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Epipactis leptochila (Godfrey) Godfrey and E. phyllanthes G. E. Sm. occurring in South Northumberland on lead and zinc soils

A. J. RICHARDS and G. A. SWAN

University of Newcastle-upon-Tyne

ABSTRACT

Epipactis leptochila (Godfrey) Godfrey has been found in 11 stations in S. Northumberland (v.c. 67), 180 miles north of the nearest previously known site. Plants appear to be typical except for short perianth segments. All sites are under birch and associated with apparently toxic heavy metal soils; one site in particular has a very high level of zinc. Most sites are on apparently natural gravels beside the Rivers Tyne and South Tyne, but one is by a disused lead mine. At another lead mine E. phyllanthes G. E. Sm. var. pendula D. P. Young is reported. This species is new to South Northumberland, the nearest previously reported station being in south-west Furness (v.c. 69b). On lead spoils at another site E. helleborine was found; depauperate forms of this species resemble E. leptochila vegetatively. The significance of Epipactis on heavy metal sites in Northumberland is discussed.

INTRODUCTION

Epipactis leptochila (Godfrey) Godfrey was said by Young (1962a) to be confined in England to calcareous areas in the south, where it is frequent very locally 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 Mendips, and in two localities in Devon (Perring & Walters 1962). It also occurs in widely separated localities in France, Germany, Denmark, Sweden and Switzerland. The plant is said to be strongly calcicolous – much more so than any other European species of Epipactis. Every station for which geological data are available is on calcareous rock, and these comprise the great bulk of records. Conversely no station had been recorded on neutral or acid rocks. The usual habitat is in beech-woods under heavy shade, and with only a sparse ground flora; it often occurs with E. helleborine (L.) Crantz and E. purpurata Sm. From these, and from other related Epipactis species, it is readily distinguished by rather narrow, yellowish, two-ranked leaves, relatively few, yellowish flowers, which are held in an inclined position and which lack a rostellum, with rather long, narrow perianth segments, and a patent epichile which is longer than broad, and which equals or exceeds the hypochile. The anthers are borne on a stalk (cinandrium) in such a way that when viewed sideways a distinctive hole is visible between the column and anther (Young 1962a). As such it is usually a rather distinct species, and it has not normally been considered as being a critical member of this difficult genus.

It was therefore surprising to receive from M. Rawes and B. M. Cunliffe, towards the end of 1973, a record of E. leptochila from birch scrub on the east bank of the River South Tyne near Williamsonst, S. Northumberland (v.c. 67), 4 miles north-north-east of Alston (grid references of all sites are withheld, but have been deposited with the Biological Records Centre, Monks Wood). This identification had been confirmed by Dr J. T. Knight. It later transpired that the same colony had been observed and photographed a month earlier on the 21st July 1973 by Dr A. W. Williams, who had known it for some years.

HABITAT AND DISTRIBUTION

The colony was located on the 14th July 1974 by G. A. and M. Swan, although on that date it was only in bud, and a further search by A. J. Richards and G. A. Swan on 31st July revealed that
it was part of a larger colony of Epipactis with about 290 flowering spikes within a limited area. A voucher specimen was taken (herb. Swan) and some mature flowers were pickled in 70% ethanol. Reference in the field to Clapham (1962) and Young (1962a) established that the colony consisted of typical E. leptochila, differing only in short outer (mean 7.4 mm) and inner (mean 5.9 mm) perianth segments. All mature flowers examined in this and other populations lacked a rostellum and possessed a clinandrium. In addition, all had a narrow, patent, triangular epichile. In view of the apparent lack of floral measurements in the literature (except Godfery 1933), those from one population of E. leptochila and two of E. helleborine are presented in Table 1, together with measurements made from Ross-Craig's (1971) excellent scale drawings.

At this locality the River South Tyne forms a broad valley at an altitude of 700 ft (220 m) with level gravels in the immediate vicinity of the river. To the east of the gravels, away from but scarcely raised above the river, is a thinly grassed bank on which birch scrub grows. E. leptochila occurs in scattered colonies both within and at the margin of this scrub. We noted the following species growing within 1m of E. leptochila:

<table>
<thead>
<tr>
<th>Species</th>
<th>Species</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angelica sylvestris</td>
<td>Conopodium majus</td>
<td>Leontodon hispidus</td>
</tr>
<tr>
<td>Anthoxanthum odoratum</td>
<td>Dactylorhiza fuchsii</td>
<td>Ranunculus acris</td>
</tr>
<tr>
<td>Armeria maritima</td>
<td>Epipactis helleborine</td>
<td>Salix nigricans</td>
</tr>
<tr>
<td>Arrhenatherum elatius</td>
<td>Equisetum arvense</td>
<td>Silene dioica</td>
</tr>
<tr>
<td>Betula pubescens</td>
<td>Geum rivale</td>
<td>Succisa pratensis</td>
</tr>
<tr>
<td>Carex ovalis</td>
<td>Holcus lanatus</td>
<td>Trifolium repens</td>
</tr>
<tr>
<td>Centaurea nigra</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Open gravel and pathside within 5m of E. leptochila colonies, to the south and east, also supported:

<table>
<thead>
<tr>
<th>Species</th>
<th>Species</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer pseudoplatanus</td>
<td>G. verum</td>
<td>Trisetum flavescens</td>
</tr>
<tr>
<td>Aegopodium podagraria</td>
<td>Hieracium sp.</td>
<td></td>
</tr>
<tr>
<td>Agrostis canina</td>
<td>Linum catharticum</td>
<td></td>
</tr>
<tr>
<td>A. tenuis</td>
<td>Lotus corniculatus</td>
<td>V. sepium</td>
</tr>
<tr>
<td>Campanula rotundifolia</td>
<td>Luzula sylvatica</td>
<td>Viola lutea</td>
</tr>
<tr>
<td>Cerastium fontanum</td>
<td>Minuartia verna</td>
<td></td>
</tr>
<tr>
<td>Crucifera laevipes</td>
<td>Parnassia palustris</td>
<td>BYU hymatocitcum</td>
</tr>
<tr>
<td>Deschampsia cespitosa</td>
<td>Plantago lanceolata</td>
<td>B. capillare</td>
</tr>
<tr>
<td>Euphorbia nemorosa</td>
<td>Rubus idaeus</td>
<td>Pleurozium schreberi</td>
</tr>
<tr>
<td>Festuca rubra</td>
<td>Rumex acetosa</td>
<td>Polyclinthium juniperinum</td>
</tr>
<tr>
<td>Filipendula ulmaria</td>
<td>Sorbus aucuparia</td>
<td>Rhytidiodilus squarrosus</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>Thlaspi alpestre</td>
<td>Tetraplopon mnioides</td>
</tr>
<tr>
<td>Galium saxatile</td>
<td>Thymus drucei</td>
<td>Weissia controversa var. densifolia</td>
</tr>
</tbody>
</table>

The open nature of these gravels, which are almost bare in places, and the occurrence of species such as Armeria maritima, Minuartia verna, Thlaspi alpestre and Weissia controversa var. densifolia led us to suspect that the mineral content of the soil might be unusual. In the vicinity of Alston, lead, zinc and barium ores have been mined in the past. Soil samples were therefore taken from 2–10 cm below the surface in the immediate vicinity of E. leptochila, and from the bare patches in the adjacent open gravel. These were analysed by Dr K. Shaw (Agricultural Development and Advisory Service, Kenton Bar, Newcastle-upon-Tyne) (Table 2). The Epipactis sites are remarkable, with high levels of extractable zinc, of an order likely to result in toxicity in many plants (Bradshaw et al. 1965), although if the calcium level (unknown) is high relative to magnesium, there would be a less severe effect. However, the zinc levels are nearly twice the 'critical' level suggested by Halliday (1960). Levels of extractable lead are also rather high. The levels of extractable phosphorus and potassium are very low although not untypical of many upland soils, particularly those with a high pH. The pH of these soils is about 7 (neutral), which is unusual in this predominantly acidic area, and may well be comparable with the southern chalk soils on which this species has been previously reported.

The bare gravel areas are not dissimilar, although the figures are less extreme, particularly with regard to zinc, which is only a tenth of the Epipactis soils. This, coupled with the relatively high levels of lead and the low levels of phosphorus, are sufficient to account for the sparse but floristically interesting vegetation found in these areas. Nevertheless, it is noteworthy that the more
extreme soils, under birch, support a more vigorous ground vegetation. This may be due to such ameliorating factors as the shade, moisture and higher humus of these areas, and the higher pH. It may be that the open nature of the gravel communities owes much to free drainage, high leaching and low humus content, as Halliday (1960) has suggested that little direct heavy metal toxicity is associated with lead/zinc spoil soils in the Pennines.

Similar possibly toxic gravels are found beside the River South Tyne from Williamson down to the junction with the River North Tyne at Warden, and species such as Armeria maritima, Thlaspi alpestre and Minuartia verna occur beside the combined River Tyne even below Wylam, only 7 miles west of Newcastle. Since we thought that birch scrub growing on apparently toxic Tyne gravel might constitute a habitat for *E. leptochila*, we went downstream on the same day in search of other examples of this type of habitat, and indeed we never failed to find the *Epipactis* in suitable areas.

South-east of Harper Town, the South Tyne forms a bend, on the western (and southern) bank of which a fairly level area is covered with birch scrub at an altitude of 500 ft (160 m). Here, growing in the scrub and also on an open grassy bank just above the river, we saw about 1,000

**TABLE 1. FLORAL CHARACTERS OF *EPIPACTIS LEPTOCHILA* AND *E. HELLEBORINE***

<table>
<thead>
<tr>
<th>Origin</th>
<th>Sample size</th>
<th>Outer perianth segment (mean) Length</th>
<th>Inner perianth segment (mean) Length</th>
<th>Epichile (mean) Length</th>
<th>Epichile L Hypochile L (mean) Length</th>
<th>Ros-tellum</th>
<th>Clin-andrium</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>L/B</td>
<td>L/B</td>
<td>L/B</td>
<td>Tip patent</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. leptochila</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Williamson</td>
<td>9</td>
<td>7-4</td>
<td>2-1</td>
<td>5-9</td>
<td>1-75</td>
<td>3-5</td>
<td>1-9</td>
</tr>
<tr>
<td>Clapham (1962)</td>
<td>—</td>
<td>12-15</td>
<td>ca. 10</td>
<td></td>
<td>Tip patent</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ross-Craig (1971)</td>
<td>—</td>
<td>10</td>
<td>1-9</td>
<td>9-6</td>
<td>1-8</td>
<td>4-5</td>
<td>2-2</td>
</tr>
<tr>
<td><em>E. helleborine</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haydon Bridge</td>
<td>10</td>
<td>9-6</td>
<td>1-6</td>
<td>7-9</td>
<td>1-5</td>
<td>2-4</td>
<td>0-8</td>
</tr>
<tr>
<td>Langley</td>
<td>9</td>
<td>8-8</td>
<td>1-5</td>
<td>7-0</td>
<td>1-4</td>
<td>3-0</td>
<td>0-7</td>
</tr>
<tr>
<td>Clapham (1962)</td>
<td>—</td>
<td>ca. 10</td>
<td></td>
<td></td>
<td>Tip recurved</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ross-Craig (1971)</td>
<td>—</td>
<td>11-0</td>
<td>1-55</td>
<td>9-6</td>
<td>1-5</td>
<td>5-0</td>
<td>0-8</td>
</tr>
</tbody>
</table>

All measurements in mm

spikes of *E. leptochila*. These were very similar to those at Williamson, although some were much bigger plants. There was also one plant of *E. helleborine*. The associated species were very similar to those at Williamson, but the following additional species were also noted:

*Anthyllis vulneraria*  
*Geranium sylvaticum*  
*Polygala vulgaris*  
*Rhinanthus minor*  
*Taraxacum unguiolobum*

Two further sites were visited the same day. On the southern bank, west of Beltingham, 13 spikes were found; and on the northern bank, near Crow Hall, 6 spikes were discovered after a long search. In both these sites, birch occurred on riverside gravels, but there was little evidence of soil toxicity and none of the characteristic gravel plants were present. The vegetation under the birch was much more rank and species-rich, and the *Epipactis* were poorly developed and apparently suffering from competition. This was also true of the other six riverside sites subsequently discovered downstream to Wylam during August. All were on riverside gravels or banks associated with birch, and in some cases (as at Wylam and Haltwhistle) open gravel or banks with
Armeria, Minuartia and Thlaspi occurred nearby. Nevertheless, colonies were invariably small both in number of spikes (2–20) and height, occurring in areas with vigorous ground cover. It is suggested that these birch woods might have colonized toxic gravels, and have developed a deep humus above the gravels, allowing more vigorous ground cover to develop.

In view of the association of *E. leptochila* with apparently toxic sites under birch, spoil heaps from disused lead mines were examined. Some of these proved negative, but a thriving colony of more than 50 spikes, accompanied by *E. helleborine*, was discovered in birch scrub on spoil heaps (altitude 450 ft, 140 m) some distance north of the River Tyne at Hexham.

**TABLE 2. ANALYSES OF SOIL SAMPLES FROM WILLIAMSTON**

<table>
<thead>
<tr>
<th>Site</th>
<th>pH1</th>
<th>P2</th>
<th>K3</th>
<th>Mg4</th>
<th>Cu5</th>
<th>Zn6</th>
<th>Pb6</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. leptochila</em></td>
<td>7.2</td>
<td>3</td>
<td>56</td>
<td>99</td>
<td>26</td>
<td>2,370</td>
<td>692</td>
</tr>
<tr>
<td><em>E. leptochila</em></td>
<td>7.0</td>
<td>4</td>
<td>54</td>
<td>113</td>
<td>18</td>
<td>2,300</td>
<td>300</td>
</tr>
<tr>
<td>Open gravel</td>
<td>5.2</td>
<td>6</td>
<td>91</td>
<td>61</td>
<td>12</td>
<td>192</td>
<td>540</td>
</tr>
<tr>
<td>Open gravel</td>
<td>5.2</td>
<td>6</td>
<td>91</td>
<td>48</td>
<td>15</td>
<td>222</td>
<td>720</td>
</tr>
</tbody>
</table>

All element concentrations as p.p.m. of air-dry soil.

1 Measured by glass electrode on 1:2 soil:water mixture.

2 Extracted in sodium bicarbonate and determined by the phosphomolybdate procedure.

3 Extracted in N ammonium nitrate and determined by flame-photometer.

4 Extracted in N ammonium nitrate and determined by atomic absorption spectrophotometer.

5 Extracted in EDTA and determined by atomic absorption spectrophotometer.

6 Extracted in 0.5N acetic acid and determined by atomic absorption spectrophotometer.

On 11th August 1974, G. A. and M. Swan visited the old heaps of a lead mine (altitude 400 ft, 125 m) north of Haydon Bridge. Although birch was abundant they failed to find *E. leptochila*. However, this disappointment was more than compensated for by the discovery of a flourishing colony of *E. phyllanthes* G. E. Sm. var. *pendula* D. P. Young. About 50 spikes were present, growing particularly under *Corylus avellana*, along with *Salix* spp., *Alnus glutinosa*, and *Betula* sp. Although the plant occurred to within 5 m of the edge of a lead spoil tip 20 m high, and the ground vegetation was open, it was under heavy shade, and there was no external indication that the spoil was in any way affecting the soil or the vegetation. However, patches of birch scrub adjacent to and on the heaps held magnificent colonies of *E. helleborine*, of which there were several hundred spikes. The nearest records for *E. phyllanthes* to Haydon Bridge appear to be in W. Lancs. (v.c. 60) and S.E. Yorks. (v.c. 61) (Young 1962b), and south-west Furness (v.c. 69b) (Young 1952). The Lancashire record is known to be of var. *pendula*. This locality, therefore, is not only the first record of *E. phyllanthes* for S. Northumberland but it is also the northernmost known in the British Isles. The record from Holy Island (Cheviot, v.c. 68) cited by Swinton (1967) must surely be an error for *E. dunensis* (T. & T. A. Stephenson) Godfrey, which is well known there (Young 1962a). Comparison of the Haydon Bridge plants (voucher in herb. Swan) with the account in Young (1952) shows these attractive and distinctive little plants to be in agreement with var. *pendula* in every characteristic.

We also inspected the heaps at the site of the disused lead smelting works at Langley (altitude 700 ft, 220 m) where very many magnificent plants of *E. helleborine* were growing, particularly under conifers. Among birch scrub on these heaps were also some smaller, yellower plants with leaves in two ranks, which had the superficial appearance of *E. leptochila*. However, the flowers of both possessed a rostellum, lacked a clinandrium, and had an epichile and perianth segments indistinguishable from the Haydon Bridge population of *E. helleborine* (Table 1). Doubtless, they were merely odd and rather depauperate forms of this species.

**DISCUSSION**

The origin of *E. leptochila* in the Tyne Valley is quite unknown, although it can give rise to some interesting speculation. In view of the constancy of its habitat elsewhere it may be supposed that
it originally arose in woodland sites on chalk and limestone where it is widespread in this country and abroad. The majority of its close relatives are also most usually found in this type of habitat. In common with most members of the Orchidaceae it possesses a very light seed which is very readily windborne, perhaps over large distances on occasion. Thus the natural colonization of suitable habitats in Northumberland from the south of England is not beyond question. The Tyne Valley sites are not apparently of very recent origin. *Helleborine latifolia* Druce is recorded from open sites by the banks of the Tyne near Haltwhistle by Blackburn (1927), and her report is accompanied by an editorial note from J. E. Hull that he knew it in similar situations at Featherstone in 1897. Since *E. leptochila* had not been distinguished at that time, it has probably been present in the Tyne Valley for at least 80 years.

The Tyne Valley habitats share with southern sites features of shade, rather sparse ground flora, and, in one case at least, a neutral pH. Furthermore, they seem to be attractive to other species of *Epipactis*, *E. helleborine* being larger and more frequent here than elsewhere in Northumberland, and the very local *E. phyllanthes* occurring in one site. Nevertheless, the relatively high altitude (up to nearly 800 ft) must render these sites much colder than those in the south, and the unusual mineral content of the soil would be thought to pose many problems to these plants. However, it apparently has the effect of creating open ground suitable for these species; the poor showing of *Epipactis* in downstream sites with good ground cover was notable, and it may be that previously vigorous colonies have suffered from the progressive colonization of heavy metal gravels by birch, with subsequent increase of ground cover.

REFERENCES


(Accepted May 1975)
Studies on variation and evolution in *Centaurium erythraea* Rafn and *C. littorale* (D. Turner) Gilmour in the British Isles

1. Taxonomy and biometrical studies

R. A. E. UBSDELL

*Department of Botany, University of Reading* *

ABSTRACT

Analysis of populations of *Centaurium erythraea* Rafn subsp. *erythraea* and *C. littorale* (D. Turner) Gilmour subsp. *littorale* has shown that both show a wide range of morphological variation. Much of this variation is retained in cultivation and five varieties are recognized of subsp. *erythraea* and four of subsp. *littorale*. Despite this variation the two subspecies are quite distinct.

Analysis of mixed populations of the two species from the coasts of Anglesey and Lancashire has shown that some plants are, to varying degrees, intermediate and probably of hybrid origin. In the majority of populations from the Lancashire coast, backcrossing to *C. littorale* appears to have taken place, although two suggest backcrossing to *C. erythraea*. This is in contrast to the situation in the population from Anglesey in which only F₁-like hybrids were present. Analysis of two populations from northern Germany show all plants to be intermediate and F₁-like.

INTRODUCTION

The genus *Centaurium* Hill (*Erythraea* Borkh. *nom. illegit.*) of the Gentianaceae is widespread in Europe, especially around the Mediterranean. Taxonomic investigations of the genus have presented great difficulties since the species are extremely variable. Parallel variation in several characters is common in the groups of related species, and there have also been reports of natural hybrids. Species and infra-specific taxa are, therefore, often difficult to define and the literature is full of nomenclatural confusion.

However, Zeltner's work (1970) has led to a better understanding of relationships within the genus. He concentrated primarily on cytological studies, but correlated this with evidence from morphology, ecology and geographical distribution. He showed that in Europe the genus consists of certain ancient, morphologically distinct species, together with a number of taxonomically difficult complexes. It is in the subsections *Parviflorae* (Ronninger) Melderis, *Vulgaria* Melderis and *Centaurium* of the section *Centaurium* that the nomenclature is particularly confusing since the principal species of each, *C. pulchellum* (Sw.) Druce, *C. littorale* (D. Turner) Gilmour and *C. erythraea* Rafn, show parallel variation in many of the characters and numerous subspecies and varieties of each have been described without adequate study.

Subsection *Parviflorae* consists of two annual species, *C. pulchellum* and *C. tenuiflorum* (Hoffmanns. & Link) Fritsch, both of which grow in the British Isles. The former is hypotetraploid (*2n* = 36), while the latter has both diploid (*2n* = 20) and tetraploid (*2n* = 40) races, of which only the diploid is found in the British Isles.

Subsection *Vulgaria* consists of the narrow-leaved, biennial species. Three are diploid (*2n* = 20) and confined to Spain, Portugal and southern France, while another two are tetraploid (*2n* = 40). Of the latter, one is found only in Spain and Portugal, while *C. littorale* is present in central and northern Europe and is the only species of this subsection found in the British Isles. There is a sixth species, confined to Spain and Portugal, for which no chromosome count is available.

Subsection *Centaurium* consists of the broad-leaved, biennial species. One of these is diploid and confined to the Mediterranean region, while *C. erythraea* is the most widespread species of the

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genus and is the only one of this subsection present in the British Isles. It has both diploid and tetraploid races, the diploids being confined to the Mediterranean region while the tetraploids have spread into central and northern Europe including Russia and the British Isles. The tetraploids also appear to have been introduced into North America and Australia.

Zeltner's work and Melderis's recent account of the genus for *Flora Europaea* (Melderis 1972a & b) have cleared up much of the nomenclatural confusion surrounding the European species of these three subsections. However, little experimental work has been carried out on the taxa of northern Europe, especially on *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale*. Both are extremely polymorphic and numerous varieties of each have been described, particularly in the British Isles (Wheldon & Salmon 1925, Gilmour 1937). There is still much confusion over the status of many of these varieties as they are based upon poorly defined characters and given only vague descriptions.

Four varieties of *C. erythraea* subsp. *erythraea* were recognised by Gilmour and named under *C. umbellatum* Gilib. as follows:

i) Var. *centaurium* (L.) Gilmour is the typical, tall variety of the species.

ii) Var. *fasciculare* (Duby) Gilmour is distinguished by its numerous axillary branches (the plant is often as broad as it is tall). It occurs in exposed places on the coasts of Scotland and Ireland.

iii) Var. *subcapitatum* (Corb.) Gilmour is strictly maritime and distinguished by its solitary stem, crowded cauline nodes, compact inflorescence and dwarffness. It has been confused with *C. capitatum* (Willd.) Borbás, a dwarf, maritime plant with the stamens inserted at the base of the corolla tube. *C. capitatum* was originally treated as a distinct species but is now included in *C. erythraea* subsp. *erythraea* as var. *capitatum* (Willd.) Melderis (Melderis 1972b).

iv) Var. *sublittorale* (Wheldon & Salmon) Duce was thought (Wheldon & Salmon 1925) to be a hybrid between *C. erythraea* and *C. littorale* as it has certain characteristics of both species, but without definite evidence they treated it as a variety of the former.

These varietal names will be used throughout this account since the combinations under *C. erythraea* do not exist, although Melderis (1972b) has shown that the name *C. umbellatum* Gilib. is an invalidly published, nomenclatural synonym of *C. erythraea* Rafn.

Gilmour also recognized four varieties of *C. littorale* subsp. *littorale*. Two from the coasts of north-eastern England and eastern Scotland are glabrous, while the other two from the coasts of North Wales, north-western England and south-western Scotland are scabrid with a dense covering of small papillae on the stem, leaves, bracts and calyx:

i) Var. *occidentale* (Wheldon & Salmon) Gilmour is the common scabrid variety found on the coasts of North Wales, north-western England and south-western Scotland.

ii) Var. *bayleyi* (Wheldon & Salmon) Gilmour is distinguished from the former by its dwarf, much branched habit (the plant is as broad as it is tall), compact inflorescence, longer leaves and larger flowers. It is reported from the coasts of Anglesey and Lancashire.

iii) Var. *littorale* is a dwarf, glabrous variety distinguished by its habit, short calyx and long capsules. It is reported from the coasts of north-eastern England and eastern Scotland.

iv) Var. *minor* (Hartm.) Gilmour is reported from a few places on the coasts of north-eastern England and eastern Scotland, but it is difficult to see how it differs from var. *littorale* except in the lengths of the calyx and capsule.

There have also been reports of hybrids, plants morphologically intermediate between the two species, from mixed populations on the coasts of Lancashire and North Wales, and these add to the confusion.

Wheldon (1897) described in detail the characteristics of some plants which he collected from Hightown, S. Lancashire, v.c. 59 in 1894 (specimens in BM). He thought them to be hybrids between *C. littorale* and *C. erythraea* since they had some of the characteristics of both, but named them *Erythraea littoralis* var. *intermedia* Wheldon as they resembled *C. littorale* more closely and were also highly fertile.

Salmon & Thompson (1902) referred to a series of plants collected by them from Ansdell, W. Lancs., v.c. 60 (in BM). Some of them were clearly *C. erythraea*, others *C. littorale*, while the rest were intermediate and sterile. They thought that the latter might be hybrids.
Wheldon & Salmon (1925) later described a variety of *C. erythraea* under the name of *Erythraea centaurium* var. *sublitoralis* Wheldon & Salmon from western England and Wales, which they considered to be a hybrid between *C. erythraea* and *C. littorale*. However, without definite evidence of this they treated it as a variety of the former, and the name *C. umbellatum* var. *sublitorale* (Wheldon & Salmon) Druce was later given to it (Druce 1926).

O’Connor (1955) described the results of an investigation of *Centaurium* from the dunes at Freshfield, S. Lancs., v.c. 59 carried out by her in 1954. She found distinct populations of each species, and other populations which contained both species together with plants that could not be referred to either. Vohra (1970) also looked in detail at populations from Freshfield and Ainsdale, S. Lancs., and his results were the same as those of O’Connor.

O’Connor also remarked that plants possessing characters similar to those classed as intermediates in mixed populations from the west coast have been reported from East Anglia, although *C. littorale* is not known there.

A detailed biosystematic study was therefore carried out by the present author to investigate and describe the variation patterns shown by populations of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* in the British Isles and northern Europe. It was hoped that an experimental approach to this problem would both help to reduce some of the taxonomic confusion surrounding the numerous varieties of these two subspecies and explain the nature of the morphologically intermediate plants in mixed populations. This work formed the contents of a thesis accepted for the degree of Ph.D. by the University of Reading (Ubsdell 1973) and will be presented in three papers.

This first paper is concerned with a biometric analysis of morphological characters. The purpose of this study was to assess the extent of the variation in certain morphological characters, and by so doing to delimit the range of variation shown by these two species. This information was then used as a basis for assessing the morphological evidence for hybridization.

An account of the cytology will be given in a second paper, and a final paper will deal with the isolating mechanisms which normally keep these two species distinct in the wild.

### TABLE 1. LOCALITIES OF POPULATIONS SAMPLED

<table>
<thead>
<tr>
<th>Centaurium erythraea</th>
<th>Centaurium littorale</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Kevington, W. Kent, v.c. 16</td>
<td>A. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>2. Headley, Surrey, v.c. 17</td>
<td>D. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>3. Box Hill, Surrey, v.c. 17</td>
<td>F. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>4. Orpington, W. Kent, v.c. 16</td>
<td>G. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>5. Folkstone, E. Kent, v.c. 15</td>
<td>H. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>6. Luccombe, Isle of Wight, v.c. 10</td>
<td>BA. Newborough, Anglesey, v.c. 52</td>
</tr>
<tr>
<td>7. Sandown, Isle of Wight, v.c. 10</td>
<td>N. Newborough, Anglesey, v.c. 52</td>
</tr>
<tr>
<td>8. Swanage, Dorset, v.c. 9</td>
<td>24. Holy Island, Cheviot v.c. 68</td>
</tr>
<tr>
<td>10. Bonchurch, Isle of Wight, v.c. 10</td>
<td>R. Ross, Cheviot v.c. 68</td>
</tr>
<tr>
<td>11. Freshwater, Isle of Wight, v.c. 10</td>
<td>22. Nairn, v.c. 96b</td>
</tr>
<tr>
<td>12. Steyning, W. Sussex, v.c. 13</td>
<td>EL. near Elgin, Moray, v.c. 95</td>
</tr>
<tr>
<td>23. Aberlady, Haddington, v.c. 82</td>
<td>DO. Dornoch, E. Sutherland, v.c. 107</td>
</tr>
<tr>
<td>25. Newbiggin, S. Northumberland, v.c. 67</td>
<td>Mixed populations of the two species</td>
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<td>27. Fanore, Clare, v.c. H9</td>
<td>15. Freshfield, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>I. Minsmere, E. Suffolk, v.c. 25</td>
<td>17. Freshfield, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>K. Wells, W. Norfolk, v.c. 28</td>
<td>19. Freshfield, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>L. Cley, E. Norfolk, v.c. 27</td>
<td>20. St Annes, W. Lancashire, v.c. 60</td>
</tr>
<tr>
<td>Populations of <em>C. erythraea</em> with stamens inserted at the base of the corolla-tube</td>
<td>21. Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td>29. Freshwater, Isle of Wight, v.c. 10</td>
<td>AN. Newborough, Anglesey, v.c. 52</td>
</tr>
<tr>
<td>30. Freshwater, Isle of Wight, v.c. 10</td>
<td>B, C, E, Ainsdale, S. Lancashire, v.c. 59</td>
</tr>
<tr>
<td></td>
<td>FAL. Falshőft, Schleswig-Holstein, Germany</td>
</tr>
<tr>
<td></td>
<td>S.P. St Peter, Schleswig-Holstein, Germany</td>
</tr>
</tbody>
</table>
During the summer months of 1970–72, populations of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* were sampled from many parts of the British Isles and from two localities on the coast of north-western Germany. These consisted of either a single species or mixed populations of both, and the localities are listed in Table 1.

**METHODS**

The populations of single species were subjected to detailed biometric analyses, and the results compared with those from similar analyses of mixed populations, to determine whether the overlap in variation in the mixed populations was due to variation within the species themselves or to hybridity.

Samples of seed from many of the wild populations were sown in the greenhouse and raised to maturity under uniform conditions. Mature flowering plants were pressed and measured for comparison with the wild plants. Plants of *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* from the Continent (northern Europe) were obtained as seeds from Botanic Gardens and raised in the greenhouse, as only two populations (both mixed) were sampled in the wild. Sets of voucher specimens have been deposited in BM and OXF.

**CHARACTERS CHOSEN AND METHOD OF ASSESSMENT**

After careful consideration of the characters used by Wheldon & Salmon (1925), Melderis (1932) and Warburg (1962) to distinguish between *C. erythraea* subsp. *erythraea* and *C. littorale* subsp. *littorale* including the numerous varieties of each, the following characters were chosen:

1. **Height of stem**
   This was measured vertically from the base of the basal rosette of leaves to the tip of the highest flower.

2. **Habit**
   The number of main flowering stems and cauline nodes were noted. The lengths of the internodes were also measured to see if the cauline nodes were well spaced or crowded together, and the following three categories were used for scoring:
   
   a) L = long, internodes > 2.5 cm long,
   b) M = medium, internodes 1.0–2.5 cm long,
   c) S = short, internodes < 1.0 cm long.

3. **Inflorescence**
   The total number of cymes present on each flowering stem was scored as follows:
   
   a) M = many, > 5 cymes,
   b) I = intermediate, 3–5 cymes,
   c) F = few, < 3 cymes.
   
   The length of the internodes between each cyme in the inflorescence was scored to give an estimate of the relative laxity or compactness of the inflorescence and was scored as follows:
   
   a) L = lax, > 2.0 cm long,
   b) I = intermediate, 1.0–1.9 cm long,
   c) D = dense, 0.5–0.9 cm long,
   d) VD = very dense, < 0.5 cm long.

4. **Length/breadth ratio of cauline leaves**
   This ratio was obtained by dividing the total length of the leaf (in mm) by the greatest breadth. For each plant the first three cauline leaves above the basal rosette of leaves were measured and a mean value obtained.
5. Shape of cauline leaves
All cauline leaves could be classified without much difficulty into one of the following categories:
   a) Elliptical = leaves short and broad with sides never parallel, an acute apex and 5 prominent veins,
   b) Linear = leaves long and narrow with parallel sides, an obtuse apex and 1 prominent vein,
   c) Linear-elliptical = leaves intermediate in dimensions but with sides never parallel, an acute
      apex and 3 prominent veins.

6. Indumentum
Plants were scored as follows:
   a) Scabrid = margins and midribs of cauline leaves, upper parts of stem, bracts and calyx densely
      covered in small papillae,
   b) Semi-scabrid = all parts lightly covered in papillae,
   c) Glabrous = papillae absent.

7. Calyx/corolla-tube ratio
This ratio was obtained by dividing the total length of the calyx from the base to the tip of the
   teeth (in mm), by the length of the corolla-tube. Ten flowers per plant were scored and a mean
   value obtained.

8. Length of corolla lobes
This was measured from the top of the corolla-tube to the tip of the corolla lobes on live material
   only. Ten flowers per plant were scored and a mean value obtained.

9. Diameter of the pollen grains
The pollen grains were mounted in cotton blue/lactophenol and a mean diameter calculated for
   each plant from 25 grains.

10. Shape of stigma
This could be classified into one of three categories:

   (a)  
   (b)  
   (c)  

11. Length of filaments
This was measured from their point of attachment to the corolla-tube to the base of the anther.

12. Length of capsule

RESULTS

The data derived from the morphological studies can best be considered in three sections:
   a) The variation shown by individual characters,
   b) An assessment of the overall variation shown by different populations,
   c) The correlation of the different characters within individual plants.

VARIATION OF INDIVIDUAL CHARACTERS
For each of the characters studied, the mean, standard deviation and coefficient of variation
were calculated for twenty plants in each population. The results are given for populations of
C. erythraea and C. littorale in Tables 2 and 3 respectively, and for mixed populations of the two
in Table 4. A comparison of C. umbellatum var. subcapitatum and C. erythraea subsp. erythraea
var. capitatum is given in Table 5.
<table>
<thead>
<tr>
<th>Population</th>
<th>Height cm</th>
<th>Leaf length: breadth ratio</th>
<th>Calyx: corolla-tube ratio</th>
<th>Length of corolla-lobes mm</th>
<th>Diameter of pollen μm</th>
<th>Habit</th>
<th>Inflorescence</th>
<th>Leaf-shape</th>
<th>Indumentum</th>
<th>Stigma-shape</th>
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<td>cv</td>
<td>x</td>
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</table>

1 Habit: (a) number of flowering stems, (b) number of cauline nodes, (c) length of internodes
2 Inflorescence: (d) number of cymes, (e) compactness of inflorescence
3 Leaf-shape: ELL = elliptic, LIN-ELL = linear-elliptic, LIN = linear
4 Indumentum: G = glabrous, SS = semi-scaprid, S = scabrid
5 Stigma-shape: see p. 11.
### TABLE 3. MEAN, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR CHARACTERS OF PLANTS FROM POPULATIONS OF *C. LITTORALE* (for abbreviations see Table 2)

<table>
<thead>
<tr>
<th>Population</th>
<th>Height cm</th>
<th>Leaf length: breadth ratio</th>
<th>Calyx:corolla-tube ratio</th>
<th>Length of corolla-lobes mm</th>
<th>Diameter of pollen μm</th>
<th>Habit¹</th>
<th>Inflorescence²</th>
<th>Leaf-shape³</th>
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<td>̄x s cv</td>
<td>̄x s cv</td>
<td>̄x s cv</td>
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<td>F L</td>
<td>LIN</td>
<td>S c</td>
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<td>30·0 5 5 S</td>
<td>F D</td>
<td>LIN</td>
<td>S c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>4·2 0·8 20</td>
<td>5·6 0·48 9</td>
<td>0·87 0·05 6</td>
<td>5·4 — —</td>
<td>29·0 1 1 S</td>
<td>F L</td>
<td>LIN</td>
<td>SS c</td>
<td></td>
<td></td>
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<tr>
<td>22</td>
<td>7·3 2·2 30</td>
<td>5·0 0·41 8</td>
<td>0·85 0·05 6</td>
<td>5·4 0·27 5</td>
<td>29·0 1 2 S</td>
<td>F L</td>
<td>LIN</td>
<td>SS/G c</td>
<td></td>
<td></td>
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<tr>
<td>T</td>
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<td>4·3 0·83 19</td>
<td>0·65 0·10 15</td>
<td>5·4 0·42 8</td>
<td>32·0 1 2 S</td>
<td>F L</td>
<td>LIN</td>
<td>G/SS c</td>
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<td>4·5 0·33 7</td>
<td>31·0 1 1 S</td>
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<td>LIN</td>
<td>SS c</td>
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<td>LIN</td>
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<td>0·81 0·06 5</td>
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<td>F L</td>
<td>LIN</td>
<td>G c</td>
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<tr>
<td>Population</td>
<td>Height cm</td>
<td>Leaf length: breadth ratio</td>
<td>Calyx: corolla-tube ratio</td>
<td>Length of corolla-lobes mm</td>
<td>Diameter of pollen μm</td>
<td>Habit</td>
<td>Inflorescence</td>
<td>Leaf-shape</td>
<td>Indument</td>
<td>Stigma-shape</td>
</tr>
<tr>
<td>------------</td>
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<td>0.07</td>
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<td>3.1</td>
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<td>0.14</td>
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<td>5.0</td>
<td>31</td>
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<td>34</td>
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<td>0.12</td>
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<td>5.6</td>
<td>30</td>
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<td>2.0</td>
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<td>—</td>
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<td>0.4</td>
<td>11</td>
<td>0.66</td>
<td>0.05</td>
<td>8</td>
<td>6.1</td>
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<td>4.2</td>
<td>0.66</td>
<td>12</td>
<td>0.73</td>
<td>0.09</td>
<td>12</td>
<td>5.6</td>
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</table>
## TABLE 5. MEAN AND STANDARD DEVIATION FOR CHARACTERS OF PLANTS FROM POPULATIONS OF C. ERYTHREA VAR. CAPITATUM, C. UMBELLATUM VAR. SUBCAPITATUM AND C. UMBELLATUM VAR. CENTAURIUM

(for abbreviations see Table 2)

<table>
<thead>
<tr>
<th>Character</th>
<th>C. umbellatum var. centaurium pop. 5</th>
<th>C. umbellatum var. subcapitatum pop. 11</th>
<th>C. erythrea var. capitatum pop. 30</th>
<th>C. umbellatum var. subcapitatum pop. 29</th>
<th>C. erythrea var. capitatum pop. 29</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (μm)</td>
<td>Mean (μm)</td>
<td>Mean (μm)</td>
<td>Mean (μm)</td>
<td>Mean (μm)</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>2.0 ± 0.8</td>
<td>4.4 ± 1.0</td>
<td>1.4 ± 0.2</td>
<td>5.8 ± 2.5</td>
<td>1.1 ± 0.2</td>
</tr>
<tr>
<td>Habit (a)† (b)† (c)†</td>
<td>1.5 L</td>
<td>1.4 S</td>
<td>1.3 S</td>
<td>1.4 S</td>
<td>1.2 S</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>M D</td>
<td>M VD</td>
<td>M VD</td>
<td>M VD</td>
<td>M VD</td>
</tr>
<tr>
<td>Leaf L/B ratio</td>
<td>2.8 ± 0.4</td>
<td>2.4 ± 0.3</td>
<td>2.5 ± 0.4</td>
<td>2.9 ± 0.3</td>
<td>3.3 ± 0.2</td>
</tr>
<tr>
<td>Leaf-shape</td>
<td>ELL</td>
<td>ELL</td>
<td>ELL</td>
<td>ELL</td>
<td>ELL</td>
</tr>
<tr>
<td>Indumentum</td>
<td>G</td>
<td>G</td>
<td>G</td>
<td>G</td>
<td>G</td>
</tr>
<tr>
<td>Calyx/corolla-tube ratio</td>
<td>0.55 ± 0.05</td>
<td>0.61 ± 0.06</td>
<td>1.0 ± 0.09</td>
<td>0.79 ± 0.11</td>
<td>1.2 ± 0.17</td>
</tr>
<tr>
<td>Corolla-tube length (mm)</td>
<td>8.7 ± 0.5</td>
<td>8.6 ± 0.6</td>
<td>4.6 ± 0.4</td>
<td>7.3 ± 1.0</td>
<td>4.8 ± 0.7</td>
</tr>
<tr>
<td>Corolla-lobe length (mm)</td>
<td>4.9 ± 0.9</td>
<td>5.7 ± 0.4</td>
<td>4.7 ± 0.6</td>
<td>4.8 ± 0.7</td>
<td>4.5 ± 0.4</td>
</tr>
<tr>
<td>Pollen grain diameter (μm)</td>
<td>25.0</td>
<td>25.0</td>
<td>26.0</td>
<td>25.0</td>
<td>26.0</td>
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<tr>
<td>Stigma-shape</td>
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<td>a</td>
<td>a</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>Capsule length (mm)</td>
<td>9.3 ± 0.8</td>
<td>—</td>
<td>—</td>
<td>8.9 ± 1.1</td>
<td>6.6 ± 0.8</td>
</tr>
<tr>
<td>Filament length (mm)</td>
<td>3.3 ± 0.2</td>
<td>3.5 ± 0.7</td>
<td>5.0 ± 1.7</td>
<td>3.4 ± 0.2</td>
<td>5.1 ± 0.6</td>
</tr>
<tr>
<td>Point of insertion of stamens</td>
<td>Mouth of tube</td>
<td>Mouth of tube</td>
<td>Base of Tube</td>
<td>Mouth of tube</td>
<td>Base of tube</td>
</tr>
</tbody>
</table>

### 1-3. Height, Habit, Inflorescence

All three characters are extremely variable and this is to be expected since all are strongly affected by the environment.

a) C. erythrea

All plants of this species have 4–6 cauline nodes, and most have a compound inflorescence consisting of many branches each terminating in a compound cyme (more than 5 cymes), although some plants have only 1 or 2 cymes. Populations vary in the length of the cauline internodes, and in the relative laxity/compactness of the inflorescence, and can be divided into three major groups:

i) Populations 1–7, 10, 12, 25, 26, 28, L and K are medium to tall (10–30 cm) with a single main flowering stem, 4–6 cauline nodes, long internodes with well-spaced leaves, and a dense inflorescence of more than 5 cymes, or sometimes only 1 or 2. Plants from populations 1–4, 10, 12, 26 and 28 from inland habitats, 5–7 and 25 from the bases of cliffs by the sea and L and K from pine woods near sand-dunes, became taller but otherwise retained these characteristics when grown from seed under uniform conditions.

Continental plants grown in the greenhouse resembled the British plants placed in this group.

ii) Populations 8, 11, 13, 27, I and J, together with plants from 29 with normal stamen insertion, are all dwarf (4–8 cm) with a single main flowering stem, 4 or more cauline nodes, short internodes with crowded cauline leaves, and a dense or very dense inflorescence of many (>5) or few (<3) cymes. Plants from populations 27, I and J from sand-dunes became taller and identical to plants in group (i) when cultivated under uniform conditions, whereas plants from populations 8, 11, 13 and 29 from exposed, maritime cliffs retained their original characteristics.

iii) All plants from population 30 and those from population 29 with stamens inserted at the base of the corolla-tube, are even dwarf (1.1–1.4 cm) with a single main flowering stem, 2–3 cauline nodes, very short internodes with crowded cauline leaves, and a very dense inflorescence of many cymes. These characteristics were retained in cultivation.

iv) Population 23 from sand-dunes is dwarf (4–8 cm) with several main flowering stems (the plant is as broad as it is tall), 4 cauline nodes, short internodes with crowded, cauline leaves, and a dense inflorescence of many cymes. All characteristics were retained in cultivation.

b) C. littorale

- [Text continues here]
Plants of this species can be divided into three main groups which, apart from becoming taller, remained constant in cultivation:

i) Populations A, D, F, G and H from sand-dunes on the Lancashire coast and N from Anglesey have one main flowering stem, 3 or 4 cauline nodes (the leaves are longer than the internodes) and a lax inflorescence of few (<3) cymes.

   Continental plants grown in the greenhouse resembled the British plants belonging to this group.

ii) Populations 22, 24, R, EL, DO and T from sand-dunes on the coasts of Northumberland and north-eastern Scotland have one main flowering stem, 1 or 2 cauline nodes with long leaves exceeding the internodes in length, and a lax inflorescence of few (<3) cymes.

iii) Population BA from sand-dunes on the coast of Anglesey has several main stems (the plant is as broad as it is tall), several crowded, cauline nodes, and a dense inflorescence of few (<3) cymes. It thus resembles group (iii) of C. erythraea.

c) Intermediate plants

These are plants from mixed populations on the coasts of Anglesey and Lancashire which are intermediate between C. erythraea and C. littorale in a number of characters and cannot be referred to either. These plants are tall (over 10 cm) with 3–6 well-spaced cauline nodes and an intermediate inflorescence of 3–5 cymes.

Many of these characters seem to be adaptations to local environmental conditions and are of little use for separating the two species.

4, 5. Length/breadth ratio and shape of cauline leaves

These leaf characters have proved easy to score and are of great use for separating the two species.

a) C. erythraea

Plants of this species can be divided into two groups which remained constant in cultivation:

i) The majority of plants have a mean cauline leaf length/breadth ratio falling within the range 2:1–3:3 and elliptical leaves.

ii) Populations J and L have a higher mean leaf ratio with values of 3:5 and 4:7 respectively. These are the narrow-leaved variety with linear-elliptical leaves reported by previous authors from Norfolk and Suffolk.

b) C. littorale

Populations of this species show more variation, both within and between populations, although the leaf-shape is linear in all plants. Three main groups can be recognized and all remain constant in cultivation:

i) Populations A, D, F, G and H from the Lancashire coast, 24 and R from Northumberland, 22 and EL from the coast of north-eastern Scotland and plants from the Continent grown in the greenhouse have a mean leaf ratio within the range 5:0–6:3.

ii) Populations BA and N from the coast of Anglesey have a higher mean leaf ratio within the range 7:1–7:6.

iii) Populations DO and T from the coast of north-eastern Scotland have a lower mean leaf ratio within the range 4:1–4:3.

c) Intermediate plants

As all mixed populations in the British Isles occur on the coasts of Lancashire and Anglesey, the value of C. littorale is taken to be above 5:0 and that for C. erythraea below 3:3. Plants of these two species from the Continent also fall within these values. The leaf ratios of the intermediate plants from the British Isles and Germany fall within the range 3:5–4:8 and the leaves are linear-elliptical. The mean leaf ratios of the mixed populations fall within the range 3:1–5:3.

6. Indumentum

a) C. erythraea

All populations are glabrous, and this character is retained in cultivation.

b) C. littorale

Populations vary in this character and fall into three main groups which remain constant in cultivation.

i) Populations A, D, F, G, H from the Lancashire coast and N from the coast of Anglesey corresponding to var. occidentale and population BA from Anglesey corresponding to var. bayleyi are densely scabrid.

ii) Populations 22, 24, EL, DO, R and T from the east coast and corresponding to var. littorale and var. minor are either glabrous or semi-scabrid.
iii) Plants from the Continent are completely glabrous.

c) Intermediate plants
As all plants of _C. erythraea_ from single species populations are glabrous and all plants of _C. littorale_ from single species populations on the coasts of Lancashire and Anglesey are scabrid, this character can be used to separate them in mixed populations from the British Isles. The intermediate plants vary in this character, as in some mixed populations all are glabrous while in the rest all intermediates are scabrid.

Intermediate plants from mixed populations in Germany were glabrous as are all Continental plants of _C. erythraea_ and _C. littorale_ subsp. _littorale_.

7. Calyx/corolla-tube ratio
This character proved easy to calculate and is one of the best for separating the two species.

a) _C. erythraea_
Populations of this species fall into three main groups:

i) Most have a mean value within the range 0·44–0·59, but this increases in cultivation to 0·64–0·71.

ii) Populations 26, 27, 28 from Wales and western Ireland, plants of this species from mixed populations on the coasts of Lancashire and Anglesey, and population L from eastern Norfolk, have a slightly higher mean value, 0·63–0·64, which increases in cultivation to 0·74–0·76.

iii) Population 30 and plants from 29 with stamens inserted at the base of the corolla-tube have a mean value of 1·0–1·2, which is much higher than that of all other plants of this species. The rest of the plants from population 29 with normal stamen insertion also have a higher mean value of 0·79. Examination of the length of the calyx and corolla-tube shows that the calyx of these plants is of the same length as the calyx of typical _C. erythraea_, and the difference in ratio is the result of the very short corolla-tube of the plants from populations 29 and 30.

b) _C. littorale_
Populations of this species fall into three main groups:

i) Most have a mean value within the range 0·80–0·87, but this increases in cultivation to 0·88–0·97.

ii) Populations N and BA from Anglesey have an even higher value of 0·97–0·98.

iii) Populations DO and T from Sutherland and Ross have a lower mean value of 0·50–0·65.

This is atypical of the species and in fact falls within the range of _C. erythraea_.

c) Intermediate plants
Plants of _C. littorale_ from the coasts of Lancashire and Anglesey can be clearly separated from plants of _C. erythraea_ using this character. Intermediate plants from mixed populations in the British Isles vary with some falling within the range of _C. littorale_ from the west coast, others falling within the range of _C. erythraea_, while the rest are intermediate and fall within the range 0·72–0·78. Mixed populations have mean values of 0·66–0·82.

Intermediate plants from Germany have mean values of 0·66–0·73, which is intermediate between the values of Continental plants of _C. erythraea_ and _C. littorale_.

8. Length of corolla lobes
This character can only be accurately measured on living material.

a) _C. erythraea_
All populations of this species have mean values of 4·4 to 5·5 mm and remain constant in cultivation.

b) _C. littorale_
Populations of this species are more variable and fall into two main groups:

i) Populations from the coasts of Lancashire and Anglesey, and plants from the Continent have mean values within the range 5·8–6·6 mm.

ii) Populations 24, R, 22, EL, DO and T from the east coast have lower mean values within the range 4·5–5·4 mm.

c) Intermediate plants
This character can be used to distinguish plants of _C. littorale_ from the coasts of Lancashire and Anglesey from plants of _C. erythraea_. Intermediate plants from mixed populations have mean values within the range 5·4–6·1 mm.

9. Diameter of the pollen grains
No mention of this character has been made by previous authors, yet it has proved easy to measure accurately and is of great value in separating _C. erythraea_ from _C. littorale_.

a) *C. erythraea*
All plants of this species were found to have pollen grains ranging from 23 to 26 \( \mu m \) with mean values for populations within the range 24-26 \( \mu m \).

b) *C. littorale*
All plants of this species were found to have larger pollen grains ranging from 28 to 32 \( \mu m \) with mean values for populations within the range 29-32 \( \mu m \).

c) Intermediate plants
Although some of the intermediate plants from mixed populations have mostly sterile and distorted pollen, most have fertile, spherical pollen grains, like those of *C. erythraea* and *C. littorale*, ranging in diameter from 26 to 30 \( \mu m \) and with population mean values from 27 to 28 \( \mu m \), which is intermediate between the two species.

10. **Shape of the stigma**
No mention of this character has been made by other authors, yet it has proved easy to score and is of great value in separating living material of the two species. Stigmas of intermediate plants from mixed populations are clearly intermediate in shape between those of the two species.

11. **Length of filaments**
Most plants of *C. erythraea*, and all of *C. littorale* and the intermediates have the filaments ranging in length from 3.0 to 3.8 mm (mean values for populations of 3.3-3.5 mm) and they are inserted at the mouth of the corolla-tube.

All plants of *C. erythraea* from population 30 and some from 29 have the filaments ranging in length from 4.8 to 6.0 mm (mean values for populations of 5.0-5.1 mm) and they are inserted at the base of the corolla-tube.

12. **Length of capsule**
Most plants of *C. erythraea*, and all of *C. littorale* and the intermediates have a similar range (mean values for populations of 8.9-9.3 mm) and the capsules are equal in length to the corolla-tubes.

Plants of *C. erythraea* from populations 29 and 30 with the filaments inserted at the base of the corolla-tube differ. These have shorter capsules (mean value 6.6 mm) which are longer than the stunted corolla-tubes.

**SUMMARY OF INDIVIDUAL CHARACTERS**
As mixed populations of the two species are found only on the coasts of Lancashire and Anglesey, only the variation shown by plants of *C. littorale* from these areas needs to be considered when selecting characters to distinguish this species from *C. erythraea* in mixed populations from the British Isles. The above analysis of individual characters has shown that the best ones are those listed in Table 6.

**TABLE 6. CHARACTERS USED TO DISTINGUISH C. ERYTHRAEA FROM C. LITTORALE VAR. OCCIDENTALE AND VAR. BAYLEYI**

<table>
<thead>
<tr>
<th>Character</th>
<th>C. erythraea</th>
<th>Intermediate</th>
<th>C. littorale</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Leaf length: breadth ratio</td>
<td>2.1-3.3, short and broad</td>
<td>3.4-4.9, intermediate</td>
<td>5.0-7.6, long and narrow</td>
</tr>
<tr>
<td>2. Leaf-shape</td>
<td>elliptic, sides never parallel, 5-veined, apex acute</td>
<td>linear-elliptic, sides never parallel, 3-veined, apex acute</td>
<td>linear with sides parallel, 1-veined, apex obtuse</td>
</tr>
<tr>
<td>3. Indumentum</td>
<td>glabrous</td>
<td>semi-scabrid</td>
<td>scabrid</td>
</tr>
<tr>
<td>4. Calyx:corolla-tube ratio</td>
<td>0.40-0.64, calyx about half as long as corolla-tube</td>
<td>0.65-0.75, intermediate</td>
<td>0.76-0.98, calyx nearly as long as corolla-tube</td>
</tr>
<tr>
<td>5. Corolla-lobe length</td>
<td>4.5-5.4 mm</td>
<td>5.5-5.6 mm</td>
<td>5.7-6.2 mm</td>
</tr>
<tr>
<td>6. Diameter of pollen grains</td>
<td>24-26 ( \mu m )</td>
<td>27-28 ( \mu m )</td>
<td>29-32 ( \mu m )</td>
</tr>
<tr>
<td>7. Stigma-shape(^1)</td>
<td>a</td>
<td>b</td>
<td>c</td>
</tr>
<tr>
<td>Score for each</td>
<td>0</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Total hybrid-index score</td>
<td>0</td>
<td>Intermediate</td>
<td>70</td>
</tr>
</tbody>
</table>

\(^1\) See page 11.
To arrive at an assessment of the total variation shown by each plant, a total hybrid-index score was calculated using the characters and numerical scores given in Table 6. Thus, the total hybrid-index score for a plant with all *C. erythraea* characters would be 0 and for a plant with all *C. littorale* characters would be 70. Hybrid-index histograms were constructed to give an indication of the proportion of *C. erythraea*-like, *C. littorale*-like, and intermediate plants present in each population (Figs 1 & 2).

**SINGLE SPECIES POPULATIONS OF C. ERYTHRAEA**

Even in single species populations it can be seen that some plants will have a hybrid-index slightly higher than the theoretical value of 0 (Fig. 1: a–h; Fig. 2: i–m, v). Thus plants with a score of 0, 5, 10 and 15 can be considered to be characteristic of *C. erythraea*.

Plants from the East Anglian populations J (Suffolk) and L (Norfolk) have noticeably higher scores than all other plants of this species (Fig. 2: n & o).

In cultivation, plants of this species range from 0 to 15 (Fig. 2: s) except those from East Anglia, which fall within the range 15–25.

**SINGLE SPECIES POPULATIONS OF C. LITTORALE**

Populations of this species are far more variable in their hybrid-index scores than those of *C. erythraea*.

a) Plants from the coasts of Lancashire and Anglesey have scores of 65–70 (Fig. 1: 1–5; Fig. 2: 7 & 8).

b) Plants from the coasts of Northumberland, Easterness, Moray and those from the Continent grown in the greenhouse, have scores of 50–65, which are slightly lower than the theoretical value (Fig. 1: 6; Fig. 2: 9 & 10, w).

c) Plants from the coasts of E. Ross and E. Sutherland are very different from all other populations of this species since, with values of 30–35 (Fig. 2: 12) and 40–45 (Fig. 2: 11), they fall within the range considered to be intermediate between all other plants of *C. littorale* and *C. erythraea*.

All plants of this species except those from E. Ross and E. Sutherland, which unfortunately were not cultivated, showed scores of 55–70 in cultivation (Fig. 2: t).

**MIXED POPULATIONS**

The normal range of variation shown by the single species populations does not cause any overlap in the hybrid-index values of the two species, except for plants from E. Ross and E. Sutherland. This is in contrast to the situation shown by mixed populations from the coasts of Lancashire, Anglesey and Germany.

a) Histograms i–vii (Fig. 1) for populations from Hightown, St Annes, Ainsdale, Freshfield and Anglesey all show a broken and uneven transition from *C. erythraea* to *C. littorale*. Obviously there are some plants that are referable to *C. erythraea* with scores of 0–15, and others with scores of 55–70 that are referable to *C. littorale*. The rest are intermediate in a number of characters, and with scores of 20–50 cannot be referred to either.

b) Histograms viii (Fig. 1) and ix (Fig. 2) for other populations from Freshfield show that there are some plants referable to *C. erythraea* and the rest are intermediate.

c) Histograms x and xi (Fig. 2), for other populations from Ainsdale and Freshfield respectively, show some plants referable to *C. littorale* while the rest are intermediate.

d) Histogram xii (Fig. 2) for another population from Freshfield, and x and y (Fig. 2) for German populations show that only intermediate plants are present.

The presence of plants in mixed populations with scores intermediate between those of *C. erythraea* and *C. littorale* is not unreasonable evidence of hybridization.

It is possible that of these intermediate plants those with a score of 25–40 might belong to the F₁ generation, those with scores of 45–50 might be backcrosses to *C. littorale*, and those with scores of 15–20 might be backcrosses to *C. erythraea*. If this is so, it would seem that backcrossing and introgression to *C. littorale* has taken place in population 14 at Hightown (Fig. 1: i), populations 16–19 at Freshfield (Fig. 1: viii; Fig. 2: ix, xi & xii), and in populations 21 and E at Ainsdale (Fig. 1: iii & vi). By contrast, populations 15 from Freshfield and 20 from St Annes (Fig. 1: ii & v) appear to consist of backcrosses to *C. erythraea*. 
In populations B and C from Ainsdale (Fig. 1: vii; Fig. 2: x), and those from Anglesey (Fig. 1: iv) and Germany (Fig. 2: x & y) individual plants with scores of 20, 25, 35 and 40 are present.

In cultivation, the progeny of plants from single species populations together with plants of *C. erythraea* and *C. littorale* from mixed populations show hybrid-index values identical to those shown by them in the wild. However, the progeny of intermediate plants from Ainsdale, Freshfield and Hightown show a variety of intermediate scores (Fig. 2: u). A few had values of 25–30 but the majority ranged from 40 to 50, thus resembling *C. littorale* more closely than *C. erythraea* and strongly suggesting backcrossing to the former species.

**THE CORRELATION OF DIFFERENT CHARACTERS WITHIN INDIVIDUAL PLANTS**

A more detailed picture of the characters of the individual plants, particularly those of the hybrids, can be seen from pictorialized scatter-diagrams. As space does not allow presentation of all populations examined by this method, only a few representative examples are given.
SINGLE SPECIES POPULATIONS OF C. ERYTHRAEA

Figs. 3 and 4 show the range of characters found in typical individuals of C. erythraea from populations in Surrey (v.c. 17), E. Kent (v.c. 15), Dorset (v.c. 9), Haddington (v.c. 82) and Clare (v.c. H 9). All the characters fall within the range characteristic of C. erythraea subsp. erythraea.

These studies show that all plants from single species populations of C. erythraea subsp. erythraea, except those from populations J (E. Suffolk), L (E. Norfolk), 29 and 30 (Isle of Wight), are very similar in most characters, and the only variation is shown by plants from exposed, coastal situations. The three varieties described by Gilmour (1937) under C. umbellatum as var. centaurium, var. fasciculare and var. subcapitatum can be recognized, but, as Melderis (1972b) has shown that the correct name for this species is C. erythraea Rafn, these three varieties should be placed under C. erythraea subsp. erythraea as follows:

i) C. erythraea subsp. erythraea var. erythraea
C. umbellatum Gilib. var. centaurium sensu Gilmour, Kew Bull., 10: 497 (1937)
Plants of this variety, the type variety of the species (Melderis 1972b), are tall (9-30 cm high) with a single main stem, 4-6 cauline nodes, long internodes with well-spaced leaves and a dense
Figure 3. Scatter diagram representing populations of *C. erythraea* from Box Hill, Surrey (v.c. 17) (O, pop. 3) and Folkestone, E. Kent (v.c. 15) (●, pop. 5), and populations of *C. littorale* from Ainsdale, S. Lancs. (v.c. 59) (▲, pop. G) and Holy Island, Cheviot (v.c. 68) (△, pop. 24).

Figure 4. Scatter diagram representing populations of *C. erythraea* from Swanage, Dorset (v.c. 9) (●, pop. 8), Aberlady, Haddington (v.c. 82) (O, pop. 23) and Fanore, Clare (v.c. H9) (●, pop. 27), and populations of *C. littorale* from Newborough, Anglesey (v.c. 52) (▲, pop. BA), Ainsdale, S. Lancs. (v.c. 59) (▲, pop. D) and Nairn (v.c. 96b) (△, pop. 22).
inflorescence of usually at least 5 cymes. It is represented in this study by populations 1–7, 10, 12, 25, 26, 28 and K from inland or sheltered, maritime habitats in parts of southern and northern England, southern Wales and western Ireland, and also by plants from the Continent (northern Europe) raised from seed in the greenhouse.

ii) *C. erythraea* subsp. *erythraea* var. *fasciculare* (Duby) Ubsdell, comb. nov.
*C. erythraea* subsp. *erythraea* var. *fasciculare* (Duby) Ubsdell, comb. nov.

This usually maritime variety is distinguished by having several main stems, or one main stem and many axillary branches, which often make it as broad as it is tall. It is represented in this study by population 23 from sand dunes on the coast of Haddington (v.c. 82), and in this area is dwarf (4–8 cm) with 4 cauleine nodes and short internodes, and each axillary branch terminates in a dense inflorescence of at least 5 cymes. Other much branched, but taller specimens from coastal regions, which retain all these characteristics in cultivation, should be included in this variety.

iii) *C. erythraea* subsp. *erythraea* var. *subcapitatum* (Corb.) Ubsdell, comb. nov.

This variety is strictly maritime and dwarf (4–8 cm) with 4–6 cauleine nodes. It is distinguished from var. *fasciculare* by its solitary, dwarf flowering-stem, extremely short internodes with crowded, cauleine leaves, and its very dense, capitate inflorescence of at least 5, crowded cymes. It is represented in this study by populations 8, 11, 13 and plants of population 29 with filaments inserted at the mouth of the corolla-tube. These are all from exposed, maritime cliff-tops in southern England. All its characteristics are retained in cultivation.

Plants of populations 27, J and I from sand dunes in western Ireland and East Anglia resemble this variety, but in cultivation became taller with well-spaced, cauleine nodes, and so must be included in var. *erythraea*.

Two other varieties remain to be considered:

iv) *C. erythraea* subsp. *erythraea* var. *capitatum* (Willd.) Melderis (1972b)

*Melderis* has described this maritime variety as being dwarf with a capitate inflorescence and filaments inserted at the base of the corolla-tube. Although previous authors have treated it as a separate species (*C. capitatum* (Willd.) Borbas), both Zeltner (1970) and Melderis (1972b) considered it to be only a variety of *C. erythraea* subsp. *erythraea* differing from the other dwarf variant (var. *subcapitatum*) only by the level of insertion of the filaments in the corolla-tube. Insertion of the filaments in the basal or middle part of the corolla-tube, instead of at the mouth as is normal for the genus, also occurs in other species of the genus from Europe, and Melderis (1972b) also recognized the following varieties:

*C. littorale* subsp. *littorale* var. *glomeratum* (Wittrock) Melderis, from the coasts of Sweden, Denmark and Germany, has the filaments inserted at the middle of the corolla-tube.

*C. pulchellum* var. *morierei* (Corb.) Melderis, known from a single locality on the coast of northern France (Manche), has the filaments inserted in the upper third of the corolla-tube.

Such variants are usually dwarf, with crowded, cauleine leaves and a compact inflorescence. They are also rare, being restricted to either a single locality or to a few, small, separate areas, but always within range of their most closely related variety and often growing mixed with it (Jakobsen 1960, Melderis 1972b).

According to Jakobsen (1960) growth of the corolla-tube normally takes place below the insertion of the filaments, but in the above three varieties growth occurs above the insertion of the filaments, or sometimes both above and below it, and the corolla-tube is always stunted in these three. He considered these differences to be of little importance since young buds of all varieties of these three species are identical.
This present study has shown that all plants from population 30 and those from 29 with filaments inserted at the base of the corolla-tube are identical with var. capitatum as described by Melderis (1972b). Furthermore, this variety is shown to be similar in most characters to var. subcapitatum as both are dwarf, maritime varieties with a single flowering stem, crowded cauline leaves and a very compact inflorescence. Population 29 from exposed, maritime cliff-tops at Freshwater, Isle of Wight, v.c. 10, is in fact a mixture of these two varieties, while population 11 (var. subcapitatum) and 30 (var. capitatum) were found growing only a few hundred yards away. Plants of var. capitatum are shown to differ from var. subcapitatum by their more extreme dwarfishness (<2·0 cm), and compactness, by their long filaments inserted at the base of the corolla-tube, and their short, stunted corolla-tubes which equal the calyx but do not enclose the capsules.

All characteristics were retained in cultivation, and observations on floral development support Jakobsen’s (1960) observations cited above. I, therefore, agree with Melderis that plants with filaments inserted at the base of the corolla-tube should be given only varietal status as var. capitatum.

v) *C. erythraea* subsp. *erythraea* var. *sublitorale* (Wheldon & Salmon) Ubsdell, **comb. nov.**

Wheldon’s specimen (BM) of this variety, collected in 1921 from Little Sea, Dorset (v.c. 9), is accompanied by a description but it is in fact identical with *C. erythraea* subsp. *erythraea* except for its narrower leaves and longer calyx, and does not fit the original description of *Erythraea centaurium* var. *sublitoralis* given by Wheldon & Salmon (1925). Under another narrow-leaved specimen of *C. erythraea* var. *erythraea* collected from St Annes, W. Lancs. (v.c. 60) in 1884 (BM) Wheldon has written that this plant comes close to without being identical to his *sublitoralis*, which he considered to be a hybrid between *C. erythraea* and *C. littorale*. Examination of other narrow-leaved plants of *C. erythraea* (BM) from S. Hants. (v.c. 11), E. Suffolk (v.c. 25), E. Norfolk (v.c. 27) and W. Norfolk (v.c. 28) by the present author has shown them to be very similar to the plant labelled by Wheldon as var. *sublitoralis* and identical to var. *erythraea* in all other characteristics.

Populations J (E. Suffolk) and L (E. Norfolk) also resemble var. *erythraea* in all characters except for their narrower leaves, which are intermediate in size and shape between those of *C. erythraea* and *C. littorale*, and they are also very similar to Wheldon’s plant from Dorset. *C. littorale*, however, is not known south of a line from Northumberland to North Wales, and so it seems unlikely that these narrow-leaved plants from southern England can be of hybrid origin.

Plants from mixed populations on the coast of S. Lancs. (population 15, Freshfield) and W. Lancs. (population 20, St Annes), considered by the present author to be backcrosses to *C. erythraea* var. *erythraea*, resemble the original description of var. *sublitoralis* in most characters but not the specimen named by Wheldon as var. *sublitoralis*. It seems, therefore, that Wheldon & Salmon confused plants of hybrid origin from Lancashire with narrow-leaved plants of *C. erythraea* from parts of England from which *C. littorale* is absent. Although the original description of var. *sublitoralis* (Wheldon & Salmon 1925), obviously refers to a hybrid, they do not cite any specimens, and as the only named specimen (BM) refers to a narrow-leaved variety of *C. erythraea*, then the name is fixed to the latter. Such narrow-leaved plants of *C. erythraea* from southern England should, therefore, be included under the new combination of *C. erythraea* subsp. *erythraea* var. *sublitorale* (Wheldon & Salmon) Ubsdell and the name cannot be used for plants of hybrid origin.

**SINGLE SPECIES POPULATIONS OF C. LITTORALE**

Figs. 3 & 4 also show the range of characters found in individuals of *C. littorale* from populations on the coasts of S. Lancs. (v.c. 59), Anglesey (v.c. 52), Cheviot (v.c. 68) and Nairn (v.c. 96b). All the characters fall within the range characteristic of *C. littorale* subsp. *littorale*.

These studies show that it is possible to recognize four varieties within this subspecies. Two from the coasts of North Wales, north-western England and south-western Scotland are scabrid, while the other two from the coasts of north-eastern England and eastern Scotland are glabrous.

i) *C. littorale* subsp. *littorale* var. *occidentale* (Wheldon & Salmon) Gilmour (1937)
This is the common scabrid variety found on the coasts of North Wales, north-western England
and south-western Scotland. It usually has a single stem, 3 or 4 cauline nodes, a lax inflorescence of 1 or 2 cymes, and varies in height from 4–12 cm. It is the variety used to represent *C. littorale* in this study in order to distinguish it from *C. erythraea* in mixed populations of the two from the coasts of Anglesey and Lancashire (see Table 6 for other characteristics). It is represented by populations A, D, F, G, H (S. Lancs., v.c. 59) and N (Anglesey, v.c. 52), and is the variety of this species found in all the mixed populations (14–21, B, C, E, AN). All its characteristics were retained in cultivation.

ii) *C. littorale* subsp. *littorale* var. *bayleyi* (Wheldon & Salmon) Gilmour (1937)
This is a second scabrid variety from the coasts of Anglesey and Lancashire. It is distinguished from the former by its numerous flowering-stems and axillary branches, which make it as broad as it is tall, its longer, narrower leaves, longer calyx, larger flowers and more compact inflorescence which is subequalled by long, leaf-like bracts. It is also dwarf (4–8 cm). It is represented in this study by population BA from Anglesey (v.c. 52), but unfortunately it was not grown in cultivation.

The two glabrous (or sometimes semi-scabrid) varieties can also be recognized but their nomenclatural history is confused. *C. littorale* (D. Turner) Gilmour was based on *Chironia littoralis* D. Turner described by Turner (1805) from material collected by Winch in Cheviot (Holy Island and sea coast near Hartley and Bamburgh Links). Melderis (1972b) chose as the lectotype of *Chironia littoralis* a specimen ex Herb. Hooker from Holy Island from Winch’s material (BM) which agreed with the original description. Gilmour’s var. *minor* agrees with typical material of *Chironia littoralis* as exemplified by Winch’s specimen, and he used var. *littorale* for the rather atypical form of *Chironia littoralis* from north-eastern Scotland, the first name for which is *Erythraea turneri* Wheldon & Salmon (1925). The nomenclature of these two varieties is, therefore, as follows:

iii) *C. littorale* subsp. *littorale* var. *littorale*

This is the typical glabrous or semi-scabrid variety from the coasts of north-eastern England (Cheviot, v.c. 68) and eastern Scotland (Moray, v.c. 95, and Nairn, v.c. 96b), and is distinguished from the two scabrid, west coast varieties (Table 6) mainly by its lack of scabridity but also by its shorter, broader leaves (ratio 5:0–5:6) fewer cauline nodes (1 or 2), smaller flowers and more compact inflorescence. It ranges in height from 4 to 11 cm, and Wheldon & Salmon (1925) placed the taller plants, including those from the Continent (northern Europe), under *Erythraea compressa* Hayne var. *friesii* Wheldon & Salmon, and the smaller plants, notably those from Holy Island on which *Chironia littoralis* was based, under *E. compressa* var. *friesii* forma *minor*. However, apart from the variation in height, they are identical and should be included as a single variety (var. *littorale*). This variety is represented in this study by populations 24 and R (Cheviot), 22 (Nairn) and EL (Moray), and also by plants from elsewhere in northern Europe raised from seed in the greenhouse.


This second glabrous or sometimes semi-scabrid variety has a rather distinct habit, being dwarf (3–6 cm) with a persistent basal rosette of leaves and usually only a single, cauline node. It is distinguished from var. *littorale* mainly by its shorter, broader leaves (ratio 4:1–4:3), shorter non-attenuated sepals (calyx:corolla-tube ratio 0:50–0:65), its shorter but very distinctive concave,
Figure 5. Scatter diagram representing a mixed population of *C. erythraea* and *C. litorale* from Hightown, S. Lancs. (v.c. 59) (pop. 14).

Figure 6. Scatter diagram representing two mixed populations from Freshfield, S. Lancs. (v.c. 59) (hollow symbols pop. 18, solid symbols pop. 19).
almost cup-shaped corolla-lobes, and its capsules, which are 2-3 times the length of the calyx, instead of equalling it as in all other varieties of C. littorale. It is represented in this study by populations T (E. Ross, v.c. 106) and DO (E. Sutherland, v.c. 107). It is also represented by all other material of this species examined from these localities, and by all plants of this species from Golspie (E. Sutherland) and Munlochy (E. Ross), and by some plants from Campbelltown (Nairn) and Findhorn (Moray).

It is rather different from all other varieties of C. littorale as it resembles C. erythraea in the calyx:corolla-tube ratio and length of the corolla-lobes, and is intermediate between the two species for leaf length:breadth ratio. Its status is difficult to decide as C. erythraea is absent from this part of Scotland, but as it most resembles C. littorale, and as plants of var. littorale from the coasts of north-eastern England and eastern Scotland have shorter leaves, shorter calyx and smaller flowers than the west coast varieties, it should be included in C. littorale as a variety.

MIXED POPULATIONS OF C. ERYTHRAEA AND C. LITTORALE

Figs. 5-9, representing mixed populations from the coasts of S. Lancs. (v.c. 59), W. Lancs. (v.c. 60) and Anglesey (v.c. 52), show typical plants of both C. erythraea and C. littorale var. occidentale, while the rest are intermediate.

Fig. 10, representing two populations from northern Germany, shows all plants to be intermediate in most characters between C. erythraea and C. littorale var. littorale.

Careful examination of the combinations of intermediate characters found in the natural hybrids shows that most of the plants can be placed under one of several types (Table 7):

a) By far the commonest hybrid plant is that represented by type 1 (Hybrid-index 45-50), to which belong nearly all the hybrids from populations 14 (Hightown), 16-19 (Freshfield) and 21 Ainsdale), and a few from B and C (Ainsdale). It is possible that these plants are backcrosses to C. littorale.

b) All hybrid plants from populations 15 (Freshfield) and 20 (St Annes) belong to type 2 (Hybrid-index 15-20), and it is possible that these are backcrosses to C. erythraea.

TABLE 7. TYPES OF NATURALLY OCCURRING HYBRID PLANTS

<table>
<thead>
<tr>
<th>Hybrid-type</th>
<th>of C. erythraea</th>
<th>Characters of Intermediate</th>
<th>Characters of C. littorale</th>
<th>Populations in which present</th>
<th>Hybrid-index</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>—</td>
<td>Leaf characters, length of corolla-lobes, stigma, pollen</td>
<td>Scabridity, calyx/corolla-tube ratio</td>
<td>14, 16, 17, 18, 19, 21, B, C</td>
<td>45-50</td>
</tr>
<tr>
<td>2</td>
<td>Scabridity, length of corolla-lobes, stigma, pollen</td>
<td>Leaf characters, calyx/corolla-tube ratio</td>
<td>—</td>
<td>20</td>
<td>15-20</td>
</tr>
<tr>
<td>3</td>
<td>Leaf characters</td>
<td>Stigma, pollen</td>
<td>Scabridity, floral parts</td>
<td>B, C, 14</td>
<td>40</td>
</tr>
<tr>
<td>4</td>
<td>Leaf characters, scabridity</td>
<td>Stigma, pollen</td>
<td>Floral parts</td>
<td>C</td>
<td>35</td>
</tr>
<tr>
<td>5</td>
<td>Floral parts</td>
<td>Leaf characters, stigma, pollen</td>
<td>Scabridity</td>
<td>AN</td>
<td>30</td>
</tr>
<tr>
<td>6</td>
<td>Scabridity</td>
<td>Leaf characters, stigma, pollen</td>
<td>Floral parts</td>
<td>AN</td>
<td>40</td>
</tr>
<tr>
<td>7</td>
<td>Scabridity, floral parts</td>
<td>Leaf characters, stigma, pollen</td>
<td>—</td>
<td>AN</td>
<td>25</td>
</tr>
<tr>
<td>8</td>
<td>Stigma</td>
<td>Leaf characters, stigma, pollen</td>
<td>Floral parts</td>
<td>16, 20</td>
<td>35</td>
</tr>
<tr>
<td>9</td>
<td>—</td>
<td>Leaf characters, scabridity, pollen</td>
<td>Floral parts</td>
<td>17, E</td>
<td>40</td>
</tr>
<tr>
<td>10</td>
<td>Leaf characters, scabridity</td>
<td>Floral parts, stigma, pollen</td>
<td>—</td>
<td>B</td>
<td>25</td>
</tr>
<tr>
<td>11</td>
<td>—</td>
<td>All characters</td>
<td>—</td>
<td>FAL, SP</td>
<td>25-40</td>
</tr>
</tbody>
</table>
Figure 7. Scatter diagram representing a mixed population from Ainsdale, S. Lancs. (v.c. 59) (pop. 21).

Figure 8. Scatter diagram representing a mixed population from St Annes, W. Lancs. (v.c. 60) (pop. 20).
CENTAURUM ERYTHRAEA AND C. LITtorALE: MORPHOLOGY

Figure 9. Scatter diagram representing a mixed population from Newborough, Anglesey (v.c. 52) (pop. AN).

Figure 10. Scatter diagram representing two populations from Falshöft (solid symbols) and St Peter (Schleswig-Holstein) (hollow symbols).
c) Types 3–10 (Hybrid-index 25, 30, 35, 40) are represented by a few individuals present in many of the mixed populations from the British Isles. Many appear F₁-like, and, in populations in which backcrosses predominate, they merge with them.

d) Type 11 (Hybrid-index 25-40) is represented by all plants from the two populations (FAL. and S.P.) from northern Germany, and they are F₁-like.

It seems, therefore, that on the Lancashire coast backcrossing to C. littorale is commoner than to C. erythraea. Neither seems to have happened in the population from Anglesey, in which only three F₁-like plants were found amongst a large number of plants of C. erythraea and C. littorale. All plants in the populations from northern Germany were F₁-like and there were no plants referable to either of the parental species.

SUMMARY

Morphological analysis of single-species populations of C. erythraea subsp. erythraea and C. littorale subsp. littorale has shown that both show a wide range of morphological variation, most of which is retained in cultivation.

It is possible to recognize five varieties of C. erythraea subsp. erythraea from the British Isles. They include the two named by Melderis (1972b) as var. erythraea and var. capitatum, and three others to be known as var. subcapitatum (Corb.) Ubsdell, comb. nov., var. fasciculare (Duby) Ubsdell, comb. nov. and var. sublitorale (Wheldon & Salmon) Ubsdell, comb. nov., all of which were included by Melderis in his var. erythraea.

It is also possible to recognize four varieties of C. littorale subsp. littorale from the British Isles, all of which were included in var. littorale by Melderis (1972b). Two are the scabrid, west coast varieties named by Gilmour (1937) as var. occidentale and var. bayleyi, while the two glabrous, east coast varieties are var. littorale (sensu Melderis 1972b) and var. turneri (Wheldon & Salmon) Ubsdell, comb. et stat. nov.

Despite this variation the two species can be clearly distinguished on the basis of a number of characters.

Analysis of mixed populations of C. erythraea and C. littorale from the coasts of Lancashire and Anglesey have shown that, while some plants are clearly referable to C. erythraea and others to C. littorale, the remainder are hybrids between the two. Analysis of two populations from the coast of northern Germany have shown all plants to be F₁-like.

In the majority of populations on the Lancashire coast backcrossing to C. littorale has taken place, although backcrossing to C. erythraea has also occurred. This is in contrast to the situation in the population from Anglesey, in which only F₁-like hybrids were present.

The nomenclature of the hybrids has been confused in the literature and will be discussed in detail in the third paper of this series.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr D. M. Moore under whose supervision this work was initiated and completed. I am also very grateful to Professor V. H. Heywood for providing facilities in the Department of Botany at the University of Reading.

This work was carried out during the tenure of a grant awarded by the Science Research Council.

REFERENCES


(Accepted March 1975)
Studies on variation and evolution in Centaurium erythraea Rafn and C. littorale (D. Turner) Gilmour in the British Isles

2. Cytology

R. A. E. UBSDELL

Department of Botany, University of Reading*

ABSTRACT

Chromosome counts of Centaurium erythraea Rafn and C. littorale (D. Turner) Gilmour from northern Europe are given. They confirm those made by Zeltner (1970) and show both species to be tetraploid (2n = 40) with regular meiosis.

Morphologically intermediate (F₁-like) plants from Ainsdale, S. Lancs. (v.c. 59), were found to be tetraploid with irregular meiosis. They were almost sterile, as were F₁-like plants from Newborough, Anglesey (v.c. 52), and were almost identical in their morphology and cytology to artificial F₁ hybrids.

Morphologically intermediate plants from northern Germany were found to be tetraploid, but with regular meiosis and a high fertility. It is suggested that they are stabilized derivatives of the F₁ hybrid.

Hybrid plants from St Annes, W. Lancs. (v.c. 60), which resemble C. erythraea in their morphology and are probably backcrosses to this species, were found to be tetraploid with regular meiosis and a high fertility.

Hybrid plants from Ainsdale, Freshfield and Hightown, S. Lancs. (v.c. 59), which closely resemble C. littorale in their morphology, were found to be hexaploid (2n = 60) with regular meiosis and a high fertility. They are shown to breed true, to be isolated from their tetraploid parents and other (tetraploid) hybrids by a difference in chromosome number, and to be able to compete successfully with their parents. They are, therefore, considered to constitute a new species, and a possible origin involving hybridization and polyploidy is discussed.

INTRODUCTION

Prior to Zeltner's work (1961, 1962, 1963, 1966, 1967) only four species of the genus Centaurium Hill had been examined cytologically, and the results obtained by different authors contradicted each other so much that it was impossible even to establish a basic number for the genus (Wulff 1937, Warburg 1939, Rork 1949, Mesquita Rodrigues 1953, Khoshoo & Khusnu 1966, Brink 1967).

Zeltner made numerous, reliable chromosome counts of all the European species and finally produced a comprehensive treatment summarizing his work on the genus (Zeltner 1970). He found all the karyotypes to be very similar and decided that they were of no taxonomic value. He also established two basic chromosome numbers for the European species, of x = 11 for C. spicatum (L.) Fritsch and x = 10 for all the other species. Six of the latter were found to be diploid (2n = 20), two tetraploid (2n = 40) and the other three species were found to have both diploid and tetraploid races, the diploids occurring in the Mediterranean region and the tetraploids in central and northern Europe. His work showed the importance of polyploidy, and of the resulting genetical isolation, in the evolution of the genus.

CENTAURIUM ERYTHRAEAE RAFN

The first chromosome count (2n = 42) for this species was determined by Rork (1949) on a plant from New York. Zeltner (1962) carried out chromosome counts on 113 populations from Europe.

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Of these, 16 from southern Europe were found to be diploid (2n = 20) with regular meiosis, while the other 97, all from northern Europe, were found to be tetraploid (2n = 40) with regular meiosis. It is not known how the tetraploids arose, but Zeltner suggested that it could have been by autopolyploidy.

*C. capitatum* (Wild.) Borbás, which is now considered to be only a variety of *C. erythraea* (Melderis 1972, Ubsdell 1976), was also found by Zeltner to be tetraploid with regular meiosis.

**CENTAURIUM LITTORALE (D. TURNER) GILMOUR**
The first chromosome count (n = 19) for this species was determined by Wulff (1937) on material from northern Germany. Warburg (1939) recorded 2n = 38 and 2n = 56 on material from the British Isles, while Brink (1967) reported that most plants of this species from the Netherlands had 2n = 40 although she had found a few plants with 2n = 38 or 2n = 42. Zeltner (1962) examined 15 populations from Europe and similarly found all to be tetraploid with regular meiosis. The diploid relatives of this species are confined to the Iberian peninsula and southern France, and Zeltner suggested that *C. littorale* could have been derived from them either by autopolyploidy or by allopolyploidy.

**NATURALLY OCCURRING HYBRIDS**
Zeltner (1970) examined some hybrid plants (*C. erythraea × C. littorale*) from Ainsdale, S. Lancs. (v.c. 59). He found 40 chromosomes at mitosis, but observations of meiosis showed some of the cells dividing regularly to give two equal groups of 20 chromosomes, and others showing irregular division with groups of 20/24 and 16/24. 80% of the pollen was distorted and sterile.

K. Jakobsen (in litt. 1972) reported that tetraploid hybrids between these two species occur on the coasts of Denmark. Some of the hybrids were almost sterile with irregular meiosis, while others appeared to be cytologically stable.

This paper is concerned with the cytology and pollen fertility of plants of *C. erythraea* and *C. littorale* from northern Europe (chiefly from the British Isles), their naturally occurring hybrids (Ubsdell 1976) and artificial hybrids.

**METHODS**

**CHROMOSOME COUNTS**
Somatic chromosomes were examined at mitosis in the root-tips. Initially they were difficult to count as all the chromosomes tended to conglomerate on the metaphase plate. Eventually, however, pre-treatment with saturated, aqueous paradichlorobenzene for twelve hours before fixation in 3:1 ethanol:acetic acid was found to give satisfactory preparations with the chromosomes well spread. After fixation the root-tips were softened in N HCl for three minutes before washing and staining in propionic-orcein.

Buds were fixed in 3:1 ethanol:acetic acid and stored in 70% ethanol. After softening in 1:1 ethanol:concentrated HCl, good results were obtained for the meiotic chromosomes by staining in propionic-orcein; acetic-orcein and acetocarmine gave poor results.

All preparations were made permanent by freezing with Arcton 12, dehydrating in ethanol and mounting in Euparal.

**POLLEN FERTILITY**
Fresh pollen grains were mounted in cotton blue/lactophenol. Spherical pollen grains took up the stain and were considered to be viable, while unstained, distorted, elliptical grains were considered to be infertile. 100 pollen grains were scored for each plant.

**RESULTS**
Details of the chromosome number, pairing at meiosis and pollen fertility are given for various collections of *C. erythraea* (Table 1), *C. littorale* (Table 2), and their natural (Table 3) and artificial (Table 4) hybrids.
### TABLE 1. CHROMOSOME NUMBER, MEIOTIC PAIRING AND POLLEN FERTILITY OF *C. ERYTHRAEA*

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>4. Orpington, W. Kent, v.c. 16</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>84%</td>
<td></td>
</tr>
<tr>
<td>5. Folkestone, E. Kent, v.c. 15</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>93%</td>
<td></td>
</tr>
<tr>
<td>6. Lucombe, Isle of Wight, v.c. 10</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>92%</td>
<td></td>
</tr>
<tr>
<td>7. Sandown, Isle of Wight, v.c. 10</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>8. Swanage, Dorset, v.c. 9</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>89%</td>
<td></td>
</tr>
<tr>
<td>10. Bonchurch, Isle of Wight, v.c. 10</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>89%</td>
<td></td>
</tr>
<tr>
<td>11. Freshwater, Isle of Wight, v.c. 10</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>12. Steyning, W. Sussex, v.c. 13</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>96%</td>
<td></td>
</tr>
<tr>
<td>23. Aberlady, Haddington, v.c. 82</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>92%</td>
<td></td>
</tr>
<tr>
<td>25. Newbiggin, S. Northumberland, v.c. 67</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>87%</td>
<td></td>
</tr>
<tr>
<td>27. Fanore, Clare, v.c. H9</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>86%</td>
<td></td>
</tr>
<tr>
<td>28. Funshin, S.E. Galway, v.c. H15</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>91%</td>
<td></td>
</tr>
<tr>
<td>J. Minsmere, E. Suffolk, v.c. 25</td>
<td>20</td>
<td>—</td>
<td>2n = 40</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>L. Minsmere, E. Suffolk, v.c. 25</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>90%</td>
<td></td>
</tr>
</tbody>
</table>

**Mixed populations**

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>14. Hightown, S. Lancs., v.c. 59</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>82%</td>
<td></td>
</tr>
<tr>
<td>15. Freshfield, S. Lancs., v.c. 59</td>
<td>20</td>
<td>—</td>
<td>2n = 40</td>
<td>80%</td>
<td></td>
</tr>
<tr>
<td>20. St Annes, W. Lancs., v.c. 60</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>21. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>96%</td>
<td></td>
</tr>
<tr>
<td>AN. Newborough, Anglesey, v.c. 52</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>86%</td>
<td></td>
</tr>
</tbody>
</table>

Continental plants raised in greenhouse (all seed obtained from Botanic Gardens)

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rügen, Germany</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>Wageningen, Netherlands</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>92%</td>
<td></td>
</tr>
<tr>
<td>Copenhagen, Denmark</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>90%</td>
<td></td>
</tr>
</tbody>
</table>

### TABLE 2. CHROMOSOME NUMBER, MEIOTIC PAIRING AND POLLEN FERTILITY OF *C. LITTORALE*

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>94%</td>
<td></td>
</tr>
<tr>
<td>G. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>H. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>89%</td>
<td></td>
</tr>
<tr>
<td>BA. Newborough, Anglesey, v.c. 52</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>79%</td>
<td></td>
</tr>
<tr>
<td>N. Newborough, Anglesey, v.c. 52</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>86%</td>
<td></td>
</tr>
<tr>
<td>24. Holy Island, Cheviot, v.c. 68</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>84%</td>
<td></td>
</tr>
<tr>
<td>22. Nairn, v.c. 96b</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>92%</td>
<td></td>
</tr>
</tbody>
</table>

**Mixed populations**

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>86%</td>
<td></td>
</tr>
<tr>
<td>21. Ainsdale, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>14. Hightown, S. Lancs., v.c. 59</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>16. Freshfield, S. Lancs., v.c. 59</td>
<td>20</td>
<td>2n = 40</td>
<td>2n = 40</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>20. St Annes, W. Lancs., v.c. 60</td>
<td>20</td>
<td>—</td>
<td>—</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>AN. Newborough, Anglesey, v.c. 52</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>80%</td>
<td></td>
</tr>
</tbody>
</table>

Continental plants raised in the greenhouse (all seed obtained from Botanic Gardens)

<table>
<thead>
<tr>
<th>Single species populations</th>
<th>Meiosis (No. of bivalents)</th>
<th>Metaphase I</th>
<th>Anaphase I</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rügen, Germany</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>Blidö, Sweden</td>
<td>20</td>
<td>2n = 40</td>
<td>—</td>
<td>89%</td>
<td></td>
</tr>
<tr>
<td>Helsinki, Finland</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>88%</td>
<td></td>
</tr>
<tr>
<td>Copenhagen, Denmark</td>
<td>—</td>
<td>—</td>
<td>2n = 40</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>Cultivation code and status</td>
<td>Metaphase I (No. of bivalents, univalents and quadrivalents)</td>
<td>Meiosis</td>
<td>Anaphase I (pattern of segregation and diploid no.)</td>
<td>Root-tip mitosis</td>
<td>Pollen fertility</td>
</tr>
<tr>
<td>----------------------------</td>
<td>----------------------------------------------------------</td>
<td>---------</td>
<td>-------------------------------------------------</td>
<td>----------------</td>
<td>----------------</td>
</tr>
<tr>
<td>14. Hightown, S. Lancs.</td>
<td>30 II</td>
<td></td>
<td>30–30 (2n = 60)</td>
<td>2n = 60</td>
<td>81–90%</td>
</tr>
<tr>
<td>Progeny in cultivation</td>
<td></td>
<td></td>
<td>31–26 (2n = 57)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R60</td>
<td></td>
<td></td>
<td>29–28 (2n = 57)</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>31–25 (2n = 56)</td>
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<td></td>
<td></td>
<td></td>
<td>26–25 (2n = 51)</td>
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<td></td>
<td></td>
<td></td>
<td>26–24 (2n = 50)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16. Freshfield, S. Lancs.</td>
<td>30 II</td>
<td></td>
<td>28–28 (2n = 56)</td>
<td>2n = 60</td>
<td>81–90%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>27–27 (2n = 54)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
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<td>28–27 (2n = 55)</td>
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<td></td>
<td></td>
<td></td>
<td>29–29 (2n = 58)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>27–25 (2n = 52)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30–29 (2n = 59)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Progeny in cultivation R61

| 20. St Annes, W. Lancs.   | 20 II                                                   |         | 20–20 (2n = 40)                                 |                | 88%            |
| 21. Ainsdale, S. Lancs.   | —                                                       |         | 2n = 40                                         |                | 0–10%          |
| B. Ainsdale, S. Lancs.    | —                                                       |         | 2n = 60                                         |                | 80–90%         |

Progeny in cultivation R10

| R11                        | 29/30 II                                               |         | 29–29 (2n = 58)                                 | 2n = 60        | 81–82%         |
| R31                        | 30 II                                                  |         | 30–30 (2n = 60)                                 | 2n = 60        | 78–89%         |
| R51                        | 30 II                                                  |         | 30–30 (2n = 60)                                 | 2n = 60        | 80–87%         |
| R52                        | 30 II                                                  |         | 30–30 (2n = 60)                                 | 2n = 60        | 81–87%         |

Selfed progeny of R10, R11

| 30 II                      | 30–30 (2n = 60)                                        | 2n = 60 | 80–90%                                        |

C. Ainsdale, S. Lancs.

| —                         | 2n = 40                                                |         | 0–10%                                         |
| —                         | —                                                      |         | 67–80%                                        |

Progeny in cultivation R23

| 20 II                      | 2n = 40                                                | 2n = 40 | 0–10%                                         |
| 19 II + 2 I                |                                                        |         |                                               |
| 17 II + 6 I                |                                                        |         |                                               |
| R50                        | 29 II                                                  |         | 31–29 (2n = 60)                                 | 2n = 60        | 67–87%         |
| 28 II + 1 IV               | 31–27 (2n = 58)                                        |         |                                               |
| 26 II + 4 I                | 30–25 (2n = 55)                                        |         |                                               |
| E. Ainsdale, S. Lancs.     | —                                                      |         | 2n = 40                                         | 0–10%          |

Progeny in cultivation R28

| 18 II + 4 I                | 2n = 40                                                | 2n = 40 | 0–10%                                         |
| 18 II + 1 IV               |                                                        |         |                                               |
| 15 II + 1 IV + 6 I         |                                                        |         |                                               |
| 14 II + 1 IV + 8 I         |                                                        |         |                                               |
| 13 II + 1 IV + 6 I         |                                                        |         |                                               |

and as for R23

AN. Newborough, Anglesey

| —                         | —                                                      |         | 0–10%                                         |

FAL. Falshöft, Germany

| 20 II                      | 20–20 (2n = 40)                                        |         | 77–85%                                        |

S.P. St Peter, Germany

| 20 II                      | 20–20 (2n = 40)                                        |         | 78–82%                                        |
### TABLE 4. CHROMOSOME NUMBER, MEIOTIC PAIRING, POLLEN FERTILITY AND SEED SET OF ARTIFICIAL HYBRIDS

<table>
<thead>
<tr>
<th>Cultivation code and status</th>
<th>Meiosis</th>
<th>Root-tip mitosis</th>
<th>Pollen fertility</th>
<th>Seed set per capsule by open pollination</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>20 II</td>
<td>24-20 (2n = 44)</td>
<td>2n = 40</td>
<td>0 - 10%</td>
</tr>
<tr>
<td>3</td>
<td>19 II + 2 I</td>
<td>23-20 (2n = 43)</td>
<td>2n = 40</td>
<td>0 - 6</td>
</tr>
<tr>
<td>4</td>
<td>17 II + 6 I</td>
<td>20-20 (2n = 40)</td>
<td>2n = 40</td>
<td>67%</td>
</tr>
<tr>
<td></td>
<td>18 II + 1 IV</td>
<td>20-18 (2n = 38)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>17 II + 1 IV + 2 I</td>
<td>19-19 (2n = 38)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>16 II + 1 IV + 4 I</td>
<td>19-17 (2n = 36)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>15 II + 2 IV + 2 I</td>
<td>20-15 (2n = 35)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>14 II + 2 IV + 4 I</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>15 II + ch. of 5 + 5 I</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetraploid hybrid</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R23 × C. erythraea 5</td>
<td>20 II</td>
<td>20-20 (2n = 40)</td>
<td>2n = 40</td>
<td>6 - 9%</td>
</tr>
<tr>
<td></td>
<td>18 II + 1 IV</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>15 II + 2 IV + 2 I</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetraploid hybrid</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R23 × C. littorale 6</td>
<td>Not clear but II, III and IVs</td>
<td>20-1-1-17 (2n = 40)</td>
<td>2n = 40</td>
<td>6 - 9%</td>
</tr>
<tr>
<td>Hexaploid hybrid × C. erythraea 7</td>
<td>24 II + 2 I</td>
<td>28-22 (2n = 50)</td>
<td>2n = 50</td>
<td>50 minute</td>
</tr>
<tr>
<td></td>
<td>22 II + 2 III</td>
<td>26-24 (2n = 50)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(reciprocal crosses) 19 II + chs. of 4, 6</td>
<td>25-5-20 (2n = 50)</td>
<td>26-22 + 1 II (2n = 50)</td>
<td>21-21 + 4 II (2n = 50)</td>
<td>malformed</td>
</tr>
<tr>
<td>Hexaploid hybrid × C. littorale 9</td>
<td>20 II + chs. of 3, 3, 4</td>
<td>25-25 (2n = 50)</td>
<td>2n = 50</td>
<td>3 - 25%</td>
</tr>
<tr>
<td></td>
<td>19 II + chs. of 4, 4 + 2 I</td>
<td>25-1-24 (2n = 50)</td>
<td></td>
<td>10 minute</td>
</tr>
<tr>
<td>(reciprocal crosses) 19 II + chs. of 6 + 6 I</td>
<td>24-8-18 (2n = 50)</td>
<td></td>
<td></td>
<td>malformed</td>
</tr>
<tr>
<td>18 II + chs. of 4, 6 + 2 I</td>
<td>20-15-15 (2n = 50)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18 II + rgs. of 4, 4 + 4 I</td>
<td>20-3-27 (2n = 50)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 II + chs. of 3, 3, 4, 6</td>
<td>20-30 (2n = 50)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 II + chs. of 3, 3, 4, 4 + 2 I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 II + chs. of 4, 4, 4, 6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 II + chs. of 3, 4, 6 + 4 I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 II + rgs. of 4, 4 + 4 I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 II + chs. of 3, 3, 5, 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hexaploid hybrid ×</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hexaploid hybrid 11</td>
<td>30 II</td>
<td>30-30 (2n = 60)</td>
<td>2n = 60</td>
<td>79 - 89%</td>
</tr>
</tbody>
</table>

**CENTAURIUM ERYTHRAEA**

All plants of this species, both from single species populations and from mixed ones, were found to be tetraploid (2n = 40) with regular meiosis. All plants were highly fertile, with a pollen fertility of over 80% in single species and mixed populations (Table 1).
**CENTAURIUM LITTORALE**

All plants of this species, both from single species populations and from mixed ones, were also found to be tetraploid (2n = 40) with regular meiosis. All plants were highly fertile, with a pollen fertility of over 79% in single species and mixed populations (Table 2).

**NATURALLY OCCURRING HYBRIDS**

These hybrids showed a variety of chromosome numbers and meiotic irregularities, and seemed to fall into three main cytological types.

1. This is represented by the morphologically intermediate, F₁-like plants from Ainsdale, S. Lancs. (Table 3: populations C, E & 21). These plants were tetraploid (2n = 40) with irregular meiosis. No clear metaphase counts were made, but preparations of first anaphase showed lagging chromosomes, fragments and apparent chromatid bridges. All plants had a very low pollen fertility of 0–10%.

   Seed collected from these hybrids in the field was sown in the greenhouse and the progeny raised to maturity. These cultivated plants, which were at least second generation hybrids (Table 3: R23 & R28), were also found to be tetraploid (2n = 40) and to have irregular meiosis. The number of bivalents varied from 13 to 20, the other chromosomes forming univalents or occasionally a quadrivalent (Fig. 1: a & b). There were lagging chromosomes and other irregularities at first anaphase, and despite the large number of bivalents all plants had a low pollen fertility (0–10%).

   Morphologically intermediate, F₁-like plants from Newborough, Anglesey (v.c. 52) (Table 3: population AN), also had a low pollen fertility, but unfortunately no chromosome counts were made.

2. This is represented by plants from St Annes, W. Lancs. (v.c. 60). Table 3, population 20), which closely resemble *C. erythraea* in their morphology and may be backcrosses to this species, and also by the morphologically intermediate plants from the northern German populations (Table 3: populations FAL. & S.P.). These plants were found to be tetraploid (2n = 40) with regular meiosis, and all were highly fertile with a pollen fertility comparable to that of the parents. Unfortunately, no progeny were raised in the greenhouse.

3. This is represented by the majority of hybrid plants from Ainsdale, Freshfield and Hightown, S. Lancs. (Table 3: populations 14, 16 & 21), which closely resemble *C. littorale* in their morphology and may possibly be backcrosses to this species. These plants were found to be basically
hexaploid \((2n = 60)\), but meiotic counts of 50, 51, 52, 54, 55, 56, 57, 58 and 59 were also made, more than one number often being counted from the same individual. Three preparations of first metaphase showed complete pairing with 30 bivalents, but many other preparations were not clear enough for a count to be made. Twenty preparations of first anaphase showed cells dividing regularly into two equal groups of from 27 to 30 chromosomes, while a further ten preparations showed cells dividing irregularly into groups of 24/26, 25/26, 25/31, 27/28, 26/31, 28/29 chromosomes (Fig. 2). These plants showed a wide range of pollen fertility \((45-96\%)\), but the majority were quite fertile (over \(80\%\)).

![Figure 2](image)

**Figure 2.** Hexaploid hybrids (a) anaphase I of meiosis \((2n = 50)\), (b) anaphase I of meiosis \((31-26, 2n = 57)\), (c) anaphase I of meiosis \((30-30, 2n = 60)\).

Wild-collected seed from these hybrids was sown in the greenhouse and the progeny raised to maturity. All plants were found to be basically hexaploid (counts of \(2n = 60\) for root-tip chromosomes). A few plants (Table 3: R50) showed irregular meiosis, the number of bivalents varying from 26 to 29 with the other chromosomes forming univalents or occasionally a quadrivalent. Anaphase segregation was unequal, and the pollen fertility of these plants fell within the range \(67-87\%\). However, the majority of plants (Table 3: R10, R11, R31, R51, R52, R60, R61) showed regular meiosis with complete pairing (30 bivalents) and equal anaphase segregation into two groups of 30 chromosomes. The pollen fertility of these cytologically stable, hexaploid plants was high \((74-90\%\)\) and comparable to that of the parents.

Seed set by selfing these hexaploid hybrids in the greenhouse produced progeny identical to the parents in their morphology, cytology and fertility (Fig. 3, R10).

**ARTIFICIAL F1 HYBRIDS AND THEIR PROGENY**

These hybrids resulted from crosses made in the greenhouse between *C. erythraea* and *C. littorale*. All were found to be morphologically intermediate between the parents (Fig. 3: 1–4), and tetraploid \((2n = 40)\) with irregular meiosis (Table 4: 1–4). The number of bivalents varied from 14 to 20, the other chromosomes forming univalents and multivalents (Fig. 1c). There were also lagging chromosomes and other irregularities at first anaphase. Despite the large number of bivalents, pollen fertility was low \((0-10\%)\) and all plants set very little seed by artificial self-pollination.
Figure 3. Scatter diagram comparing all artificial hybrids with plants of *C. erythraea*, *C. littorale* and their natural hybrids raised in the same greenhouse in the same year.

**OTHER ARTIFICIAL HYBRIDS**

Crosses between natural, almost sterile, tetraploid hybrids (R23) and natural, hexaploid hybrids produced pentaploid (2n = 50) progeny with irregular meiosis and a very low pollen fertility and seed set. No such plants were found in the wild.

Using the same natural, tetraploid hybrid (R23), backcrosses were made to *C. erythraea* and *C. littorale*. Surprisingly the two backcrosses had very different fertility. That to *C. littorale* was morphologically intermediate between the tetraploid and hexaploid hybrids, had irregular meiosis, a low pollen fertility and seed-set (Table 4: 6), and was unlike any plant found in the wild. By contrast, the backcrosses to *C. erythraea* closely resembled that species and had a more regular meiosis, higher pollen fertility and better seed set than both the natural and artificial F₁ hybrids.
CENTAURIUM ERYTHRAEA AND C. LITTORALE: CYTOLOGY

These plants strongly resembled the fertile, tetraploid hybrids (Table 3: population 20) from St Annes, W. Lancs. in their morphology, cytology and fertility.

Backcrossing the natural, hexaploid hybrids (R10, R11) to C. erythraea produced progeny intermediate in morphology between the F1 hybrid and C. erythraea (Fig. 3: 7 & 8), but the backcrosses to C. littorale closely resembled the hexaploid parents (Fig. 3: 9 & 10). Both backcrosses were pentaploid (2n = 50) with irregular meiosis, a low pollen fertility and poor seed-set (Table 4: 7–10). No plants with these characteristics were found in the wild.

**DISCUSSION**

Chromosome counts of C. erythraea and C. littorale from northern Europe show both species to be tetraploid (2n = 40) with regular meiosis. These results confirm those of Zeltner (1970) and Brink (1967), but contradict those of Wulff (1937), Warburg (1939) and Rork (1949). It is possible that faulty observation of this cytologically difficult material might explain the counts of 2n = 42 for C. erythraea made by Rork (1949), and 2n = 38 for C. littorale made by Wulff (1937) and Warburg (1939). It also seems probable that the count of 2n = 56 for C. littorale by Warburg (1939) was made from the hexaploid hybrid between this species and C. erythraea, since the hexaploid hybrids closely resemble C. littorale and are easily mistaken for this species.

The artificial F1 hybrids are shown to be tetraploid (2n = 40) with fairly good pairing at first metaphase, but irregularities at first anaphase and a low pollen fertility. It therefore seems likely that the morphologically intermediate (Hybrid-index 25–40 (Ubsdell 1976)), tetraploid plants from Ainsdale, S. Lancs., and Newborough, Anglesey, with irregular meiosis and low pollen fertility also belong to the F1 generation, as do those examined by Zeltner (1970).

The morphologically intermediate, tetraploid plants (Hybrid-index 25–40) from northern Germany with regular meiosis and a high pollen fertility seem unlikely to belong to the F1 generation, since artificial F1 hybrids produced by crossing plants of C. erythraea and C. littorale from northern Germany were found to have irregular meiosis and a low pollen fertility similar to those produced by crossing British plants. It is possible that they are segregates of the F1 hybrid which have become cytologically stable, and a similar suggestion was made by Jakobsen (in litt. 1972) to explain the origin of cytologically stable, fertile, tetraploid hybrids found in populations on the coast of Denmark.

The highly fertile, hexaploid, hybrid plants from Ainsdale, Freshfield and Hightown, S. Lancs. (Hybrid-index 45–50) could have been formed by one of several methods.

While it is possible that it may have been derived from an octoploid parent and a normal, tetraploid parent, this seems very unlikely since the number 2n = 80 has never been recorded in Centaurium. It seems more likely that the hexaploid was produced from two tetraploid parents, C. littorale and C. erythraea, and this must almost certainly have involved an unreduced gamete, possibly as a result of non-disjunction and restitution during first meiotic division.

It is possible that the unreduced gamete was from C. littorale since the hexaploids most closely resemble this species. With three sets of chromosomes, two of which would be from C. littorale, they would also have at least 20 bivalents and it is possible that some of the C. erythraea chromosomes might also pair. Those that do not pair might get lost during anaphase segregation and this would explain the numbers of 2n = 50–59 observed at anaphase in some of the natural, hexaploid hybrids.

This theory, however, assumes that non-reduction has only occurred in C. littorale since no hexaploid hybrids resembling C. erythraea have been found, although it is possible that they might be formed but do not survive in the wild.

It seems more likely that non-reduction occurred in a hybrid plant, since natural and artificial, tetraploid F1 hybrids are almost sterile owing to meiotic irregularities. Furthermore, it has been shown that neither selfing the artificial F1 hybrids nor crossing between them increases their fertility so there would be a strong selective advantage for genotypes that could overcome their sterility by some other means.

It has been shown that artificially backcrossing the natural, almost sterile, tetraploid hybrids from Ainsdale to C. erythraea produces tetraploid plants closely resembling this species in their morphology, and with regular meiosis and high fertility. Such plants closely resemble the fertile,
tetraploid hybrids from St Annes, W. Lancs. (Hybrid-index 15–20), and so these plants may have originated in this way. By this method, the fertility of the hybrids has been increased at the tetraploid level.

However, it has also been shown that artificially backcrossing the same Ainsdale hybrids to *C. littorale* does not increase the fertility at the tetraploid level, all such backcrosses being almost sterile. If, therefore, fertilization occurred between a non-reduced, tetraploid hybrid gamete and a normal, reduced, diploid gamete of *C. littorale*, the more fertile hexaploid genotypes might be at a selective advantage. By this method, the hexaploids would resemble *C. littorale* more closely in their morphology and pairing at metaphase and anaphase segregation would also be the same as it would have been if non-reduction had occurred in *C. littorale*.

Experiments have also shown that crossing the hexaploid hybrids with either of the tetraploid parents, or with the tetraploid hybrids, produces a few almost sterile, pentaploid plants of varying morphology, none of which has been found in the wild. It seems, therefore, that the hexaploids are isolated from their tetraploid parents and all tetraploid hybrids by a difference in chromosome number, and so in order to persist must either self or cross with each other. As has already been shown, the hexaploids are characterized by a more or less regular meiosis and good seed-set; they also breed true.

Since these hexaploids are as abundant as their parents in certain populations at Ainsdale, Freshfield and Hightown, S. Lancs., and since they breed true and are also isolated from their parents by a difference in chromosome number, they should be considered to constitute a new species. Their nomenclature will be discussed in the third and final paper in this series. This study has consequently shown that, in addition to introgression, which might have been expected, hybridization between *C. erythraea* and *C. littorale* has resulted, in certain areas, in the evolution of a new species.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr D. M. Moore under whose supervision this work was initiated and completed. I am also very grateful to Professor V. H. Heywood for providing facilities in the Department of Botany at the University of Reading.

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REFERENCES


(Accepted April 1975)
Notes on British Rubi, 4

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ABSTRACT

The names of seven brambles on the British list are discussed and the following new names are proposed: Rubus painteri for R. eifeliensis sensu W. C. R. Wats. ex parte, non Wirtg., R. turritus for R. apricus sensu W. C. R. Wats. ex parte, non Wimm., R. infestior for R. infestus sensu W. C. R. Wats., non Weihe ex Boenn., and R. anglohirius for R. hirtus sensu W. C. R. Wats. ex parte, non Waldst. & Kit. R. pampinosus Lees is shown to be an earlier name for R. favonii W. C. R. Wats. and R. infestus Weihe ex Boenn. for R. taeniarcum Lindeb. R. condensatus P. J. Muell. is confirmed as a British species.

R. buttii Barton & Riddelsd. in Riddelsd., Hedley & Price, Fl. Gloucester, 148 (1948)

There is a specimen in Babington’s herbarium (no. 233) in CGE named R. pampinosus Lees, which is undoubtedly the same taxon as R. favonii W. C. R. Wats. It is a good specimen mounted on two sheets, one bearing a panicle in advanced fruit and the other a piece of the first-year stem with two leaves. It was collected by W. Mathews from ‘open hedge banks in the Forest of Wyre’, Worcester, v.c. 37, 25/9/1851, and named by E. Lees. Babington had determined it R. villicaulis Weihe & Nees and maintained that opinion in later years (1869, p. 144). In his original description Lees (1852) described the stem as ‘polished’ and referred to the long, leafy panicle with wide-spreading branches. He called it ‘a very remarkable bramble, with leaves so large and numerous as almost to conceal the stem’ and said it grew in dense thickets in Cowleigh Park, v.c. 37. Later on (1867) he gave the Wyre Forest as a second locality. I have seen this bramble both in Cowleigh Park and in the Wyre Forest and have several specimens, including one from the Wyre Forest, Salop, v.c. 40, collected by W. C. R. Watson, 15/7/1953. This specimen is unnamed but is no doubt the source of Watson’s record (1958) of R. favonii for the Wyre Forest. R. buttii Barton & Riddelsd. is the same taxon.

R. favonii must now be known as R. pampinosus. It is locally common in woods in the west of England from Staffordshire through Gloucestershire to Dorset. Exsiccata from the following vicinities have been examined by A. Newton or myself: 6, 9, 11, 33, 36-40, 46.

2. Rubus condensatus P. J. Muell., Flora (Regensb.), 41: 167 (1858)

Among the specimens which Sudre (1911) cited to illustrate this taxon is a series (Sudre’s Rubi rari no. 68) collected by P. J. Mueller from Reissbach, Alsace, the locus classicus, 20/7/1857. There is a good example in MANCH which tallies well with the original description. Watson (1958) thought that a bramble he found on Harrow Weald Common, Middlesex, v.c. 21, was R. condensatus. But his specimen in my herbarium does not match the MANCH specimen closely. However a bramble of central England, which has puzzled batologists for many years, clearly does. There are specimens of this bramble in MANCH and SLBI collected by A. Ley, 25/8/1904, from the Wyre Forest, Salop, v.c. 40, which Ley named R. serpens Weihe with the approval of W. M. Rogers. But they differ from Rogers’ (1900) description of R. serpens, which, however, may not be reliable. The true R. serpens Weihe ex Lejeune & Court. has often been misinterpreted, but it was evidently a hairy, very glandular bramble with many quinate as well as some ternate leaves. There is another specimen in BIRM collected by Ley, 2/9/1909, from Wenlock Edge, Presthope, Salop, which Ley called R. serpens forma.
Watson, to whom I sent a Staffordshire specimen collected in 1953, associated it with *R. scaber* Weihe & Nees, and B. A. Miles told me *(in litt. 1968)* that he had seen Staffordshire specimens, collected by J. Fraser in 1877 and 1878, which had also been named *R. scaber*. *R. condensatus* resembles *R. scaber* in having ternate leaves, small white petals and erect sepals. But there are many differences, particularly in the armature and glandular development of the stem and rachis and in the shape, texture and serration of the leaflets.

The following description of the Wyre Forest bramble was prepared before I had seen the MANCH specimen or had read Mueller’s original account. It is offered for comparison with Mueller’s description and as a substitute for Watson’s *(1958):*

Stems bluntly angled, becoming reddish purple in exposure, thinly pilose, with a few scattered acicles and glandular hairs. Prickles small, often shorter than the diameter of the stem, declining or sometimes slightly curved, unevenly arranged.

Leaves ternate. Leaflets plicate, thinly strigose and shining green above, paler below and almost glabrous apart from a few hairs on the veins. Margins shallowly crenate. Terminal leaflets obovate-oblong, acuminate, emarginate or cordate, three to four times as long as their petiolules. Petioles with a few weak, declining or curved prickles.

Flowering branches with adpressed and short, spreading hairs, frequent short acicles and a few glandular hairs. Prickles slender, declining or curved. Lower leaves ternate, upper leaves simple, broad, cordate, nearly glabrous on both sides. Panicles dense with interlacing pedicels and subsidiary clusters on long, suberect peduncles in the axils of the leaves.

Sepals sparingly aculeolate and glandular, long-pointed, white-margined, reflexed in flower, erect in young fruit. Petals white, spaced, obovate, 10 × 5 mm. Stamens white, equalling the green styles. Anthers pilose or subpilose. Carpels densely hairy at first, bearded later.

*R. condensatus* is frequent in the Wyre Forest, GR 32/7.7, and in south-western Staffs., v.c. 39. I have a series of specimens in my herbarium from Kinver, GR 32/8.8, Codsall, GR 33/8.0, and Wrottesley, GR 33/8.0.

3. **Rubus painteri** E. S. Edees, sp. nov.

*R. eifelliensis* sensu W. C. R. Wats. ex parte, non Wirtg.

Turiones pilis patentibus, albis, simplicibus dense vestiti. Glanduli stipitati pauci vel nulli. Aculei pilosi, numerosi (15–20 per 5 cm), ad angulos dispositi, aequo longi ac diametrum caulis, patentes vel paulo declinati.

Folia ternata vel quinata pedata. Foliola utrinque griseoviriditia, superne strigosa, inferne pilis multis ad nervos disposita, villosa, aequaliter duplicato-serrata. Foliolum terminale late obovatum vel paene rotundatum, stipitatum, basi emarginatum vel subcordatum, petiolo proprio triplo longius. Foliola infima breviter petiolumata (2–3 mm). Petioli pilis albis patentibus dense vestiti aculeisque parum curvatis muniti.

Rami floriferi aculeis pilisque illis caulis similibus instructi. Inflorescentiae late elongatae, usque ad apicum foliiferae, infra foliis ternatis, supra bracteis foliaceis et longe petiolatis praeditae. Foliola utrinque cinerascentia, subtus ad nervos molliter pilosa. Ramuli inferiores (usque ad 5 cm longae) adscendentes, superiores (2–4 cm) patuli, omnes floribus breviter pedicillatis ornati.


Stems densely hairy with patent, white, simple hairs. Glandular hairs rare or absent. Prickles hairy, numerous (15–20 per 5 cm length of stem), situated on the angles, equal in length to stem diameter, patent or slightly declining.

Leaves ternate or quinque-pedate. Leaflets greyish green on both surfaces, strigose above and soft with many hairs on the veins beneath, evenly but coarsely serrate. Terminal leaflets broadly obovate or nearly round, with a cuspidate point and emarginate or subcordate base, three times as long as their petiolules. Basal leaflets with short petiolules (2–3 mm). Petioles with dense, spreading, white hairs and nearly patent, slightly curved prickles.
Flowering branches armed and clothed like the stems. Panicles, when well developed, broadly cylindrical and leafy to the summit, the lower ternate leaves giving place to leafy bracts on long petioles. Leaflets ashy grey on both sides and soft with many hairs on the veins beneath. Lower panicle branches ascending, about 5 cm long, upper branches patent and decreasing in length from 4 to 2 cm, all bearing clusters of flowers on short pedicels.

Sepals hairy, aculeolate, loosely reflexed. Petals white or pale pink, obovate-cuneate, 12x7 mm. Stamens white, longer than the pale styles. Receptacles hirsute.

**HOLOTYPE:** Raven’s Clough, Rushton, GR 33/91.63, Staffs., v.c. 39, 22/7/1944, W. D. Graddon (herb. E. S. Edees 3824)

This is a common bramble on the foothills of the Pennines in Staffordshire and Cheshire. When Watson visited Staffordshire in 1950 he examined several bushes in the field and later on identified them with *R. eifelliensis* Wirtg., a bramble which he claimed to have found already at Boar's Hill, near Oxford, Berks., v.c. 22. But the Staffordshire and Cheshire bramble, of which I have several specimens and which I know well in the field, is not identical with Watson's specimen from Boar's Hill, 7/7/1936, in my herbarium, nor with authentic specimens of *R. eifelliensis* Wirtg. Indeed the Boar's Hill bramble is not a close match for *R. eifelliensis* either, nor is another specimen in my herbarium from Fancy, near Plymouth, S. Devon, v.c. 3, 20/7/1939, collected by Watson and also named *R. eifelliensis*. No British exsiccata which can be unequivocally named *R. eifelliensis* have yet been seen.

*R. eifelliensis* was first described by Wirtgen in 1858 on the labels of specimens sent out as Herbarium Ruborum Rhenanorum, ed. 1, no. 94. It was a very brief description, stating simply that the bramble resembled *R. silesiacus* Wehre, but differed in having a shaggy inflorescence, spreading and leafy below, and large, reddish petals. I have not seen a specimen of this number, but I have one of Herb. Rub. Rhen., ed. 2, no. 69, in my herbarium, gathered by E. Ley from the *locus classicus* in 1860 and sent out by Wirtgen under the same name. There are certainly resemblances between the Staffordshire and Eifel plants, but the Eifel bramble has more finely toothed leaflets, more strongly curved prickles on the stem, felted leaflets and is said to have red petals. A. Newton, who saw the German plant in situ in 1974, considers it quite different from the Cheshire and Staffordshire bramble we both know well. The German plant has a much stronger development of glands and acicles, is dark green rather than grey-green and has pink to deep pink petals. *R. painteri*, on the other hand, is notable for its white petals, nearly eglandular stem, nearly patent prickles, soft but not felted leaflets and strongly hirsute receptacles. Like *R. eifelliensis* it is a very shaggy bramble.

In addition to the holotype I have Staffordshire paratypes collected by myself (herb. E.S.E.) from Biddulph, GR 33/89.59, Black Bank, near Newcastle, GR 33/81.47, Highshutt, near Cheadle, GR 43/03.43, and Meerbrook, GR 33/98.59, and one from Congleton, GR 33/89.62, Cheshire, v.c. 58. The name commemorates the work of W. H. Painter (1835–1910), who took a special interest in *Rubi*. There are specimens of *R. painteri* in MANCH, collected by Painter from Biddulph in 1889 and 1890, under the name *R. pyramidalis* Kalt.

4. Rubus turritus E. S. Edees, sp. nov.

*R. apricus* sensu W. C. R. Wats. ex parte, non Wimm.

Turiones obtuse angulati, faciebus planis, glabrescentes, purpurascentes. Aculei maiores tenues, declinati, subaequales, diametro caulis paulo longiores, plerumque ad angulos dispositi. Aculei minores inaequalia sed non in ceteros abeuntes. Aculeoloi numerosi, glandulii stipitati aliquantum sparsiores.

Folia quinta pedata vel rarius ternata. Foliola utrinque viridia, supra glabra, infra pilosa sed non tomentosa, plus minusve aequaliter serrata. Foliolium terminale obovatum, longe acuminatum, in basin emarginatum saepe angustatum, petiulo proprio triplo longius. Petioli glandulosi et leviter villosi aculeis tenuibus aculeolisque armati. Stipulae lineares, glandulosae.

Rami floriferi inferne leviter pilosi aculeolis tuberculisque muniti, superne dense villoso-tomentosi, glandulosi, aculeolati. Aculei tenues, debiles, declinati, aequales, diametro caulis vix longiores.
Folia ternata. Foliola obovata, utrinque viridia. Inflorescentiae apicem versus late cylindraceae pedunculis longis, subaqualibus, 1–3-floris.


Stems bluntly angled with flat sides, green, becoming purple on the angles, glabrescent. Prickles slender, declining, somewhat variable in length, the longest slightly exceeding the diameter of the stem, mostly confined to the angles. Prickles and acicles numerous and varying in size but distinct from the main prickles. Glandular hairs frequent, but less numerous than the prickles and acicles.

Leaves sometimes ternate but usually quinate-pedate. Leaflets green on both surfaces, glabrous above and hairy, though not felted, beneath; regularly toothed except sometimes towards the tip. Terminal leaflets obovate, acuminate, often with straight sides converging to a narrow, emarginate base, three times as long as their petiolules. Petioles with slender declining prickles, acicles and glandular hairs, and thinly clothed with patent white hairs. Stipules narrow and fringed with glandular hairs.

Flowering branches with sparse, white spreading hairs and numerous prickles and tubercles below, felted above with dense, spreading simple hairs, glandular hairs and acicles. Prickles slender, weak, declining and of even length, scarcely longer than the stem-width. Leaves ternate with obovate leaflets, green on both sides. Panicles broadly cylindrical, with long, subequal peduncles, each bearing 1–3 flowers.

Flowers 2.5 cm in diameter. Sepals densely hairy, aculeolate, glandular, long-pointed and erect. Petals white, though sometimes pinkish in bud, spaced, obovate-lanceolate, 15 × 6 mm, glabrous. Stamens white, slightly longer than the green styles. Carpels glabrous. Receptacles hairy.

**HOLOTYPUS:** Hanchurch Hills, on the south side of the water-tower enclosure, GR 33/840.397, Staffs., v.c. 39, 1/8/1972, E. S. Edees 20823 (herb. E. S. E.)

This is another local bramble which is abundant on Hanchurch Hills and distributed over a wide area of north Staffordshire. I have paratypes in my herbarium from Barlaston, GR 33/92.39, Fulford, GR 33/93.38, Leigh, GR 43/00.33, Mucklestone, GR 33/74.37, Sandon, GR 33/93.33, Stone, GR 33/90.37, Swynnerton, GR 33/84.41, and Whitmore, GR 33/82.41, in addition to several specimens from Hanchurch Hills. Watson, who saw the bramble in situ, identified it with *R. apricus* Wimm. But it does not match closely specimens of *R. apricus* from the original station, of which I have seen several. I have two in my own herbarium and there is one in K, collected by F. Schwarzer in 1869, 'Am Streitberg in Schlesien', with a note, 'Specimen typicum in statione originali autoris lectum', pasted on to the sheet. Prof. H. E. Weber, to whom I sent a specimen of the Staffordshire bramble with Watson's suggested name, replied 'Very far away from the true plant which I know from original specimens'. Nor is *R. turritus* closely related to *R. bercheriensis* (Druce ex Rogers) Rogers, which Watson (1935) described as *R. apricus* var. *sparsipilus* W. C. R. Wats.


*R. taeniarum* Lindeb., *Nov. Fl. Scand.*, 5 (1858)

There is a widely distributed bramble in northern England and southern Scotland which Rogers (1900) identified with *R. infestus* Weihe ex Boenn. and Watson (1958) with *R. taeniarum* Lindeb. Apart from Heslop-Harrison (1968), most living botanists agree that these are two names for the same taxon. Many Continental botanists have for long held this view. Even Lindeberg admitted a close relationship between *R. taeniarum* and *R. infestus*. A specimen of his Herbarium Ruborum Scandinavie no. 19 in MANCH from the locus classicus for *R. taeniarum*, 'In insula Oroust Bahusiae, August 1880', has a Latin description which begins: 'R. infesto Whe proximus eiusque quasi forma borealis.' But Lindeberg thought that the grooved, more lightly-armed stem, with fewer glandular hairs, the felted leaflets and compound panicles sufficiently distinguished it. Focke (1877, 1914) cited *R. taeniarum* as a synonym of *R. infestus* and Sudre (1911) described it
as a variety of *R. infestus* having a rhomboid terminal leaflet, with a nearly entire base, and a lax inflorescence.

Of the two numbers which Sudre (1911) cited to illustrate *R. infestus*, one at least (Sudre’s Batotheca Europaea no. 37) is identical with *R. taeniarum*. There is a good example in BM which I have carefully examined. The petals are rounded and notched and said to be rose-coloured, the stamens are scarcely longer than the styles and the carpels are strongly pilose. I quickly concluded that this was *R. taeniarum* and then I discovered a note with one of Watson’s specimens in my herbarium which stated that in Watson’s opinion too Sudre’s no. 37 was *R. taeniarum*. The other number which Sudre cited for *R. infestus* was no. 122 of the Set of British Rubi. Unfortunately pieces for this number were cut from bushes from two widely separated areas, viz. Thursley Common, Surrey, v.c. 17, and Bethesda, Caernarvon, v.c. 49, and represent two different taxa. The Bethesda bramble is *R. taeniarum*, but the bramble of Thursley Common is *R. infestus* sensu Watson, non Weihe ex Boenn., which (see below) it is proposed to call *R. infestior*. Both were distributed as *R. infestus* and Sudre (1904) said of the specimen or specimens he saw: ‘Espèce bien caractérisée’.

Watson (1931, 1949) followed Neuman (1915) in thinking *R. infestus* and *R. taeniarum* to be distinct. At first he thought that the bramble recorded for northern England and Scotland should be called *R. spurius* Neuman, a name which according to Weber (1972) was given to a weak specimen of *R. infestus* from its original German station. When Watson visited Staffordshire in 1950 he called several bushes, which we examined together in the field, *R. spurius*, maintaining that the true *R. infestus* was a quite different bramble. In his *Handbook* (1958) he substituted the name *R. taeniarum* for *R. spurius*. There is a note on one of his specimens in my herbarium, dated 1951 and followed by his initials, with the equation *R. taeniarum = R. spurius*. Watson (1931) claimed that the true *R. infestus* had white flowers and imbricate leaflets reminiscent of the *Suberecti* and was more fiercely armed, and he applied this name to a bramble which he had seen in several places in south-eastern England, as, for example, on Farnborough Common, Hayes Common and in Barnet Wood, W. Kent, v.c. 16, and on Netley Heath and in the Roughs near Guildford, Surrey, v.c. 17. This is a well marked taxonomic resemble the plate of *R. infestus* in *Rubi Germanici* (Weihe & Nees 1825) to some extent, but not the lectotype at Kiel. The lectotype, designated by Professor Weber in 1975, was labelled by Weihe ‘Rubus infestus Weihe, Minden’, and is a good specimen of the taxonomic which Lindenberg later called *R. taeniarum*.

*R. infestus* was first recorded for Minden, West Germany, where Weihe & Nees (1825) said it was far from rare and easily recognized. Focke (1877) said it was plentiful in that province in the neighbourhood of Menninghüffen. There is a specimen in K of Focke’s Rubi Selecti no. 66 from Minden, ‘In Hecken und Gebüsch zu Heddingsen bei Menninghüffen’, collected by H. Banning in 1871. Weber sent me a recent specimen from the same place, collected by himself in 1968, and told me (in litt. 1975) that it was still very common. These specimens match one another and also specimens of *R. taeniarum* collected by Lindeberg and others from Sweden and Denmark, of which there is a good series in MANCH, leaving no doubt that *R. infestus* Weihe and *R. taeniarum* Lindeb. are conspecific. Nor is there any doubt that the bramble of northern England and southern Scotland, which Watson called *R. taeniarum* and his predecessors *R. infestus*, was also correctly identified. British exsiccatae have been compared with authentic specimens of *R. taeniarum* and the Minden specimens of *R. infestus* and match them both. But *R. infestus* is the earlier name. Accordingly specimens which have been determined *R. taeniarum* for British collectors should now be re-named *R. infestus*.

The bramble from south-eastern England requires a new name.

6. Rubus infestior E. S. Edcees, sp. nov.

*R. infestus* sensu W. C. R. Wats., non Weihe ex Boenn.

Turriones angulati, glabrescentes. Aculei crebri, e basi lata declinati vel curvati, inter se valde diversi, maiores diametro caulis parum longiores, minores multo breviores, haud ad angulos omnino dispositi. Aciculi glandulique stipitati vulgo sparsi.

Folia quinata subdigitata. Foliola nonnunquam imbricata, utrinque viridia, supra glabrescentia, subitus pallide pubescentia, inaequaliter serrata. Foliolum terminale ovatum, cordatum, acu-
The minatum, circa 8 × 6 cm, petiolulo proprio triplo longius. Petioli aculeis falcatis aculeolisque inaequalibus confertim obsiti.

Rami floriferi aculeis declinatis falcatis et aculeolis multis dense armati. Aciculi glandulique stipitati, quorum plurimi minus quam 1 mm longi, praesertim in pedunculis pedicellisque numerosi.

Inflorescentiae angustae, ramulis brevibus, adscendentibus, paucifloris instructae.


Stems angled, glabrescent. Prickles crowded, base-based, declining and curved, varying greatly in size from prickles much shorter than the stem-width to prickles which are a little longer than it, occurring on the faces as well as the angles. Aciciles and glandular hairs usually few.

Leaves quinate-subdignite. Leaflets frequently imbricate, green on both sides, nearly glabrous above, soft with short hairs and paler below, rather coarsely serrate. Terminal leaflet ovate, cordate, acuminate, about 8 × 6 cm, three times as long as its petiolule. Petioles strongly armed with falcate prickles and many pricklets of variable length.

Flowering branches densely armed with crowded falcate and declining prickles and pricklets of various sizes. Aciciles and glandular hairs, which are usually less than 1 mm long, mostly on the peduncles and pedicels. Panicles narrow, with short, ascending, few-flowered branches.

Sepals aculeolate, loosely reflexed or patent. Petals white. Stamens white, longer than the green styles. Carpels glabrous.


The strong, unequal prickles, which are sometimes so crowded, especially on the rachis, that they touch one another, place this bramble in the section Glandulosi series Hystrixes of Watson's arrangement. The flowers were well described by Watson (1931): 'The flowers are very characteristic; white, cup-shaped, with the upper parts of the petals inflexed. The petals are roundish but they taper below into a rather long claw... the white stamens are much longer than the green styles. The young carpels are glabrous.' The true R. infestus (R. taeniarum) differs from R. infestor in having smaller and more numerous flowers, with pink, notched petals, short stamens and hairy carpels, and is less heavily armed. It belongs to the section Appendiculati in Watson's classification. R. infestor differs from R. setulosus Muell. & Lefèvre, which Watson (1958) cited as a synonym, in several ways. P. J. Mueller's definitive specimen in Lausanne (LAU) (Bois du Roi, Oise, France, 1856, L. V. Lefèvre), which I have examined, has obovate terminal leaflets, strongly cuneate in the panicle, and a much weaker armature. R. marianus (Krause) H. E. Weber (R. infestus var. marianus Krause), of which Professor Weber has sent me a specimen collected and determined by himself, also differs most markedly from R. infestor in armature. It has not been recorded for the British Isles.


R. infestor is locally common in the south-eastern counties of England. In addition to the holotype I have paratypes in my herbarium from Hayes Common, GR 51/401.657, W. Kent, v.c. 16, Thursley Common, GR 41/9.4, Surrey, v.c. 17, and Yateley Common, GR 41/84.59, and Bramshott Common, GR 41/85.33, N. Hants., v.c. 12.

7. Rubus anglohirtus E. S. Edees, sp. nov.

R. hirtus sensu W. C. R. Wats. ex parte, non Waldst. & Kit.

Turiones obtuse angulati vel teretiusculi, in apricis rufescentes, pruinosi, breviter et dense pilosi, glandulius stipitatis aciculisque obsiti. Aculei tenues, parvi (saepe diametro caulis dimidio breviores), paulo declinati.

Folia quinata pedata. Foliola utrinque viridia, supra strigosa, subtilis ad nervos pilosa, inaequaliter serrata. Foliolum terminalis circa 10 × 7 cm, obovatum, interdum subincisum, cuspri-
datum, basi emarginatum vel cordatum, petiolo propio triplo vel quadruplo longius. Petioli pilis illis caulis similibus vestiti et aculeis tenuibus, declinatis vel curvatis armati.


Sepala aculeolata, appendiculata, primo reflexa, demum erecto-patentia. Petala alba, late elliptica (14 × 7 mm), ad marginem glabra. Stamina alba stylus pallidus parum superantia. Carpella et receptacula pilosa.

Stems bluntly angled or nearly round, dull red in exposure, with many short, simple and stellate hairs, glandular hairs and acicles, pruinose. Prickles slender, small (often not more than half the stem-width), slightly declining.

Leaves quinate-pedate. Leaflets light green on both surfaces, strigose above, hairy on the veins below, with somewhat irregular teeth. Terminal leaflet about 10 × 7 cm, obovate, sometimes shouldered or incised, with a cuspidate point and marginate or cordate base, three to four times as long as its petiolule. Petioles clothed like the stem and with slender, declining or curved prickles.

Flowering branches densely hairy with short spreading hairs, many short glandular hairs and acicles of more or less equal length. Prickles slender, weak, declining or curved. Panicles lax, with spreading peduncles above the leaves and long, ascending lower branches, truncate. Peduncles and pedicels densely covered with adpressed hairs and many glandular hairs of variable length.

Sepals aculeolate, leafy-pointed, at first reflexed, later patent to erect. Petals white, broadly elliptic (14 × 7 mm), glabrous on the margin. Stamens white, slightly exceeding the pale styles. Carpels and receptacles pilose.

**Holotypus:** Ropsley Rise Wood, near Grantham, GR 43/97.34, S. Lincs., v.c. 53, 27/7/1965, E. S. Edees 19015 (herb. E.S.E.)

This is one of several taxa which Watson (1958) called *R. hirtus* Waldst. & Kit., but Professor H. E. Weber, to whom I sent a specimen, told me *(in litt. 1975)* that it is quite different from the bramble to which Continental batologists have usually applied this name and corresponds with nothing known to him. *R. hirtus* has not been typified and as generally understood is a notoriously aggregate taxon. Rogers (1900) said he could not define it and quoted Focke as saying that it was a polymorphic species with countless indefinable varieties. I have seen no specimen of *R. hirtus* named by the original authors, but the bramble described and illustrated by Weihe & Nees (1827) is different from ours. A specimen of *R. hirtus* forma *borealis* G. Braun (Herbarium Ruborum Germaniae no. 60) in K is closer to *R. anglohirto* but is not identical with it.

*R. anglohirto* is a constant and easily recognized taxon with a wide distribution in eastern England, occurring in woods from S. Lincs., v.c. 53, to E. Kent, v.c. 15. In addition to the holotype I have paratypes in my herbarium from Twyford Forest, near Bourne, GR 43/95.23, Row Wood, near Bourne, GR 53/07.26, Spring Wood, near Bourne, GR 53/06.23, Ponton Park Wood, near Grantham, GR 43/94.31, all in S. Lincs., v.c. 53, and from Alsa Wood, near Stansted, GR 52/5.2, Birchanger Wood, GR 52/503.225, Broom Wood, Ugley, GR 52/510.285, N. Essex, v.c. 19.

**Acknowledgments**

I am greatly indebted to Professor H. E. Weber, whose recent book (1972) has stimulated interest in the relationship of the British and Continental Rubi and prompted a fruitful correspondence and exchange of specimens. I must also once more express my gratitude to A. Newton for some references and many helpful suggestions and to the curators of the national herbaria mentioned in this paper for the loan of specimens.

**References**


*(Accepted May 1975)*
Chromosome number of *Puccinella maritima* (Huds.) Parl. in the British Isles

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ABSTRACT

Chromosome counts were made on root-tip cells of *Puccinella maritima* plants representing a wide range of localities and growth forms. All plants examined had $2n = 56$.

INTRODUCTION

The most frequently quoted chromosome number for British *Puccinella maritima* (Huds.) Parl. is $2n = 63$ (Mills 1967, Newton 1965), which is nonaploid if $x = 7$ for the genus, and consistent with the suggestion (Tutin 1955) that the species usually reproduces vegetatively and may be apomictic. Mills also reported $2n = 56$, which is commonly listed for foreign material (Bernström 1948, Church 1949, Sørensen 1958). Other British counts are $2n = 14, 49, 77$ (Brown-Packer 1961), and from foreign material $2n = 42$ (Church 1949), $c = 60$ (Castro & Fontes 1946) and $70$ (Wulff 1937, Rodrigues 1953).

The counts made by Mills (1967) and Newton (1965) are listed in Table 1, and suggest the possibility of differences in distribution of the octoploid and nonaploid plants in Britain. Because it also seemed possible that the wide range of phenotypic variation observed in the species might correspond to different cytological races, chromosome counts were made on a large number of plants collected as part of a study of infraspecific variation. Plants were sampled from a wide range of habitats and locations (Table 2), different growth forms being included when found adjacent to one another in the field. Growth form differences, often very large, were usually maintained after a period of collateral cultivation (Table 3).

The object of the work presented here was to relate chromosome number to the growth forms and geographical races of the plant.

**TABLE 1. PREVIOUS LOCALIZED CHROMOSOME COUNTS FOR Puccinella maritima IN THE BRITISH ISLES**

<table>
<thead>
<tr>
<th>Author</th>
<th>Location</th>
<th>No. of plants counted</th>
<th>Chromosome Number $2n$</th>
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<tr>
<td>A. R. Mills</td>
<td>Parkgate, Cheshire, v.c. 58</td>
<td>8</td>
<td>51–62</td>
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<td>3</td>
<td>51–56</td>
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<td>A. R. Mills</td>
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<td>$e = 60$</td>
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<td>Tollesbury, N. Essex, v.c. 19</td>
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<tr>
<td>A. R. Mills</td>
<td>Mudeford, S. Hants., v.c. 11</td>
<td>1</td>
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<tr>
<td>L. E. Newton</td>
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<td>1</td>
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</tr>
<tr>
<td>L. E. Newton</td>
<td>Tollesbury (tall plant), N. Essex, v.c. 19</td>
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</tr>
<tr>
<td>L. E. Newton</td>
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<td>Yantlet Creek, W. Kent, v.c. 16</td>
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TABLE 2. SITES OF *PUCCINELLIA MARITIMA* WITH $2n = 56$ DETERMINED IN THE PRESENT STUDY

<table>
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<th>Location</th>
<th>Habitat type</th>
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<td>34/465.795</td>
<td>Armside, Westmorland, v.c. 69</td>
<td>Grazed saltmarsh</td>
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<td>P 7</td>
<td>J/51.64</td>
<td>Strangford Lough, Down, v.c. H38</td>
<td>Ungrazed saltmarsh</td>
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<td>54/355.032</td>
<td>Tetney, N. Lines., v.c. 54</td>
<td>Tidal riverbank</td>
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<td>P 28</td>
<td>34/202.758</td>
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<td>Cattle-grazed saltmarsh</td>
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<td>Warton, W. Lancs., v.c. 60</td>
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<td>P 118</td>
<td>53/926.457</td>
<td>Wells, W. Norfolk, v.c. 28</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 119</td>
<td>53/926.457</td>
<td>Wells, W. Norfolk, v.c. 28</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 120</td>
<td>53/926.457</td>
<td>Wells, W. Norfolk, v.c. 28</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 124</td>
<td>51/028.014</td>
<td>Littlehampton, W. Sussex, v.c. 13</td>
<td>Sandflats</td>
</tr>
<tr>
<td>P 127</td>
<td>63/487.065</td>
<td>Breydon Water, E. Suffolk, v.c. 25</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 152</td>
<td>51/935.193</td>
<td>Rye Harbour, E. Sussex, v.c. 14</td>
<td>Creek bank</td>
</tr>
<tr>
<td>P 156</td>
<td>51/444.082</td>
<td>Beddingham, E. Sussex, v.c. 14</td>
<td>Tidal riverbank</td>
</tr>
<tr>
<td>P 165</td>
<td>40/183.918</td>
<td>Mudeford, S. Hants., v.c. 11</td>
<td>Sandy mudflat</td>
</tr>
<tr>
<td>P 167</td>
<td>30/255.907</td>
<td>Axmouth, S. Devon, v.c. 3</td>
<td>Stony, tidal river shore</td>
</tr>
<tr>
<td>P 177</td>
<td>20/116.579</td>
<td>Lostwithiel, E. Cornwall, v.c. 2</td>
<td>Stony, tidal river shore</td>
</tr>
<tr>
<td>P 183</td>
<td>21/205.064</td>
<td>Bud, E. Cornwall, v.c. 2</td>
<td>Stony, tidal river shore</td>
</tr>
<tr>
<td>P 188</td>
<td>31/550.753</td>
<td>Avon Gorge, W. Glouce., v.c. 34</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 236</td>
<td>34/208.855</td>
<td>Foxfield, Furness, v.c. 69b</td>
<td>Grazed saltmarsh</td>
</tr>
<tr>
<td>P 241</td>
<td>34/184.694</td>
<td>Vickerstown, Furness, v.c. 69b</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 254</td>
<td>28/847.853</td>
<td>Morrich More, E. Ross, v.c. 106</td>
<td>Sandflats</td>
</tr>
<tr>
<td>P 255</td>
<td>16/715.821</td>
<td>Ulva Islands, S. Ebudes, v.c. 102</td>
<td>Gravelly shore</td>
</tr>
<tr>
<td>P 259</td>
<td>53/555.578</td>
<td>Gibraltar Point, N. Lines., v.c. 54</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 282</td>
<td>27/096.587</td>
<td>Loch Leven, Argyll Main, v.c. 98</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 295</td>
<td>18/897.547</td>
<td>Loch Torridon, W. Ross, v.c. 105</td>
<td>Grazed saltmarsh</td>
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<tr>
<td>P 299</td>
<td>29/354.540</td>
<td>Kyle of Tongue, W. Sutherland, v.c. 108</td>
<td>Grazed saltmarsh</td>
</tr>
<tr>
<td>P 304</td>
<td>39/166.294</td>
<td>Dunbeath, Caithness, v.c. 109</td>
<td>Quay top</td>
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<tr>
<td>P 322</td>
<td>37/342.294</td>
<td>Kingoodie, Fife, v.c. 85</td>
<td>Ungrazed saltmarsh</td>
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<tr>
<td>P 326</td>
<td>46/082.426</td>
<td>Lindisfarne, Cheviot, v.c. 68</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 329</td>
<td>54/384.018</td>
<td>North Cotes, N. Lines., v.c. 54</td>
<td>Ungrazed saltmarsh</td>
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<tr>
<td>P 332</td>
<td>62/048.212</td>
<td>Wivenhoe, N. Essex, v.c. 19</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 333</td>
<td>23/405.672</td>
<td>R. Cefni, Anglesey, v.c. 52</td>
<td>Ungrazed saltmarsh</td>
</tr>
<tr>
<td>P 337</td>
<td>33/648.512</td>
<td>Nantwich, Cheshire, v.c. 58</td>
<td>Inland saltmarsh</td>
</tr>
<tr>
<td>P 342</td>
<td>53/920.448</td>
<td>Wells, W. Norfolk, v.c. 28</td>
<td>Ungrazed saltmarsh</td>
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<tr>
<td>P 358</td>
<td>53/939.450</td>
<td>Wells, W. Norfolk, v.c. 28</td>
<td>Ungrazed saltmarsh</td>
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</tbody>
</table>

METHODS

Tillers taken from individual plants in the field were grown in plastic pots containing John Innes No. 3 potting compost and a basal layer of moss-peat. Portions of root-tip c 30 mm long were taken from the peat, where they were grit-free, pre-fixed for 3 hours in dilute 8-hydroxyquinoline at 5°C, fixed for 3 hours in 3:1 ethanol/acetic acid, and hydrolyzed for 10 minutes at 60°C in 1 N HCl, followed by staining in Feulgen reagent for 1.5 hours. After staining, the tips were treated in pectinase (Osterhren & Heneen 1962) to facilitate cell spreading. The preparations were squashed in 45% acetic acid, and temporary mounts were made by ringing coverslips with rubber solution. Whenever possible chromosome counts were taken from replicated root-tips and plants.
TABLE 3. GROWTH FORM DIFFERENCES BETWEEN TWO CLONES OF Puccinellia Maritima FROM WELLS, NORFOLK

<table>
<thead>
<tr>
<th>Accession code</th>
<th>3rd leaf-blade length (cm)</th>
<th>Maximum vegetative tiller height from ground (cm)</th>
<th>No. of tillers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(13/6/72 in field)</td>
<td>(13/6/72 in field)</td>
<td>(18/4/73 at Norwich)</td>
</tr>
<tr>
<td>P 348</td>
<td>2.26 (0.129)</td>
<td>2.68 (0.292)</td>
<td>19.5 (2.53)</td>
</tr>
<tr>
<td></td>
<td>3.76 (0.108)</td>
<td>7.42 (0.684)</td>
<td></td>
</tr>
<tr>
<td>P 353</td>
<td>8.38 (0.443)</td>
<td>7.94 (0.534)</td>
<td>11.25 (2.29)</td>
</tr>
<tr>
<td></td>
<td>7.54 (0.389)</td>
<td>14.64 (1.13)</td>
<td></td>
</tr>
</tbody>
</table>


CHROMOSOME NUMBERS

*P. maritima* has chromosomes which are relatively long and thin, which makes counting difficult because they are often intermingled with one another in imperfect squashes. In over-spread preparations splitting of chromatids frequently occurred, adding another difficulty to counting. In good cells 56 chromosomes were usually present, but a few cells appeared to contain numbers in the range 53–55, suggesting a degree of somatic aneuploidy. All plants, including representatives of extremes of growth form, had a number at or just below \(2n = 56\), the octoploid \((x = 7)\) level (Fig. 1). Some other counts ranged from 50 to 64, but in all instances where aberrant counts were investigated repetition on new material of the same plants led to the conclusion that \(2n = c 56\).

![Figure 1. A root-tip cell of Puccinellia maritima showing a full complement of chromosomes, \(2n = 56\) (accession P 35).](image)
Preparations were insufficiently clear for full karyotype analysis but Fig. 2 summarizes five categories of chromosome size and form. About six pairs of small acrocentric chromosomes are present; the rest are metacentric ranging in size up to twice as long as the acrocentrics. At least two pairs of the largest metacentrics have distinct satellites, and identical chromosomes have been seen in other species of the genus Puccinellia. All chromosomes showed bands of more intense staining which matched in several pairs and could be valuable in karyotype analysis.

DISCUSSION AND CONCLUSIONS

Chromosome number was found to be constant in plants of different growth form coming from a wide range of sites, suggesting that it is not a facet of variation in the species in the British Isles. The widespread occurrence of octoploids \((2n = 56)\) with little aneuploidy is consistent with results of our unpublished breeding experiments which show that *P. maritima* is an active out-breeder with a low selfing rate.

The presence in its karyotype of sets of many similar chromosomes supports the idea that the species is a polyploid, but meiosis appears to be regular (Church 1949), and the plants are highly interfertile. Our evidence suggests that British plants are octoploid, but allowing for difficulties with counting it is not possible to rule out the existence of aneuploids. The wide range of morphological variability of the species is likely to be the produce of environmental selection on populations whose gene systems perform normal segregation and recombination, and not the expression of isolated lines maintained after a breakdown of sexuality.

ACKNOWLEDGMENTS

We thank W. E. Hughes, B. M. G. Jones, and A. R. Mills for information on *Puccinellia*. L. F. La Cour gave valuable advice on methods, and we are grateful to Miss N. Meek whose patient work added many new counts during 1974. F. T. Last and D. S. Ranwell made valuable comments on the text.

REFERENCES


ROYAL IRISH ACADEMY

Robert Lloyd Praeger Fund
for Field Natural History

Grants, not normally exceeding £50 in any one year, will be awarded for field work relevant to the Natural History of Ireland. Application forms, which should be returned before February 15, may be obtained from The Secretary, Royal Irish Academy, 19 Dawson Street, Dublin 2, who will also be glad to give further information.
Nomenclature of the British taxa of the Carex muricata L. aggregate

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ABSTRACT

The nomenclatural problems surrounding the Carex muricata L. aggregate are discussed. The taxa as at present understood should be known as C. spicata Hudson, C. lumnitzeri (Rouy) Krecz., C. muricata L. subsp. muricata, C. muricata L. subsp. paireai (F. W. Schultz) Čelak., C. polyphylla Kar. & Kir., C. leersiana Rauschert, C. diculsa Stokes and C. chabertii F. W. Schultz.

The Carex muricata L. aggregate comprises all the European taxa of Carex section Muehlenbergianae Tuckerm., and of these C. polyphylla Kar. & Kir., C. diculsa Stokes, C. spicata Hudson and C. muricata L. (to quote the names included in Dandy (1958)) are commonly recognized as British plants. Their nomenclature, however, has undergone a multiplicity of confusions. This has been primarily due to uncertainty as to what is the Linnaean type; but the initial error has been compounded by subsequent mistakes in determination (especially confusions with C. otrubae Podp.), by inadequate descriptions that often emphasize characters that are in fact indecisive, and by differing opinions as to the rank of the taxa included within the aggregate.

Linnaeus (1753) described C. muricata as follows: 'muricata. 8. CAREX spiculis subovatis sessilibus remotis andrognis, capsulis acutis divergentibus spinosis. Fl. suec. 753. Gmel, sib, I p. 148.' This original diagnosis could apply to several taxa in the aggregate; but Linnaeus' herbarium (LINN) contains a Swedish specimen marked in Linnaeus' own handwriting '8 muricata'. The use of the identical number and name directly connects the diagnosis and the specimen.

Nevertheless nineteenth-century botanists failed to notice this connection. Most of them, for example Koch (1837), merely lumped all taxa of the aggregate under the Linnaean name. The case of Crépin (1859) is instructive, for it illustrates both the failure of the earlier botanists to find satisfactory criteria for the distinguishing of the individual taxa, and the distinctiveness of the taxa when such criteria are found. Crépin cited two varieties of 'C. muricata': a genuina Grenier & Godron, and β sirens Koch. From each of these he segregated a subvariety, incrassata, distinguished by the thickened base of its utricle. Such utricles are found only in the taxon isolated by Hoppe (Sturm 1833) as C. contigua and now known as C. spicata Hudson. Evidently each of the varieties cited by Crépin was in itself a conglomerate of several taxa of the aggregate, including C. spicata, which he correctly separated out from each of the two conglomerates.

Other attempts were made, as for example by Andersson (1849) and by Neuman (1901), to distinguish the individual taxa of the aggregate at least as subspecies or varieties, but these attempts appear to be no more soundly based than those of Grenier & Godron or of Koch. There was, however, through the century, a growing tendency, exemplified in Ascherson & Graebner (1902), to apply the Linnaean name not in its original sense but to C. contigua. Nelmes (1942) following Mackenzie (1935), produced evidence that the correct prior name for C. contigua is C. spicata Hudson. Though that evidence is not very weighty, the identification and the name have been generally accepted.

To the original uncertainty about the identity of C. muricata a further complication was added by Linnaeus' Swedish pupil, Johann Andreas Murray, who (Murray 1770) described Carex echinata. Formerly in LINN, but in January 1963 transferred to BM, is a sheet of four stems collected by Murray near Götingen and inscribed by him 'Carex echinata'. These specimens in fact belong to a taxon of the C. muricata aggregate identical with or near to Linnaeus' type-specimen of C. muricata. Attempts to resolve this contradiction have followed two opposing lines. On the one hand, Kükenthal (1905, 1909) took C. echinata Murray to be the correct name of C. muricata
and rejected the latter altogether as a nomen delendum on the grounds that it covered several members of the aggregate. In support of this view he observed (1909, p. 156 note 2) that the Linnaean herbarium contained, in addition to the specimen labelled C. muricata, an unnamed specimen of C. diculsa (which is true) and also an unnamed specimen of C. contigua. There is, however, no specimen of this last taxon in Linnaeus’ own collection. It was probably in one of the subsidiary collections (e.g. Murray’s) that have lately been transferred by the Linnean Society to other herbaria. On the other hand Mackenzie (1923), arguing with some force and citing not only Linnaeus’ Species Plantarum but also his Flora Suecica which describes C. muricata as a plant of wet ground, took C. muricata L. to be the correct name for C. echinata Murray, which he dismissed as a later synonym. In this Mackenzie was followed by Kreczetovicz (1935) in Flora URSS.

Britten (1907), followed by Kovacs (1910), Briquet (1910), Fernald (1917), and de Lange (1944), had shown, however, that Murray’s published description of C. echinata referred without any possible doubt to the sedge otherwise known as C. stellulata Good.; and Nelmes (1959) implicitly rejected Mackenzie’s argument, maintaining that, as Linnaeus labelled both his description and his specimen with the same reference number, ‘8 muricata’, no confusion exists apart from the misidentifications of others, and that the name C. muricata should stand. Nelmes’ conclusion is surely right, although Hylander (1966), who appears to have been unaware of Nelmes’ 1959 paper (it was published in Russian), again rejected the name C. muricata as a nomen ambiguum.

The question remains: what is in fact the plant labelled C. muricata by Linnaeus? Nelmes (1947, emended 1959) distinguished a northern and eastern taxon growing on limestone, and a western taxon preferring acid sands and gravels. Linnaeus’ type-specimen of C. muricata belongs to the northern taxon, although the glumes, which should be dark brown, are now quite bleached and the specimen is a less robust form than that described by Hylander (1966) as C. pairae [sic] subsp. borealis. As another example of the northern taxon Nelmes (1959) claimed C. loliacea sensu Schkuhr, non L. nec Schreber, as illustrated (the description is borrowed and applies to C. loliacea L.) in Plate Ee No. 91 of Schkuhr (1801).

Two other names, C. nemorosa Lumn. and C. cuprina (Sándor ex Heuffel) Nendtivich ex A. Kern, have also been referred to the northern taxon. Schultz (1871) thought that he had shown C. nemorosa to be synonymous with C. loliacea Schkuhr non L. and therefore (in his eyes) with his own C. pairaei of which it might, he thought, be the correct prior name. But in BM there is a specimen from the herbarium of J. J. Roemer (1763–1819) inscribed by him ‘Carex 3 nemorosa Lumnitzer ... Ab ipso accepi beatae memoriae D. Lumnitzer’; and this plant appears to be an immature specimen of that currently known as C. otrubae. It is certainly neither C. muricata L. nor its western relative. The name ‘C. cuprina (Sándor) Nendtivich’ was adopted by Kreczetovicz (1935) as the correct name of the northern taxon after he had taken C. muricata to be the correct name for C. echinata. Nendtivich’s name was not accompanied by a description and was therefore discarded by Hylander (1966) as a nomen nudum; but it was based on a Hungarian specimen in Sándor’s herbarium which had been validly published, with a description, as C. nemorosa β cuprina Sándor. Sándor’s specimen, however, as reported by Rauschert (1973), has lately been determined by Soó as C. otrubae, of which C. cuprina would apparently appear to be the correct prior name. Küenthal (1909, p. 156) is justified in his note: ‘Alia quoque nomina non paqua quoad synonymiam semper in dubio remanent, cum species supra laudatae ante cl. Fr. Schultz, Étude sur quelques Carex (1868), Flora LIII. (1870) et LIV. (1871) non certe distinctae sint, insuper confusio cum C. vulpina timenda.’ Both C. nemorosa Lumn. and ‘C. cuprina (Sándor) Nendtivich’ are included in Küenthal’s list of nomina dubia and both should now disappear from the synonymy of the C. muricata aggregate.

The history of the naming of the western taxon is even more complicated. In June 1868 Michel Paira, of Geudertheim in Bas-Rhin (Alsace), sent to F. W. Schultz specimens of a sedge that grew plentifully in his neighbourhood. Schultz confessed that till then he had overlooked it, recognized that it differed both from C. spicata (which he then knew as C. muricata) and from C. divulsa, and proposed to describe it as a new species under the name C. pairaei in honour of its discoverer. As ‘Paira’ and ‘Pairaei’ are equally acceptable Latin forms of Paira’s name, there is no need to make, as Hylander did, an orthographical correction to ‘pairae’.

Meanwhile there was further correspondence between the two men, in the course of which Paira said that he had taken his sedge to be the same as C. loliacea sensu Schkuhr non L.; and to show what he meant he sent Schkuhr’s illustrations (Schkuhr 1801) to Schultz who did not himself

Nelmes (1947) took C. pairaei to be the western taxon; and well he might, for Schultz's full Latin description (1868b) contains at least two sentences ('habitat ... in montibus graniticis' and 'Carex muricata [i.e. C. spicata Huds] differt ... tempore florenti, in isidem locis, multo precociori') that apply only to the western taxon and not at all to the northern. By 1959 Nelmes' colleague, A. A. Bullock, had called his attention to the fact that Schultz, in his first paper (1868a), had equated his C. pairaei with C. loliiacea sensu Schkuhr and that, as the actual specimen described by Schultz could not be certainly identified, Schkuhr's illustration was the only type upon which Schultz's name could be based. As Schkuhr's plant was in Nelmes' view the northern taxon, it followed that C. pairaei, based upon it, could by the International Code of Botanical Nomenclature be regarded only as yet another synonym for that taxon (= C. muricata L. sensu stricto). In that case the western taxon still lacked a name, and Nelmes (1959) supplied it by describing the western plant as C. bullockiana Nelmes.

Now it is true that Schultz's first paper (1868a) is headed 'Carex muricata var. β Schkuhr (C. loliiacea Schk., non Linné) als gute Art aufgestellt' and that he positively identified Pairea's sedge with Schkuhr's illustration, though he did question whether the enlargement of the utricle can be a true representation. Yet in the same paper he made it very clear that what he set out to describe were the specimens sent to him by Pairea, and he announced his intention to do two things: to issue a full description of Pairea's plant, and to preserve the specimens as vouchers 'in der 12 Centurie meines herbarium normale.' In this first paper (Schultz 1868a) there is in fact no adequate description or reference to one, so that C. pairaei is there a nomen nudum. One must conclude that Schkuhr's illustration (even if the discrepancy in the utricle is disregarded) was not intended by Schultz to be a type; as explained above, he intended Pairea's specimens to be the types. It may also be added that the source of Schkuhr's plant is unknown. He obtained it from an unnamed friend and the illustration did not indicate habitat or time of flowering. The only diagnostic characters that could be shown in a plate are the degree of divergence of the ripe utricles, their shape, and the colour of the glumes. On the first point Schkuhr's plate is ambivalent: the utricles are somewhat divergent but not more so than can be found in the western taxon. The illustration of the utricle is, as Schultz remarked, unsatisfactory: it does not correspond with that of either taxon. On the last point the evidence varies from copy to copy of the book according to the individual colourist responsible. For example, the copy in the Department of Botany, British Museum (Natural History), shows dark glumes contrasting with grey-green utricles—the northern taxon. The two copies owned by the Linnean Society show glumes and utricles that are almost concolorous—the western taxon. It is really not possible to say whether the plant illustrated is the one or the other.

Valid publication of C. pairaei was achieved, as Schultz had promised, in his Étude sur quelques Carex (Schultz 1868b). This contains a full Latin description, together with a drawing by Pairea, both of which can only refer to the western taxon, while of the 'quelques cents exemplaires' received from Pairea (Schultz 1868b) those distributed to a number of major herbaria are certainly that plant. They constitute genuine type-material, and I choose as lectotype the sheet ('déc. et rec. M. Pairea') in K dated 27 June and 9 July 1868. C. pairaei can therefore be retained as the name of the western taxon, while C. bullockiana, which (perhaps because it was published in a Russian journal) has never received much currency, becomes a later synonym.

In fact I am of the opinion, which is shared by Mr A. O. Chater, that the two taxa, while clearly distinct, do not merit more than subspecific rank. In that case the name of the northern taxon would be C. muricata L. subsp. muricata, and that of the western taxon C. muricata L. subsp. pairaei (F. W. Schultz) Čelak. It is ironical that the correctness of Čelakovský's combination is accidental, for his C. muricata is certainly not Linnaeus' and his C. pairaei is probably not Schultz's. C. muricata subsp. pairaei is not uncommon in Britain. C. muricata subsp. muricata is a rare plant there, and has at present been refound in only one of the four localities recorded by Nelmes (David & Kelcey 1975).

A plant apparently related to C. spicata, but of greater stature and with widely interrupted inflorescences, was described as C. muricata Race II lunmitzeri by Rouy (1912). Rouy noted that it
has ‘écailles et utricules concolorès, d’un vert blanchâtre.’ This is more a character of *C. leersii* F. W. Schultz (see below) and Rouy may have been referring to that taxon, though he also listed *C. muricata* Race III *leerseana*, with uncharacteristic ‘écailles ± brunâtres.’ *C. lunulizera* was, however, accorded specific rank by Kreczetovicz (1935), who reported it to be widespread in western Europe and equated it with *C. contigua var. γ longissima* Tauscher ex Vollmann (Vollmann 1903). Kükenthal (1909) followed Vollmann in giving the plant this varietal rank but cited only a restricted distribution (Hungary). In Britain I have seen only two plants (in a single locality) that answer to the description of *C. lunulizera*, and there was some likelihood that they were hybrids between *C. spicata* and *C. otubae*. A specimen from Tauscher’s own herbarium, collected by him on 26 July 1869 and now in K (ex herb. Churchill), has no mature fruit and looks as if it might also be of this hybrid origin.

The one member of the aggregate whose name has never really been in doubt is *C. divulsa* Stokes (published in 1787), though for a time the name was given a later authority, *C. divulsa* Good. (published in 1794), which allowed the problematical *C. virrens* Lam. (published in 1791) to qualify as a claimant for priority; and the plant, like all other members of the aggregate, has sometimes been reduced to subspecific or varietal rank.

Another taxon that has been put forward as the plant intended by Lamarck under his *C. virrens* is the one later known as *C. leersii* F. W. Schultz. Lamarck’s description is, however, quite inadequate and his specimen was reported by Winter (1870) to be even then in such poor condition that no conclusion whatever could be drawn from it. One may hope that the last to be heard of *C. virrens* is the *requiescat* pronounced by Vollmann (1903) on this ghost-name that has troubled taxonomic discussion for so long and to such little effect.

*C. leersii* F. W. Schultz is almost certainly what Hoppe understood by *C. muricata* and illustrated under that name in Sturm (1833). The description by Schultz (1870) is, however, the first in which the plant was clearly differentiated, though the name *C. leersii* is, as a species, invalidated by Willdenow’s earlier use of it as an illegitimate substitute for *C. echinata* Murray. Nelmes (1947) followed Kreczetovicz (1935) and Kükenthal (1911) in identifying Schultz’s sedge with *C. polypyilla* Kar. & Kir. (Karelin & Kirilov 1841). Kreczetovicz seems himself to have had two opinions about this, for in a note headed ‘Herbarium Florae Asia Medie ab Universitate Asiae Mediae editum Fasc. XXIII Julio a 1934’ and attached to a specimen in K of *C. polypyilla* from its original locality in the Targabatai mountains, he wrote: ‘Cette espèce appartient à une série avec le C. Leersii F. Schultz de l’Europe occidentale duquel elle se distingue par les épillets fortement divisés, de plus larges feuilles à ligule aplatie et une autre forme des utricules.’ Unfortunately Kreczetovicz did not particularize the difference in the shape of the utricles; but those of the specimen are very large (over 5 mm long) and their form, with rounded base and narrowly tapered beak, is more akin to that found in *C. spicata* than to the smaller (4-5 mm), neater ‘diamonds’ of *C. leersii*. The true *C. polypyilla* is not in Britain and probably not in Europe.

If Schultz’s sedge is to have specific rank, its name must be *C. leersiana* Rauschert, but it may be no more than a subspecies of *C. divulsa* and would then be subsp. *leersii* (Aschers. & Graebn.) W. Koch. The dividing line between these two taxa is the most difficult to draw in the whole taxonomy of the aggregate.

Lastly there is *C. chabertii* F. W. Schultz, actually named ‘Chaberti’ in Schultz (1871). Schultz’s description has not received proper attention, and the name, from the time of Kneucker’s collections (late nineteenth century) onwards, has been incorrectly applied to a number of plants intermediate between *C. divulsa* and *C. leersiana* and possibly of hybrid origin, as they do not seem to mature fruit. The true *C. chabertii*, as seen in specimens in K that originated from Schultz, is characterized by a comparatively short and closely-packed inflorescence of long (over 5 mm), upward-pointing (i.e. not patent) utricles, and appears to have been reported only from the Rhine-land and Palatinate, Germany, from the département of Drôme and the Pyrenees, France, and possibly from Bulgaria. As it is said to be a very local plant of woods on dry and stony ground in the mountains it is unlikely to occur in Britain.

Hybrids within the aggregate, and between members of the aggregate and sedges in other sections of subgenus *Vignea*, are reported from time to time in Britain and elsewhere. The majority if not quite all of them are more probably atypical plants of one or other of the taxa; and of the specimens that I have seen so far, either in the field or in herbaria, the only ones of whose hybrid origin I am convinced have been the cross between *C. divulsa* and *C. otubae*. This is occasionally
ACKNOWLEDGMENTS

This paper is part of a wider study of the *C. muricata* aggregate, in which I am collaborating with Mr J. G. Kelcey; and it owes much to discussions with him. For general guidance in its preparation I am deeply indebted to Mr A. O. Chater, Mr A. C. Jermy, and especially to Mr P. D. Sell who has also set in order the synonymy and references. For particular advice on the difficult nomenclatural problem of *Carex pairaei* I am grateful to Mr J. E. Dandy, Mr R. Ross, and Dr W. T. Stearn.

REFERENCES


This list includes those names that have significantly affected taxonomic discussion or that mark clear stages in the taxonomic argument. Many *nomina dubia*, and such names as *Carex orsiniana* Tenore and *C. lititiosa* Chaubard, which appear to be merely the result of error, have been omitted. Names not validly published are enclosed in square brackets.

**APPENDIX**

**MAIN SYNONYMS OF TAXA CONSIDERED**

*CAREX SPICICATA* Hudson, *Fl. Angl.*, 349 (1762)

*C. contigua* Hoppe in Sturm, *Deutschl. Fl.*, fasc. 61 (1833)

[C. muricata *sensu* Koch, *Syn. Fl. germ.*, 751 (1837) *pro parte*, non L. (1753)]


[C. muricata *sensu* Aschers. & Graebn., *Syn. mitteleur. Fl.*, 2(2): 38 (1902), non L. (1753)]

*CAREX LUMNITZERI* (Rouy) V. Krecz. in Komarov, *Fl. URSS*, 3: 154 (1935)


*C. muricata race lumnitzi Rouy, Fl. Fr.*, 13: 412 (1912)


*CAREX MURICATA* L.

subsp. *MURICATA*

*C. muricata* L., *Sp. Pl.*, 974 (1753)


[C. *echinata* *sensu* Kükenthal in Engler, *Pflanzenreich*, 38 (IV.20): 160 (1909), non Murray (1770)]

[C. cuprina *sensu* V. Krecz. in Komarov, *Fl. URSS*, 3: 155 (1935), non Sándor ex Heuffel (1862)]


*C. pairaei* F. W. Schultz, *Etude quelques Carex*, 9 (September 1868)


[C. *muricata* *sensu* Hoppe in Sturm, *Deutschl. Fl.*, fasc. 61 (1833), non L. (1753)]

*C. leersii* F. W. Schultz, *Flora, Jena*, 53: 459 (1870), non Willd. (1787)


*C. muricata subsp. leersii* Aschers. & Graebn., *Syn. mitteleur. Fl.*, 2(2): 40 (1902)


[C. *polyphyl* *sensu* V. Krecz. in Komarov, *Fl. URSS*, 3: 155 (1935), non Kar. & Kir. (1841)]


Vignea guestphalica Boenn. ex Reichenbach, *Fl. Germ. Excurs.*, 130 (1830)
Carex guestphalica (Boenn. ex Reichenbach) C. F. Lang, *Flora, Jena*, 26: 147 (1843)
Carex chabertii F. W. Schultz, *Flora, Jena*, 54: 21 (1871)

(Accepted April 1975)
BSBI ABSTRACTS

ABSTRACTS FROM LITERATURE RELATING TO THE VASCULAR PLANTS OF THE BRITISH ISLES

Compiled by D. H. Kent. Published annually

Includes abstracts of botanical papers published in many journals throughout the Temperate World. Subject headings include History, Biography, Floras and Catalogues, Chromosome Surveys, Systematics, etc.

The Systematic Section, which is the bulk of the periodical, is arranged alphabetically under families and genera.

THE TARAXACUM FLORA OF THE BRITISH ISLES

By A. J. RICHARDS


The genus Taraxacum, commonly known as Dandelions, has been largely neglected in the British Isles, although it is of botanical, ecological and economic importance. Most accounts of the genus in this country consider only four species, which are too general in scope to be of much service.

In the present account the author shows that, due to the apomictic (non-sexual) means of reproduction usual in the genus, a much larger number of clear-cut species can be recognised in Britain, 132 in all, and that these demonstrate characteristic ecological and distributional behaviour.

A substantial introduction, with notes on the taxonomic history, biology, genetics, taxonomy, distribution, identification, cultivation and collection of the British species, is followed by a key to the species. In the main account, each species is treated individually, with nomenclature, a full description, breeding behaviour, ecology, British distribution (including a vice-county list), European distribution and general notes and comments repeated in each case.

Each species is illustrated with line drawings and there is a full index.

Although our knowledge of the British species of the genus is still incomplete, it is hoped that this work will form a standard reference for a number of years and thus should be valuable to Universities, Colleges, Field Stations, Museums and to all botanists interested in the higher plants of the British Isles.

Details from E. W. CLASSEY LTD,
PARK ROAD, FARINGDON, BERKSHIRE, SN7 7DN
Short Notes

DIPSACUS STRIGOSUS WILLD. IN CAMBRIDGESHIRE, V.C. 29

Dipsacus strigosus Willd., a native of southern Russia and western Asia, was reported as an alien in Britain by Hansen (1963), and a later note by Gerrans (1964) tabulated the characters that separate it from D. pilosus L., which it closely resembles. D. strigosus is most easily distinguished from D. pilosus by the capitulum size, 30–45(–60)mm wide (15–25mm in D. pilosus) and the length of the receptacular bracts, 15–20(–30)mm (7–22mm in D. pilosus). These measurements are from Cambridgeshire material.

Hansen’s records show that the plant has occurred as an alien in the vicinity of Oxford, Cambridge, Kew and Bristol, which suggests that it originated from the Botanic Gardens in the first three localities. Examination of material in the Cambridge University Herbarium (CGE) reveals three additional records from v.c. 29:
- ‘Hinton, Cambridge 18 July 1828 J. S. Henslow’ (as D. pilosus)
- ‘Waste ground W. of Botanical Laboratory, Cambridge 18 July 1921 A. J. Crosfield’ (as D. pilosus)
- ‘Churchyard, Little St. Mary’s church, Cambridge 1967 S. M. Walters’ (as D. strigosus). Stock from this locality is now growing in the Cambridge Botanic Garden; otherwise the plant has not apparently been grown there in recent years.

In addition to these, in July 1974, J. O. Mountford found six plants of what proved to be D. strigosus on an earth tip on the west side of the Gogmagog golf course, 3½ miles south-east of Cambridge.

Crosfield’s record above ties in with two given by Hansen: ‘Waste ground near Botanic Garden, Cambridge 1863 F. J. Hanbury’ (BM) and ‘Waste ground, Cambridge 1908 R. S. Adamson’ (BM); and also with a specimen collected by N. D. Simpson in 1913 on Coe Fen (BM). Coe Fen lies directly west of the Cambridge Botanic Garden. These records suggest that the plant has occurred as an alien in the south-western part of the City of Cambridge over a period of at least 112 years. Little St Mary’s, where the plant was first recorded by W. B. Gourlay in 1949 (as D. pilosus—in card index of Cambridgeshire Flora in CGE), still supported the species in the less tended parts of the churchyard in 1974.

The Hinton record is the earliest so far traced for this species in the British Isles. Recent searches in the field have revealed that the plant still occurs in Lime Kiln Close, Cherry Hinton (2½ miles south-east of Cambridge city centre), presumably the area that Henslow referred to. In 1972 and 1973 there was one large flowering plant, in 1974 five flowering plants were found, and 23 rosettes were counted in February 1975. This increase is best interpreted as a response to the opening up of the habitat (heavily cloaked with Clematis vitalba) by children playing in the pit and making new paths. Thus D. strigosus may have been established at Cherry Hinton for 147 years, though recorded as D. pilosus for much of that time. It certainly justifies a place in our Floras.

Perring et al. (1964), who did not distinguish D. strigosus, listed five recent records for ‘D. pilosus’. Two of these (Little St Mary’s and Cherry Hinton) are D. strigosus and of the others only that at Hildersham (9 miles south-east of Cambridge) can be confirmed as true D. pilosus by a specimen in CGE. D. pilosus has recently been rediscovered in Bottisham Park (7 miles north-east of Cambridge).

It will be interesting to record the persistence of D. strigosus in its present sites in v.c. 29 and any further spread. Does it persist elsewhere, e.g. near Oxford, Kew or Bristol? Is it still unrecognized in other sites?

ACKNOWLEDGMENTS

I should like to thank Miss M. B. Gerrans, Mr P. D. Sell and Dr S. M. Walters for help in preparing this note.
RUBUS PLATYACANTHUS MUELL. & LEFÈV. AND ITS ALLIES IN BRITAIN

In Newton (1974) I gave specific rank to Rubus carpinifolius var. laxus Sudre under the name R. laxissimus, based on A. Ley’s gathering from Mitcheldean Meend (v.c. 34) named by Sudre and issued as his Rubi rari no. 3.

At the same period Professor H. E. Weber was researching the R. carpinifolius group of brambles, during which he referred several of the sheets in BM cited by me as examples of R. laxissimus to R. platyacanthus Muell. & Lefèv. Further, he was of the opinion that many British and German specimens named R. carpinifolius by Focke, Rogers and others in the past should also be called R. platyacanthus, claiming in support the view of A. Neumann, a distinguished German botanist, who had verified R. platyacanthus in its locus classicus in France.

Weber (1973) has renamed as R. adspersus Weihe ex Weber the plant formerly known as R. carpinifolius Weihe & Nees, since this name had previously been used (by J. & C. Presl) for a different taxon. In this article he described the features distinguishing the two taxa, emphasizing the stouter, denser stem-prickles, the ovate, gradually acuminate terminal leaflet and gland-dotted bracts in the panicle as characters of R. adspersus, and the elliptical, shortly cuspidate leaflets with rounded rather than subcordate bases, the sparser, rather finer stem armature and the eglandular panicle-bracts in R. platyacanthus.

In the light of these investigations, and following inspection in company with Professor Weber of both species growing in Germany, I have re-examined many British sheets of R. laxissimus and R. carpinifolius with the holotype of R. platyacanthus (Lefèvre, Forêt de Retz, France, 1856, as R. niildus, hb. P. J. Müller in LAU) in front of me. Most of the British material named R. carpinifolius is indeed exactly R. platyacanthus, and despite slight variations in terminal leaflet-shape and indumentum in R. laxissimus, and the consistently broad panicles, I am now convinced that these features are not sufficient to support a distinct taxon at specific rank; R. laxissimus is also to be included within R. platyacanthus.

What is the relative status of R. platyacanthus and R. adspersus in Britain? Examination of sheets in several herbaria indicates that R. platyacanthus is by far the more widespread and common of the two; I have seen specimens either in the field or herbarium from v.c. 11–19, 21–24, 27, 30, 34–36, 38–40, 43, 53–59 and 62–64. R. adspersus appears to be confined to the areas of Flitwick Moor (v.c. 30), Milford Heath (v.c. 17, the specimens of ˚ R. carpinifolius flore roseo’ collected and issued as Set of British Rubi no. 28), Holme and Woodwalton Fens (v.c. 31), and the ancient Knutsford Heath (v.c. 58); doubtless it is present in other localities, but before this can be established a more comprehensive review of the available specimens will be necessary.

In the herbarium, specimens of the two are sometimes difficult to distinguish, particularly on badly collected or incomplete sheets. In the field, however, they can often be distinguished at a glance: R. platyacanthus exhibits a uniformly fresh green appearance, whereas R. adspersus has a characteristic yellowish-green cast (at least in the open) due to the reddish-spotted pigmentation of stems and panicles reflected in the name adspersus; also the petals are pale pink or pink-tinted, unlike those of R. platyacanthus which are nearly always pure white.

REFERENCES

SHORT NOTES

NOTES ON SOME WOOL-ALIEN CYPERACEAE FROM BLACKMOOR, N. HANTS.

The Cyperaceae form a huge natural family, with some 90 genera comprising 4,000 species, and are especially well represented in both temperate and warmer regions of the world where sheep are reared. Very few species have been recorded as wool-aliens in the British Isles, e.g. one species of *Cyperus* by Hayward & Druce (1919), two species of *Cyperus* by Lousley (1961), one species each of *Cyperus* and *Carex* by Dony (1969) and two species of *Carex* by Jermy & Tutin (1968), although on the Continent Probst (1949) listed about 20 species, and several other more recent records are scattered through the literature. The rather surprising lack of records is probably due to the ease with which different species in the field may be overlooked, because in the early vegetative stage many Cyperaceae look alike, and also to the difficulty in getting mature specimens for identification.

During the past six years (1969–1974) over 30 species have been collected from Blackmoor, N. Hants (v.c. 12), and these are listed below together with a few earlier records. Relatively few species were seen flowering in the field, the remainder having been cultivated under glass to protect them from frost. Many proved difficult to grow successfully, and took several years to produce even one inflorescence. For satisfactory determinations it is essential to obtain mature flowering material with good rootstocks, especially in *Cyperus* and *Carex*. Several plants have not yet flowered and remain undetermined.

A number of *Carex* species which are common British natives have been included, since these occurred regularly with undoubted wool-aliens. The geographical distributions of the species are mostly taken from the monographs by Kükenthal (1909, 1935), but it is likely that they have been introduced into many other countries, e.g. Australia and S. America. For *Carex*, the more recent accounts by Nelmes (1944), on Australian, and by Moore & Edgar (1970), on New Zealand species, have proved very useful. Voucher specimens are in my herbarium, and also some (K) at Kew.

**CYPERUS L.** 550 species

- *C. clarus* S. T. Blake Australia 1971 (K) det. SSH
- *C. congestus* Vahl Originally S. Africa, widespread Frequent (K) det. SSH
- *C. dactyloides* Benth. Australia 1973 det. SSH
- *C. eragrostis* Lam. (*C. vea* <i>Willd.</i>) Originally S. America, widespread Frequent det. SSH
- *C. esculentus* L. Widespread 1973 conf. SSH
- *C. gunnii* Hook. f. Australia 1971, 1972 (K) conf. SSH
- *C. longus* L. var. *tenuiiflorus* (Rottb.) Kük. Widespread AB and MMcCW 1973 det. JEL
- *C. luzulae* (L.) Retz. S. America 1973 (K) conf. SSH
- *C. rigidifolius* Steud. E. Africa 1973 (K) conf. SSH
- *C. rotundus* L. Cosmopolitan 1971 det. SSH
- *C. rutilans* (C. B. Clarke) Maiden & Betche Australia ACL, TBR 1969 (K) det. DMN
- *C. sporobolus* R. Br. N. Australia 1973 conf. SSH
- *C. tenuis* Schwartz S. and tropical Africa, Mexico, S. America 1971 (K) det. SSH
- *C. ustulatus* A. Rich. New Zealand 1971 det. SSH

**KYLLINGA** Rottb. 60 species

- *K. erecta* Schum. Africa 1972 (K) det. SSH
- *K. odorata* Vahl Africa and America AB 1973 conf. SSH

**SCIRPUS L.** 300 species

- *S. holoschoenus* L. Europe, Asia and the Mediterranean MMcCW e 1969
- *S. nodosus* Rottb. S. Africa, S. America, Australia and New Zealand TBR, ACL 1971 (K) conf. SSH

**ELEOCHARIS** R. Br. 200 species

- *E. nodulosa* (Roth) Schultes S. America 1971 det. TBR

**BULBOBLYSTIS** Kunth 100 species

- *B. humilis* Kunth S. Africa MMcCW 1964; 1972, 1973 (K) conf. SSH
CAREX L. Over 1,500 species
C. appressa R. Br. Australia, New Zealand, New Guinea and New Caledonia MMcCW 1968; 1971
C. devia Cheesem. New Zealand 1971 det. SSH
C. flacca Schreb. Europe, W. Asia, N. America, introduced in New Zealand Frequent
C. flagellifera Col. New Zealand 1972 det. SSH
C. hirta L. N. temperate regions 1971 det. EJC
C. hubbardii Nelmes Queensland 1972 conf. SSH
C. inversa R. Br. Australia and New Zealand 1971
C. muricata L. N. temperate regions Frequent conf. SSH
C. ovalis Good. N. temperate regions, introduced in New Zealand Frequent
C. secta Boott New Zealand MMcCW 1964 det. SSH
C. solandri Boott New Zealand MMcCW 1970 det. SSH
C. tereticaulis F. Muell. Australia MMcCW 1968; 1972 conf. SSH
C. virgata Sol. ex Boott New Zealand MMcCW 1968; 1969 (K) det. SSH
C. vulpinoidea Michx. N. America, Colombo, naturalized in Europe 1968 (K) det. SSH

Key to initials used in the list:
AB A. Brewis EJC E. J. Clement SSH S. S. Hooper
ACL A. C. Leslie JEL J. E. Lousley DMN D. M. Napper
TBR T. B. Ryves MMcCW M. McCallum Webster

ACKNOWLEDGMENTS

I am grateful to Miss S. S. Hooper for identifying many of the specimens, to Lady Anne Brewis for permission to visit Blackmoor Fruit Farm, and to Miss M. McCallum Webster for giving me some of her interesting collections of Carex. Some of the species listed were also collected by other members of the London Natural History Society.

REFERENCES


T. B. RYVES

NOTES ON SOME WOOL-ALIEN MALVACEAE

The Malvaceae form a moderately large family (1,000 species in 75 genera) in tropical and temperate regions. Many species have big, handsome flowers and are commonly grown in gardens, including Hibiscus trionum L., which is also one of our most attractive wool-alien plants.

Probst (1949) listed 26 species of Malvaceae which were associated with shoddy on the Continent, and 14 species from Britain were listed by Lousley (1961). Most of the latter have recurred in the
past six years in the two areas at present under review, but the purpose of this note is to give records only of species which were either not included or noted only once in Lousley's list. Several of them have also been recorded more recently by Dony (1969). *Modiola* appears to have been previously recorded as a British wool-alien only by Hayward & Druce (1919), from Galashiels 60 years ago.

The commonest wool-alien species were *Malva parviflora*, *M. sylvestris* and *M. neglecta* (the two latter, however, possibly being native weeds), followed by *Sida spinosa*, *S. cordifolia* and *Pavonia*. The *Sida* species hardly ever flowered in the field, although in the exceptionally fine hot summer of 1973 several very large plants of *S. rhombifolia* flowered freely and set good fruit at Blackmoor. Most of the alien Malvaceae were sensitive to slight or moderate frost, but nearly all the attempts made to grow them on through the winter were abortive, and several new species died before they could be induced to flower and hence identified. Exceptionally, *Pavonia* and *Modiola* proved relatively easy to cultivate and grew strongly under glass.

The following 12 species were found at Blackmoor, N. Hants., v.c. 12, and Maulden, Beds., v.c. 30. Records are my own unless otherwise stated.

**ABUTILON** Miller Over 100 species

*A. malvifolium* (Benth.) Domin Australia Blackmoor 1973

**MALOPE** L. 4 species

*M. trifida* L. W. Mediterranean Maulden 1969 E. J. Clement & T. B. Ryves

**MALVA** L. 40 species

*M. neglecta* Wallr. Europe Blackmoor and Maulden Common, perhaps native

*M. sylvestris* L. Europe Blackmoor and Maulden Common, perhaps native

**MALVASTRUM** A. Gray 12 species

*M. multicaule* (Schlecht.) Britton S. America Blackmoor and Maulden Single plants in several years

*M. peruvianum* (L.) A. Gray (?) S. America Blackmoor 1970 det. C. C. Townsend

**MODIOLA** Moench 1 species

*M. caroliniana* (L.) G. Don America, naturalized in Australia, S. Africa and Asia Blackmoor 1970, 1973

**PAVONIA** Cav. 200 species

*P. urens* Cav. Africa Blackmoor A few plants in most years

**SIDA** L. 200 species

*S. cordifolia* L. Tropics Blackmoor A few plants in most years

*S. rhombifolia* L. Tropics Blackmoor 1973, 1974

*S. spinosa* L. Tropics Blackmoor A few plants in most years

**UROCARPIDIUM** Ulbr. 11 species


**ACKNOWLEDGMENTS**

I wish to thank Lady Anne Brewis for permission to visit Blackmoor, Dr and Mrs J. G. Dony for their help in locating good areas to search in Bedfordshire, and various members of the London Natural History Society for general assistance in finding specimens.

**REFERENCES**


T. B. Ryves
Townsend (1959) first reported the presence in Britain of *Vulpia australis* (Steudel) Blom, an alien from South America. This addition to the British list was based on a gathering by C. W. Bannister and C. C. Townsend in 1955 from the docks at Sharpness, W. Gloucs., v.c. 34, of which we have seen material in K and herb. J. E. Lousley. Townsend appears to have identified *V. australis* by comparing his specimens with material so-determined in K, where there are several sheets from South America of plants agreeing with the Sharpness specimen and labelled *V. australis* (in particular by the American agrostologist A. S. Hitchcock). Such plants do not, however, agree with the original description nor with the type-specimen of this species.

*V. australis* (Steudel) Blom is based on *Festuca australis* [Nees ex Steudel], which was in turn based on *Festuca tenella* var. α Nees, non Willd. The description given by Nees (1829) mentions few characters which one could use to separate the closely related species in the section *Vulpia* of the genus *Vulpia*, but he described the lower glume as half as long as the lowest lemma on the same side, and the upper glume as about as long as the lowest lemma on the same side. Taken in their strict application these features agree very closely with those of *V. bromoides* (L.) S. F. Gray, but less so with those of other related species or with those of the Sharpness specimen. The only specimen cited by Nees was collected by Sellow at Montevideo and seen by Nees in B. No such specimen exists at B now, but a duplicate of it, sent from B in 1840 (after Nees' publication), is at K. It is clearly *V. megalura* (Nutt.) Rydb., a taxon to which Nees' description does not strictly apply, and quite different from the Sharpness plant. The true identity of *V. australis* as understood by Nees is thus uncertain, and will be discussed by us more fully in a later paper.

The Sharpness specimen is a typical representative of the plant generally known as *V. hybrida* (Brot.) Pau or *V. broteri* Boiss. & Reut., a western Mediterranean species which is widely naturalized in South America, and Townsend's (1959) description gives a good idea of the differences between it and *V. bromoides*. Several other British specimens, mostly wool-aliens, have been identified as *V. australis* since 1959, and the name has been used in the literature (e.g. Lousley 1961). All specimens we have seen so-labelled have been referable to *V. broteri*, or (presumably representing mis-identifications) to *V. bromoides*, *V. myuros* (L.) C. C. Gmel. or *V. megalura*, all of which occur as aliens in South America. We have seen material of *V. broteri* from Scilly, v.c. 1a; N. Hants., v.c. 12; W. Kent, v.c. 16; Beds., v.c. 30; and W. Gloucs., v.c. 34.

The correct name for *V. broteri* (*V. hybrida*) is, however, *Vulpia muralis* (Kunth) Nees, a combination based on *Festuca muralis* Kunth, which was in turn based by Kunth on his own earlier concept of *F. myuros* L. (*V. myuros*) as it occurred in South America, but which he came to believe was a distinct species. There is an isotype of *F. muralis* (from garden walls, Quito, Ecuador) in BM, and it is a perfect match for the European *V. broteri*. The name *F. muralis* was published in 1822 and easily predates *V. broteri* or *V. hybrida*.

*Vulpia megalura*, the second subject of this note, has been known as a wool-alien species in Britain for many years. It was described (as *Festuca megalura* Nutt.) from Californian material, and it is very widespread in both North and South America. Nevertheless it is scattered throughout the European and North African range of *V. myuros*, to which it is very closely related, in places where it is most unlikely to have been introduced (in contrast to its casual status in Britain), and we are convinced that it was introduced to America from the Mediterranean region. The same conclusion has been recently reached by Lonard & Gould (1974).

*V. megalura* differs from *V. myuros* only in its lemmas, which are ciliate distally. Such variation is found in several species of *Vulpia*, and we fully agree with Lonard & Gould (1974) that the two taxa are conspecific. Lonard & Gould included *V. megalura* in *V. myuros* var. *hirsuta* Hackel. However, we consider that the rank of forma is more appropriate, and the combination *V. myuros* f. *hirsuta* (Hackel) Blom already exists (Blom 1934). But the basionym *V. myuros* f *hirsuta* Hackel referred to a Portuguese plant with dorsally hairy (not marginally ciliate) lemmas (Hackel 1880). Plants of this sort are also scattered throughout the range of *V. myuros*, and we consider them to represent a distinct forma.


It is interesting to note that these two plants, *V. muralis* and *V. myuros* f. *megalura*, are both
Mediterranean taxa which have become naturalized in America, were both first named in America, and have both been re-introduced into Europe as wool-aliens from America.

REFERENCES


C. A. STACE & R. COTTON

FESTUCA GLAUC AUCT. AND FESTUCA CAESIA SM.

In a recent paper (Trist 1973), I discussed the glaucous fescue confined to a limited area of the Suffolk Breckland. It had been considered that one species with two varieties could be identified, but the results of a field study showed that only one taxon should be recognized.

As pointed out in that paper, the uncertainty of the identification of this glaucous Breckland fescue has been a contention of botanists for over 160 years. Smith (in Sowerby & Smith 1808), who studied this plant and collected it from the Breckland site, gave it specific rank as Festuca caesia Sm. and after much study concluded that it was quite distinct from Festuca ovina L. and Festuca duriuscula auct. (F. longifolia Thuill.). Hackel (1882) placed both of the varieties referred to by Trist (1973) under Festuca ovina sensu lato, as F. ovina subsp. eu-ovina var. glauca (Lam.) Hack. and F. ovina subsp. eu-ovina var. glauca subvar. caesia (Sm.) Hack. Richter (1890) similarly subordinated Smith’s F. caesia to F. glauca Lam. as F. glauca Lam. e. caesia (Sm.) K. Richter, which has been regarded as a subspecies by some (e.g. Auquier 1973) and as a variety by other authors (e.g. Hubbard 1954).

In the circumstances, it seems reasonable to doubt that a comparison of the English and Continental glaucous fescues has been fully made; in fact it must be admitted that a full understanding of the taxonomy of this group of glaucous fescues has still not been reached. Dr. P. Auquier of Liège University (1973 in litt.) has told me that the date of Lamarck’s description of F. glauca was 1788 and not 1786, as previously thought. This was one year later than the notes published on F. glauca by Villars (1787). Villars would have known of Lamarck’s work, but were the plants described by each of them the same or different? Auquier (1973 in litt.) also informed me that his studies have conclusively shown that F. glauca sensu Villars has distinct differences from the Breckland plants and also from the plants of the locus typicus of Lamarck in the Massif Central; Lamarck’s plants also differ from those found in the Suffolk Breckland.

Auquier (1973) discussed the Suffolk plants and those from the loci typici of Villars and Lamarck and presented the results of a very detailed study. He has made a valuable contribution to our knowledge of this group of glaucous fescues. It now appears clear that the two fescues of Villars and Lamarck cannot both be referred to the same taxon; also it is shown that the Breckland fescue is different from either. It therefore follows that the name of the Breckland plant must be reconsidered. In considering the present state of our knowledge of the F. ovina group, Auquier (1973 in litt.) has suggested that the Breckland fescue be referred to the original name given by J. E. Smith, i.e. F. caesia Sm.

ACKNOWLEDGMENTS

I am grateful to Dr P. Auquier for information through his publications and correspondence, which gave invaluable guidance, and also to Dr C. E. Hubbard for his continued interest and assistance in this complicated group of fescues.
REFERENCES

Auquier, P. (1973). Qu’est-ce que le Festuca caesia Sm. (Poaceae)? Lejeunia, n.s., 70.

P. J. O. Trist
Plant Records

Records for publication must be submitted in the form shown below to the appropriate vice-county Recorder (Watsonia, 8: 435-447 (1971), and not to the Editors.

Records are arranged in the order given in the List of British Vascular Plants by J. E. Dandy (1958) and his subsequent revision (Watsonia, 7: 157-178 (1969)) but Taraxacum is arranged according to A. J. Richards (Watsonia, 9, Suppl. (1972)). With the exception of collectors' initials, herbarium abbreviations are those used in British Herbaria by D. H. Kent (1958).

The following signs are used:

* before the record: to indicate a new vice-county record.
† before the species number: to indicate that the plant is not a native species of the British Isles.
[] enclosing a previously published record: to indicate that the record should be deleted.


†27/1. Azolla filiculoides Lam. *1, W. Cornwall: Ding Dong, near Penzance, GR 10/44.34. Pool in old quarry. B. Sturdy, 1971, field record.


†395/1. PENTAGLOTTIS SEMPERVIRENS (L.) Tausch *78, Peebles: Traquair, GR 36/3.3. C. Morrison, 1972, field record.


555/1. MYCELIS MURALIS (L.) Dumort. *96b, Nairn: Holme Rose, GR 28/81.48. M. McC. Webster, 1974, E.


560/42. **Taraxacum euryphyllum** (Dahlst.) M.P.Chr. *1, W. Cornwall *99, Dunbarton.

560/44. **Taraxacum praestans** H.Lindb.f. *1, W. Cornwall.


560/50. **Taraxacum naevosum** Dahlst. *95, Moray.

560/51. **Taraxacum laetifrons** Dahlst. *61, S.E. Yorks.

560/58. **Taraxacum strictophyllum** Dahlst. *96, Easternness.


560/69. **Taraxacum sellandii** Dahlst. *56, Notts.

560/70. **Taraxacum anistrolobum** Dahlst. *1, W. Cornwall *96b, Nairn *99, Dunbarton.


†560/74. **Taraxacum procerum** Hagl. *1, W. Cornwall *56, Notts.


†560/76. **Taraxacum linguatum** Dahlst. ex M.P.Chr. & Wiinst. *85, Fife *95, Moray.


560/94. Taraxacum ekmanii Dahlst. *94, Banff *95, Moray.
560/97. Taraxacum copidophyllum Dahlst. *61, S.E. Yorks.
560/122. Taraxacum hemipolyodon Dahlst. *95, Moray.


†646/1. ACRUS CALAMUS L.  *68, Cheviot: by R. Tweed, ½ mile S. of Norham, GR 36/89.46. G. A. & M. Swan, 1974, field record.


656/6. ELEOCHARIS UNIGLUMIS (Link) Schult.  *45, Pembroke: Landshipping Ferry, GR 22/01.11. Upper salt-marsh. T. A. W. Davis, 1974, NMW. 1st localized record. (Nature Wales, 14: 202 (1975)).


663/71. CAREX REMOTA L.  *78, Peebles: Dawyck, GR 36/16.34. D. J. McCosh, 1972, herb. D.J.M.


677/1. CATABROSAAQUATICA (L.) Beauv.  67, S. Northumberland: by Bothal Burn, near Pegswood, GR 45/23.87. C. A. & M. Swan, 1974, field record. 1st record for over 100 years.


701/4. AGROSTIS GIANTEA Roth  *109, Caithness: Thurso railway station, GR 39/11.67. C.S.S.F. field meeting, 1972, field record.


Book Reviews


Guernsey is a small, geologically uniform island of 63 square kilometres, smaller than a grid square in the Atlas. Its soils are fertile, and its forests were completely cleared by Norman times, while few of its marshes remain undrained; it has no nature reserves. It has been densely populated for at least a thousand years, and currently supports 51,500 people, so that its population density is nearly three times that of Belgium or Holland. The local people are skilled and efficient horticulturists, who have radically changed their pattern of land use in the last hundred and fifty years, so that about ten per cent of the island is now under glass. Given these facts, we might expect the flora to be a poor one, with few surviving native species. In fact, David McClintock has been able to list 1,340 plant species which have been found on the island, compared with 684 listed by Babington in 1839 and 957 by Marquand in 1901.

The new Flora combines immense botanical and historical erudition without ever becoming too technical: it is designed to be read as well as consulted. It is a very critical work, both in rejecting the unusually large number of spurious records and in the care with which correct names have been cited (though purists may disapprove of the retention of the initial capital for some specific epithets). It gives much information on local variations, so important in island floras, for example in Spergula arvensis, Oxalis latifolia and Salsola verbenaca (now lumped with S. marquandii). It includes all aliens, a policy which I approve, since this is a region where naturalization takes place rapidly. It gives excellent brief notes on status, frequency, history, horticultural merit, occurrence on other Channel Islands, local uses and names: English, Latin and local names are all indexed together.

Inevitably this Flora will be compared with Lousley’s Flora of the Isles of Scilly (1971), and the comparison reveals several omissions in the Guernsey work. The lack of almost all background information on geology, soils, physical features and climate is compensated by listing references to these topics in an appendix. More important, no attempt is made to interpret the remarkable facts presented concerning the occurrences and absences of native and introduced plants. No mention is made of the fact that the more interesting natives fall into several different categories with regard to their European distribution—Matthews’ ‘Mediterranean’, ‘Oceanic’ and ‘Continental Southern’ groupings. Comparative tables of the numbers of naturalized species from different parts of the world might have analytic and predictive value. A number of the introduced species recorded in this work are not mentioned in Flora Europaea. This Flora gives no keys, e.g. for the following genera, which contain taxa on Guernsey which are not covered by standard British Floras: Agropyron, Asplenium, Calystegia, Centaurea, Mentha, Narcissus, Olearia, Pilosella, Rosa, Solanum and the hardy bamboos. Simple keys, or more hints on identification of the unfamiliar species, would greatly increase the value of the work to visiting botanists. The thumbnail sketches of rarities in the text only give an idea of the plants, but their ‘jizz’, to use David McClintock’s own word, is more easily learnt from clear descriptions or magnified drawings of critical parts.

The book is stoutly bound, the paper is of rather poor quality, and the number of misprints is small (e.g. amygdaloïdes mis-spelt on page 143). One small printing defect concerns the spacing of authors’ names and Guernsey names after the Latin name of each species. The uninitiated may be led into thinking that the islanders refer to Rosy Bindweed as Brummit and Wavy Bitter-cress as Withering. Despite these minor defects, this book is a worthy addition to the long list of British local Floras. It is essential reading for all visiting botanists, and deserves a wide sale among Islanders and holiday visitors.

H. J. M. Bowen

This modest, but valuable, paper-back publication provides a survey of the Cormophyta, and is primarily intended for students. This term, which is not very familiar to British botanists, embraces the bryophytes, pteridophytes and flowering-plants. Concise family descriptions are provided, in a sequence following Takhtajan's system, along with brief notes on economic plants and other points of interest. Numerous excellent plates by Bent Johnsen illustrate the diagnostic features of flowers and fruit, through habit drawings, floral details and floral diagrams. In common with the reviewer, most British botanists will lack the knowledge of the Danish language which would permit them to make free use of the text. However, the first-class illustrations speak clearly and in a thoroughly international tongue, and these in themselves are sufficient to commend the work to British readers. In a concise work for students, some restriction of coverage is both appropriate and essential. Naturally in this case, the selection favours families well represented in N.W. Europe, supplemented by some others, especially those in which major economic species are included. Nevertheless, the choice sometimes seems rather capricious, as when the Apocynaceae and Asclepiadaceae are allowed two lines between them, and the Verbenaceae fares little better. In contrast, the Bromeliaceae, Myrtaceae and Commelinaceae are allotted 18, 13 and 10 lines respectively. The reviewer understands that an English edition is under consideration and believes that there is a real need for a simple, concise review of the higher plants, a role that this book is well fitted to fill for amateur botanists as well as students. The outstandingly good illustrations are both highly informative and aesthetically attractive, and merit an English text, which would make them available to a much wider circle of users.

J.F.M. Cannon


This long-delayed publication is a 5-year résumé, in compact, cyclostyled format, of the botanical literature of Czechoslovakia. All fields of botany are covered, and the arrangement of the 8,318 entries (which include the full titles of all the papers cited) is like that in the similar publication for 1965–1966 reviewed in *Watsonia*, 9: 161 (1972). Many additional subjects are cited by means of cross-references at the end, and there are very useful indexes to geographical regions, plant names, and authors of articles. Libraries will find this a valuable reference-work, and more convenient than the annual bibliographies already available.

A. O. Chater


Previously issued between 1954 and 1965 in three separate parts, this unrevised reprint in a single volume is the outcome of 'academic and public demand'. It is not a full Flora with comprehensive species descriptions but has the form of hand-written illustrated keys reproduced from printings of the original manuscripts. In addition there are explanatory notes on 'How to use this book' (for those without formal botanical training), a glossary, and separate indices to the three constituent parts.

Despite its limitations and present incompleteness—twelve families (Solanaceae to Compositae) are still to come, in a later, promised volume—it is easy to see why there is the demand in (West) Australia for the publication of these keys in one handy volume. Australia, with many thousands of plant species, still has no comprehensive Flora other than Bentham's *Flora Australiensis* (published between 1863 and 1878) and but few modern regional Floras. This volume must therefore be a welcome addition.

The European botanist, not directly concerned with the Australian flora, will probably be more interested in the methods and techniques of presentation used. There is a general key to
BOOK REVIEWS

families, which also enables one to refer a plant to the twelve families of the future volume. The dichotomous keys to genera and species form the body of the book; they incorporate numerous drawings as an integral part of the keys. The precision given by the 'visual description' and the elimination of all non-essential information produces a clarity and apparent simplicity of procedure.

The facsimile handwriting is quite acceptable where entries are not crowded on the page; but many drawings are far from successful, especially in Part I where they are much reduced in size. There are many improvements in Parts II and III. The indices contain additional data: season of flowering and synonymy (Part III), distribution (Parts II and III), authorities for the Latin names (which are used throughout) (Parts II and III), but not in that for Part I, which fills over half the book. There are oddities in the sequence of families, by and large Englerian: Myrtaceae has been added to Part I and Goodeniaceae to Part II. There are some discrepancies in the treatment of the three parts which may be misleading: the change of scale of the drawings is signalled in the explanatory notes.

Not being familiar with Western Australian species I cannot properly judge the efficacy of the keys; but, using specimens from New South Wales, I found the Key to families reasonably easy to use and had moderate success with appropriate genera and species. But is it really necessary to observe 'fruit without vittae, compressed laterally' (the drawing of which is unrecognizable) before Conium can be keyed out?

Of course there are snags; without corroborative descriptions a faulty identification may go unrecognized. But this method, pioneered (?) by Bonnier many years ago, has a lot to commend it, especially when it results in a single light-weight serviceable volume covering, in this case, 90% of the families represented in temperate Western Australia. It should be considered by anyone contemplating the writing a working handbook to a comparably extensive flora. This is surely an invaluable handbook; it is excellently produced, sturdily bound in flexible covers and printed on glossy hard-wearing paper. And it costs only £6.60.

A. P. CONOLLY


Prior to May 1840, when the control of the Royal gardens at Kew passed from the Crown to the Commissioners of Woods and Forests, and Sir William J. Hooker was appointed as its first Director, there was no library or herbarium at Kew. The dried plant collections sent home by Kew collectors such as Caley, Good and Masson as well as many of their manuscripts were at the time in the possession of Sir Joseph Banks, and are now in the Department of Botany, British Museum (Natural History).

No scientific establishment, however, can function efficiently without a comprehensive library, and soon after Sir William Hooker became Director he set about the formation of one at Kew. The founder collections were the libraries of Dr W. A. Bromfield (presented in 1852), George Bentham (presented in 1854) and Sir William Hooker (purchased in 1867). Today the library of the Royal Botanic Gardens, Kew, is one of the finest botanical libraries in the world, covering taxonomy, economic botany, plant geography, cytology, anatomy, physiology, and biochemistry. Adequate staffing in recent years has enabled them to maintain an excellent author catalogue and also to classify their entire stock and so provide a subject catalogue. The classification schedules used are not those of one particular well-known scheme, but a mixture of Bentham & Hooker for flowering plants, Kew's own geographical schedule for Floras and an adaptation of the Dewey Decimal Classification for the remainder. It is important to note that the author catalogue includes pamphlets and a major part of the library's very extensive collection of reprints. Important articles in obscure journals can often be found in a reprint collection and Kew are to be congratulated on having catalogued their vast collection and so being able to include them in their author catalogue. These volumes are a major contribution to botanical and horticultural bibliography. Printing directly from card catalogues is far from ideal but, alas, gone are the days of type-set-printed catalogues.

P. I. EDWARDS

Thd third volume of this Flora (see Watsonia, 6: 390–1 (1968) for a review of Volumes 1 & 2) is devoted to the Leguminasles. The Caesalpiniaeaceae and Mimosaceae are very sparsely represented in Iraq, mainly by introduced species; the Papilionaceae, however, with some 40 native genera and 300 species, form a significant part of the country's flora. This family is also of paramount economic importance, since its members provide essential foodstuffs (pulses, forage and fodder crops) and many other products: gums and resins, tanning agents, fibres, vegetable oils, dyes, perfumes, medical substances and poisons and timber, as well as ornamental plants. The Flora of Iraq is unusual in placing a strong emphasis on the uses of plants, and this makes it of interest to a wide range of readers. In the present volume, for example, there are three whole pages concerned with manna and two with gum tragacanth.

Volume 3 is written by the editors, working as a team: Mr Townsend is the taxonomist, while Mr Guest provides the economic and distributional notes and the Iraqi names of plants and plant products.

The tribes of the Papilionaceae are delimited according to Hutchinson (1964), and yet, surprisingly, they are arranged in the order of Bentham & Hooker (1865). As was explained in Volume 2, the Flora of Iraq is modelled on Hutchinson's (1959) treatment of the angiosperms and so it is odd to find this return to B. & H., especially as the Turkish legumes have so recently been revised and arranged in Hutchinson's order. The latter is surely more natural; for example, it places the tribes Vicieae—Ononideae—Trifolicieae in sequence, whereas Bentham & Hooker removed the Vicieae far from the Trifolicieae, which were linked instead to the Genisteae.

The present volume is notable for its careful, accurate and detailed species descriptions and for the fine accompanying illustrations. The format is clear and attractive and there are very few printing errors. It also continues a feature which other Floras would do well to emulate: there is a series of addenda comprising a gazetteer, a history of botanical exploration in Iraq, a glossary, indices to abbreviations, signs and symbols, author's names and abbreviations for periodicals and other publications, and a selected bibliography. This part is not unwieldy, and is a great help to the working taxonomist. It would be useful if the frontispiece map of Volume 1 were reproduced in future volumes, so that the regions referred to in the distributional paragraphs—MAM, FPF, DLJ, etc.—could be more easily visualized.

We look forward to the publication of the remaining five volumes of this admirable Flora.

REFERENCES


F. K. KUPICHA


Here are 13 chapters of literary appreciation on works of 11 'non-fiction prose writers of the English Countryside'. They range from Walton to Williamson, and the author, Professor of English in the University of Toronto, presupposes a familiarity with their writings. His commentaries will no doubt be appreciated by aficionados, but on actual plants, or animals, there is just nothing.

D. MCCINTOCK

In this pocket-size book, one of a series in which flowers and fungi are to be included, the author returns to a subject well-treated in her Nature Photography, Its Art and Techniques, Fountain Press, 1972. Here, one of our leading wild-life photographers has produced a practical guide to tree photography in field and studio. A mass of hints and techniques are provided and those who desire to obtain better photographic records will find the book invaluable. A basic groundwork of photography is assumed but a useful photographic glossary is included together with an equipment list, bibliography and index. Used as a recording instrument, the modern camera with its apparent simplicity has tended to produce far too many mediocre photographs. Those of us who take a camera into the field should not be satisfied in obtaining a mere record; with such a guide to technique we can only improve. Future titles are awaited with interest.

G. A. MATTHEWS


When he investigates the course of evolution of supraspecific taxa and the factors involved therein, the student is denied recourse to experiment. When, as is often the case in flowering plants, he is also denied effective fossil evidence on which to make decisions, how should be proceed? At this point many workers give up the effort, muttering 'It is all speculation' or words to that effect. G. Ledyard Stebbins, who has already made so many original contributions to the study of various aspects of evolution, has not given up. Instead, in this fascinating and important work he gives detailed consideration to the main source of data that is available, namely evolutionary trends. Indeed, the titles of the two parts of the book speak for themselves: 'Factors that determine evolutionary trends' and 'Trends of angiosperm phylogeny'.

Stebbins begins by discussing certain principles of evolution, from which he proceeds to derive his own evolutionary philosophy. He believes that evolutionary trends have resulted from a succession of complex interactions between organisms and their environment, by means of natural selection; and that, in any organism, there exist several different gene combinations that might adapt it to any changed environment, the particular adaptive combination that does become established being dependent largely on the nature of the gene pool already present. In other words, recurrent natural selection results in an evolutionary trend, the direction of which depends on the state of the organism when the selective force begins to act.

Having shown how trends can and do occur in any character, the author goes on to discuss how they can be recognized. In the second part, in which trends of various types in the angiosperms are considered, he throws new and fascinating light on such familiar problems as the evolution of the flower and the origin and development of the monocotyledons.

One could expatiate on so many topics that are discussed, agreeing with some of the views expressed, disagreeing to various extents with others; but the fact remains that this synthesis of Stebbins' mature ideas on evolutionary processes and their results is a 'must' for anyone at all interested in evolution, despite the high cost of the book.

Similarly, one could list some errors (one or two factual, a fair number typographical) that appear in the text; but these seem of relatively little importance. The format, however, makes the book less pleasing to read than it might have been, particularly the two unjustified columns per page and the reproductions of some illustrations at too small a scale. Nevertheless, this is a book to buy, to read and to keep at hand.

N. K. B. ROBSON


The appearance of a textbook of almost 500 pages on the subject of plant cell-walls and written by Professor Preston is a noteworthy event. The inevitable comparison with the late P. A. Roelofsen's masterpiece The Plant Cell Wall (1959) is made by Preston himself in his Preface,
BOOK REVIEWS

where he pleads his case for the restriction in subject matter that has been necessitated by the vast amount of literature which has accrued since 1959. In fact this book, which claims to deal with aspects of the plant cell-wall covered by the term 'physical biology', is primarily an exposition of those topics which have interested the author during nearly 50 years of research (Preston's Ph.D. thesis, completed in 1931, was entitled The organisation of the cell wall applied to the elucidation of problems associated with growth).

The first third of the book (chapters 2–6) deals with introductory physico-chemical topics, in particular chemical bonding and structure, X-ray diffraction, and polarizing and electron microscopy. The rest of the book deals with cell-wall structure (chapters 7–10), visco-elastic properties of cell-walls (chapter 11), and cell-wall growth and biosynthesis (chapters 12 and 13). As examples of the author's self-imposed restrictions one may cite his lack of mention of scanning electron microscopy, and his confinement to algae and phanerogams. The strength of this book, however, lies in the authoritative manner in which the topics covered are reviewed and discussed by one who has been intimately concerned with the development and application of many of the relevant techniques.

The reader with even a slight knowledge of the subject matter will not be in the least surprised at the relative emphasis placed by the author on the various aspects of his subject, nor will he be disappointed by it. With this slight reservation, one can safely predict that this treatise will swiftly become a standard textbook.

C. A. Stace


This is an original and remarkable text. It gives first a good account of the protocaryotes, though not treating the bacteria in great detail. It continues with eucaryotes in three large chapters of equal length. These deal first with the morphology and anatomy of the thallus, secondly with reproduction, and thirdly with thallophytes in the environment and the biosphere. In each of these three chapters, topics are treated in a perfectly general way, cutting across the systematic categories. For example, vegetative reproduction, types of life-history, cell structure, symbiosis, are all considered synthetically, and not as separate algal and fungal fractions. The book ends with a short chapter on the main lines of classification of the leading algal and fungal groups. It is copiously and excellently illustrated, with many original drawings and diagrams and some good electron micrographs. It is packed with information and is well written and printed. The level is about that of a second year course in a British university. Expensive, but highly recommended.

D. H. Valentine
Obituaries

CATHERINE MURIEL ROB
(1906–1975)

Kit Rob died on 6th February, 1975 as the result of a grave illness of some months' duration. She died at Catton Hall, near Thirsk, where she was born on 21st February, 1906. Educated at home by a governess, she later carried heavy domestic responsibilities for very many years, ultimately caring first for her sick mother, who died in 1959, and then for two elderly aunts, the last one dying in her hundredth year in 1974. Once a part-time dispenser and then a lecturer, she was latterly employed full-time as a member of the Yorkshire Rent Assessment Panel. During the war she served as a cook at Catterick Military Hospital.

A noted, highly experienced amateur field-botanist, Kit was also a great character and a wonderful friend to many. With a sound working knowledge of the British flora, she was the unrivalled authority on the distribution of vascular plants in North Yorkshire for at least 36 years. Self-educated botanically, she was justly proud of being elected a Fellow of the Linnean Society in 1947 in recognition of her services to Yorkshire botany. Permanent testimony to her knowledge and continual effort ‘in the field’ is to be found in her numerous contributions to The Naturalist, particularly the valuable accounts of the plants of specified North Yorkshire localities in excursion circulars and reports from 1935–69. Her greatest contribution to botanical knowledge is to be found in the Atlas of the British flora. She was responsible for collecting records for the whole North Yorkshire area (v.c. 62 and 65), a tremendous task, and yet this is one of the best-covered areas due mainly to her own great personal enthusiasm and effort. Her account of the plants of the moors and dales in the Forestry Commission Guide North Yorkshire forests will continue to be of great help and interest to the visitor to the area. Her great knowledge of folk-lore and English names was invaluable in the preparation of the recently published English names of wild flowers (Dony, Perring & Rob, 1974). Kit had an important private herbarium which contained 5,000 specimens in 1959.

Kit's interest in wild plants had begun early in life. She joined the Wild Flower Society at the age of 17 and it was to her activities in this Society, together with the personal help and encouragement of Tom and Gertrude Foggitt, that she owed her wide basic knowledge of plant identification. Her active membership of four societies in particular was of great mutual benefit to the societies concerned. Always an outstanding member of the Wild Flower Society, Kit soon worked her way up to the heights of ‘Valhalla’, becoming secretary of its lower section in 1930 and succeeding Mrs Foggitt as secretary of the upper section in 1949, a position she held until 1971. A succession of Presidents have been grateful for her help and advice always readily given. One of the longest-serving members in the B.S.B.I., Kit joined the Botanical Society and Exchange Club of the British Isles in 1932, soon became a regular exchange member and was promptly made local secretary for North Yorkshire. It was a tribute both to her knowledge of British plants and to her ability to handle people tactfully that she was appointed distributor in 1946. When exchange was abandoned, referees and recorders were appointed in addition to local secretaries and Kit became all three for North Yorkshire until two of these offices ceased to exist; she was still recorder at the time of her death, as well as referee for popular names. She served on the Council of the B.S.B.I. as representative of the North-East Region from 1950–3, 1956–60 and from 1967–71, and was Vice-President from 1960–4. She joined the Yorkshire Naturalists’ Union in 1934 and became one of its most prominent and highly respected members. She held important offices including that of Hon. General Secretary from 1958–62, Hon. Excursions Secretary, 1963, and Divisional Secretary from 1939–63. She was plant recorder for North Yorkshire from 1938–71 and was responsible for the publication of plant records for all Yorkshire from 1957–65. She was elected President of the Union in 1969 being only the third woman to be so honoured. Always interested in conservation, she took a keen interest in the Yorkshire Naturalists’ Trust from the time of its foundation in 1946. She was Hon. Secretary of the Trust from 1952–7, when it owned
only two nature reserves, and she laid the foundations for the much wider influence that it gained subsequently. Since 1957, she continued to serve the Trust in many ways: as a council member from time to time, as chairman of two reserves and as a member of the north-west area group committee. She had also been a member of the council of the Yorkshire Philosophical Society and was its secretary from 1954-9.

Both botanizing and meeting botanists were enjoyed to the full. Kit organized excursions for the B.S.B.I. and the W.F.S. and annually for the Y.N.U. over a long period of time, all in her own inimitable style. She was in great demand as a lecturer and gave generously of her time to various Natural History Societies, often travelling long distances, and in recent years she conducted adult education lectures, which were well attended. Completely at ease in front of a microphone, Kit took part in radio programmes concerned with the northern country-side, and the invitation to take part in the television series ‘The North-Country Naturalist’ was recognition greatly appreciated.

What Kit Rob was able to do for Yorkshire botany and conservation owes as much to her personal qualities as to her botanical knowledge and even her many other interests played their part. Her own warmth of personality and genuine interest in others meant that she made friends with people in all walks of life, including land-owners and others of influence. Widely known and respected, her name was household, not only in Yorkshire but far beyond its boundaries. There was great satisfaction in honest endeavour and achievement. Not only did Kit become an eminent amateur botanist, but also in recent years a highly successful breeder of dogs which won prizes at shows all over the country, one of her Cardigan corgis winning a best-of-breed award at Cruft’s.

The amount of knowledge which Kit Rob disseminated during 40 years or so is inestimable, and this was particularly valuable in the case of the more critical species and aliens. She is remembered by botanists all over the British Isles for her patient, kindly and valuable help to them, especially as beginners. The effect of her influence in stimulating botanical field-work in the whole of Yorkshire is incalculable. Personally I owe her much; soon after I took up field botany seriously we became regular correspondents and there were frequent invitations to stay at Catton Hall to examine her fine herbarium or to use her extensive library. Numerous botanists, both experts and humble beginners, have enjoyed similar generous hospitality. On those special occasions when one needed the support of a staunch friend Kit was somehow reassuringly there. She also did much to enrich the life of her friends by bringing into contact those who could be mutually helpful. Arrangements have been made for her herbarium to be sent to the offices of The Yorkshire Naturalists’ Trust Ltd., 20 Castlegate, York.

A measure of the high regard and great affection with which she was held was demonstrated at the funeral service when the local parish church at Skipton Bridge was full to overflowing on a very foggy day. The B.S.B.I. was represented by David McClintock and others.

Kit Rob will be greatly missed. We were privileged to know such a unique character; her spirit of service and friendship and her great sense of humour will be remembered.

I am indebted to Dr J. G. Dony; also to Charles Rob, Mrs V. Scherdt of the Wild Flower Society and Clifford Smith of the Yorkshire Naturalists’ Trust for assistance in the preparation of this appreciation.

F. E. CRACKLES

VICTOR SAMUEL SUMMERHAYES
(1897–1974)

With the death of Victor Summerhayes on 27th December 1974, at the age of 77, the B.S.B.I. has lost a most valuable member and I have lost a personal friend of long standing. When I first went to Kew in 1928 I soon got to know Victor, who by that time was well established on the permanent staff in the Herbarium, where he was in charge of the systematic Orchidaceae section as well as the geographical Australasia and Polynesia section, both of which he was expected to run single-handed! In the following year, as general herbarium dogsbody, I was given the task of naming the extensive collection of plants from Fiji made by W. F. N. Greenwood, and so came
under Victor’s personal tuition, when I was greatly impressed not only by his thoroughness and attention to detail, but by his great patience in initiating a tiro into the finer points of taxonomy and nomenclature.

I soon found common ground with Victor in our mutual interest in ecology and it was not long before I was invited to join the team of volunteers who were working on an ecological survey of Richmond Park under W. B. Turrill. Victor was keeping most of the records of the survey, and I used to spend many enjoyable evenings in his home in West Park Avenue, Kew, helping by marking the distributions of plant species on to record maps, while Victor wrote up the notes.

Here, in Victor’s home, I soon got to know his wife, Dolly and their two boys, John and Gerald. I have very happy memories of those evenings, when the work was followed by interesting conversations and discussions and an excellent light supper provided by Dolly.

I was not to work for long on Fiji, for early in 1930 I was told I would be seconded to the Colonial Office for attachment in May to the Aerial Survey of Northern Rhodesia. Victor was interested to learn about the orchids I came across in Africa, very few in fact as the expedition was held during the dry season.

The following year I exchanged my motor cycle for a B.S.A. 3-wheeler, and I was able to take Victor into the country to study orchids. One of the most memorable of our many outings was one to Dorset when, following an early start, we met Sir Maurice Abbot-Anderson at 10 o’clock at Wareham for a conducted tour of various marsh orchid sites, ending up at Toller Porcorum. After a late tea at Beaminster we drove 135 miles back to deposit a very weary Victor at his home.

Victor was particularly interested in hybrid swarms of Dactylorhiza species and I learnt from him the technique for studying such populations, a technique I found most useful when I came across hybrid swarms of orchids and other plants in Africa.

Dolly and Victor spent much of the Second World War at Kew, when many of his colleagues were evacuated with sections of the Kew herbarium collections to Oxford or Gloucestershire. They luckily escaped injury when one of the first V2 rockets fell on the nearby Chrysler Works and shattered all the windows and brought down all the ceilings but one of their home, for the kitchen ceiling had been boarded up following an earlier bomb.

After the War, Victor started his intensive field work in preparation for his Wild orchids in Britain published in the New Naturalist series (Summerhayes, 1951). This book is packed with original observations obtained by Victor personally during this period. Trained largely as an ecologist, he paid particular attention to the nature of the habitats. He visited as many as possible of the species in the field, making notes of the plants commonly associated with each. He obtained willing help from a number of B.S.B.I. members, and became closely associated with the late Donald Young in his detailed study of Epipactis.

When the B.S.B.I. launched its mapping scheme, Victor Summerhayes joined in, and he and I spent several holidays recording in various parts of Britain, including Wales and southern Scotland. He had a very sound knowledge of the British flora, and his ecological training had enabled him to identify many plants, including a large number of grasses, from sterile material.

The highlights of Victor’s early career and of his ecological work have been well covered by Brenan (1975). I would, however, like to emphasise the tremendous amount of background work which resulted in his paper on the effect of voles on vegetation (Summerhayes, 1941). For several consecutive years he took leave in the summer and travelled by road with his friend, A. D. Middleton of the Bureau of Animal Population, Oxford, to Newcastle on in Roxburghshire and Corris in Merioneth, where he carried out, meticulously, the sampling of the vegetation in areas of upland grassland, often under most unpleasant weather conditions.

Victor Summerhayes had a delightful sense of humour, and he saw the funny side of many situations. One summer we were recording for the B.S.B.I. in a remote square in, I think, Roxburghshire, when we came across a field full of arable weeds. We had not been in it long when the farmer approached to find out who we were and what we were doing. Victor, with a surreptitious wink, put the fear of God into him by telling him we were on the staff of the Ministry of Agriculture, and so we were! The farmer was clearly worried, but did not feel he could turn us off, so we went on recording satisfactorily, whilst he went away expecting he would receive a rocket for having a field in such a neglected state. Victor thoroughly enjoyed an incident such as this.

When, early in the fifties, a large part of the only British site for Orchis simia in Oxfordshire was destroyed by ploughing, Victor was one of the volunteer conservationists who visited the
remaining part of the site one Sunday each winter to keep it clear of scrub. He took part in this annual activity organized jointly by botanists at Kew and Oxford until 1964, when he retired and went to live in Devon.

I am refraining from dealing, here, with Victor Summerhayes’ outstanding work on the African Orchidaceae. This is well covered by Peter F. Hunt in *Orchid Review* (1975). I would, however, like to mention his tremendous foresight and tenacity in starting and building up a collection of orchids and other fleshy or zygomorphic flowers and of berried fruits preserved in spirit solution. For years it was a question of putting into and getting nothing out of the collection and, with no assistant, undaunted, Victor did much of the initial labelling of the bottles and specimens himself. Time and again he resisted pressure to discontinue the collection. When I went out to Northern Rhodesia in 1937 he asked me to collect specimens in spirit, and I believe my collection from Mwinilunga was the first major Kew collection to be accompanied by material in spirit. This has now become normal collecting procedure, resulting in the Kew spirit collection being far ahead of any other such collection in the world, and in families like Orchidaceae, Asclepiadaceae and genera such as *Utricularia* the chances are that the plant one needs to study will be represented.

Victor was a small man with slight physique, but mentally always very much alive. He had a wonderful habit of gesticulating when, in conversation, he was describing the features of a particular orchid flower which he imagined before him enormously magnified! His clenched fist would be the rostellum whilst with his other hand he would outline the relative position of the pollinia and other essential parts. Another of his characteristics was his use of the word ‘svecies’ instead of ‘species’, a rather delightful pronunciation the reason for the use of which I never discovered. His wonderful botanical hat, which rivalled mine for dilapidation, had many amusing vicissitudes. More than once it parted from its owner when speeding in Donald Young’s open MG, and on one occasion it was abandoned in a pub at Carmarthen when we were staying at Haverfordwest, necessitating a return journey to Carmarthen to collect it next day. I remember one night, as I was leaving their home, Dolly commented on the disgraceful state of Victor’s hat on the hat-stand in the hall, only to dissolve into a state of acute embarrassment when I claimed the offending object!

B.S.B.I. members who consulted him always found him helpful, and he had many friends among its members. His loss will leave a gap in British botanical circles that will be hard to fill.

**REFERENCES**


E. Milne-Redhead
Reports

ANNUAL GENERAL MEETING, MAY 31st, 1975

The Annual General Meeting of the Society was held in the lecture room of the Loreburn Primary School, Dumfries, Scotland, on Saturday, 31st May, 1975 at 12 noon. 40 members were present, with Dr S. M. Walters (retiring President) in the Chair.

The minutes of the last Annual General Meeting, as published in Watsonia, 10: 321–322 (1975), were adopted unanimously.

REPORT OF COUNCIL
The adoption of the Report for the year 1974, as circulated to members, was proposed by Mr A. C. Jermy, seconded by Dr F. H. Perring and carried unanimously.

TREASURER’S REPORT AND ACCOUNTS
Mr J. E. Lousley, in supporting the Treasurer, expressed the hope that the Society would not be rushed into precipitous action in effecting economies. He felt that the Accounts showed no cause for undue despondency. The Treasurer hoped that Mr Lousley would be proved right, and the Secretary reported that the decision on any significant change in our publications had been postponed until Spring 1976 when the saving in costs through changes in format could be determined. The Treasurer reported that one Warburg Memorial Fund Award of £75 had been returned, and that a number of items on the 1974 expenditure account were non-recurring. The adoption of the Treasurer’s Report, together with the Accounts for the year 1974, was then proposed by Mr J. E. Lousley, seconded by Mrs O. M. Stewart, and carried unanimously.

INCREASE OF MEMBERSHIP SUBSCRIPTIONS
The Treasurer proposed an increase in subscriptions from 1st January, 1976, as circulated to members:

Ordinary £5 (from £3)  Family 75p (from 50p)
Junior £2 (from £1)  Subscriber £5 (from £3)

This was seconded by Miss M. Dickinson and, with some reluctance, was approved by the meeting and carried unanimously.

ELECTION OF PRESIDENT
Dr S. M. Walters from the Chair welcomed the nomination by Council of Mr E. L. Swann. This was seconded by Mr R. J. Pankhurst and unanimously carried. Mr Swann then took the Chair, expressing thanks to Dr Walters on behalf of the Society for his wise counsel and active furtherance of the Society’s aims during his Presidency.

ELECTION OF OFFICERS
The re-election of Mrs H. R. H. Vaughan, Dr W. T. Stearn and the election of Dr C. T. Prime as Vice-Presidents was proposed by Miss M. McC. Webster, seconded by Miss E. R. T. Conacher and carried unanimously. The following officers were then proposed and elected without dissent: Mrs M. Briggs Honorary General Secretary, proposed Miss E. Young, seconded Mrs A. H. Sommerville; Mr M. Walpole Honorary Treasurer, proposed Dr S. M. Walters, seconded Mr B. W. Ribbons; Dr G. Halliday, Dr N. K. B. Robson and Dr C. A. Stace Honorary Editors, proposed Mr E. F. Greenwood, seconded Dr R. W. M. Corner; and the following officers en bloc: Dr J. T. Williams Honorary Meetings Secretary, Mrs G. Beckett Honorary Field Secretary, Mrs R. Hamilton Honorary Membership Secretary, proposed Dr A. J. Richards, seconded Miss E. J. Rich. Dr C. T. Prime and Dr J. T. Williams were welcomed as new officers, and warm thanks were expressed to all officers for the great deal of work and time given to the Society’s
affairs. Particularly thanked was Mr E. F. Greenwood who retired after 9 years as an Honorary Editor.

ELECTION OF NEW MEMBERS OF COUNCIL
Nominations had been received for Professor D. H. Valentine, Mr G. Messenger, Mr B. S. Brookes and Mrs Y. Heslop-Harrison to fill the four vacancies on Council. These members were unanimously elected and their order of precedence, as given, was determined by ballot.

ELECTION OF HONORARY MEMBER
Council had recommended the election of Mrs J. G. Dony, a member of the Society since 1948 and Honorary Membership Secretary from 1964 to 1974. The President, proposing from the Chair, said this would be the first time a botanist and his wife were both Honorary Members of the Society. The nomination was seconded by Mr R. Mackechnie and carried unanimously and with pleasure by the meeting. The nomination had not been a surprise to Mrs Dony (Dr and Mrs Dony proof-read the Annual Report) and a letter of thanks if elected, sent by Mrs Dony, was read.

ELECTION OF HONORARY AUDITORS
Council’s recommendation for the re-election of Messrs Thornton Baker & Co. was proposed by Mr M. Walpole, seconded by Mr J. E. Lousley and carried unanimously. The Treasurer pointed out that auditing our accounts represented a loss of business to the auditors, and it was agreed that the Society was most grateful to them for the continuance of their valuable service.

ANY OTHER BUSINESS
Miss M. McC. Webster raised the problem of botanical communications in northern Scotland. Mr R. Mackechnie commented on the thin spread of membership in that area, and Mrs A. H. Sommerville said that the C.S.S.F. had done marvellous work in co-ordination. Some B.S.B.I. members thought that there was a lack of representation and an undertaking was given to refer this to the B.S.B.I. Co-ordinating Committee for consideration.

The Director of Education for Dumfriesshire was thanked for permission to use the school; the C.S.S.F., in particular Miss E. R. T. Conacher, C.S.S.F. Honorary Meetings Secretary, and the local botanists and friends who had helped organise the meeting were appreciatively applauded.

The meeting closed at 13.05.

M. BRIGGS

COMMITTEE FOR THE STUDY OF THE SCOTTISH FLORA

TWENTIETH ANNUAL REPORT TO 31ST DECEMBER, 1974

The Committee met twice in Perth and arranged an Exhibition Meeting at the University of Glasgow (by kind permission of the Regius Professor of Botany). 11 field meetings were included in the Scottish programme for the year.

The Exhibition Meeting was held on Saturday, 2nd November, 1974 and about 100 people were present. The following exhibits were shown: posters on plant conservation and Society activities (B.S.B.I.); Ruppia cirrhosa and other aquatic plants from Uist (Mrs J. Clark); photographs of places visited in Easternness during the C.S.S.F. survey (Miss E. R. T. Conacher); some sedges and grasses of Ireland (A. Copping); Glen Affric, 1974 (R. W. M. Corner); six species new to East Ross (Miss U. K. Duncan); mapping in 1974 of Groenlandia densa, Littorella lacustris, Myosurus mininus and Orchis morio (Miss L. Farrell); Ranunculus flammula? subsp. scoticus, other records and maps from the Glen Strathfarrar field meeting, 1974 (D. Kingston); New Zealand Epilobium spp. in Scotland, Gunnera in the British Isles and Polygonum? molle in Britain (D. McClintock); progress in and publications concerned with the C.S.S.F. Inverness-shire Survey (B. W. Ribbons); a Wardian case: an aid to plant study (Miss A. Rutherford); flower paintings and records from Kirkcudbright (Mrs O. M. Stewart); variation in frond morphology in Polypodium australis, and Rubus scoticus, a recently described bramble of the Clyde area (A. McG. Stirling); Hebridean and Icelandic plants (E. C. Wallace); the Eildon Hills: a vegetation study (Scottish
Wildlife Trust, Tweed Valley Branch). After tea, Dr S. M. Walters, Director of the University Botanic Garden, Cambridge, and President of the B.S.B.I., spoke on priorities in botanical conservation. Following a buffet supper in the University of Glasgow Refectory, colour transparencies of C.S.S.F. field meetings held in 1974 and of the meeting in Lapland in 1973 were shown by Miss E. R. T. Conacher, R. W. M. Corner, D. Kingston, R. Mackechnie, J. D. S. Martin, B. W. Ribbons, Mrs A. H. Sommerville and R. E. Thomas.

Of the 11 field meetings in the programme, two were cancelled (Strathdearn and north-western Lochaber); one (to Beinn Laoigh) was arranged on 29 June by the Alpine Botanical Secretary of the B.S.E. (for report see B.S.E. News no. 14); and the other meetings were held at Brodick, Isle of Arran, Clyde Isles (21–24 June with the Andersonian Naturalists of Glasgow) led by Mrs A. H. Sommerville (11), in Mamore Forest, Westernness (28 June–1 July) led by A. A. P. Slack (5), at Fort William, Westernness (13–20 July) led by A. A. P. Slack (8), in Glen Affric Forest, Easternness (20–27 July) led by R. W. M. Corner (4), at Tomatin, Easternness (20–27 July) led by Miss E. R. T. Conacher (3), at Kindroan Field Centre, East Perth (24–31 July) led by A. C. Jermy (11), in Glen Strathfarrar, Easternness (27 July–3 August) led by Miss E. R. T. Conacher (7), and at Fort Augustus (3–10 August) led by H. A. McAllister (5). The attendance figures are given in brackets. For reports of these meetings see Watsonia, 10: 456–462 (1975) and B.S.E. News nos 15 and 16.

The eight elected members appointed Mr G. H. Ballantyne, Dr U. K. Duncan, Mr A. A. P. Slack and Mr A. McG. Stirling as members of the committee for the calendar year 1975. Mr R. Mackechnie was appointed Chairman, Mr B. W. Ribbons Honorary Secretary, Mrs A. H. Sommerville Honorary Treasurer, Miss E. R. T. Conacher Honorary Meetings Secretary, Mr A. McG. Stirling Honorary Field Meetings Secretary and Mr R. Mackechnie a member of the B.S.B.I. Conservation and Records Committees for 1975. Mr Stirling resigned as Honorary Field Meetings Secretary in October and in December Mr B. S. Brookes was appointed to this office. The Chairman was represented at B.S.B.I. Council on 19 February and 29 October by Mr Ribbons and on 4 May by Miss Conacher. He was represented by Mr Brookes at the B.S.B.I. Conservation Committee on 26 September and by Mr Ribbons at the B.S.B.I. Records Committee on 25 January and 30 August.

The Organizing Committee for the Inverness-shire Survey met twice in 1974, in February and September; all five members attended the earlier meeting and four were present in September. Number 3 of the Inverness-shire Newsletter was issued in February. The progress of the survey was illustrated by an exhibit prepared jointly by the recorder for Easternness and the Honorary Secretary of the C.S.S.F., and mounted at the C.S.S.F. Exhibition meeting in Glasgow early in November, and again at the B.S.B.I. Exhibition meeting in London later in the same month. A working party was appointed to arrange for the publication of the results of the Survey.

The list of recorders for the Scottish vice-counties was kept under review and recommendations were made to the B.S.B.I.; no entries for the Red Data Book were received for checking during the year; a leaflet briefly outlining the aims and functions of the Committee was printed; arrangements were made for the forthcoming Annual General Meeting of the B.S.B.I. in Dumfries. Various administrative matters were discussed with the officers and councils of the parent societies.

The accounts showed a deficit of £37.90. This has been refunded in equal sums by the two parent societies who also made grants to cover the cost of printing the leaflet on the aims and functions of the Committee.

The Committee wishes to express thanks to Mr A. McG. Stirling for serving as Honorary Field Meetings Secretary 1971–74, to the officers of the parent societies, to the leaders of the field meetings and the exhibitors at the Exhibition Meeting and to other members and friends who helped the Committee during the year.

B. W. RIBBONS
FLORA OF A CHANGING BRITAIN
Edited by F. H. Perring

The Report of the 1969 Conference which reviewed factors responsible for changes in the British flora, particularly since the end of the Second World War, and endeavoured to predict other changes which might take place between the present time and the end of the century.

Topics covered included the effects on the flora of climatic changes, atmospheric and other pollution, changes in transport systems, etc.

PLANTS WILD AND CULTIVATED
Edited by P. S. Green

An account of the Conference held by the Royal Horticultural Society and the Botanical Society of the British Isles in September 1972. All the papers read at this Conference on horticulture and field botany are included.

Demy 8vo., 231 pages, with 8 half-tone plates, and figures in the text.

THE CONSERVATION OF THE BRITISH FLORA
Edited by E. Milne-Redhead

The Report of an important and most successful Conference held by the Botanical Society of the British Isles at Durham in April 1963. This report includes most of the papers read at the Conference, together with a verbatim account of the discussions that followed.

Demy 8vo., 80 pages. Bound in buckram

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Papers must be submitted in final, fully-corrected form. They should be typewritten, with wide margins, double-spaced, on one side of the paper only. If possible, two copies should be sent, of which one must be a top copy. Authors should keep a fully-corrected carbon copy of their typescripts for reference.

Write clearly and concisely, rigorously excluding extraneous matter. It sometimes helps the clarity of an argument to place extensive experimental or tabular data in appendices, rather than in the main text. Technical terms are of value only as aids to clarity, precision and conciseness of expression. Take care that they are used consistently, and defined where necessary. Ill-defined or general terms often need definition in a particular context, and can often with advantage be replaced by something more precise, as by the ‘deme’ terminology of Gilmour and Gregor in genealogy. Make certain that the main conclusions of the paper are clearly displayed to the reader.

Avoid complicated hierarchies of headings, and check carefully the consistency of those that you use; a table of contents, setting out the full hierarchy of headings with the MS. page numbers, is often helpful even if it is not to be printed with the paper. Avoid footnotes as far as possible, and keep cross references by page number to a minimum.

Tables, unless very small, should be typed on separate sheets and attached at the end of the typescript. They should be kept within a reasonable size, and as simple in structure as possible.

Keys should be in one of the generally accepted forms; Flora of the British Isles by Clapham, Tutin and Warburg (2nd ed., Cambridge, 1962) and Flora Europaea (Cambridge, 1964–72) provide suitable patterns.

Names of genera and species should be underlined, but any other typographical indications should be inserted lightly in pencil. Names of vascular plants should normally follow the List of British Vascular Plants by J. E. Dandy (British Museum (NH) and BSBI, London, 1958) and changes published in Watsonia, 7: 157–178 (1969) or Flora Europaea (Cambridge, 1964–72) and may then be cited without authorities. Otherwise authors' names must be cited, at least on the first occasion where they appear in the text and followed by the ‘Dandy' or Flora Europaea name in parenthesis. Authors must follow strictly the International Code of Botanical Nomenclature (Utrecht, 1972). Synonyms should be cited in chronological order; misapplied or illegitimate names should be placed in square brackets. Examples will be found in recent parts of Watsonia.

Except for citations of the place of publication of plant names, which may be given in abbreviated form in the text, full references should be listed in alphabetical order of authors' names at the end of the paper; the form used for references in a recent part of Watsonia should be followed carefully. Names of periodicals should be abbreviated as in the World List of Scientific Periodicals (4th ed., London, 1963–65), and references to herbaria should follow the abbreviations given in British Herbaria (BSBI, London, 1958) and Index Herbariorum Part I (5th ed., IAPT, Utrecht, 1964). Foreign language references should, where necessary, be transliterated into the roman alphabet according to a recognized convention; for Cyrillic script (Russian, etc.) the Royal Society (BS 2979: 1959) or UNESCO schemes are acceptable. Unless authors expressly indicate that they cannot get access to the necessary literature, the editors will assume that they have checked the correctness of all titles, abbreviations, transliterations and references.

Papers should begin with a short abstract, in the form of a piece of connected prose conveying briefly the content of the paper, and drawing attention to new information, new names and taxa, and the main conclusions.

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If in doubt about the citation of names or references, or the presentation of illustrations or tabular matter, contributors are advised to consult the editors before submitting their typescripts.


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Twenty-five offprints are given free to authors of papers. Further copies may be obtained at the Society’s current price, and must be ordered when the proofs are returned.

The Society as a body takes no responsibility for views expressed by authors of papers.

Papers and short notes should be sent to Dr G. Halliday, Dept. of Biological Sciences, The University, Ballrigg, Lancaster. Books for review should be sent to Dr N. K. B. Robson, Dept. of Botany, British Museum (Natural History), Cromwell Road, London, SW7 5BD. Plant records should be sent to the appropriate vice-county recorders.
Contents

RICHARDS, A. J. and SWAN, G. A. *Epipactis leptochila* (Godfery) Godfery and *E. phyllanthes* G.E.Sm. occurring in South Northumberland on lead and zinc soils ... ... ... ... 1–5

UBSDELL, R. A. E. Studies on variation and evolution in *Centaurium erythraea* Rafn and *C. littorale* (D. Turner) Gilmour in the British Isles, 1. Taxonomy and biometrical studies ... ... ... ... 7–31

UBSDELL, R. A. E. Studies on variation and evolution in *Centaurium erythraea* Rafn and *C. littorale* (D. Turner) Gilmour in the British Isles, 2. Cytology ... ... ... ... ... ... 33–43

EDEES, E. S. Notes on British *Rubi*, 4 ... ... ... ... ... ... 45–52

SCOTT, R. and GRAY, A. J. Chromosome number of *Puccinellia maritima* (Huds.) Parl. in the British Isles ... ... ... ... ... ... 53–57

DAVID, R. W. Nomenclature of the British taxa of the *Carex muricata* L. aggregate ... ... ... ... ... ... 59–65

SHORT NOTES ... ... ... ... ... ... ... ... ... ... ... ... 67–74

PLANT RECORDS ... ... ... ... ... ... ... ... ... ... ... ... 75–82

BOOK REVIEWS ... ... ... ... ... ... ... ... ... ... ... ... 83–88

OBITUARIES ... ... ... ... ... ... ... ... ... ... ... ... 89–92

REPORTS

Annual General Meeting, May 31st, 1975 ... ... ... ... ... ... 93–94

Committee for the Study of the Scottish Flora ... ... ... ... ... ... 94–95