given, and there is a good glossary.

The book embodies the results of many years of botanical exploration carried out by Professor and Fru Weimarck, at first by bicycle and later by car, with the assistance of a number of others. It is excellently printed and strongly bound, and provided with a useful map. It can be strongly recommended to anyone interested in Swedish plants and is a necessity for botanists visiting the beautiful and still largely unspoiled province of Skåne.

T. G. Tutin

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