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The Aizoaceae naturalized in the British Isles

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ABSTRACT

An introduction is given to the Aizoaceae with particular emphasis on the subfamilies Mesembryanthemoideae and Ruschioideae. It is followed by a detailed account of the complicated floral parts and fruits of the species of these groups. A conspectus of the subfamilies and genera naturalized in the British Isles is followed by a key to the species. Accounts of the nomenclature, typification, morphology, distribution, habitat and reproductive biology of *Aptenia cordifolia* (L.fil.) Schwantes, *Ruschia caroli* (L. Bolus) Schwantes, *Lampranthus roseus* (Willd.) Schwantes, *L. falciformis* (Haw.) N.E.Br., *Oscularia deltoides* (L.) Schwantes, *Disphyma crassifolium* (L.) L. Bolus, *Drosanthemum floribundum* (Haw.) Schwantes, *Erepsia heteropetala* (Haw.) Schwantes, *Carpobrotus edulis* (L.) N.E.Br. var. *edulis*, var. *rubescens* Druce, var. **chrysophthalmus** C. D. Preston & P. D. Sell, **var. nov.**, and *C. glaucescens* (Haw.) Schwantes, follow. An Appendix by R. D. I'Ons gives the chromosome numbers.

INTRODUCTION

The Aizoaceae are a large family, with their centre of distribution in South Africa (Rowley 1978). Two of its component subfamilies, the Mesembryanthemoideae and the Ruschioideae, are sometimes removed as a separate family, the Mesembryanthemaceae. All the species in these two subfamilies were once included in the genus *Mesembryanthemum* L., but have since been divided into as many as 125 genera which contain about 2000 species (Rowley 1978).

South African Aizoaceae have long been cultivated in British gardens. A detailed account of the botanical exploration of South Africa is given by Gunn & Codd (1981). Although Bartolomeu Dias rounded the Cape of Good Hope in 1488, it was not until 1605 that any plant specimen from South Africa was described in print. Live bulbs were collected from the beginning of the 17th century and increasing numbers of plants from South Africa, including some 'mesembs', were introduced by the Dutch in the second half of that century. James Petiver received live material of the Aizoaceae from the Temple Garden, London, in 1706 (Edwards 1968). The collection grown by James Sherard at Eltham in Kent was illustrated by Dillenius (1732) in the important *Hortus Elthamensis*, which provides an almost complete coverage of the 'mesembs' then known in cultivation (Gunn & Codd 1981). There is at Oxford, in the library of the Department of Plant Sciences, a copy coloured by Dillenius himself. We have also seen a similarly coloured copy in a private collection.

Two botanists are pre-eminent in the interpretation of early 'mesemb' names. Adrian Hardy Haworth (b. 1768, d. 1833) described 206 species in his *Synopsis* (Haworth 1812). His descriptions were based on living plants, including many grown by himself as well as some in the collections at Kew. His herbarium was bought by H. B. Fielding, who threw most of the specimens away. Fortunately, a great many coloured drawings were made by George Bond and Thomas Duncannon between 1822 and 1835 of the plants Haworth had seen at Kew (Brown 1920), and these are available for selection as neotypes. In the facsimile of all Haworth's works on succulent plants, Stearn (1965) has written an informative introduction.

Prince Salm-Dyck (b. 1773, d. 1861) was an enthusiastic cultivator and student of succulent plants. His most important work is the *Monographia Generum Aloes et Mesembryanthemi*, published in seven parts (Salm-Dyck 1836–1863). It is a collection of lithographed and partly hand-coloured plates accompanied by Latin descriptions. A detailed account of the work has been published by Stearn (1938).

A number of 'mesembs' have become naturalized by the sea in the British Isles, and these are described in this paper. We regard species as naturalized if they are established in semi-natural vegetation. It is not necessary that a species should reproduce by seed to satisfy this criterion, although some of the naturalized species certainly do so. The extent to which the individual species are naturalized is discussed in the accounts that follow.

The localities where 'mesembs' are naturalized are all coastal. The species' tolerance of salt-laden gale-force winds enables them to grow very close to the sea, where the microclimate is most equable. In such positions naturalized colonies often escape low winter temperatures which severely damage or kill plants of the same species growing in gardens a short distance inland. Even if extensively damaged, colonies can regrow from vegetative parts or seed (Preston 1988).

Lousley (1973) regarded the naturalized Aizoaceae as "plants dependent on a run of mild winters and deliberate planting". We consider that this underestimates their ability to persist and spread. *Carpobrotus edulis*, in particular, is now a characteristic feature of the seaside landscape in many parts of south-western England. Betjeman (1945) mentions it growing with stonecrop on a Cornish cliff in his poem *Sunday Afternoon Service in St Enodoc Church, Cornwall* and Rowse (1941), describing Henry VIII's castle at St Mawes, says "it remains unchanged, the walls of its three-lobed batteries but weathered to a silver grey, the grass slopes covered with mesembryanthemum and rock-plants down to the edge of the water". Flowers of *Carpobrotus* and plants of *Lampranthus* are featured on picture postcards and sometimes protected by wild-flower lovers. This protection is unnecessary: *Carpobrotus* competes so effectively with native species that its continued spread is a source of anxiety to conservationists (Hopkins 1979; Frost 1987).

TAXONOMY OF THE AIZOACEAE

Commenting on attempts to identify one naturalized species, J. P. M. Brenan (*in litt.* to L. J. Margetts 1970) wrote that "one would have to be a magician to give it a name . . . the whole family is in a state of chaos". Four factors have contributed to this unhappy state of affairs:

i. Many of the species were originally described from material cultivated in European gardens. The precise origin of the cultivated stock was not known, so the names are difficult to relate to plants in their native habitats. Often type specimens were not preserved, or have not survived.

ii. Herbarium specimens of these succulent plants are difficult to identify, as leaf shape and flower colour are destroyed when the plant is pressed and dried. Pressed specimens can often be identified only to generic level. Even if type specimens exist they are often of little use. Good coloured illustrations, or photographs, are more useful than specimens. For this reason we have selected illustrations as lectotypes when they are available.

Recently Fuller & Barbe (1981) have described a method of pressing succulent plants, including *Carpobrotus edulis*, using a microwave oven. We have not experimented with this technique.

iii. Although many enthusiasts have studied the 'mesembs', their efforts have been devoted to the description of more and more new species. H. M. L. Bolus alone described 1445 species but "she did not regard all these as true new species" (Herre 1971). Descriptions of new taxa have rarely been accompanied by a key or a conspectus to the species in the genus, and few generic monographs are available.

iv. Very little is published about the ecology, reproductive biology and cytology of 'mesemb' species. Within genera or closely related groups of species the taxa seem to be either geographically or ecologically isolated, and it is not known if they are interfertile. In the absence of this information, it is impossible to interpret the described taxa biologically.

Lousley's (1971, 1973) studies of the Aizoaceae naturalized in the Isles of Scilly are the most valuable published accounts of the British species. McClintock's (1975) and le Sueur's (1984) studies of the Channel Island species are also useful. Recently Kent (1982) listed the species reported from the British Isles.

METHODS OF STUDY

Initially we collected living material of the Aizoaceae naturalized in the British Isles and grew this in a greenhouse at Cambridge University Botanic Garden. Descriptions were first prepared from these cultivated plants, then compared in the field with wild populations. It was necessary to modify the descriptions of cultivated material both because plants grown in the greenhouse lacked the vigour of plants in the wild, and because of the greater environmental variation present in wild populations. The cultivated plant material was used to count the chromosome numbers of the naturalized species (see Appendix).

Some herbarium specimens, and a larger number of colour photographs, have been deposited in **CGE**. Full details of all records available to us have been deposited at the Biological Records Centre, Monks Wood Experimental Station.

We are conscious that our work is only a preliminary contribution to the elucidation of the taxonomy and nomenclature of the species naturalized in Britain. In particular, further work on the British species of *Lampranthus* is needed. However, we believe that progress is more likely to result from studies of the taxa in their native habitats rather than from more intensive studies of the species in Britain.

MORPHOLOGY OF FLOWERS AND FRUIT

Some authors treat the outer perianth segments as sepals, while others consider them to be the divided part of the calyx. The latter view is taken here and they are regarded as calyx lobes. They are very unequal in size and some of them usually have wide scarious flaps which cover the petals in bud. The petals and stamens are usually situated between the point where the segments join the remainder of the calyx and the top of the half-inferior ovary. The whole arrangement is similar to the hypanthium in the Rosaceae.

The inner perianth segments are usually considered to be derived from stamens. They are here called petals and include those inner ones that are often narrower and smaller than the outer. Only when they are in the form of stamens, but without anthers, are they called staminodes. There is sometimes a graded sequence between stamens and petals, both in form and colour. In *Aptenia cordifolia* the petals are united at the base to form a short corolla tube; the stamens arise from this tube. The nectaries are sunk in a hollow around the rim of the ovary. In the other species naturalized in Britain the petals are free, and the nectaries form a slight crest around the rim of the ovary.

The capsules of the Aizoaceae are extremely complicated in structure. An illustrated survey is given by Schwantes (1957). In most species growing in the British Isles the capsule is hygrochastic, i.e. it opens when it becomes moist and closes when it dries out again. In the simplest case (*Aptenia*) the capsule has axile placentation with open loculi, so that raindrops can easily wash out the seeds. In the tribe Ruschieae the capsules are much more complex and the placentation is parietal. There are five loculi and partition walls. The lid of the capsule is opened and closed by the expansion of the epidermal lining of the loculus when it becomes wet. The cells of expanding tissue have a rhomboidal shape, the inner shorter axis elongating considerably while the outer longer axis remains almost unchanged. The result is a pronounced elongation of the expanding tissue in one direction while the remaining tissues of the capsule do not change appreciably, thus causing the valves to unfold outwards. In some species a membrane covers the loculi so that the seeds are not exposed when the capsules open. The membranes are elastic and are never found in the middle of the loculus. The division is always brought about by the valve wings which are formed by the splitting of the false septum which projects into the loculus from above. The valve wings always remain firmly attached to the valve. When the capsule opens for the first time they act like the rip-cords of a parachute and bring about the exact division of the parts of the covering membrane. The membrane never covers the loculus completely, as a portion of the endocarp on the roof of the loculus is required for the formation of the expanding mechanism. The opening remaining is sometimes reduced to two minute openings by a swelling of the placenta (tubercle).

SYNOPSIS OF THE CLASSIFICATION OF THE BRITISH GENERA

In the synopsis below we follow the classification proposed by Schwantes (1971) for the Mesembryanthemaceae. Unless otherwise stated, the number of species per genus is taken from Herre (1971). Critical revision of the larger genera would almost certainly reduce the number of recognized species considerably.

SUBFAMILY MESEMBRYANTHEMOIDEAE

Nectaries sunken in a hollow. Placentation axile.

Tribe Aptenieae

Petals soft, not rigid.

Aptenia N.E.Br. in *Gdnrs' Chron.*, ser. 3, **78**: 412 (1925). Holotype species: *A. cordifolia* (L. fil.) Schwantes, cf. *J. Bot., Lond.* **66**: 139 (1928). Number of species: 2.

SUBFAMILY RUSCHIOIDEAE

Nectaries forming a slight crest round the rim of the ovary. Placentation parietal.

Tribe Ruschieae

Fruit a dry hygrochastic capsule with numerous seeds.

Ruschia Schwantes in *Z. SukkulKde* **2**: 186 (1926). Holotype species: *R. rupicola* (Engler) Schwantes. Number of species: c. 350.

Lampranthus N.E.Br. in *Gdnrs' Chron.*, ser. 3, **87**: 71 (1930). Holotype species: *L. multiradiatus* (Jacq.) N.E.Br. Number of species: 178 according to Herre (1971), 56 according to Glen (1980).

Oscularia Schwantes in *Möllers dtsch. Gärt.-Ztg* **42**: 187 (1927). Holotype species: *O. deltoides* (L.) Schwantes. Number of species: 1 (Glen 1986).

Disphyma N.E.Br. in *Gdnrs' Chron.*, ser. 3, **78**: 433 (1925). Lectotype species: *D. crassifolium* (L.) L. Bolus, chosen by L. Bolus in *Fl. Pl. S. Afr.* **7**: t. 276 (1927). Number of species: 5 or 1 (see below).

Drosanthemum Schwantes in *Z. SukkulKde* **3**: 14, 29 (1927). Holotype species: *D. hispidum* (L.) Schwantes. Number of species: c. 95.

Erepsia N.E.Br. in *Gdnrs' Chron.*, ser. 3, **78**: 433 (1925). Lectotype species: *E. inclaudens* (Haw.) Schwantes, chosen by N. E. Brown in E. P. Phillips, *Gen. S. Afr. Fl. Pl.* 248 (1926). Number of species: 38.

Tribe Carpobroteae

Fruit fleshy, indehiscent, the outer wall becoming tough and leathery, the seeds embedded in mucilage.

Carpobrotus N.E.Br. in *Gdnrs' Chron.*, ser. 3, **78**: 433 (1925). Lectotype species: *C. edulis* (L.) N.E.Br., chosen by N.E. Brown in E.P. Phillips, *Gen. S. Afr. Fl. Pl.* 249 (1926). Number of species: 29.

KEY TO SPECIES NATURALIZED IN THE BRITISH ISLES

1. Leaves flat, ovate; petals connate at base, forming a short tube; calyx lobes and stigmas 4 .... 1. *Aptenia cordifolia*
1. Leaves triangular, cylindrical or rarely narrowly obovoid in section; petals free; calyx lobes (4–)5–6; stigmas 5 or 10–14 2

2. Leaves ± dentate on at least one of the angles 3

2. Leaves not dentate on the angles 4

3. Leaves broadly triangular-obovoid in outline, deltate in section, less than twice as long as broad; petals exceeding calyx lobes; stigmas narrowly ovoid with curved apex .... 5. *Oscularia deltoides*

3. Leaves asymmetrically oblanceolate in outline, triangular in section, at least twice as long as broad; petals shorter than calyx lobes; stigmas small, roundish in outline .... 8. *Erepsia heteropetala*

4. Stems with numerous hairs; leaves cylindrical or narrowly obovoid, covered with glass-like tubercles .... 7. *Drosanthemum floribundum*

4. Stems glabrous; leaves ± triangular in section, not covered with glass-like tubercles 5

5. Leaves in groups of 3–10, narrowly linear-lanceolate or linear-oblanceolate in outline, with a row of almost flat papillae on the angles; stigmas ending in a long awn .... 6. *Disphyma crassifolium*

5. Leaves not obviously in groups of 3–10 and some obviously decussate, without flat papillae on the angles; stigmas plumose or long-acute but not ending in a long awn 6

6. Leaves 1·5–5·0 mm wide; flowers 10–50 mm in diameter; stigmas 5; fruit a dehiscent capsule 7

6. Leaves 5–15 mm wide; flowers 35–90 mm in diameter; stigmas 10–14; fruit fleshy and indehiscent (*Carpobrotus* spp.) 9

7. Leaves 15–70 × 2–5 mm; stigmas long-acute at apex .... 2. *Ruschia caroli*

7. Leaves 6–24 × 1·5–4·5 mm; stigmas plumose (*Lampranthus* spp.) 8

8. Most stems and branches erect; leaves 10–16 × 2·0–2·5 mm in cultivation, rather dark bluish-green .... 3. *Lampranthus roseus*

8. Most stems and branches prostrate; leaves 6–13 × 1·5–2·5 mm in cultivation, taken as a whole shorter and fatter, markedly pruinose .... 4. *Lampranthus falciformis*

9. Petals yellow, tinged pink when old .... 9a. *Carpobrotus edulis* var. *edulis*

9. Petals mainly purple, orange-pink or reddish-purple 10

10. Petals pale to deep purple throughout .... 9b. *Carpobrotus edulis* var. *rubescens*

10. Petals purple, orange-pink or reddish purple with obvious white or yellow bases 11

11. Petals pale orange-pink, pale reddish purple or pale purple .... 9a × b. *Carpobrotus edulis* inter var. *edulis* et var. *rubescens*

11. Petals deep purple 12

12. Leaves (20–)35–125 × 5–15 mm; base of petals yellow; filaments yellow with whitish bases .... 9c. *Carpobrotus edulis* var. *chrysophthalmus*

12. Leaves 20–70 × 5–8 mm; base of petals white; filaments whitish, sometimes with a little yellow at apex .... 10. *Carpobrotus glaucescens*

ACCOUNT OF SPECIES

1. **Aptenia cordifolia** (L. fil.) Schwantes in *Gartenflora* **77**: 69 (Feb. 1928); N.E.Br. in *J. Bot., Lond.* **66**: 139 (May 1928).

Mesembryanthemum cordifolium L. fil., *Suppl.* 260 (1781). Described from the Cape of Good Hope. NEOTYPE: Salm-Dyck, *Monogr. Aloes Mesembr.* **61**: fig. 1 (1842), designated here.

Litocarpus cordifolius (L. fil.) L. Bolus in *Fl. Pl. S. Africa* **7**: sub. t. 261 (1927).

Vernacular names: Heart-leaf Ice-plant, Heart-leaf Mesembryanthemum.

Illustrations: Herre, *Gen. Mesembr.* 79 (1971); Salm-Dyck, *Monogr. Aloes Mesembr.* **61**: fig. 1 (1842), pro *Mesembryanthemum cordifolium*; Bichard & McClintock, *Wild Fl. Channel Is.* no. 87 (1975).

Description: Rather succulent, short-lived perennial, but not infrequently behaving as an annual. Stems up to 60 cm, pale yellowish-green, sometimes tinted brownish and angled, prostrate, much-branched, covered with dense greyish papillae; internodes 1·2–9 cm. Leaves 10–35 × 10–30 mm, green, decussate, flat, more or less ovate, obtuse to subacute at apex, entire, more or less cordate, truncate or cuneate at base, covered with greyish papillae; petiole up to 15 mm. Flowers solitary, 5–16 mm in diameter, terminal at the end of branches or axillary; peduncles up to 13 mm, sometimes 5-angled. Calyx green, covered with greyish papillae; lobes 4, the 2 outer 10–15 × 4–13 mm, ovate to narrowly ovate, subobtuse to acute at apex, slightly to distinctly keeled and curved outwards, entire, the inner 5–10 × 2–6 mm, lanceolate or linear-lanceolate, obtuse to acute at apex, entire, curved outwards. Petals numerous, 3–7 mm, reddish-pink, linear or linear-oblanceolate, obtuse at apex, united at the base into a short tube. Stamens numerous, arising from the corolla tube in a mass; filaments 2–3 mm, whitish, glabrous; anthers cream. Staminodes numerous, 2–3 mm, whitish, forming a ring between the stamens and the corolla tube. Stigmas 4, greenish, small, sessile. Nectaries sunken in a hollow. Capsule 12–15 × 8–10 mm, green, 4-locular, obovoid, valves broader than long, with the apex so abruptly thickened that the basal termination of the thickening is quite vertical, middle of inner surface of the 4 valves with a bright yellow keel reaching from the central column to the end of the flat part, each keel consisting of 2 parallel ridges, without marginal wings or flaps, with 4 narrow strips arranged like a star between the central column and the point of origin of keels; loculi roofs and tubercle absent; placentation axile. Seeds c. 40, 1·0–1·2 × 1·0–1·2 mm, dark reddish-brown, subrotund or broadly ovate, compressed, tuberculate, with funicles up to 1 mm. $2n = 18$.

Nomenclature and typification: There are no specimens in the Linnaean herbarium (**LINN**) and no additional references in the protologue. The name has always been applied to the same taxon and the Salm-Dyck illustration is chosen here as the neotype, and reproduced as Fig. 1.

Taxonomy and variation: Le Sueur (1984) has noted that in Jersey a single plant at Grouville differed from a large population at St Brelade in colour, leaf shape and flower size. Otherwise little variation is recorded in naturalized populations except in plant size. A variegated form is sometimes grown in gardens.

Reproductive biology: Flowers from May to August. Reproduces by seed. Poorly grown plants are said to behave as annuals, dying after they have produced seed, but we have no observations on the reproductive biology of the species in the British Isles. Some, but not all, populations in Jersey failed to survive the severe 1962–63 winter (le Sueur 1984).

Distribution and habitat: Naturalized on banks and stone walls on Bryher, St Martin's and St Mary's, Isles of Scilly, and on Guernsey and Jersey. A large population in Jersey is naturalized under coniferous trees. Recorded as a casual on rubbish tips in W. Kent and Herts.; it perhaps occurs elsewhere in such localities. According to Higgins (1956), *Aptenia* was first introduced into British gardens in 1774. It was recorded in Guernsey in 1928, but there were no subsequent records until naturalized populations were discovered in Jersey in the early 1950s and on St Mary's, Isles of Scilly, in 1956. Although it is thoroughly established in some localities, *Aptenia* has not invaded semi-natural habitats to the same extent that *Carpobrotus* and *Disphyma* have done. It is a native of the eastern coastal districts of Cape Province, South Africa (Herre & Friedrich 1959).

2. **Ruschia caroli** (L. Bolus) Schwantes in *Z. SukkulKde* **3**: 20 (1927).
Mesembryanthemum caroli L. Bolus in *Ann. Bolus Herb.* **3**: 129 (1922). Described from living plants in the Kirstenbosch Botanic Garden and in Dr C. Juritz's garden at Three Anchor Bay, Cape Town, South Africa. Not typified.

Description: Low, spreading shrub, up to 60 cm. Stems up to 60 cm, much branched from the base upwards, greyish-brown or reddish-brown with darker brown elliptical spots, straight and ascending or decumbent, irregularly striate or ridged, glabrous; internodes 1–3 cm. Leaves 15–70 × 2–5 mm, rather unequal in size, more or less erect, bluish-green, faintly pink at apex, loosely decussate with each pair with a connate base enclosed in a brown sheath, linear in outline, 3-angled, sometimes recurved, obtuse or subacute at apex, sessile, covered with green spots and smaller white dots when young, becoming irregularly muriform when mature. Flowers 1–4, 10–30 mm in diameter, terminal

FIGURE 1. *Aptenia cordifolia* (L.fil.) Schwantes, illustrated as *Mesembryanthemum cordifolium* in Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi* **61**: fig. 1 (1842). The coloured plate is the neotype of *M. cordifolium* L. fil.

at the end of branches; peduncles 10–25 mm. Calyx pale green; lobes 5, 3·5–4·0 × 2·0–2·5 mm, triangular-ovate, 2 with a pale narrow margin and subacute at apex, 3 with a broad scarious flap and a reddish subacute apex. Petals c. 30, 4·5–10·0 × 1–2 mm, free, purplish, with a darker central longitudinal line and slightly whitish at base, narrowly oblanceolate, obtuse and entire at apex. Stamens numerous, some outer without anthers; filaments 3–3·5 mm, purplish with white bases, with numerous, pale, slightly clavate hairs at base; anthers yellow. Stigmas 5, green, narrowly triangular-ovoid with a long acute apex and a few hairs near the base. Nectary glands united to form a crenulate ring round the ovary. Capsule not seen in British material, but said to have much diverging valve keels; loculi roofs present with a large tubercle; placentation parietal. We cannot trace a description of the seeds. 2n = 18.

This description is based solely on plants from a naturalized population cultivated in Cambridge. We have not had an opportunity to compare it with plants in the field.

Taxonomy and variation: Little variation has been recorded in our naturalized populations, but in South Africa the species seems to produce much larger leaves than in Britain.

Reproductive biology: Flowers in April and May. We have no observations on the reproductive biology of the species in the British Isles.

Distribution and habitat: Only recorded from the Isles of Scilly, where it is naturalized on walls on St Mary's and Tresco. The only record from semi-natural habitats is a note by Lousley on a specimen in **RNG** that *Ruschia* occurs "in 'wild' places or rocks" at Carn Friars, St Mary's, Isles of Scilly. Lousley (1971) says that there is a specimen in **K** sent from Tresco Abbey in 1897, nearly 30 years before the species was described. The first collection from a naturalized population was made in 1959. *Ruschia caroli* is a native of Cape Province, South Africa.

3. **Lampranthus roseus** (Willd.) Schwantes in *Reprium nov. Spec. Regni veg.* **43**: 230 (1938).
Mesembryanthemum roseum Willd., *Enum. Pl. Horti Berol.* 535 (1809). Described from the Cape of Good Hope. Not typified.

Vernacular name: Rosy Dew-plant.

Illustrations: Marloth, *Fl. South Africa* **1**: pl. 53A (1913); Salm-Dyck, *Monogr. Aloes Mesembr.* **29**: fig. 4 (1849), pro *Mesembryanthemum roseum*; Polunin, *Flowers Med.* t. 12 (1965).

Description: Low evergreen shrub. Stems up to 20 cm, decumbent to erect, 4-angled, glabrous, brownish or purplish, much branched, the branches short, ascending or patent; internodes 0·3–3·5 cm, sometimes with narrow wings on the angles. Leaves 10–16 × 2–2·5 mm, decussate just under the flowers, becoming more numerous and dense lower down the fertile stems and branches and on the sterile stems and axillary shoots, the terminal pairs on axillary sterile shoots often pressed together giving a flattened appearance, dark glaucous green, mostly triangular in section with fairly acute angles, more or less acute at apex and sometimes red-tipped, rounded at the sessile base with each pair touching in their upper part and together encircling the stem, covered with dense pellucid dots. Flowers 1–3 together, terminal or at the end of lateral shoots, 20–50 mm in diameter; peduncles 12–20 mm. Calyx with dense pellucid dots; lobes 5, all red-tipped; 2 of the lobes 5–7 mm, triangular-lanceolate, acute at apex, green (darker towards apex) with a scarious margin up to 0·5 mm wide in the lower half; remaining 3 lobes with a green part similar to the other 2 but with a deep rusty orange, subapical, often asymmetrical appendage up to 3 mm wide on the inner side and extending to the base where it is joined to that of the next lobe, the true apex of the lobe reflexed. Petals numerous (over 100), very variable in length, 6·5–18·0 × 0·4–2·0 mm, free, shining light purple or salmon pink sometimes on same plant, inner short and narrowly linear becoming gradually larger to outer which are narrowly linear-oblanceolate, obtuse at apex, broader ones slightly emarginate, with pale lines on back. Stamens numerous (100–150), more or less as long as stigmas; filaments 3–4 mm, pale greenish-yellow; anthers yellow. Stigmas 5, greenish, outline more or less triangular and formed from 3 plumose rays. Nectary glands united to form a crenulate ring round the ovary. Capsule 6–7 × 7–8 mm, 5-locular, each valve with diverging keels and a membranous wing; loculi roofs present, without a tubercle; placentation parietal. Seeds numerous, 1·0 × 1·2 mm, pale brown, obovoid, with shallow, obtuse tubercles. 2n = 36.

The above description is based on material cultivated at Cambridge from Bec du Nez, Guernsey, and Lizard Head.

Taxonomy and variation: We find the taxonomy of *Lampranthus* difficult and unsatisfactory. The two species accepted here looked quite different when grown side by side in the Cambridge Botanic Garden, but their differences were very difficult to put into words. In the wild differences tend to be masked by phenotypic variation. Thus the plant of *L. roseus* illustrated by Bichard & McClintock (1975) seems to have the habit and leaves of *L. falciformis*. *L. roseus* shows considerable variation in flower colour, purple and pink flowers occasionally occurring on the same plant.

Reproductive biology: Most *Lampranthus* species are thought to be self-sterile. *L. roseus* flowers from late May to July. Seedlings have been seen at Portelet Bay, Jersey, at Beaucette and Bec du Nez, Guernsey, and at Poldhu Cove. Some plants in the Lizard Point population were killed by frost in the 1978–9 winter and all *Lampranthus* plants in Jersey were killed in the 1962–3 winter, but reappeared from seed. Seed collected at Lizard Point, Cornwall and Bec du Nez, Guernsey germinated freely.

Distribution and habitat: Naturalized on sea cliffs, coastal rocks and walls in several localities in Guernsey and also collected from Alderney, Herm and Sark. In W. Cornwall naturalized on cliffs at Lizard Point and Poldhu Cove. A *Lampranthus* naturalized on cliffs by Beau Port and on an artificial scree of stone blocks at Portelet Bay, Jersey, is probably also referable to this species. The earliest collection was made in Sark in 1924. Native of South Africa.

4. **Lampranthus falciformis** (Haw.) N.E.Br. in *Gdnrs' Chron.*, ser. 3, **87**: 212 (1930).
Mesembryanthemum falciforme Haw., *Syn. Pl. Succ.* 299 (1812). Described from a specimen grown in a London garden. NEOTYPE: coloured illustration made between 1822 and 1835 from the plants on which Haworth worked (**K**), designated here.

Vernacular name: Sickle-leaved Dew-plant.

Illustrations: Salm-Dyck, *Monogr. Aloes Mesembr.* **29**: fig. 1 (1836), pro *Mesembryanthemum falciforme* (reproduced here as Fig. 2).

Description: Low evergreen shrub. Stems up to 80 cm, mostly spreading and prostrate, but a few erect, 4-angled, glabrous, greyish or brownish, much-branched, the branches short, ascending or patent; internodes 0·2–1·7 cm, sometimes with narrow wings on angles. Leaves 6–13 × 1·5–2·5 mm, decussate just under the flowers, becoming more numerous and dense lower down the fertile stems and branches and on the sterile stems and axillary shoots, the terminal pairs on the axillary shoots often pressed together giving a flattened appearance, pale bluish-green with thick waxy covering, half obovoid, flattened on one surface and rounded and keeled on the other making them more or less triangular in section, more or less acute and sometimes with a red dot at apex, semi-connate at the sessile base, covered with dense pellucid dots. Flowers 1–2 together, terminal or at the end of lateral shoots, 35–45 mm in diameter; peduncles 5–20 mm. Calyx with dense pellucid dots; lobes 5, all red-tipped; 2 of the lobes 5.0–10.5 mm, triangular-lanceolate, acute at apex, green with a scarious margin up to 0·5 mm wide in the lower half; remaining 3 lobes with a green part similar to the other 2, but with a subapical, often asymmetrical appendage up to 3 mm wide on the inner side and extending to the base where it is joined to that of the next lobe, the true apex of the lobes reflexed. Petals numerous, very variable in length, 6·5–21·0 × 0·4–2·5 mm, free, pale pink, the inner very pale, or purple, narrowly linear, becoming gradually larger to outer which are narrowly linear-oblanceolate, obtuse at apex, broader ones slightly emarginate, with pale lines on back. Stamens numerous, more or less as long as stigmas; filaments 3–4 mm, whitish, with a tuft of whitish hairs at base; anthers pale yellow. Stigmas 5, greenish, outline more or less triangular and

FIGURE 2. *Lampranthus falciformis* (Haw.) N.E.Br., illustrated as *Mesembryanthemum falciforme* in Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi* **29**: fig. 1 (1836).

formed from 3 plumose rays. Nectary glands united to form a crenulate ring. Capsule 6–7 × 7–8 mm, 5-locular, each valve with diverging keels and a membranous wing. Seeds numerous, 1·0–1·2 mm, pale brown, obovoid, with shallow, obtuse tubercles.

The above description is based on plants cultivated at Cambridge from Pembrokeshire and St Mary's, Isles of Scilly.

Nomenclature and typification: The obvious neotype is the coloured drawing at Kew made from plants on which Haworth worked.

Taxonomy and variation: The only variation noted is in flower colour which varies from pale pink to purple.

Reproductive biology: Most *Lampranthus* species are thought to be self-sterile. *L. falciformis* flowers from May to July. It is very susceptible to frosts and there may be little or no flowering after a bad winter, but some parts of the plant usually survive and soon regenerate vegetatively. At The Gann, Pembrokeshire, it normally regenerates abundantly from seed. It seems to be immune from grazing by cattle and rabbits (Davis 1978).

Distribution and habitat: Supposedly introduced into British gardens in 1805 (Higgins 1956). There are specimens in **K** from Tresco Abbey Gardens in the Isles of Scilly collected in 1895. It is now naturalized on St Mary's, Tresco, St Martin's, St Helen's and Round Island in those islands, growing on coastal rocks, cliffs and stone walls near the sea in shallow soil on ledges and in crevices. Both St Helen's (where it is particularly abundant) and Round Island are uninhabited and the *Lampranthus* was presumably carried there by sea birds. It was collected on Lundy (**K**) as naturalized in 1908 and 1911. It was planted in a long disused quarry at The Gann, St Ishmael, Pembrokeshire in 1919 and 30 or more plants still occur on the almost perpendicular face of a natural rock outcrop of rhyolite. In the 1920s or early 1930s it was introduced from this quarry to Dale Point, 2 km south of The Gann, where a few plants were still present in 1978 (Davis 1978). Plants from Three Castle Head, W. Cork, and on sandy cliffs at Roches Point, E. Cork, are probably referable to this species. Native of South Africa.

5. **Oscularia deltoides** (L.) Schwantes in *Möllers dtsch. Gart.-Ztg* **43**: 187 (1927).

Mesembryanthemum deltoides L., *Sp. Pl.* 482 (1753). Described from Africa. Lectotype: Dillenius, *Hort. Eltham.* 255, t. 195, fig. 246 (1732), pro *Mesembryanthemum deltoides, & dorso, & lateribus muricatus, minus*, in the copy in the Department of Plant Sciences, Oxford University, coloured by Dillenius; designated here.

Lampranthus deltoides (L.) Glen ex D. O. Wijnands, *Bot. Commelins* 148 (1983), comb. invalid., basion. non cit.

Lampranthus deltoides (L.) Glen in *Bothalia* **16**: 55 (1986).

Vernacular name: Deltoid-leaved Dew-plant.

Illustrations: Salm-Dyck, *Monogr. Aloes Mesembr.* **30**: fig. 3 (1840), pro *Mesembryanthemum muricatum*; Herre, *Gen. Mesembr.* 245 (1971); Lousley, *Fl. Scilly* 216, fig. 10 (1971).

Description: Low, sprawling shrub. Stems up to 50 cm, ascending or decumbent, glabrous, when young bluish-green, heavily tinged reddish, soon becoming reddish- or orange-brown, older growth woody, terete or slightly angled, glabrous, with short, erect or patent branches; internodes 0·2–2·5 cm, often with narrow wings on the angles. Leaves 6–18 × 3–10 mm, unequal or more or less equal in size, pruinose with a pinkish-red apical point and apices of teeth, waxy, in decussate, clustered pairs with each pair slightly connate at base, smooth, 3-angled, widest towards the shortly acute apex, narrowed towards the sessile base, dentate-apiculate on the angles. Flowers 1–3 together, 12–18 mm in diameter, terminal at the ends of branches, almond-scented; peduncles 2–3 mm. Calyx yellowish-green; lobes 5, 3·0–3·5 × 2–3 mm, triangular-ovate, 2 with a pale, narrow margin and up to 4 pinkish-red points at the apex, 3 with a broad scarious flap and a subapical, pinkish-red tipped point. Petals 40–50, 4–6 × 0·5–1·5 mm, free, purplish, paler towards the base, narrowly oblanceolate, obtuse and entire at apex. Stamens numerous, some outer without anthers; filaments 2–3 mm, white with rather pale simple eglandular hairs at base; anthers yellow. Stigmas 5, green, narrowly ovoid with a curved apex. Nectary glands forming a crenulate ring round the ovary but in 5 distinct groups, dark green. Capsule 6–7 × 5–6 mm, 5-locular, obovoid; each valve with expanding narrowly winged keels diverging from the base and half as long as the valves; loculi roofs present, without a tubercle; placentation parietal. Seeds 1·0–1·2 mm, nearly black, ovoid or pyriform with a nipple, minutely tuberculate, on a funicle up to 2 mm. 2n = 18.

The above description of flowers and fruit is based on plants from a naturalized population cultivated in Cambridge. We have not had an opportunity to compare it with plants in the field.

Nomenclature and typification: *Mesembryanthemum deltoides* was described by Linnaeus (1753) in *Species Plantarum*. His diagnosis *Mesembryanthemum caulescens, foliis deltoidibus triquetris dentatis* is taken from the *Hortus Cliffortianus* (Linnaeus 1738) without change. There are no specimens in the herbarium of the Hortus Cliffortianus (**BM**), nor in the Linnaean Herbarium in London (**LINN**). Two synonyms follow the diagnosis: *Mesembr. deltoides & dorso & lateribus muricatis* Dill. *elth*. 255. t. 195. f. 246 and *Ficus aizoides africana erecta folio triangulari breviusculo, fimbriato, floribus roseis odoratis* Volk. *hesp*. 223. t. 224. f. 5. They are also cited in the *Hortus Cliffortianus*. Both illustrations are referable to the plant usually called *Oscularia deltoides*, as is a specimen in Dillenius' herbarium (**OXF**). Glen (1986) cited the illustration in *Hortus Elthamensis* as the iconotype and the specimen at **OXF** as the typotype, but did not select either as the lectotype. More information can be obtained from the coloured illustration in Dillenius' own copy of his work than from the shrunken herbarium specimen so we select it as the lectotype. An uncoloured version of this illustration, which is an excellent portrait of the plant, is reproduced here as Fig. 3.

Taxonomy and variation: British plants show little variation. Lousley (1971) questioned whether the allied *Oscularia caulescens* (Miller) Schwantes occurs as a naturalized species in the Isles of Scilly, but all the British plants seem to be *O. deltoides*. In fact, Glen (1986) considers that the three names published in the genus *Oscularia* belong to the same species. Glen (1980) also thinks that *Oscularia* and *Lampranthus* should be united and proposes that *Lampranthus* (1930) be conserved over *Oscularia* (1927) as it is a much larger genus. The Committee for Spermatophyta (*Taxon* **32**: 282 (1983)) recommended the acceptance of this proposal. Despite the fact that Glen (1980) says that his monograph of *Lampranthus* is in press, it has not yet been published. He did not justify his transfer of *Oscularia* to *Lampranthus* (Glen 1986), but merely cited an unpublished thesis in support of this move. We are thus unable to assess his proposals and for the time being retain *Oscularia* as a separate genus.

Reproductive biology: Flowers in April. *Oscularia* is a sprawling shrub, which can spread to cover large areas of walls. Seedlings have been observed by G. D. Rowley (in litt. 1988) on walls on Tresco, Isles of Scilly, and by J. R. Palmer on a wall in Guernsey (D. McClintock in litt. 1987).

Distribution and habitat: Naturalized in the Isles of Scilly on St Martin's, St Mary's and Tresco. It is cultivated but not naturalized in the Channel Islands. It was introduced into British gardens before 1732, but not noted as a naturalized plant until Lousley collected it in Tresco in 1953. When Lousley (1971) compiled his Flora, it was only known from walls. In 1982 it was found growing in small quantity on a coastal rock outcrop, associated with *Sedum anglicum*, where it was still present in 1987. It will be interesting to see if it continues to spread into semi-natural habitats. It is a native of the south-western part of Cape Province, South Africa (Herre 1971).

6. **Disphyma crassifolium** (L.) L. Bolus, *Fl. Pl. S. Africa* **7**: t. 276 (1927).
Mesembryanthemum crassifolium L., *Sp. Pl.* 484 (1753). Described from Africa. LECTOTYPE: Dillenius, *Hort. Eltham*. 266, t. 201, fig. 257 (1732), pro *Mesembryanthemum crassifolium repens,*

Figure 3. *Oscularia deltoides* (L.) Schwantes, illustrated as *Mesembryanthemum deltoides, & dorso, & lateribus muricatis, minus* in *Hortus Elthamensis* 255, t. 195, fig. 246 (Dillenius 1732). The illustration coloured by Dillenius is the lectotype of *Mesembryanthemum deltoides* L.

flore purpureo, in the copy in the Department of Plant Sciences, Oxford University, coloured by Dillenius; designated here.

Vernacular name: Purple Dew-plant

Illustrations: Salm-Dyck, *Monogr. Aloes Mesembr.* **18**: fig. 3 (1836), pro *Mesembryanthemum crassifolium*; Lousley, *Fl. Scilly* 217, fig. 10 (1971).

Description: Succulent shrub. Stems up to 1 m, trailing or hanging, often rooting at the nodes, glabrous, yellowish-green, tinted reddish or brownish to pale brown, rather woody especially at the base; internodes 1·5–4·0 cm. Leaves in groups of 3–10, 12–42 × 3–9 mm, translucent yellowish-green, faintly or heavily tinted pinkish, or reddish, usually blotched red, narrowly linear-oblanceolate or linear-lanceolate in outline, triangular in section with obscure angles, rounded to a minute point at apex, sessile, when in opposite pairs slightly connate at base, with a row of almost flat papillae on the angles and covered with small pellucid dots. Flowers solitary, 30–50 mm in diameter, axillary; peduncles 4–40 mm. Calyx pale yellowish-green, sometimes tinted reddish at base of lobes, covered with small pellucid dots; lobes 5, the 2 longest 8–15 × 4–7 mm, linear or oblong, subacute at apex, the 3 shortest 6·5–10·5 × 4·0–5·5 mm, shortly oblong, obtuse at apex, with a scarious margin (except at apex) up to 5 mm wide. Petals numerous (c. 50–60), 15–24 × 1–2 mm, free, on inside purple with white bases, on outside white at base and along central line with purple margins, narrowly linear-oblanceolate, obtuse at apex. Stamens numerous, longer than the styles; filaments 3–10 mm, white, with a tuft of white simple eglandular hairs at base; anthers pale yellow. Stigmas 5, greenish, the basal 1–2 mm with a plumose inner surface, the apex with a long awn up to 4 mm. Nectary glands forming a crenulate ring round the ovary. Capsule c. 10 × 10 mm, 5-locular, pale yellowish, obovoid, each valve with a diverging keel with oblong wings; loculi roofs present, with a pale bifid tubercle; placentation parietal. Seeds 0·8–0·9 × 0·7–0·8 mm, chestnut brown, obovoid, surface irregular but smooth, on funicles c. 1 mm. 2n = 36.

Nomenclature and typification: *Mesembryanthemum crassifolium* was described by Linnaeus (1753) in *Species Plantarum*. His diagnosis *Mesembryanthemum caule repente semi-cylindraceo, foliis semicylindricis laevibus connatis apice triquetris* is taken direct from the *Hortus Cliffortianus* (Linnaeus 1738) except that the words *semicylindraceo* and *repente* are transposed. There are no specimens in the herbarium of the *Hortus Cliffortianus* (**BM**), nor in the Linnaean Herbarium in London (**LINN**). Two synonyms follow the diagnosis: *Mesembr. crassifolium repens, flore purpureo* Dill. *elth*. 266. t. 201. f. 257. and *Ficoides africana reptans, folio triangulari, viridi, flore saturate purpureo*. Bradl. *Succ*. 4. p. 16. t. 38. They are also cited in the *Hortus Cliffortianus*. Both illustrations are referable to the plant usually called *Disphyma crassifolium*. The illustration in the first of these, in the copy coloured by Dillenius, is designated as the lectotype. An uncoloured version is reproduced here as Fig. 4.

Taxonomy and variation: The living plants from the Isles of Scilly, mainland Cornwall, Sussex, Anglesey and Jersey that we have studied show little variation. The variation in peduncle length, from 4 to 40 mm, is phenotypic. Flowers on the exposed edge of a clone have short peduncles whereas those arising amongst the longer leaves in the centre of the same clone have longer peduncles.

Following Chinnock's (1971) revision of the genus in Australasia five species were recognized, two native to South Africa and three to Australasia. More recent work suggests that these might all be conspecific (Venning 1984b). If this is so, however, some infraspecific taxa surely need to be recognized. All naturalized British material belongs to *D. crassifolium* (L.) L. Bolus sensu stricto. The population on Tresco, Isles of Scilly, reported as *D. australe* by McClintock (1964), is similar to the other populations we have examined. A hybrid between *Disphyma australe* (Aiton) J. M. Black and *Carpobrotus edulis* has been recorded from New Zealand (Chinnock 1972). Hybrids between *Carpobrotus* and *Disphyma* could occur in Britain where the two genera grow together, but have not yet been recorded.

FIGURE 4. *Disphyma crassifolium* (L.) L.Bolus, illustrated as *Mesembryanthemum crassifolium repens, flore purpureo* in *Hortus Elthamensis* 266, t. 201, fig. 257 (Dillenius 1732). The illustration coloured by Dillenius is the lectotype of *Mesembryanthemum crassifolium* L.

Reproductive biology: Flowers in May and June. Viable seed is produced in Britain but we have not seen seedlings in the wild. Colonies appear to have become established from planted material and from stems discarded from cliff-top gardens onto the cliffs below. In cultivation the species roots easily from cuttings. Effective reproduction of established colonies is mainly or entirely by vegetative spread.

Disphyma is less susceptible to frost damage than other naturalized 'mesembs'. In Jersey it survived the 1962–63 winter "with ease" (le Sueur 1984). At Lizard Point, W. Cornwall, patches of *Carpobrotus edulis* were severely damaged by frost in the 1978–79 winter, but adjacent patches of *Disphyma* were unaffected. In the 1981–82 winter *Carpobrotus* at Cooden, E. Sussex, was damaged but *Disphyma* was not (K. E. Bull in litt. 1982).

Distribution and habitat: Naturalized on St Mary's and Tresco, Isles of Scilly, in W. Cornwall from Kenneggy east to Coverack on the south coast and at Constantine Bay on the north coast (Margetts & David 1981), and on Jersey, Channel Islands. It occurs on walls, sea cliffs, sand dunes and (in Jersey) on a bank under pine trees and in salt marsh conditions behind a sea wall. It is also naturalized on a sea cliff and coastal rocks north of Bwa Du on the west coast of Holy Island, Anglesey, and on a damp, sheltered cliff at Cooden, E. Sussex. It has been found elsewhere as a casual introduced with wool shoddy.

Disphyma was first recorded as a naturalized plant by J. E. Lousley in 1936 at New Grimsby, Tresco, when it was even then said to have been present for as long as anyone could remember (Lousley 1971) and where it still (1987) survives. It was noted on cliffs at the Lizard peninsula in 1951 and collected at Prussia Cove, Marazion, in 1954. *Disphyma* is now, except for *Carpobrotus edulis*, the most thoroughly naturalized of all 'mesembs' and in places (e.g. Praa Sands and Lizard Point, W. Cornwall) it occurs in abundance. It is not quite as effective a competitor as *C. edulis* and it tends to be naturalized in greatest quantity on steep cliffs or shallow soil, where the cover of other vegetation is reduced. *Disphyma crassifolium* sensu stricto is native to Cape Province, South Africa; other (possibly conspecific) taxa are native to Australia and New Zealand.

7. **Drosanthemum floribundum** (Haw.) Schwantes in *Z. SukkulKde* **3**: 29 (1927).

Mesembryanthemum floribundum Haw., *Misc. Nat.* 100 (1803). Described from plants grown in a London garden. NEOTYPE: Salm-Dyck, *Monogr. Aloes Mesembr.* **51**: fig. 7 (1840), designated here.

Mesembryanthemum candens Haw., *Rev. Pl. Succ.* 186 (1821). NEOTYPE: coloured drawing of a vegetative plant (**K**), designated here.

D. candens (Haw.) Schwantes in *Z. SukkulKde* **3**: 29 (1927).

Vernacular name: Pale Dew-plant

Illustrations: Salm-Dyck, *Monogr. Aloes Mesembr.* **51**: fig. 7 (1840), pro *Mesembryanthemum floribundum*.

Description: Low sprawling shrub forming dense prostrate to hanging patches. Stems up to 60 cm, trailing, pale brown, with numerous, very short and short, thick, pale, usually deflexed, broad-based simple eglandular hairs; branches usually weak, short and patent; internodes 0·5–3·0 cm. Leaves 6–30 × 1·0–3·5 mm, fleshy, decussate, dull pale to medium green, cylindrical or narrowly obovoid, deltate-ovate in section, sometimes curved, more or less obtuse at apex, sessile, covered with rounded, glass-like tubercles. Flowers 18–27 mm in diameter, solitary at the end of branches or axillary; peduncles 2·5–50·0 mm. Calyx hemispherical to slightly elongated, covered with glass-like tubercles; lobes 5 (–6), 3–6 mm, lanceolate or linear-lanceolate, obtuse at apex, 3(–4) with broad scarious flaps, 2 without flaps. Petals 25–35, 5–12 × 0·5–2·0 mm, free, shining white with a purple apex when young, becoming tinted lilac and finally lilac with age, narrowly linear-oblanceolate, more or less obtuse at apex, the inner much shorter than outer and sometimes bifid at apex. Stamens 30–70, from a little shorter to a little longer than styles; filaments 4–5 mm, whitish, with a group of sub-basal pale simple eglandular hairs, becoming lilac after anthesis and curving outwards to expose the stigmas and nectary glands; anthers pale yellow. Stigmas 5, linear in outline, curved outwards, brownish-yellow, sometimes tinged purplish at apex. Nectary glands forming a ring round the ovary but in disjunct groups. Capsule 2·5–5 × 4–6 mm, 5-locular, obovoid, each valve with 2 contiguous expanding keels on inner face, each keel with a membranous wing; loculi-roofs present; placentation parietal. Seeds c. 1 × 0.5 mm, brown, with ribs and tubercles. $2n = 36$.

Nomenclature and typification: The specimens in Haworth's herbarium have mostly been destroyed. There are no coloured drawings of *Mesembryanthemum floribundum* at Kew based on Haworth's material. The only illustration cited with the original diagnosis, *M. pilosum micans flore purpureo pallidiore* Dill. *Elth.* t. 214. f. 280, forms the basis for and is here designated as the lectotype of another species, *Mesembryanthemum torquatum* Haw., *Rev. Pl. Succ.* 187 (1821). Thus there is no original type material of *M. floribundum*. Fortunately the description is a good one and is in accord with the plant we have described here. It is also in agreement with Salm-Dyck's illustration (reproduced here as Fig. 5) which we designate as the neotype.

Mesembryanthemum candens Haw. was described from vegetative material. There is a coloured drawing of such a specimen at Kew, which does not in our opinion differ from *M. floribundum*, and which we designate as the neotype. Another drawing at Kew shows a single pink flower which, although not certainly the same as the vegetative plant, can be used as a guide, as it was probably made from the same clone at a later date. It also does not differ from *M. floribundum* and we conclude that the name should be placed into the synonymy of that species.

The lectotype illustration of *Mesembryanthemum torquatum* Haw. (*Drosanthemum torquatum* (Haw.) Schwantes in *Z. SukkulKde* **3**: 30 (1927)) looks rather like a pot-grown *D. floribundum*, but we have seen no plants with such long peduncles.

Taxonomy and variation: Drosanthemum floribundum shows little variation in Britain. We have studied living plants from the Isles of Scilly, the Lizard peninsula (W. Cornwall) and Guernsey and all undoubtedly belong to a single taxon. The naturalized plant is referred to *D. candens* (Haw.) Schwantes by Tutin (1962, 1964) but to *D. floribundum* by recent authors. *D. candens* is said to differ from *D. floribundum* in its narrower calyx, paler pink or nearly white petals and stigmas not exceeding the stamens (Adamson & Bolus 1950; Fernandes 1972). As described above, the flower colour and the position of the stigmas relative to the stamens of the British plants varies with age and photographs in **CGE** show white and pink flowers on the same plant.

Reproductive biology: Flowers from May to July. As its specific epithet implies, patches of *Drosanthemum* usually flower freely. We have noticed flies, bees (including *Bombus* cf. *lucorum* and *B. terrestris*) and ants visiting the flowers. *Drosanthemum* is more attractive to bees than any other 'mesemb' naturalized in Britain, and in sunny weather they are frequent visitors. Seeds are ripened in Britain, but we do not know if they are viable. We have not seen any seedlings in the wild and effective reproduction is by vegetative spread. In cultivation cuttings of *Drosanthemum* root less readily than those of *Carpobrotus* or *Disphyma*.

Drosanthemum is more susceptible to frost than *Carpobrotus* or *Disphyma*. Some colonies have not survived severe winters, e.g. a well-established clone on a wall at Cadgwith Cove, W. Cornwall, which was covered by a mass of flowers in July 1978, did not survive the severe 1978–9 winter.

Distribution and habitat: Naturalized on coastal walls, banks, rock outcrops and cliffs on St Mary's and Tresco, Isles of Scilly, at Rinsey Head and the Lizard peninsula, W. Cornwall, and on Guernsey. The largest and most vigorous plants form patches hanging down vertical walls or cliffs. Patches on less steep banks are smaller and less vigorous, and *Drosanthemum* is apparently less able than *Carpobrotus* or *Disphyma* to spread vegetatively in such habitats. There is a single record from Jersey, where it was killed in the 1962–63 winter (le Sueur 1984), and a plant collected as *Mesembryanthemum candens* at Newquay, W. Cornwall, in 1921 (**BM**) was probably this species. It is also recorded as a casual introduced with wool shoddy.

Specimens of *Drosanthemum* were collected at St Mary's in 1875 (**BM**) and 1885 (**OXF**). These were presumably cultivated plants. The first records of naturalized plants appear to be the 1921 collection from sand hills near Newquay mentioned above and a plant collected by T. G. Tutin in 1948 from a cliff at Cadgwith, Lizard peninsula (**LTR**). None of the pressed specimens can be

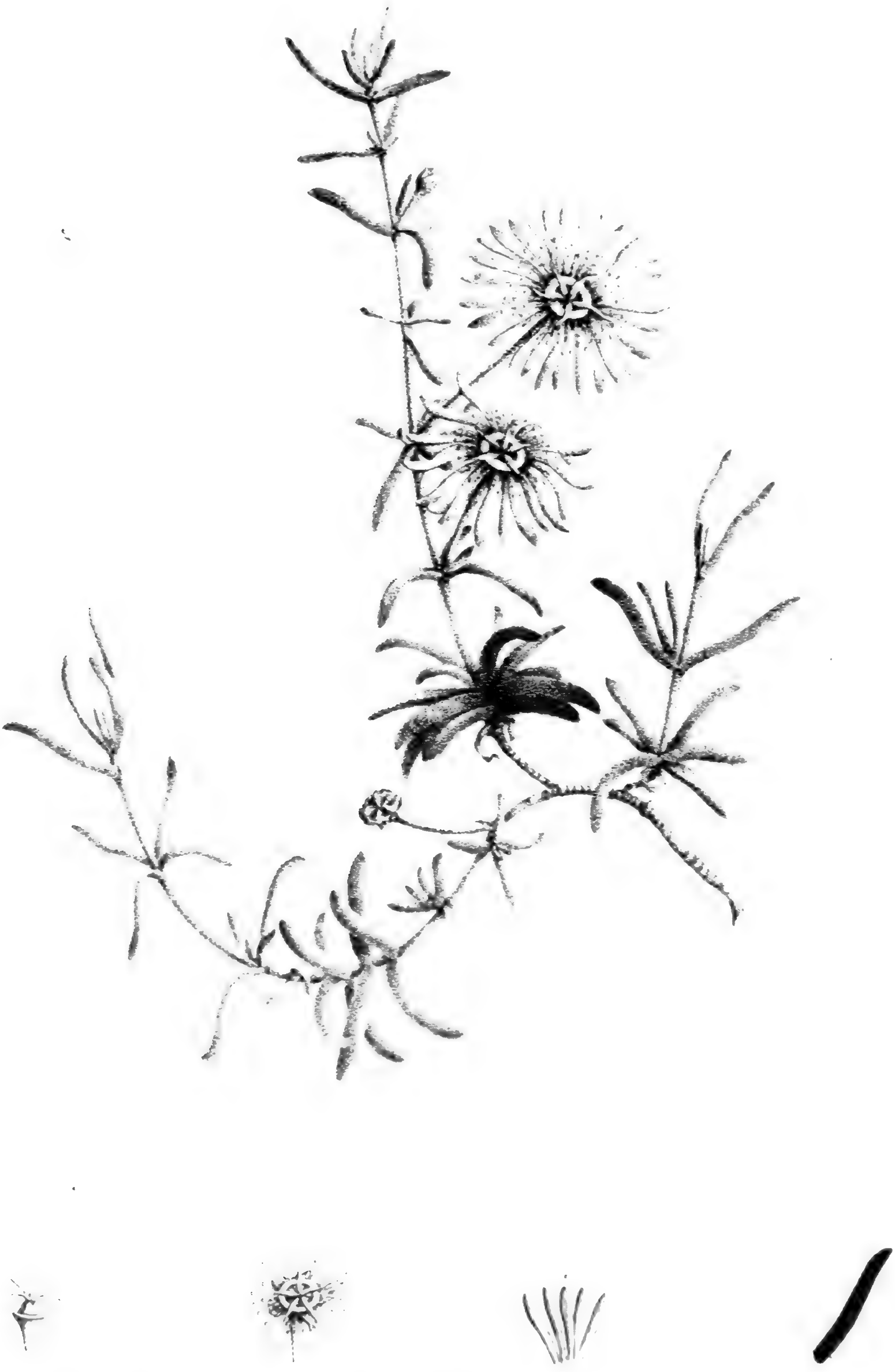

FIGURE 5. *Drosanthemum floribundum* (Haw.) Schwantes, illustrated as *Mesembryanthemum floribundum* in Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi* **51**: fig. 7 (1840). The coloured plate is the neotype of *M. floribundum* Haw.

identified as *D. floribundum* with certainty but all probably represent the same species as that currently naturalized and we have confirmed the identity of the Cadgwith plant in the field.

Drosanthemum is less thoroughly naturalized than *Carpobrotus*, *Disphyma* or *Lampranthus*. It is probably limited by its frost sensitivity and low competitive ability. It does occur, however, in natural habitats, although often only in small quantity, and will probably persist as a member of the British flora. It is a native of South Africa (Herre & Friedrich 1961).

8. **Erepsia heteropetala** (Haw.) Schwantes in *Gartenflora* **77**: 68 (1928).

Mesembryanthemum heteropetalum Haw., *Misc. Nat.* 67 (1803). Described from plants cultivated in a London garden. Neotype: Salm-Dyck, *Monogr. Aloes Mesembr.* **21**: fig. 2 (1840), pro *Mesembryanthemum heteropetalum*; designated here.

Illustrations: Lousley, *Fl. Scilly* 217, fig. 10 (2) (1971); Salm-Dyck, *Monogr. Aloes Mesembr.* **21**: fig. 2 (1840), pro *Mesembryanthemum heteropetalum*.

Description: Low, glabrous, fleshy shrub. Stems up to 35 cm, erect or decumbent, glabrous, yellowish-green or tinted brownish, often spotted purplish, slightly flattened with decussate ridges or wings; internodes up to 4·5 cm. Leaves 16–30 × 6–13 mm, with bluish-green bloom on faces and yellowish-green angles and covered with dense pellucid dots, unmarked when young, becoming tinted or spotted purplish and eventually turning purple with age, decussate, asymmetrically oblanceolate in outline, triangular in section, shortly acute at apex, sessile, irregularly dentate on one angle, often minutely denticulate on the others. Flowers solitary or 2–3 together, terminal at the end of branches and side shoots, 10–15 mm in diameter; peduncle up to 15(–25) mm. Calyx bluish-green, hemispherical, covered in pellucid dots, sometimes spotted or tinted purplish; lobes 5, erect; 2 longest lobes 11–15 mm, broadly triangular-ovate, abruptly acute to more or less obtuse at apex, entire, both usually keeled on the back, the keel continuing to the base of calyx and entire or irregularly dentate below, rarely only 1 keeled; 3 shortest lobes 8–15 mm, triangular-ovate, acute at apex, entire, not keeled, 2 with a scarious often purplish-tinted margin on both sides and one with a similar margin on one side. Petals numerous, in several irregular series, 4–11 × 0·5–0·8 mm, free, pale purple, linear-oblanceolate, obtuse and sometimes bifid at apex, outer petals more or less spreading, inner erect or inflexed. Staminodes numerous, 2·0–4·5 × 0·1–0·2 mm, whitish, linear, more or less obtuse at apex, inner inflexed and covering the stamens. Stamens numerous, inflexed; filaments 0·5–2·0 mm, white; anthers pale yellow. Stigmas 5–6, very small, pale greenish, roundish to almost globular in outline. Nectary glands minute and scarcely visible. Capsule 10–15 × 10–15 mm, 5-locular, each valve with two expanding keels which diverge towards the apex and end in broad awn-tipped membranes; loculi roofed with stiff wings, but without tubercles at the openings; placentation parietal. Seeds 1·3–1·5 × 0·8–1 mm, chestnut-brown, ovoid, flattened, tuberculate, on a funicle up to c. 1 mm. $2n = 18$.

Nomenclature and typification: Haworth's original description of *Mesembryanthemum heteropetalum* is a good one and fits our plant except that the petals are said to be white. There is a coloured drawing of a plant worked on by Haworth at Kew but as it is only a vegetative shoot we have not selected it as a neotype, preferring instead Salm-Dyck's illustration of a flowering plant. This is reproduced here as Fig. 6.

Taxonomy and variation: There is very little variation within the only population naturalized in Britain.

Reproductive biology: Flowers in May and June. The morphology of the flower suggests that it is self-pollinating. We have not seen flying insects visit the flowers (although they are visited by ants) and *Erepsia* is certainly much less frequently visited by insects than *Carpobrotus* or *Drosanthemum*. Reproduction in the wild is by seed: viable seed is produced and seedlings have been observed. We have no evidence of any vegetative reproduction.

FIGURE 6. *Erepsia heteropetala* (Haw.) Schwantes, illustrated as *Mesembryanthemum heteropetalum* in Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi* **21**: fig. 2 (1840). The coloured plate is the neotype of *M. heteropetalum* Haw.

Distribution and habitat: Only naturalized in one locality, Buzza Hill, St Mary's, Isles of Scilly, where it grows in shallow soil on the edge and face of a disused quarry and on a nearby cliff slope. It was first collected by J. E. Lousley in 1957, and was still present in 1987. In 1983 the population consisted of approximately 30 plants. *Erepsia heteropetala*, unlike the more showy 'mesembs', is not widely grown in coastal gardens in south-western England. It is a native of South Africa.

9. **Carpobrotus edulis** (L.) N.E.Br. in E. P. Phillips, *Gen. S. Afr. Fl. Pl.* 249 (1926).
Mesembryanthemum acinaciforme var. *flavum* L., *Sp. Pl.* 485 (1753). Lectotype: Dillenius, *Hort. Eltham.* 284, t. 212, fig. 272 (1732), pro *Mesembryanthemum falcatum majus, flore amplo luteo*, chosen by Blake in *Contr. Queensland Herb.* **7**: 17 (1969); the copy in the Department of Plant Sciences, Oxford University, is coloured by Dillenius.
M. edule L., *Syst. Nat.*, 10th ed., 1060 (1759), nom. nov. pro *M. acinaciforme* var. *flavum* L.

Vernacular names: Hottentot Fig, Kaffir Fig, Sally-my-handsome.

Illustrations: Ross-Craig, *Draw. Br. Pl.* **11**: 39 (1958).

Description: Prostrate or hanging, succulent perennial forming large mats. Stems up to at least 3 m, trailing or hanging, sometimes rooting at the nodes, fleshy, angled, glabrous, slightly bluish-green turning pink, pinkish-purple or orange with age; branches axillary; internodes 1·5–7·0 cm. Leaves (20–)40–140 × 5–15 mm, decussate, each pair slightly connate at base, slightly bluish-green and waxy, turning pinkish-purple and finally orange with age, covered with pellucid dots, linear or narrowly oblong in outline, triangular in section, straight to more or less curved, obtuse to acute at apex, sessile. Flowers terminal or at the end of side shoots, solitary, 40–90 mm in diameter; peduncles 6–60 mm. Calyx yellowish-green, sometimes tinged purplish, covered with pellucid dots; lobes 4–6, the 2 longest 15–65 × 8–17 mm, lanceolate to linear-lanceolate in outline, more or less acute at apex, flat on inner surface, keeled on outer surface, the keel continuing down the undivided calyx, the 2–4 short lobes 10–50 × 6–15 mm, ovate to lanceolate in outline with a curved, acute apex and a brownish scarious flap on one or both sides up to 10 mm wide, that on the shortest of the shorter lobes sometimes almost circular, exceeding the apex and adnate to its inner surface, one of the longest lobes sometimes with a flap and one of the shorter lobes sometimes without a flap. Petals 65–150, 25–45 × 1·5–3·5 mm, free, yellow or pale or deep purple, pale reddish-purple or orange-pink, sometimes with a yellow base, narrowly linear or narrowly linear-oblanceolate, entire or slightly toothed at apex. Stamens numerous; filaments 5–10 mm, yellow or brownish-orange, sometimes with a whitish base, inner with a tuft of whitish or purplish hairs at base; anthers yellow. Staminodes resembling petals sometimes present between stamens and petals. Stigmas 10–14, greenish-yellow, curved upwards and outwards, plumose on the inner surface. Nectary glands united to form a crenulate ring round the ovary. Fruit adnate to the calyx, 1·4–3·0 × 1·4–2·7 cm, obovoid; seeds 1–1·5 × 0·8–1 mm, dark brown when ripe, obovate in outline, flat, minutely and faintly reticulate, on a funicle 2–3 mm.

a. var. **edulis**

Illustrations: *Curtis's bot. Mag.* **144**: t. 8783 (1918), pro parte; Sjögren, *Açores Flores* t. 73 (1984).

Description: Leaves (20–)40–140 × 5–14 mm. Flowers 40–90 mm in diameter; petals pure yellow when freshly opened, becoming pink-tinged with age. Fruits 2·5–3·0 × 2·5–2·7 cm. 2n = 18.

b. var. **rubescens** Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **7**: 771 (1926). Not typified (see below).
Mesembryanthemum virescens auct., non Haw.
M. aequilaterum auct., non Haw.
C. deliciosus auct., non L. Bolus.

Illustrations: *Curtis's bot. Mag.* **144**: t. 8783 (1918), pro parte; Bichard & McClintock, *Wild Fl. Channel Is.* no. 67 (1975).

Description: Leaves (20–)40–100 × 5–10 mm. Flowers 45–75 mm in diameter; petals purple with little or no sign of yellow at their bases. Fruits 2·5–3·0 × 2·5–2·7 cm. 2n = 18.

c. var. **chrysophthalmus** C. D. Preston & P. D. Sell, **var. nov.** HOLOTYPE: Plant collected as living material at the sea front, Porthloo, St Mary's, Isles of Scilly, 12 January 1978, C. D. Preston, cultivated at the Botanic Garden, Cambridge, and pressed on 8 June 1979 as *P. D. Sell 79/22* (**CGE**).

C. acinaciformis sensu Lousley, *Fl. Scilly* 145 (1971).

Illustration: Lousley, *Fl. Scilly* dustcover (1971) ut *C. edulis*.

Description: Folia (20–)35–125 mm longa, 5–15 mm lata. Flores 45–70 mm in diametro; petala purpurea basi area aurei; fructus 1·4–2·5 × 1·4–1·8 cm.

Leaves (20–)35–125 × 5–15 mm. Flowers 45–70 mm in diameter; petals purple with a distinct area of yellow at their bases, which forms a ring as you look into the flower from above. Fruit 1·4–2·5 × 1·4–1·8 cm.

Nomenclature and typification: Linnaeus (1753) described *Mesembryanthemum acinaciforme* var. *flavum* based on *Mesembr. falcatum majus, flore amplo luteo*. Dill. *elth*. 284. t. 212. f. 272. and *Ficoides s. Ficus aizoides africana major procumbens, triangulari folio, fructu maximo eduli*. Herm. *lugd*. 244. t. 245. Both illustrations are referable to what is now known as *Carpobrotus edulis*. We are in agreement with Blake (1969) who selected the Dillenius plate as the lectotype, but in particular we cite the coloured copy at Oxford. An uncoloured version is reproduced here as Fig. 7. Linnaeus (1759) gave *M. acinaciforme* var. *flavum* a new name, *M. edule*. The type of *M. edule* is thus the type of *M. acinaciforme* var. *flavum*.

The purple-flowered variant, var. *rubescens*, was described by Druce in 1926. No specimens are cited in the protologue, and none of the specimens in Druce's herbarium (**OXF**) is labelled var. *rubescens* or described as *C. edulis* with red- or purple-flowers. G. H. Douglas sent plants to Druce in 1924, stating "the flowers are of two colours". In the poorly dried specimens one can no longer see any colour, but it may be that chemical analysis could distinguish them. At the moment we are unable to lectotypify var. *rubescens*. *M. aequilaterum* Haw., *M. virescens* Haw. and *Carpobrotus deliciosus* (L. Bolus) L. Bolus have all been wrongly applied to this taxon. *C. aequilaterus* (Haw.) N.E. Br. is a smaller-flowered Australian species more akin to *C. glaucescens*, but without the white bases to the petals (cf. Blake 1969). For *C. virescens* (Haw.) Schwantes see under *C. glaucescens*. Lousley (1971) thought that specimens sent in 1895 from Tresco Abbey for a drawing in *Curtis's botanical Magazine* (t. 8783) were referable to *C. deliciosus* (L. Bolus) L. Bolus. The pink-flowered specimen on this plate, however, seems to us to be indistinguishable from *C. edulis* var. *rubescens*, and furthermore the text states that the plants illustrated were collected at Caerthillian Valley, which is on the Lizard peninsula, mainland Cornwall (cf. Hutchinson 1917).

The third variety, var. *chrysophthalmus*, has the bases of the purple petals yellow, so that when looking into the open flowers one can see a golden ring round the base. This seems to be the plant Lousley (1971) called *C. acinaciformis*, although he did not mention the flower character. *Mesembryanthemum acinaciforme* was described by Linnaeus (1753). The diagnosis *Mesembryanthemum foliis acinaciformibus connatis: angulo carinali scabris, ramis angulatis* is taken verbatim from the *Hortus Cliffortianus* (Linnaeus 1738). There are no specimens in the herbarium of the Hortus Cliffortianus (**BM**), or in the Linnaean Herbarium in London (**LINN**). The diagnosis is followed by var. *purpureum* based on *Mesembr. acinaciforme, flore amplissimo purpureo* Dill. *elth*. 282. t. 211. f. 270 & t. 212. f. 271. This is also given in the *Hortus Cliffortianus*, but without a varietal name. It is clearly what Linnaeus considered to be the type variety. The plate t. 211 fig. 270 in the Oxford coloured copy is therefore designated as the lectotype of *M. acinaciforme* and shows a large-flowered, large-leaved plant which is not matched by any material from the British Isles which we have seen. It was apparently cultivated in the Isles of Scilly as the illustration in *Curtis's bot. Mag*. t. 5539 (1865) seems to be correctly named. We cannot find any described taxon which matches our plant with yellow centres to the flowers and have therefore described it as new, although we have no suggestions as to its geographical origin or derivation. The holotype is taken from the clone we have

FIGURE 7. *Carpobrotus edulis* (L.) N.E.Br. var. *edulis*, illustrated as *Mesembryanthemum falcatum majus, flore amplo luteo* in *Hortus Elthamensis* 284, t. 212, fig. 272 (Dillenius 1732). The illustration is the lectotype of *Mesembryanthemum edule* L.

most studied, and there are colour photographs in **CGE** of the plant we pressed (Sell colour film 297/30, 31 & 32).

Taxonomy and variation: Variation within var. *edulis* is described by le Sueur (1984) from Jersey, where neighbouring clones differ in leaf and flower colour. Var. *rubescens* differs only in its smaller purple flowers (though vegetatively it never seems to reach the maximum size of the yellow-flowered plant). Both these varieties are widely naturalized and often grow together. Intermediate plants with pale purple, pale reddish-purple or pale orange-pink flowers occur, and look as though they have been derived from hybridization between yellow- and purple-flowered plants. As their origin is obscure we have treated the yellow- and purple-flowered plants as varieties of the same species under the only names that seem to be available for them.

Var. *chrysophthalmus* has slightly smaller flowers, like var. *rubescens* but with the base of the petals yellow. It also has smaller fruits. The only published illustration we are aware of is on the dustcover of Lousley (1971), which most libraries will have thrown away. We can find no name for it. We originally thought it was a distinct species, as species go in 'mesembs', but have finally decided to name it as a variety of *C. edulis* as it is just possible that it arose from hybridization between the yellow and purple variants.

Reproductive biology: The main flowering period is from May to July. The flowers are visited by Coleoptera, Diptera, Hymenoptera and Lepidoptera, and snails can sometimes be seen sitting in the open flowers. Viable seed is produced and seedlings have been seen, usually growing in areas of bare soil around the fringe of naturalized clones.

Carpobrotus edulis spreads mainly by vegetative means. In the Isles of Scilly and the Channel Islands it has been planted for dune stabilization or for ornament, and elsewhere colonies often originate from stems thrown out of gardens. New colonies become established from fragments collected by gulls as nesting material, and in this way *Carpobrotus* has spread even to small uninhabited islands. Fragments of *C. edulis* root readily in cultivation: one potted up in an unheated greenhouse produced roots up to 22 cm long in 18 days.

Large areas of *C. edulis* overwhelm native vegetation, forming mats in which virtually no other species grow. These mats acidify the underlying soil down to a depth of at least 8–12 cm (Frost 1987). The spread of *Carpobrotus* is accelerated by cliff fires, which scarcely affect the succulent 'mesemb' but destroy the surrounding vegetation. In severe winters *C. edulis* is badly damaged by frost. However, stems may survive and produce new shoots even in areas in which all the existing foliage has been killed. A thick layer of litter accumulates under mats of *Carpobrotus* and this must help insulate stems from low temperatures, and certainly inhibits the colonization by other flowering plants of areas in which *Carpobrotus* has been frost-killed. Cattle sometimes eat the leaves of *Carpobrotus*, but only a few colonies grow in localities where such grazing is likely to occur. Frost (1987) reports that it is eaten "with relish" by pet rabbits.

Distribution and habitat: *C. edulis* is primarily a species of sea cliffs and sand dunes, but it also grows on coastal banks, rocks and walls. Its distribution is mapped in Fig. 8. Var. *edulis* and/or var. *rubescens* is recorded from the following vice-counties: Channel Islands, 1–4, 9–11, 14, 15, 19, 41, 45, 49, 52, 60, 71, H1, H5, H20, H21, H38. The population in v.c. 74 mapped in the *Atlas of the British flora* (Perring & Walters 1962) is *C. glaucescens* and confirmation of the identity of the plant recorded on shingle in v.c. 19 by Jermyn (1974) is desirable in view of the presence of *C. glaucescens* on the adjacent Suffolk coast. Var. *chrysophthalmus* is naturalized on Bryher and St Mary's in the Isles of Scilly and at St Brelade and St Ouen's Bay in Jersey. Lousley (1971) records "*C. acinaciformis*" – the name he apparently applied to var. *chrysophthalmus* – from St Martin's and Tresco. C. D. P. and P. Clough (formerly of Tresco Abbey Gardens) have searched for it on Tresco without success.

Carpobrotus edulis was introduced into British gardens about 1690. The history of its naturalization is difficult to reconstruct. For many years botanists did not record naturalized populations of this and other 'mesembs', and collectors of herbarium specimens sometimes fail to state whether or not they were collected from naturalized populations. *C. edulis* was recorded as "semi-wild" in Guernsey in 1886 and reported again in 1893 (McClintock 1975). A yellow-flowered 'mesemb', presumably *C. edulis* var. *edulis*, grew freely in great abundance at St Aubin's Bay, Jersey by 1886 (le Sueur 1984). In the Isles of Scilly it was planted in the mid-nineteenth century and by 1921 it was common on most of the islands (Lousley 1971). On mainland Cornwall 'mesembs' were in cultivation at Falmouth by 1871 (Baker 1871) and at The Lizard by c. 1880 (Frost 1987). Although it was not listed amongst the alien plants seen near Penzance between 1885 and 1887 by Glasson (1889), *C. edulis* was "abundant" in the Lizard peninsula in 1905 and "quite naturalised" in 1909. It was "rapidly establishing itself" at East Pentire, Newquay, in 1907 and by 1909 it had been recorded in several Cornish localities (Vigurs 1908; Davey 1909). Eight years later Hutchinson (1917) could describe it as "now so thoroughly naturalised and so characteristic a feature of the sea-slopes of Cornwall". In Devon it was collected at Torquay (v.c. 3) in 1885 and Saunton Sands (v.c. 4) in 1919. It is a native of South Africa.

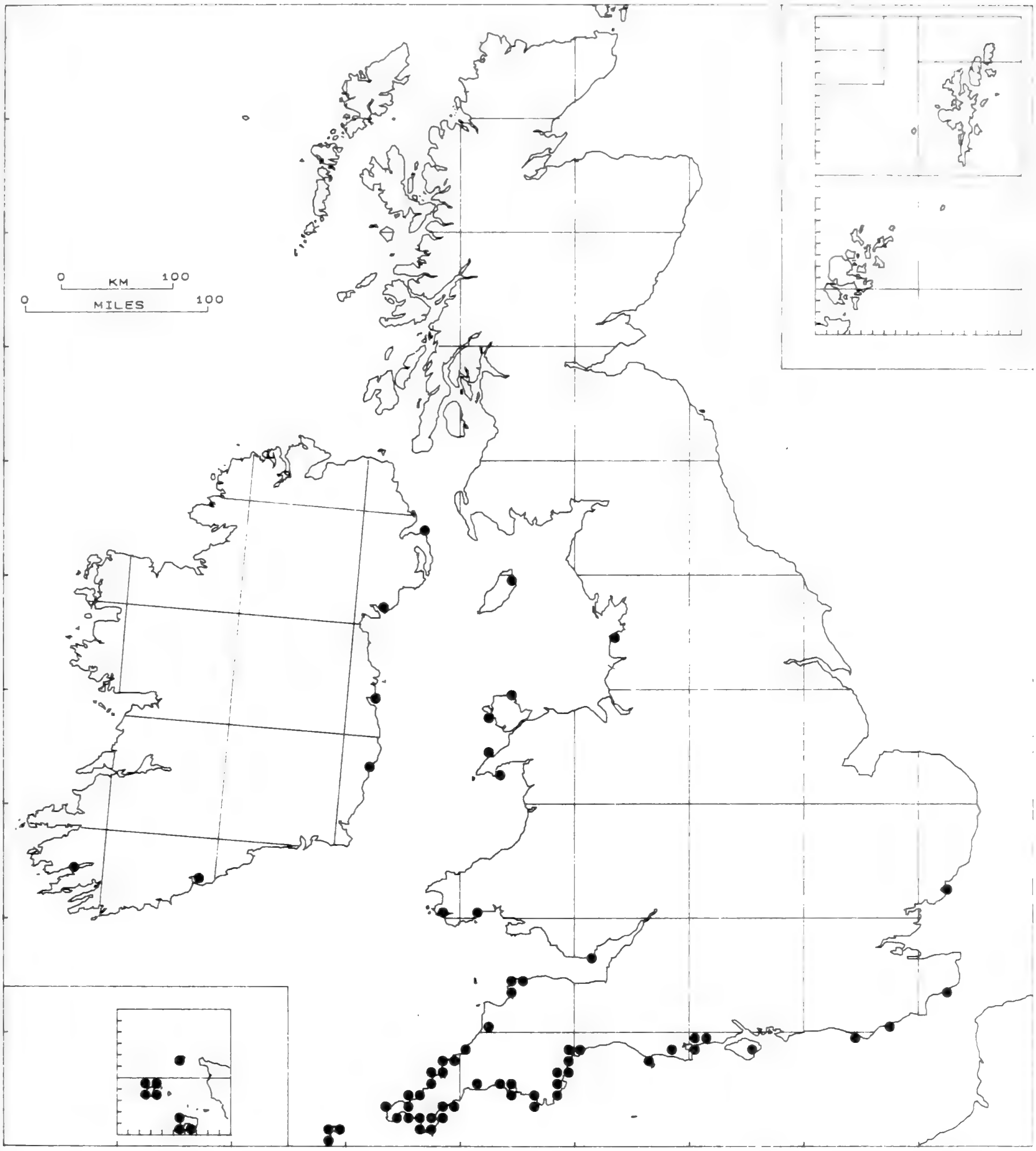

FIGURE 8. The distribution of *Carpobrotus edulis* in the British Isles. The records are plotted in the 10-km squares of the British and Irish national grids; the Channel Islands are shown as an inset with the records plotted on the UTM grid.

10. **Carpobrotus glaucescens** (Haw.) Schwantes in *Gartenflora* **77**: 69 (Feb. 1928); N.E. Br. in *J. Bot., Lond.* **66**: 324 (Nov. 1928).

Mesembryanthemum glaucescens Haw., *Syn. Pl. Succ.* 236 (1812). Described from plants from Nova Hollandia grown in a London garden. NEOTYPE: cultivated plant originating from Botany Bay, *S. T. Blake 19677* (**BRI**), vide Blake in *Contr. Queensland Herb.* **7**: 23 (1969).

Mesembryanthemum virescens Haw., *Syn. Pl. Succ.* 236 (1812). Described from plants from Nova Hollandia grown in a London garden. NEOTYPE: King George Sound, West Australia, Sept. 1959, *S. T. Blake 20910* (**BRI**), vide Blake in *Contr. Queensland Herb.* **7**: 25 (1969).

Mesembryanthemum abbreviatum Haw. in *Phil. Mag.* **68**: 329 (1826). Described from a plant from Australasia grown at Kew. NEOTYPE: Salm-Dyck, *Mongr. Aloes Mesembr.* **5**: fig. 7 (1849), vide Blake in *Contr. Queensland Herb.* **7**: 25 (1969).
Mesembryanthemum edule var. *virescens* (Haw.) Moss, *Cambr. Brit. Fl.* **2**: 151 (1914), quoad basionym, exclud. descript.
C. virescens (Haw.) Schwantes in *Gartenflora* **77**: 69 (1928).
C. abbreviatus (Haw.) Schwantes in *Gartenflora* **77**: 68 (1928).

Vernacular name: Angular Pigface is the name used for this species in Australia.

Illustrations: Bichard & McClintock, *Wild Fl. Channel Is.* no. 68 (1975).

Description: As *C. edulis* except: Internodes 0·5–3·0 cm. Leaves 20–70 × 5–8 mm, bluish-green and waxy, more or less acute at apex. Flowers 35–45(–60) mm in diameter; sessile or with a peduncle up to 10 mm. Calyx bluish-green and waxy; lobes 5, the 2 longest 15–20 × 10–12 mm, the 3 shortest 5–13 × 3–15 mm, ovate in outline with a brownish scarious flap on one or both sides up to 8 mm wide. Petals 55–80, 17–25 × 1·0–1·2 mm, purple with obvious white bases, narrowly linear, with a few teeth at the apex. Stamens numerous; filaments 4–6 mm, white, sometimes yellowish towards apex, inner sometimes with tufts of white simple eglandular hairs at base. Stigmas 10–12. Fruit 1·5–1·7 × 1·2–1·5 cm; seeds 1·0–1·2 × 0·8–1·0 mm. 2n = 18.

Nomenclature and typification: This has been satisfactorily dealt with by Blake (1969). There are in fact coloured drawings of both *C. glaucescens* and *C. virescens* at Kew not seen by Blake. We can detect no obvious difference between the drawings. *C. chilensis* (Molina) N.E.Br., the name used for the Suffolk populations of this plant by Simpson (1982), is a synonym of *C. aequilaterus*, a species which lacks white bases to the petals (Blake 1969).

Taxonomy and variation: Plants naturalized in the British Isles show little variation. Blake (1969) separated *C. glaucescens* from *C. virescens* mainly on stamen number and ascribed to them different geographical ranges, *C. glaucescens* being confined to coastal areas of eastern Australia and *C. virescens* to the south-west. Venning (1984a) retained the two species, but said that dried material was difficult to name and that not enough fresh material was available to review their status. In the few naturalized British plants in which we have counted the stamens the number is around 300 which is intermediate between the two. We therefore believe that they are not distinct species, but that there may be slight differences which could allow the upkeep of geographical races.

Reproductive biology: The main flowering period is from May to July. Flowers have, however, been seen as early as February and *C. glaucescens* shows a greater tendency than *C. edulis* to flower outside the main flowering period. Effective reproduction is by vegetative growth and spread. In cultivation vegetative fragments root readily. *C. glaucescens* is a smaller plant than *C. edulis*, and does not possess as great a competitive vigour as that species.

Distribution and habitat: Naturalized in the Channel Islands (Alderney, Guernsey, Herm and Jersey), Suffolk and Wigtownshire. On Herm it is the only naturalized *Carpobrotus* but in Guernsey and Jersey it is much less frequent than *C. edulis*. In Suffolk it is recorded from two localities near Felixstowe: it is the *C. chilensis* of Simpson (1982). In Wigtownshire it grows around the Logan Fish Pond at Port Logan. Most naturalized colonies are on sea cliffs, but it also grows on walls and roadside verges. In Australia *C. glaucescens* is recommended for planting as a stabilizer of sand dunes (Beach Protection Authority of Queensland 1981) but it has not been recorded from this habitat in Britain. It is cultivated in the Isles of Scilly but has not become naturalized there.

C. glaucescens has been known for about 25 years in Jersey (le Sueur 1984). It was first noticed in Herm in 1947, in Guernsey in 1970 and in Suffolk in 1974. Although first officially recorded in Wigtownshire in 1955 (as *C. edulis*), it is said by local people to have grown there for many years before that. It is a native of the eastern coast of Australia (Venning 1984a).

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(*Accepted May 1988*)

APPENDIX: CHROMOSOME COUNTS OF AIZOACEAE NATURALIZED IN THE BRITISH ISLES

R. D. I'ONS

Chromosome counts were made of specimens collected by C. D. Preston and Mrs F. le Sueur on which the above account was based. They were grown in pots in the University Botanic Garden, Cambridge, from which root tips were easily procured. Voucher specimens of flowers and sometimes fruits were pressed and placed in **CGE**.

The root tips were placed in 0·05% colchicine in corked tubes for 2 h at room temperature, followed by fixation in Carnoy's solution for 2h. They were then put in 1m HCl and hydrolysed, uncovered, for 6 min in an oven at 60°C, and stained in Feulgen's solution for 1–2 h. The root tips were then mounted on a slide with propionic orcein, squashed, and the chromosomes counted. The slides were made permanent by using liquid nitrogen to facilitate removal of the coverslip, passing the slide into 90% alcohol followed by absolute alcohol and xylene for 1 min each, and finally mounting in dammar xylene or Euparal. Occasionally root tips were stored in 70% alcohol overnight after fixation in Carnoy's solution, but this was less satisfactory than if the complete process was carried out on the day of collection.

Aptenia cordifolia (L.fil.) Schwantes: St Brelade's Bay, Jersey, GR WV/589.486, *Mrs F. le Sueur*; $2n = 18$. Grouville, Jersey, GR WV/706.499, *Mrs F. le Sueur*; $2n = 18$.

Carpobrotus edulis (L.) N.E.Br. var. *edulis*: near Kempt Tower, St Ouen's Bay, Jersey, GR WV/56.52, *Mrs F. le Sueur*; $2n = 18$.

Carpobrotus edulis (L.) N.E.Br. var. *rubescens* Druce: N. end of Rocquaine Bay, Guernsey, GR WV/25.78, *C. D. Preston*; 2n = 18.

Carpobrotus glaucescens (Haw.) Schwantes: south coast of Alderney, between Vallée des Gaudulons and Val l'Emauve, GR WA/564.060, *C. D. Preston*; 2n = 18.

Disphyma crassifolium (L.) L. Bolus: 'White Hut', St Ouen's Bay, Jersey, GR WV/565.516, *C. D. Preston*; 2n = 36.

Drosanthemum floribundum (Haw.) Schwantes: Newman House, St Mary's, Isles of Scilly, GR 00/898.108, *C. D. Preston*; 2n = 36.

Erepsia heteropetala (Haw.) Schwantes: Buzza Hill, St Mary's, Isles of Scilly, GR 00/905.103, *C. D. Preston*; 2n = 18.

Lampranthus roseus (Willd.) Schwantes: Le Gouffre, Guernsey, GR WV/294.743, *C. D. Preston*; 2n = 36.

Oscularia deltoides (L.) Schwantes: 'Juliet's Garden', Porthloo, St Mary's, Isles of Scilly, GR 00/909.115, *C. D. Preston*; 2n = 18.

Ruschia caroli (L. Bolus) Schwantes: Old Town Bay, St Mary's, Isles of Scilly, GR 00/90.10, *C. D. Preston*; 2n = 18.

Watsonia, **17**, 247–264 (1988)

Taxonomy, morphology and distribution of *Atriplex* hybrids in the British Isles

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ABSTRACT

A study based on field, culture and experimental work delineates six hybrids in the genus *Atriplex* indigenous to the British Isles. Detailed morphological descriptions are given and distribution maps and illustrations are provided for *A. glabriuscula* Edmondston × *A. longipes* Drejer; *A glabriuscula* × *A. praecox* Hülphers; *A. glabriuscula* × *A. prostrata* Boucher ex DC.; the variable *A. longipes* × *A. prostrata* (= **A.** × **gustafssoniana** Taschereau, **hybr. nov.**, which includes var. **gustafssoniana** and var. **kattegatensis** (Turesson) Taschereau, **comb. et stat. nov.**); *A. littoralis* L. × *A. prostrata* (= **A.** × **hulmeana** Taschereau, **hybr. nov.**); and *A. littoralis* × *A. patula* L. Hybrid derivatives involving *A. longipes*, widespread on the coasts of the British Isles, are responsible for many of the identification problems in the *A. prostrata* group.

INTRODUCTION

Jones (1975a) summarized the literature reports of *Atriplex* hybrids in the British Isles and recorded the presence of seven natural hybrids. As Jones herself noted, however, some of the hybrids reported on the basis of intermediate specimens were doubtful, and as I have explained elsewhere (Taschereau 1986), some of these reports are almost certainly wrong.

Hybrids in *Atriplex* are particularly difficult to recognize without a foundation of experimental work and field studies. One reason for this is the extensive variation, both genetic and phenotypic, exhibited by so many of the species. Genetically distinct morphs, differing in such characters as leaf shape, habit or colour, are known in several species (Taschereau 1985a). Morphological and habit changes occur also in response to environmental factors. This phenotypic plasticity of *Atriplex* has long been recognized as complicating the identification of many species. As long ago as 1860, for example, C. C. Babington wrote that, "*Atriplexes* on fat land are amongst the most undeterminable of plants" (A. M. Babington 1897).

Another complicating factor in *Atriplex* hybrid and species recognition has been the widespread occurrence of hybrid derivatives. Like their facultatively autogamous parents, hybrid derivatives perpetuate themselves by selfing. Unlike many first or second generation hybrids, they are highly fertile, often range well beyond the parent populations, and may occupy an ecological niche different from that of either of the parents. Unaware of their hybrid nature, taxonomists have dealt with these species-like entities in various ways. *Atriplex longipes* × *prostrata*, for example, has given rise to a number of more or less distinctive morphs, some of which are very widespread. Babington's (1841) *A. rosea* (non L.) is, in part, a derivative of this hybrid (see, for instance, the sheet in **E** labelled "*A. rosea*, Little Hampton Sussex, 1837 com. *L. W. Borrer*", in Babington's handwriting and printed "from Charles C. Babington"); Westerlund's (1861) type collection of *A. patula* var. *bracteata* is also a derivative of this hybrid, as is Turesson's (1925) *A. longipes* subsp. *kattegatense*.

Except for *A. laciniata* L., all the *Atriplex* species indigenous to the British Isles are known to hybridize. With the experimental studies of Turesson (1925), Hulme (1957), Gustafsson (1972, 1973a, 1973b, 1976) and my own studies (Taschereau 1985b, 1986), it is possible to distinguish many of the *Atriplex* hybrids in the British flora and to identify most of them with reasonable certainty. This paper describes and illustrates six hybrids and one hybrid variant, gives their distribution, and discusses their taxonomy.

MATERIALS AND METHODS

The field, cultivation and experimental work upon which this study is based have been set forth in detail in Taschereau (1985a, b, 1986). Data from field studies were supplemented by specimens sent to me between 1977 and 1978 by participants in the B.S.B.I. *Atriplex* Survey.

Material from the following herbaria was studied: **ABD**, **BM**, **C**, **CGE**, **DBN**, **E**, **K**, **LD**, **LIV** (incl. herb. Barbara Hulme), **LIVU**, **MANCH**, **NMW**, **OXF**, **S**, **SLBI**, **TCD** (abbreviations according to Kent & Allen (1984) and Holmgren *et al.* (1981)). I have annotated the entire holdings of the following herbaria: **ABD**, **CGE**, **DBN**, **E**, **LIV**, **LIVU**, **TCD**. Also, approximately half of the large holdings of **NMW** have been annotated by me.

My collections, including those of the B.S.B.I. Survey, are deposited in **MANCH**, except for type specimens as indicated in the text. A duplicate set of Gustafsson's (1976) hybrid collections used for reference is in my possession (**herb. Taschereau**). Each dot on the distribution maps of the hybrids is supported by one or more specimens filed in **MANCH**.

ATRIPLEX LONGIPES: A KEY TAXON

The occurrence of *A. longipes* in the flora of the British Isles was confirmed only in 1977, although its presence was earlier suspected (Hulme in Aellen 1964; Jones 1975b). Taschereau (1985b) indicated that *A. longipes* is the key to understanding much of the confusing variation within the *A. prostrata* group. *Atriplex longipes* hybridizes with *A. prostrata* and with *A. glabriuscula*; species that only rarely hybridize with each other. The hybrid derivatives involving *A. longipes* are widely distributed on the coasts of the British Isles and occur also in inland salt marshes. They are usually highly fertile and often species-like in their behaviour. Morphologically, they may resemble one or the other parent, or be distinct from either parent. They may occur in the same habitat as one or the other parent species, or occupy a different ecological niche. This situation, and some of the frequent identification problems it has given rise to, are summarized in Fig. 1.

Many of the long-recognized taxonomic problems in the *A. prostrata* group in Britain have been caused by the presence of hybrid derivatives involving *A. longipes*. There yet remains, however, a residue of plants, especially from the northern and north-western coasts of Scotland and the coasts of Shetland, which have not been satisfactorily identified except to group.

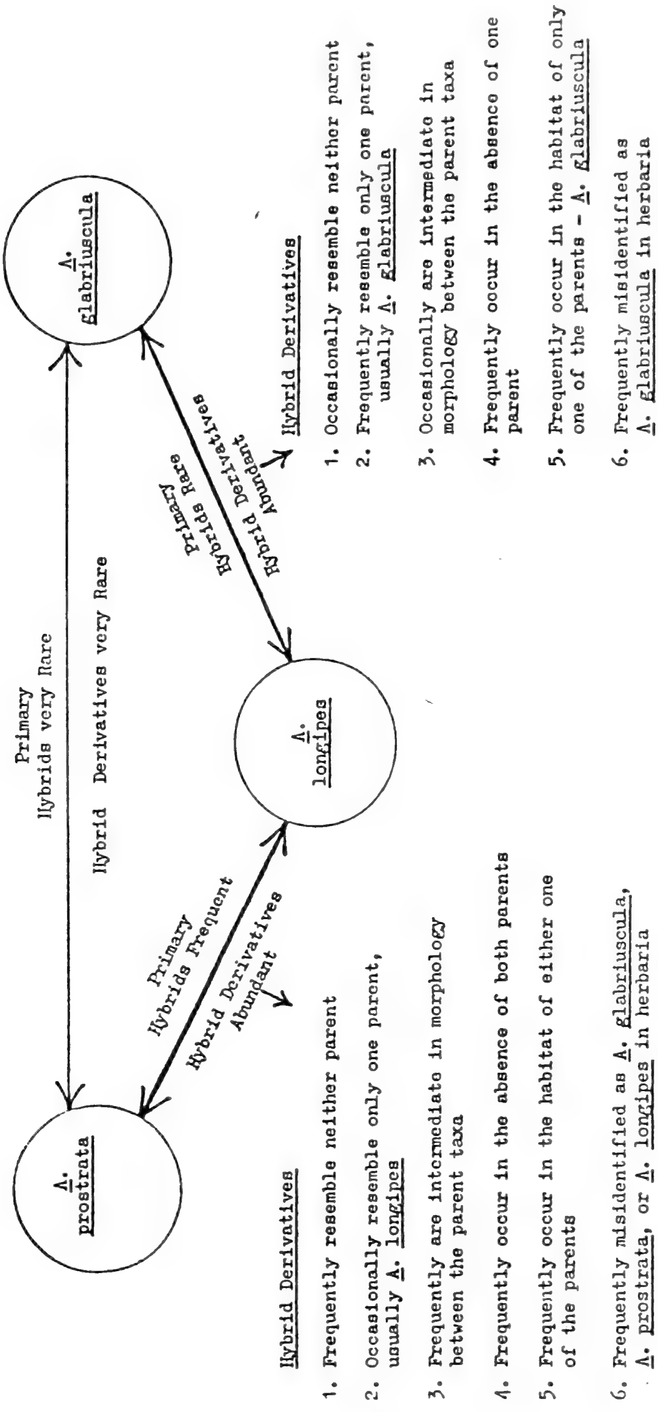
DESCRIPTIONS

1. **A. glabriuscula** Edmondston × **A. longipes** Drejer (Fig. 2)

Most plants resembling *A. glabriuscula* in habit and general morphology. Prostrate or ascending. Lower leaves triangular, or rhombic to ovate-lanceolate; base cuneate, obtuse or truncate. Bracteoles rhombic or ovate-lanceolate, herbaceous at the apex, frequently large (10–20 mm long) and foliose, some of the axillary ones stalked, margins united almost up to the middle or only near the base, thickened towards the base by a moderately to strongly developed silvery brown spongy tissue, dorsal surface often strongly reticulate-veined in the lower part.

Habitat and Distribution. Exposed coastal beaches, frequently with *A. glabriuscula*. Hybrid derivatives between *A. glabriuscula* and *A. longipes* are frequent on the coasts of northern Scotland and north-western England. Reported by Gustafsson (1976) as rare in western Scandinavia with one record from Bodö, Norway. The distribution in the British Isles is shown in Fig. 3.

Variation and Biosystematics. Hybrid derivatives, although often occurring in the same habitat as *A. glabriuscula*, are well-established and independent of the parent taxa. The hybrid was artificially synthesized by Gustafsson (1973a). Seed germination of F_1 artificial hybrids was only between 10% and 30%, although the pollen stainability of F_2 plants was between 80% and 100% (Gustafsson 1973a).



Hybrid Derivatives

1. Frequently resemble neither parent
2. Occasionally resemble only one parent, usually A. longipes
3. Frequently are intermediate in morphology between the parent taxa
4. Frequently occur in the absence of both parents
5. Frequently occur in the habitat of either one of the parents
6. Frequently misidentified as A. glabriuscula, A. prostrata, or A. longipes in herbaria

Hybrid Derivatives

1. Occasionally resemble neither parent
2. Frequently resemble only one parent, usually A. glabriuscula
3. Occasionally are intermediate in morphology between the parent taxa
4. Frequently occur in the absence of one parent
5. Frequently occur in the habitat of only one of the parents – A. glabriuscula
6. Frequently misidentified as A. glabriuscula in herbaria

FIGURE 1. Hybrid derivatives involving *A. longipes*.

FIGURE 2. *A. glabriuscula* × *A. longipes*.

The name *A. glabriuscula* f. *pedicellata* Abromeit has been applied to variants of this hybrid with large stalked bracteoles (Aellen 1960; Gustafsson 1976).

Diagnostic Characters. The hybrid is most frequently confused with *A. glabriuscula*, from which it can be distinguished by the stalks present on some of the bracteoles in the leaf axils, and the tendency of many bracteoles to develop large foliose tips and thickened, veiny basal portions.

2. **A. glabriuscula** Edmonston × **A. praecox** Hülphers (Fig. 4)

Most plants resembling *A. praecox* in leaf outline but similar to *A. glabriuscula* in bracteole morphology. Prostrate-spreading or ascending. Foliage mostly reddish or less commonly green, resembling *A. praecox*. Lower leaves lanceolate-triangular or ovate-lanceolate; base cuneate to

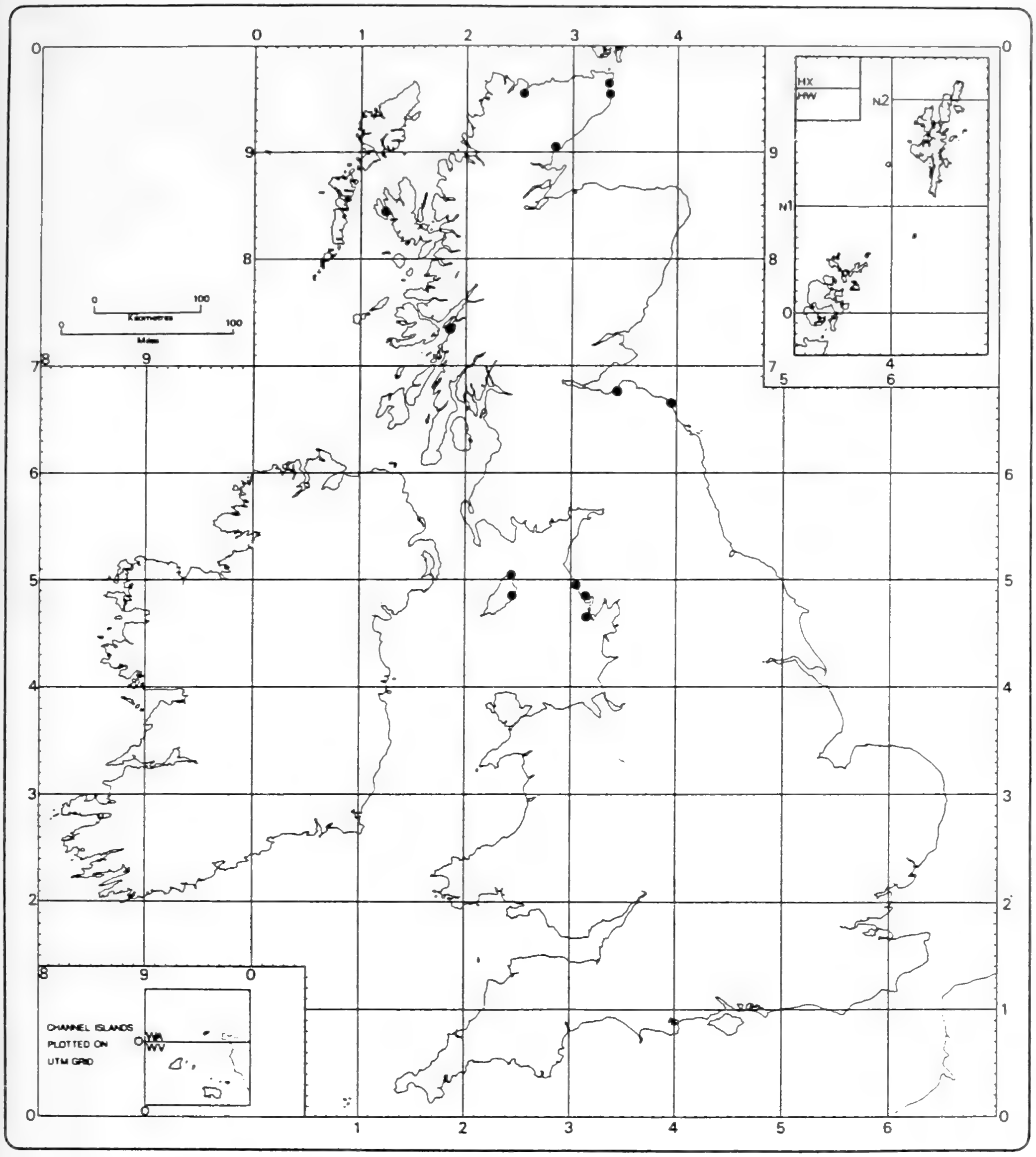


FIGURE 3. Distribution of *A. glabriuscula* × *A. longipes* in the British Isles.

obtuse. Upper leaves lanceolate to linear. Bracteoles rhombic, sessile or slightly stalked (stalks c. 0·5 mm long), margins united almost up to the middle, thick-spongy towards the base, dorsal surface smooth and without prominent veins.

Habitat and Distribution. Very rare in north-western Scotland and Shetland where it occurs with *A. praecox* and *A. glabriuscula* at the margins of protected sea inlets. Reported by Gustafsson (1976) as rare in the northernmost parts of Norway. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. The hybrid was artificially synthesized by Gustafsson (1973a). In the artificial hybrids, pollen fertility and seed germination were greatly reduced. In two crosses, one had

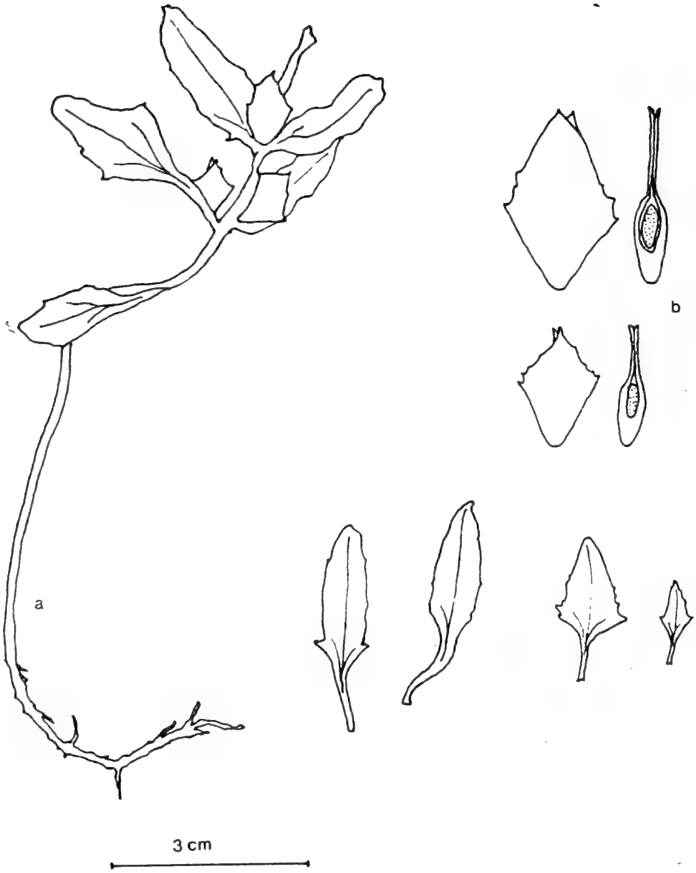


FIGURE 4. *A. glabriuscula* × *A. praecox*. a) Habit, b) Bracteoles (not to scale), c) Leaf variation.

73% and the other 67% stainable pollen, and only 40% to 50% of the seeds germinated (Gustafsson 1973a).

Diagnostic Characters. The small, often reddish, leaves resembling those of *A. praecox*, in combination with the thick-spongy bracteole characteristic of *A. glabriuscula*, will distinguish this hybrid.

3. **A. glabriuscula** Edmondston × **A. prostrata** Boucher ex DC. (Fig. 6)

Plants generally intermediate in morphology between the parent species; ascending. Lower leaves triangular as in the parents; base subcordate, truncate to obtuse. Inflorescence spiciform as in *A. prostrata*. Bracteoles sessile, smaller than *A. glabriuscula* and in more densely packed glomerules, thick-spongy, margins united almost up to the middle, dorsal surface bi-tuberculate or smooth, without prominent veins. Seeds mostly less than 3·0 mm wide, radicle variously positioned and directed.

Habitat and Distribution. Middle beach zone on coastal beaches with the parent species. Rare from southern England in v.c. 15 (Badmin 1978) to south-western Scotland in v.c. 74 and on the eastern

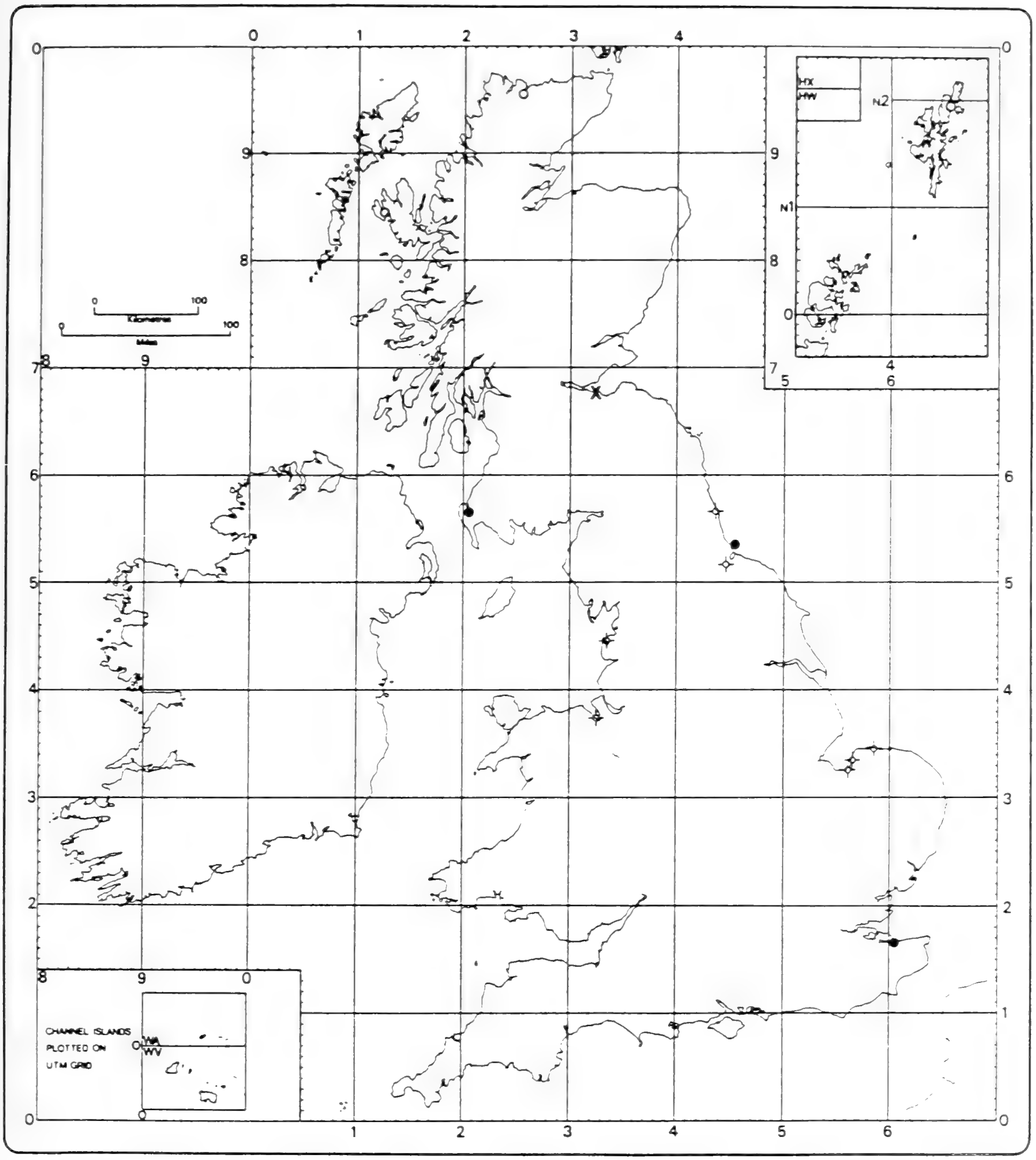


FIGURE 5. Distribution of *Atriplex* hybrids in the British Isles: ○ *A. glabriuscula* × *A. praecox*; ● *A. glabriuscula* × *A. prostrata*; -○- *A. littoralis* × *A. prostrata*; × *A. littoralis* × *A. patula*.

coast of England in v.c. 66. Reported by Gustafsson (1976) as relatively rare in the western parts of Scandinavia. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. The hybrid was artificially synthesized by Gustafsson (1973a). Most of the artificial hybrids had a high pollen stainability (four out of seven crosses had greater than 90% stainable grains), but seed germination was poor. Seeds from two of the crosses did not germinate and in the other seven crosses seed germination varied between 1% and 40% (Gustafsson 1973a).

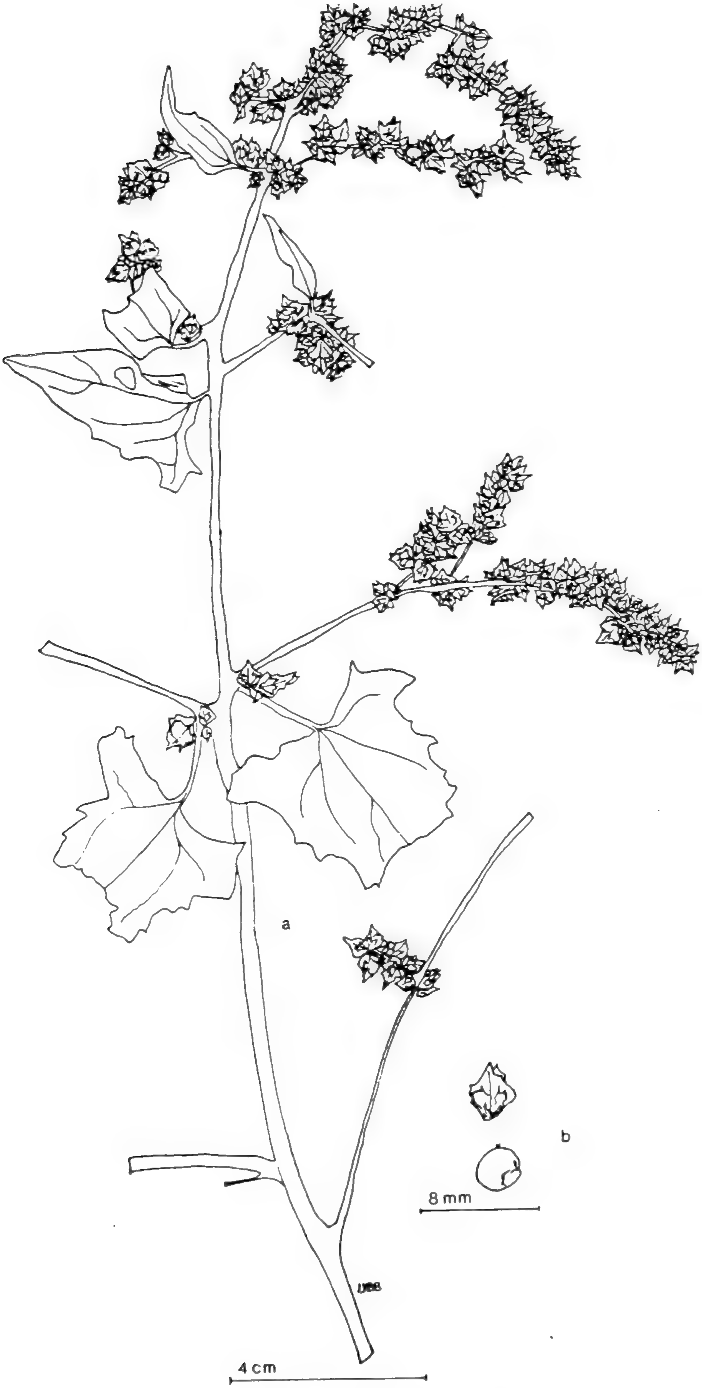


FIGURE 6. *A. glabriuscula* × *A. prostrata*. a) Habit, b) Bracteoles and seed.

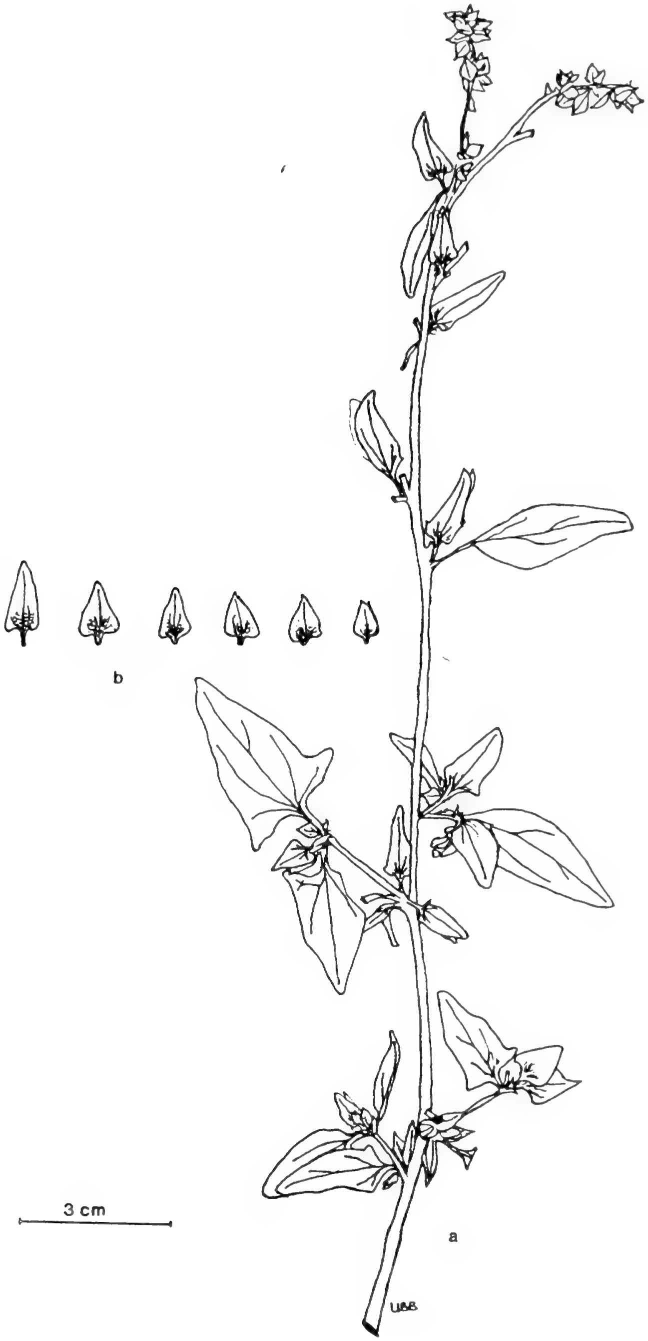


FIGURE 7. *A.* × *gustafssoniana* var. *gustafssoniana*. a) Habit, b) Variation in bracteoles.

Germination of seeds from spontaneous hybrids in nature was also low (less than 40%) (Gustafsson 1973b).

From identified material in herbaria, it is clear that hybrid derivatives of *A. longipes* × *A. prostrata* and *A. longipes* × *A. glabriuscula* have occasionally been mistaken for *A. glabriuscula* × *A. prostrata*. This hybrid is rare; it is not common as suggested by Moss & Wilmott (1914) and by Jones (1975a), and earlier records should be re-examined.

Diagnostic Characters. The size, morphology and arrangement of the bracteoles are most useful in distinguishing the hybrid from its parents: the bracteoles are thick-spongy and frequently bi-tuberculate as in *A. glabriuscula*, but generally much smaller and arranged in somewhat dense, leafless, spiciform inflorescences similar to those of *A. prostrata*.

4. **Atriplex** × **gustafssoniana** Taschereau, **hybr. nov.**
HOLOTYPUS: Snettisham, N. W. Norfolk, v.c. 28. Margin of *Phragmites australis* stand in open area of saltmarsh by the coast, 18 September 1976, *Taschereau & Libbey 76–12* (**DAO**).

Hybrida ex *A. longipes* Drejer et *A. prostrata* Boucher ex DC. orta. Folia inferiora elongato-triangularia vel ovato-lanceolata, basi truncata vel cuneata. Quidam bracteoli in axillo foliorum superiorum magni, tenuiter herbacei, petiolati, angulis lateralibus acutis saepe bene evolutis, superficie plusminusve forte reticulo-venata basin versus.

i) var. **gustafssoniana** (Fig. 7)
Atriplex patula var. *bracteata* Westerlund, *Sveriges Atriplices* 57 (1861). LECTOTYPE: Sweden, Skåne; sheet labelled "Atriplex patula Lin. – bracteata Wester., Skåne, C.A.W." (**S**); chosen by Taschereau in *Watsonia* **15**: 204 (1985).

Erect, ascending or prostrate, with long-spreading lower branches. Lower leaves elongate-triangular in erect forms, or ovate-lanceolate in some prostrate forms, usually much longer than wide (length/width ratio 1·5–2·5); base cuneate to truncate. Bracteoles 4–9 mm long, triangular, sessile or stalked but usually some with stalks 0·5–5·0 mm long present in the axils of the upper leaves and branches; thin-herbaceous, sometimes becoming foliose; margins united at the base, lateral angles pointed and often strongly developed; dorsal surface often strongly reticulate-veined toward the base.

Habitat and Distribution. Coastal sand and shingle beaches, often remote from the parent species. In coastal, estuarine and inland salt marshes, frequently in stands of *Agropyron pungens* or *Juncus maritimus* and at the margins of *Phragmites australis* stands. One of the commonest *Atriplex* taxa on the coasts and in estuaries around the British Isles and occasional in inland saltmarsh vegetation at Nantwich, Cheshire and Preesall, Lancashire. Reported by Gustafsson (1976) as common on the western coast of Sweden northwards to the southern parts of Norway, and as relatively rare in Denmark and the Baltic area. Most of the *Atriplex* populations along the Swedish western coast investigated by Gustafsson (1973b) included individuals of hybrid origin. The distribution in the British Isles is shown in Fig. 8.

Variation and Biosystematics. The cultivated progeny of most wild *A. longipes* × *A. prostrata* derivatives exhibited a mixture of parental characters. Many plants, however, showed a degree of segregation that gave some indication of their parentage (Taschereau 1986). In the artificial hybrids (Gustafsson 1973a) pollen stainability was high (16 of 22 crosses had greater than 80% stainable pollen grains), but seed germination was greatly reduced. Germination varied from 0% to 60% but in 20 out of 23 crosses less than 30% germinated. In the wild hybrids examined by Gustafsson (1973b) both pollen fertility and seed germination were reduced. The F_1 hybrids in many of the artificial crosses were morphologically similar to *A. prostrata* even when *A. longipes* was used as the female parent (Gustaffson 1973a). A similar situation has been observed in wild British plants (Taschereau 1985b). In parts of Scandinavia where grazing has disturbed the habitat, introgressive hybridization between *A. longipes* and *A. prostrata* has given rise to a more or less continual gene

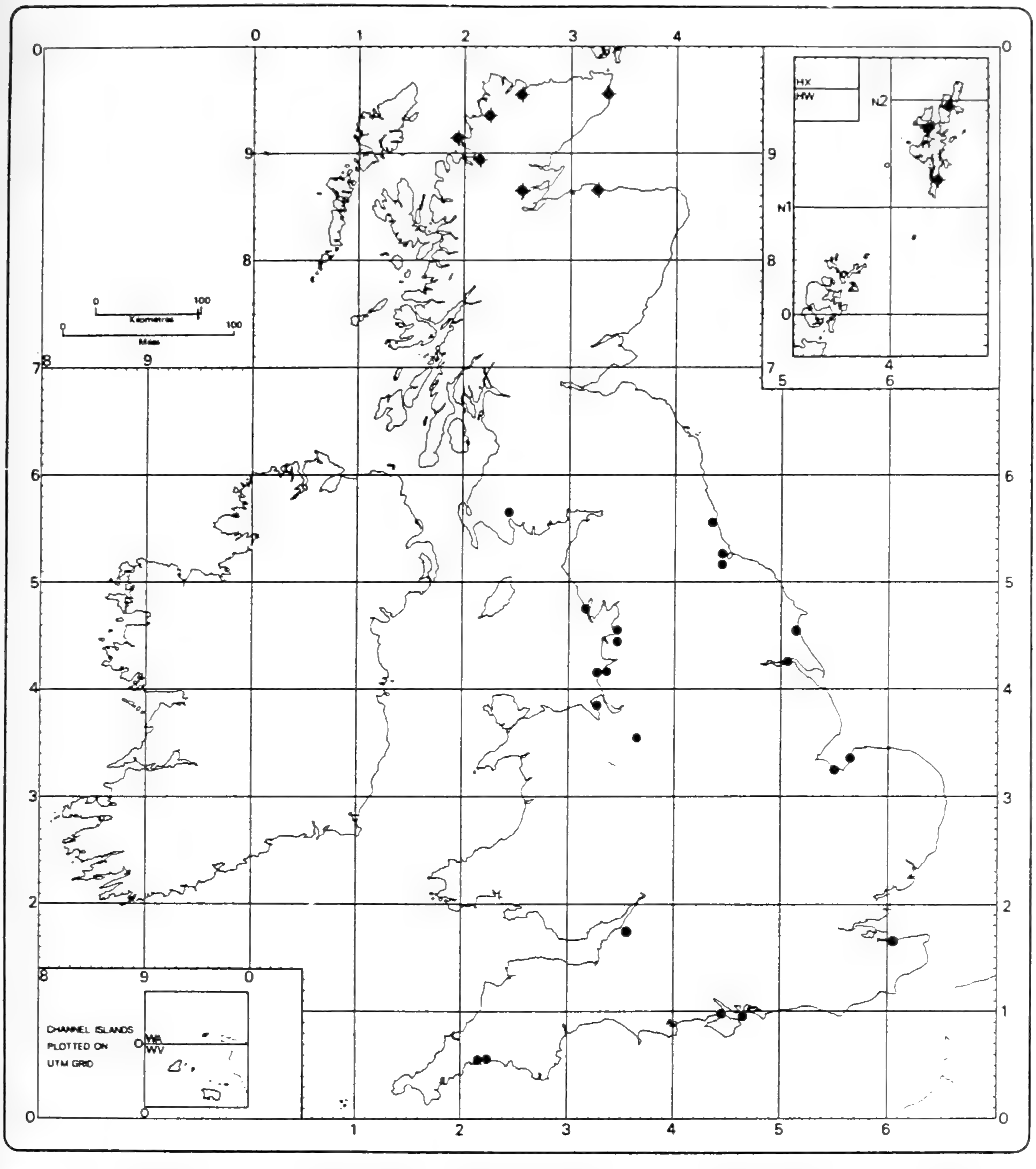


FIGURE 8. Distribution of *A.* × *gustafssoniana* in the British Isles: ● var. *gustafssoniana*, ◆ var. *kattegatensis*.

flow between these species (Gustafsson 1974). This seems to be the situation in most parts of Britain where, according to Adam (1978), undisturbed estuarine salt marsh vegetation (the habitat of *A. longipes*) is virtually non-existent.

Hybrid derivatives are well established and independent of the parent species. They are extremely variable and almost every combination of parental characters has been observed in the field. On the basis of size, habit and habitat our plants can be broadly placed into two groups: 1) Salt marsh variants. Large ± succulent plants, erect, spreading to straggling, up to 1 m high; stems strongly angled; leaves large, elongate-triangular, with cuneate to truncate base; occurring in tall salt marsh vegetation or at the margins of such communities. 2) Beach variants. Small non-succulent or more or less succulent plants, prostrate, decumbent or weakly erect; lower branches wide-spreading and often longer than the central axis; angularity of stems variable; occurring on ± exposed coastal beaches and at the margins of or in sparsely covered or open areas of coastal salt marsh vegetation.

Diagnostic Characters. In the axils of some of the upper leaves occur large thin-herbaceous, stalked bracteoles with lateral angles pointed and often strongly developed and the dorsal surface more or less strongly reticulate-veined toward the base. The occurrence of these characteristic bracteoles in combination with elongate-triangular or ovate-lanceolate lower leaves at least some of which have a more or less truncate base is diagnostic of this hybrid.

Nomenclatural Note. The type specimen of *Atriplex patula* var. *bracteata* Westerlund is a hybrid derivative between *A. longipes* and *A. prostrata*. Plants such as this are part of the myriad of beach variants comprising the hybrid derivatives described here under var. *gustafssoniana*. While I have myself seen specimens along the Swedish coast at Malmö that are similar to the type, the characters distinguishing such plants are, in my view, not constant enough to merit further formal taxonomic recognition. In addition, there has been considerable confusion regarding the application of the name var. *bracteata* Westerlund since Aellen (1960) applied it (as f. *bracteata*) to plants of *A. patula* L. s.s. with foliose bracteoles (ennatia), and Fernald (1950) applied the name *A. patula* var. *bracteata* to plants described as very similar to typical *A. patula* "but with fruiting bracts 1–1·5 cm long" occurring on marshes of Cape Breton, Nova Scotia. Fernald's specimen from Cape Breton (**GH**!) representing his var. *bracteata* is, like Westerlund's type, a hybrid derivative in the *A. prostrata* group. Furthermore, Westerlund's (1861) description is not sufficiently detailed to exclude certain variants of *A. patula* sens. str., and his statement, "Hab. rara ad vias circa Lund et in litore marino ad Malmö Scaniae" would seem to include the ruderal *A. patula* ("ad vias circa Lund"), along with the obligate halophytic derivatives of *A. longipes* × *A. prostrata* ("in litore marino ad Malmö Scaniae").

ii) var. **kattegatensis** (Turesson) Taschereau, **comb. et stat. nov.** (Fig. 9)
A. longipes subsp. *kattegatense* Turesson in *Lunds Univ. Arsskr.*, N.F. Adv. 2, **24** (4): 4 (1925).
LECTOTYPE: Sweden, Bohuslan, Tanums socken, Otteron, August 1880, *H. Thedenius* (**S**); the specimen annotated "A. longipes kattegatense Turess. nov. subsp.", to the middle-left, chosen by Gustafsson in *Opera Botanica* **39**: 29, 31 (1976).

Plants 10–30 cm, prostrate to decumbent, spreading with the lower branches longer than the central axis. Stems sub-angular, striate, green and stramineous striped or reddish. Branches opposite to sub-opposite in the lower region of the central axis but often barely separated by extremely short internodes. Foliage bluish-green, frequently reddish, succulent; mature lower and upper leaves glabrous; juvenile leaves glabrous above, sparsely farinose on the undersurface. Lower leaves 2·0–3·5 cm long, 1·0–2·5 cm wide, with a pair of outpointing to forward-curving basal lobes; margins irregularly serrate or entire; apex acute; base cuneate. Upper leaves smaller, linear-lanceolate, without or with basal lobes; margins entire or weakly toothed. Inflorescence axillary to the base of the plant and shortly terminal, leafy to the tip. Bracteoles 3·5–5·0 mm long, at least some shortly stalked (stalks 0·5–1·0 mm long), rhombic to triangular-lanceolate or ovate-lanceolate; apex acute or acuminate; base cuneate; margins entire, united at the base or somewhat higher up to the lateral angles; lateral angles pointed or rounded, not strongly developed; mostly herbaceous and thin but sometimes slightly thickened toward the base by the presence of spongy tissue; dorsal surface smooth or with a few short, weak appendages; venation obscure or somewhat prominent towards the base. Seeds polymorphic, black or brown, orbicular, 1·5–2·5 mm wide; radicle sub-basal, obliquely up-pointing.

Habit and Distribution. Exposed coastal beaches close to the salt water where the vegetation is very sparse; often with *A. praecox* on the shores of somewhat less exposed sea inlets. Frequent in northern Scotland and occasional in Shetland. Reported by Gustafsson (1973b) as common on the western coast of Sweden. The distribution in the British Isles is shown in Fig. 8.

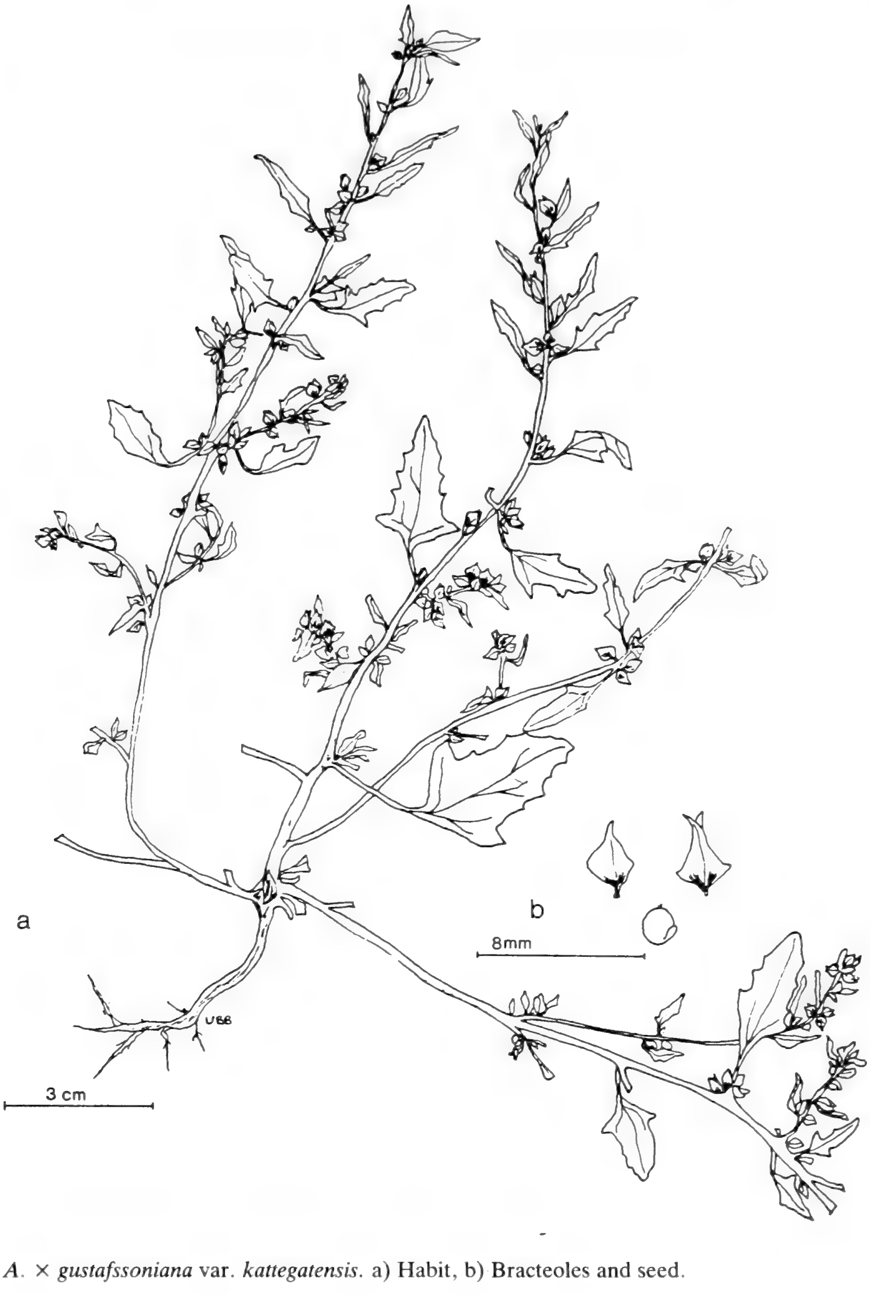


FIGURE 9. *A.* × *gustafssoniana* var. *kattegatensis*. a) Habit, b) Bracteoles and seed.

Variation and Biosystematics. Gustafsson's (1973b) experimental work with this taxon indicates it is probably a more or less well established product of hybrid origin. Some of the cultivated offspring of var. *kattegatensis* raised by Gustafsson (1973b) from seeds collected in nature showed considerable morphological variation. He observed segregates similar to *A. longipes* and to *A. prostrata* as well as intermediate forms. Some offspring, however, did not differ from the parent and showed no indication of segregation. Likewise, plants cultivated from var. *kattegatensis* collected at Ullapool, v.c. 105, did not segregate (Taschereau 1986). These non-segregating forms may represent ancient

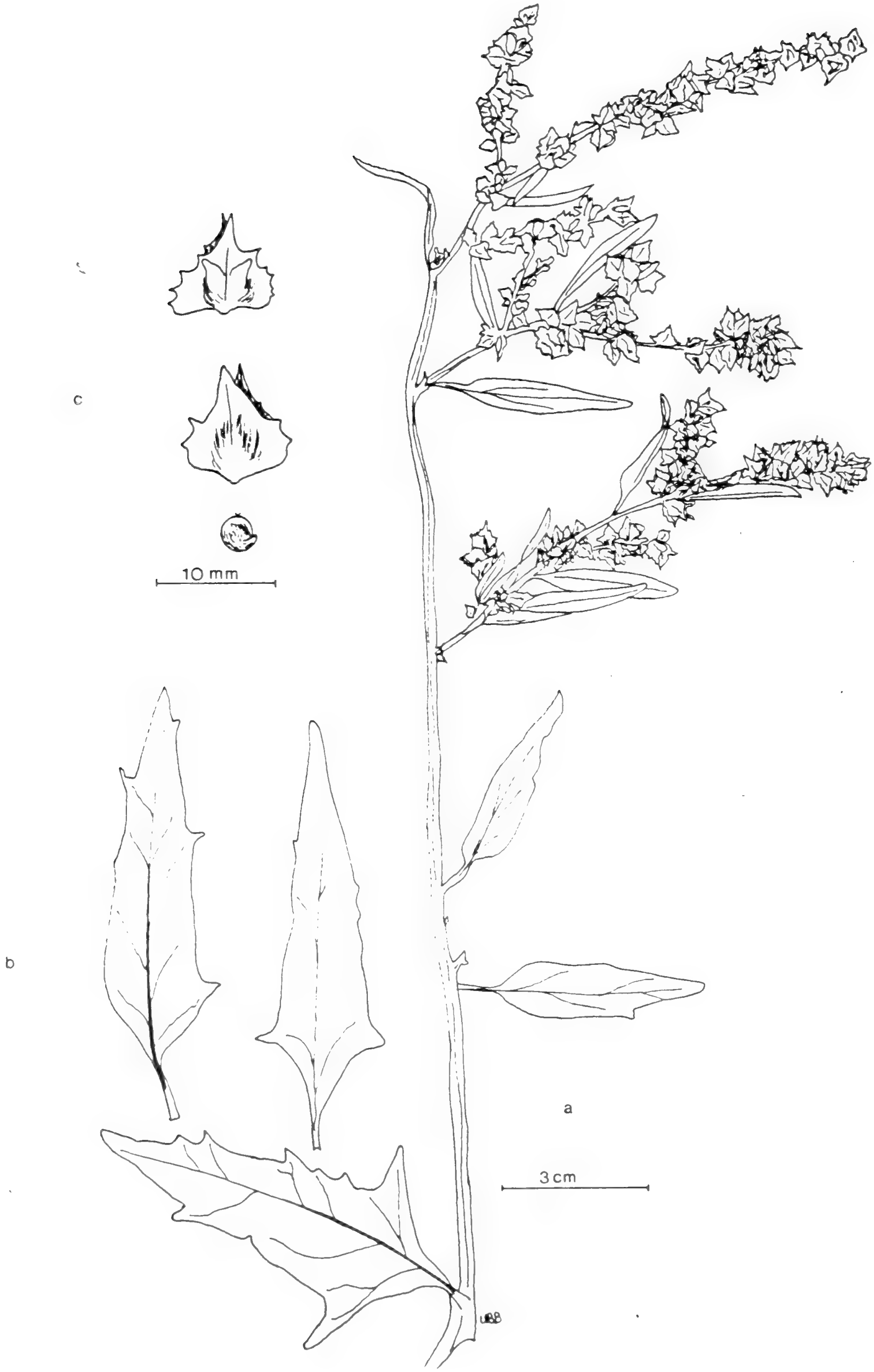


FIGURE 10. *A.* × *hulmeana.* a) Habit, b) Leaf variation, c) Bracteoles and seed.

or historical hybrids that have arisen by stabilization of an F_2 or later segregant adapted to the specialized exposed habitat that is colonized by neither of the parents. In the British Isles, var. *kattegatensis* appears to have primarily a northern distribution and specimens from southern regions such as those from v.c. 15 (Badmin 1978) require further study.

Hybrids. None have been identified from nature. Gustafsson (1973b) has made experimental hybrids between var. *kattegatensis* and *A. longipes*, *A. praecox* and *A. prostrata*. Pollen fertility in the majority of crosses was greater than 80% but hybrids with reduced fertility were common. Morphological variation in the F_1 and F_2 progenies of the experimental hybrids was considerable and difficult to categorize because of the free recombination of morphological characters that occurred.

5. **Atriplex × hulmeana** Taschereau, **hybr. nov.** (Fig. 10)
HOLOTYPUS: Wolferton, Norfolk, England, 18 September 1976, *Taschereau & Libbey 76–24* (**DAO**).

Hybrida ex *Atriplex littoralis* L. et *A. prostrata* Boucher ex DC. orta. Folia primaria succulenta, triangulari-lanceolata, cum lobis basalibus patentibus vel falcatis, basi cuneata. Bracteolae triangulares vel ovati-triangulares, crassae, spongiosae, basibus conjunctae.

The hybrid is named after Barbara Hulme, British botanist and first person to produce experimental hybrids in *Atriplex* by controlled crossing (Hulme 1957, 1958). Her elegant work provided an experimental basis for understanding the relationship of *A. patula* to *A. littoralis* and to members of the *Hastata* complex (*A. prostrata* group) in Britain.

Erect, very robust plants with thick stems and ascending branches. Foliage dark green, glabrous, very succulent. Lower leaves triangular-lanceolate with a pair of strongly developed out-pointing to forward-curving basal lobes; length at least twice the width; margins irregularly sinuate-dentate, attenuate to the apex; base strongly cuneate. Upper leaves lanceolate, without basal lobes or with a single lobe developing on one side only, entire or with few teeth. Bracteoles 5–10 mm long, sessile, broadly triangular to ovate-triangular; apex acute; base truncate to cuneate; margins denticulate or with only a few teeth, united at the base; lateral angles rounded and weakly developed; thick-spongy; dorsal surface strongly bi-tuberculate or smooth; venation obscure. About 70–80% of the bracteoles contain well-developed seed. Both large-brown and small-black seed types are frequent in the same plant. Segregants showing a wide range of character combinations sometimes occur amongst the F_1 plants described above. Many of the segregants are largely sterile and often weak-stemmed, but some are vegetatively very vigorous and develop into quite prominent plants. The following three variants appeared in cultivation and are sufficiently common in the field to be mentioned.

1. *Patula*-leaf variant. Plants with leaves like *A. patula* that possess the falcate basal lobes so characteristic of this species.
2. *Serrata*-leaf variant. Plants with markedly sinuate-dentate leaves like extremes of plants formerly called *A. littoralis* var. *serrata*.
3. *Gigas* variant. Plants up to 1 m high with thick stems and gigantic leaves with ovate-lanceolate irregularly lobed lamina up to 15 cm long and 4 cm wide.

Habitat and Distribution. Disturbed habitats where the parent species are present in abundance: disturbed banks of estuaries recently dredged, earthen sea walls less than three years old, salt marshes disturbed by rabbit grazing. Occasional on the eastern and western coasts of England in v.cc. 28, 58, 60, 66. Jones (1975a) states it has been recorded as rare in Denmark. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. See Taschereau (1986) for a detailed discussion. Jones' (1975a) report of the putative hybrid *A. glabriuscula* Edmondston × *A. littoralis* L. probably refers to *A.* × *hulmeana* as discussed in Taschereau (1986).

Diagnostic Characters. The characteristic shape of the large succulent lower leaves in combination with the spongy-thick bracteoles is diagnostic of this hybrid.

FIGURE 11. *A. littoralis* × *A. patula*.

6. **Atriplex littoralis** L. × **A. patula** L. (Fig. 11)

Erect, up to 0·5 m high. Lower leaves up to about 6 cm long and 3 cm wide, ovate-lanceolate to rhombic with a pair of forward-curving basal lobes; succulent, glabrous, dark glossy-green; margins irregularly serrate to sinuate-dentate; base strongly cuneate. Upper leaves smaller, similar to the lower ones or lanceolate to linear with or without basal lobes, entire or with a few teeth. Bracteoles rhombic, sessile; margins denticulate, united up to the middle; thick-spongy, tuberculate; occurring in dense terminal inflorescences. The majority of bracteoles are empty and collapsed. Dispersed between these sterile bracteoles, however, are occasional larger, well-formed, filled out bracteoles that contain seed. From one to five of the larger fertile bracteoles occur in the inflorescenses of most branches.

Habitat and Distribution. Disturbed weedy ground by the coast where both the parents are growing together. Known only from one locality in Scotland at Leith Docks, Edinburgh, v.c. 83. Reported by Turesson (1925) from Lomma and Torekov along Öre Sund in south-western Sweden. The distribution in the British Isles is shown in Fig. 5.

Variation and Biosystematics. This hybrid has been experimentally synthesized three times: by Turesson (1925), by Hulme (1957) and by Taschereau (1986), but its occurrence in nature is very rare. It has been looked for on numerous occasions in locations where the parents were growing together but found only once. A published record from Findhorn, v.c. 95, Scotland (Webster 1979) is a mistake. Subsequent to publication of this record, I changed my original identification of the hybrid specimen to *A. littoralis* × *A. prostrata*. For a detailed discussion of the biosystematics see Taschereau (1986).

Diagnostic Characters. The green, densely spiciform inflorescence consists mainly of small empty uniform bracteoles, but on almost every inflorescence branch, scattered among the green sterile bracteoles, one or two large grey-black seed-containing bracteoles stand out. The plants resemble *A. littoralis* in habit, but the lower leaves are similar to those of *A. patula*. The bracteoles are spongy-thick as in *A. littoralis* but united almost to the middle as in *A. patula*. In early November, the bright dark green colour of the hybrids makes them stand out strongly from the surrounding vegetation. The parent species by this time are mostly brown and dying.

ACKNOWLEDGMENTS

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Hybridization between *Polygonum mite* Schrank, *P. minus* Huds. and *P. hydropiper* L. in Northern Ireland with comments on their distinction

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ABSTRACT

Polygonum mite Schrank, *P. minus* Huds. and *P. hydropiper* L., in *Polygonum* sect. *Persicaria* (Miller) DC. occur together around Lough Neagh, Northern Ireland. Initial observations of these species had suggested the presence of intermediate plants of possible hybrid origin. Populations from two sites at the Lough were examined for hybridity using multivariate analyses, and by measurement of pollen fertility. Most plants could be assigned to one of the three species, but a few were almost certainly hybrids between *P. mite* and *P. minus* (= *P.* × *wilmsii* G. Beck). *P. hydropiper* did not appear to hybridize with the other species, although *P. mite* and *P. hydropiper* may approach each other in their vegetative morphology. The characters which best distinguish the three species are described and discussed.

INTRODUCTION

Polygonum mite Schrank, *P. minus* Huds. and *P. hydropiper* L. are closely related species within *Polygonum* sect. *Persicaria* (Miller) DC. Of the three, *P. mite* is considered to be the least common, occurring mainly in south-eastern England and Northern Ireland (Perring & Walters 1976). *P. minus* is rather rare, although scattered throughout the British Isles, while *P. hydropiper* is common and widely distributed (Lousley & Kent 1981).

Timson (1965, 1966, 1975) carried out a series of studies on hybridization in sect. *Persicaria*. He found that most species are rarely visited by insects, produce very sticky pollen and are usually self-pollinated before the flower opens. He concluded that interspecific hybridization in sect. *Persicaria* would be rare, but theoretically possible; both *P. mite* and *P. minus* are tetraploids with 2n = 40. Timson also suggested that hybridization could occur between *P. mite* and *P. hydropiper* (2n = 20), the former species being an autopolyploid derivative of *P. hydropiper*. Nevertheless Lousley & Kent (1981) noted that hybrids between each of the three species occur only rarely in Great Britain.

Webb (1984) carried out a survey of *P. mite* in Ireland, including an examination of all extant sheets of Irish material labelled *P. mite* at **TCD**, **DBN** and **BEL**. He concluded that all records for this species prior to 1969 were erroneous, being either *P. minus*, *P. hydropiper* or *P. persicaria* L. Furthermore he concluded that there is only one area in Ireland where *P. mite* could be found, this being the shores of Lough Neagh. Webb and J. R. Akeroyd visited this area in 1979 and found what they thought might be a complex hybrid swarm, which included *P. mite* and *P. minus*. *P. hydropiper* also occurs around the lake, although Webb did not regard it as part of the swarm. In the late summer of 1984, we visited a number of sites around Lough Neagh, and our observations suggested that some material was intermediate in morphology between *P. mite*, *P. minus* and *P. hydropiper*. However it was known that all three species show a wide range of phenotypic variation. Therefore we decided to investigate these populations in more detail, to establish whether any true hybrids were present.

MATERIALS AND METHODS

Plants were obtained from two sites on the shores of Lough Neagh, these being near Newport Trench harbour, Tyrone, v.c. H36 (GR H298.377) and Sands Bay, Co. Antrim, v.c. H39 (GR J312.372). At each site material of the three species was gathered randomly, and a total of 100 plants was collected and pressed. Voucher material has been deposited in **TCD**. 17 morphological characters (Table 1) were scored from this material, three observations of each character being made from each plant. Mean values per plant were then calculated for each character, and these data were analysed by Principal Components Analysis (PCA) using the BMDP4M PCA program. The data were also subjected to a Stepwise Discriminant Analysis (DSC) using the SPSS-X statistical package, to test the strength of disinctions between the species and to indicate their best distinguishing features (Parnell 1987).

TABLE 1. CHARACTERS USED IN NUMERICAL ANALYSES

1. Leaf length
2. Leaf width (maximum)
3. Distance between leaf base and widest point on leaf
4. Leaf venation (recorded on a scale of 1–2, where 1 = venation inconspicuous, 2 = venation conspicuous)
5. Mid-stem ochrea tooth length
6. Flower spike posture (recorded on a scale of 1–3, where 1 = erect, 2 = slightly nodding, 3 = nodding)
7. Spike length
8. Number of axillary flowers
9. Perianth length
10. Perianth width (maximum)
11. Perianth colour (recorded on a scale of 1–3, where 1 = red, 2 = pale pink, 3 = pink-green-white)
12. Perianth gland density
13. Nut length
14. Nut width (maximum)
15. Distance between nut base and widest point on nut
16. Degree of shininess of nut surface (recorded on a scale of 1–3, where 1 = shiny, 2 = somewhat shiny, 3 = dull)
17. Degree of roughness of nut surface (recorded on a scale of 1–3, where 1 = smooth, 2 = slightly rough, 3 = very rough)

Pollen fertility, as indicated by stainability tests, was determined using selected material of the species and their possible hybrids. Three to four ripe anthers from each specimen were dissected on a microscope slide and stained in Cotton Blue/Lactophenol for 30 minutes. The numbers of stained and unstained grains were then counted and percentage stainability calculated.

RESULTS

Most of the plants from both populations could be visually assigned to one of the three species (Figs. 1–3), and these findings were confirmed by both PCA (Fig. 4) and DSC. In the PCA, plants visually assigned to *P. mite* made up the largest group of points on the scatter plot, with smaller groups corresponding to *P. minus* and *P. hydropiper*. Principal components 1 and 2 accounted for 54% and 28% of the total variation respectively. The DSC distinguished each species at a 99·9+% level of confidence (all $F>17$, $P<0{\cdot}001$), and the characters picked out by this analysis that would best separate the species are given in Table 2. Using a combination of these it was possible to assign herbarium specimens to a taxon with little difficulty.

A few plants were found at both sites which seemed to be intermediate between *P. mite* and *P.*

FIGURE 1. *Polygonum mite* Schrank from Lough Neagh, Northern Ireland, August 1984, *Parnell & Simpson 73* (**TCD**). Scale bar = 20 mm.

TABLE 2. CHARACTERS WHICH BEST SEPARATE *POLYGONUM MITE*, *P. MINUS* AND *P. HYDROPIPER* (MEASUREMENTS ARE MEAN VALUES ± 95% CONFIDENCE LIMITS)

Character	*P. mite*	*P. minus*	*P. hydropiper*
1. Nut length (mm)	3·03±0·06	2·18±0·12	3·21±0·12
2. Nut width (mm)	1·83±0·43	1·12±0·24	2·20±0·07
3. Nut shininess	very shiny	somewhat shiny	dull
4. Perianth gland shape	flat	—	raised
5. Perianth glands, approx. no. per flower	12	0	83
6. Perianth length (mm)	3·66±0·06	2·48±0·33	4·10±0·15
7. Flower colour	pale pink to purplish-pink	usually reddish	pale pink to greenish-white
8. Spike	slightly nodding	erect	nodding
9. Mid-stem ochrea tooth length (mm)	1·76±0·09	1·67±0·26	0·30±0·16

FIGURE 2. *Polygonum minus* Huds. from Lough Neagh, Northern Ireland, August 1984, *Parnell & Simpson 32* (**TCD**). Scale bar = 20 mm.

FIGURE 3. *Polygonum hydropiper* L. from Lough Neagh, Northern Ireland, August 1984, *Parnell & Simpson 29* (**TCD**). Scale bar = 20 mm.

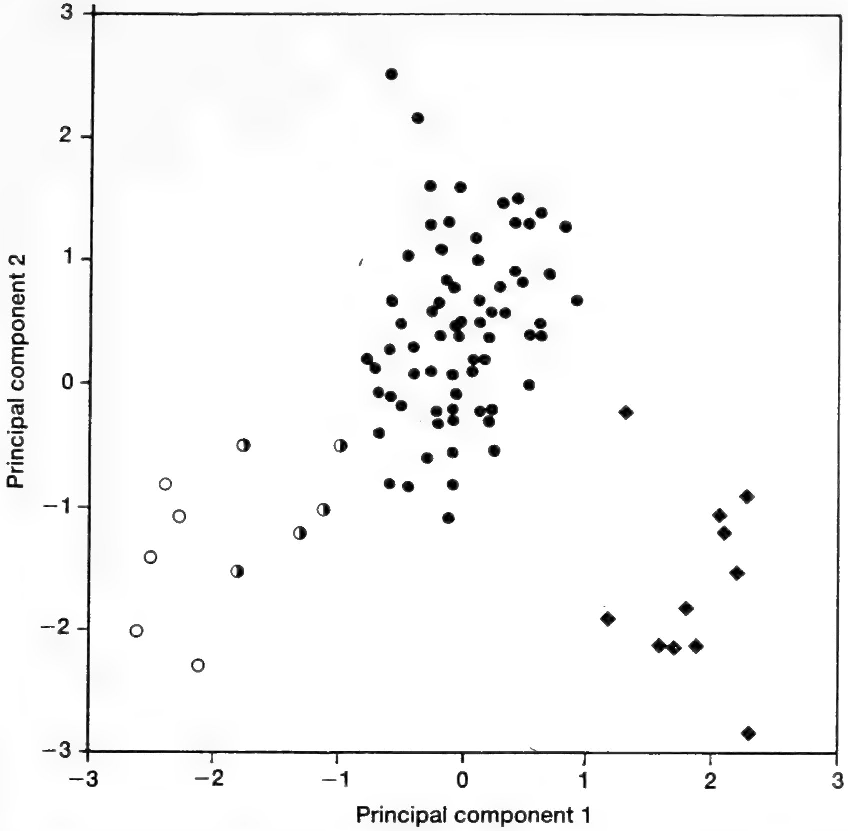

FIGURE 4. Principal components analysis on all plants sampled. ● = *P. mite*, ○ = *P. minus*, ◆ = *P. hydropiper*, ◑ = *P. mite* × *P. minus*.

minus. In particular these plants had fewer flowers than either *mite* or *minus* and produced fewer nutlets. One plant (specimen no. 71) was also found which appeared to be intermediate between *P. mite* and *P. hydropiper*. On the PCA scatter plot five points were located between the *mite* and *minus* groups and these corresponded with the visually intermediate material. One point was also located between the *hydropiper* and *mite* groups, which again corresponded with the visually intermediate plant.

The results of the pollen stainability tests are shown in Table 3. Plants which were not considered to be intermediate showed pollen stainability levels in the range 87·0–99·3%. Those plants which were intermediate between *P. mite* and *P. minus* showed a significantly reduced pollen stainability in the range 76·1–82·4% (*P. mite* (t=6·41) and *P. minus* (t=9·84), both P<0·001). However specimen no. 71, the intermediate between *P. mite* and *P. hydropiper*, at 92·7% did not have significantly reduced pollen stainability (cf. *P. mite* (t=0·76) and *P. hydropiper* (t=0·71), both not significantly different).

DISCUSSION

Our initial observations showed that as well as the three species studied, *P. persicaria* L. and *P. lapathifolium* L. were also present at both sampling sites. Webb (1984) drew attention to the difficulty in separating the two latter species from the others, particularly *P. mite*, and suggested that

TABLE 3. PERCENTAGE POLLEN STAINABILITY OF *POLYGONUM* SPECIMENS FROM LOUGH NEAGH

Specimen no.	% stainability	Identity
38	88·7	*mite*
40	89·2	*mite*
72	94·2	*mite*
73	92·2	*mite*
75	87·0	*mite*
28	94·4	*minus*
29	97·4	*minus*
32	92·0	*minus*
34	92·2	*minus*
45	98·1	*minus*
58	93·6	*minus*
19	82·3	*mite* × *minus*
30	80·7	*mite* × *minus*
35	78·9	*mite* × *minus*
49	76·1	*mite* × *minus*
D20	85·7	*mite* × *minus*
6	99·2	*hydropiper*
8	94·7	*hydropiper*
21	93·7	*hydropiper*
22	90·7	*hydropiper*
23	98·0	*hydropiper*
71	92·7	*hydropiper*

P. persicaria was also part of the hybrid swarm at Lough Neagh. Furthermore Timson (1966) had indicated that hybrids could occur between *P. persicaria* and *P. mite* or *P. minus*. However, we found *P. persicaria* and *P. lapathifolium* to be readily distinguishable from the others, including *P. mite*; the denser spike and small black patches on the leaves of *P. persicaria* and the possession of both these features, together with pedicel glands in *P. lapathifolium*, were very distinctive. In addition we found no evidence of hybridization between *P. persicaria* or *P. lapathifolium* with the other species, and for this reason we concentrated on *P. mite*, *P. minus* and *P. hydropiper*.

Five of the plants we sampled fall between pure *P. mite* and pure *P. minus*, and these intermediates are almost certainly the hybrid *P. mite* × *P. minus* (= *P.* × *wilmsii* G. Beck; Fig. 5). Do hybrids with *P. hydropiper* also occur? The plant which was morphologically intermediate between *P. mite* and *P. hydropiper* did not have reduced pollen stainability and also produced a similar number of flowers and nutlets to *P. hydropiper*. This is almost certainly not a hybrid, because an F_1 hybrid would be triploid (2n=30) and, presumably, highly sterile. Therefore it would seem that Webb (1984) was correct when he indicated the potential presence of hybridization in sect. *Persicaria* around Lough Neagh, but with hybrids only occurring between *P. mite* and *P. minus*, and not all species present.

Out of the three species studied, *P. hydropiper* is supposedly the easiest to recognize. Webb (1984) and others (Tutin 1987; Lousley & Kent 1981) have indicated that the possession of glands on the perianth of *P. hydropiper* is, apart from its taste, one of the key characters allowing its separation from both *P. minus* and *P. mite*. Surprisingly we found that virtually all of the *P. mite* plants also had perianth glands, and initially we thought these were similar to those on *P. hydropiper*. This led us to believe at first that such plants might have been hybrids. However on closer examination we found the glands to be smaller, fewer in number and almost flat compared with those on *P. hydropiper*. Similar glands were also found on the perianth of British and European material of *P. mite*, despite the fact that these glands are not mentioned in standard works on *Polygonum* (Tutin 1987; Lousley & Kent 1981). However the differences in gland structure and number are further key characters, identified by DSC, separating *P. mite* from *P. hydropiper*. We also found that some of the other characters used to separate all three species, such as nut size and

FIGURE 5. *Polygonum mite* Schrank × *P. minus* Huds. from Lough Neagh, Northern Ireland, August 1984, *Parnell & Simpson D20* (**TCD**). Scale bar = 20 mm.

leaf length:breadth ratio are rather more variable than previously thought (Webb 1984 and pers. comm.) Both these latter characters are useful for distinguishing *P. minus* from both *P. hydropiper* and *P. mite*, but not for separating the last two from each other. This is particularly emphasized by the leaf length:breadth ratio, so that the leaves of *P. minus* are up to 8·5 times as long as broad whereas those of the other two species are up to 4·5–4·8 times as long as broad. The leaf shapes and sizes of *P. hydropiper* and *P. mite* may thus be very similar. Therefore, as is often the case, it is best to use a combination of the characters given in Table 2 to delimit the species, rather than rely on only a single character.

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Two hybrids of *Equisetum sylvaticum* L. new to the British flora

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ABSTRACT

Two hybrids of *Equisetum sylvaticum* are reported, which are new to the British flora. These are **E. × bowmanii** C. N. Page, **hybr. nov.** (*E. sylvaticum* L. × *E. telmateia* Ehrh.), from Hampshire, and *E.* × *mildeanum* Rothm. (*E. pratense* Ehrh. × *E. sylvaticum* L.) from Perthshire.

INTRODUCTION

No hybrids involving Wood Horsetail (*Equisetum sylvaticum* L.) have been previously recorded from the British Isles. This paper reports the occurrence of two such hybrids new to the British flora, one of which is unknown elsewhere and is described here for the first time. These are *E.* × *bowmanii* C. N. Page, hybr. nov. (*E. sylvaticum* L. × *E. telmateia* Ehrh.), from Hampshire, and *E.* × *mildeanum* Rothm. (*E. pratense* Ehrh. × *E. sylvaticum* L.) from Perthshire. Herbarium material of each has been deposited in the herbarium of the Royal Botanic Gardens, Edinburgh (**E**).

EQUISETUM × *BOWMANII*

Equisetum × bowmanii C. N. Page, **hybr. nov.** (*Equisetum sylvaticum* L. × *E. telmateia* Ehrh.) TYPUS: Hampshire, New Forest, Minstead, near A337 Minstead Road, July 1986, *R. P. Bowman s.n.*, det. R. P. Bowman & C. N. Page (Holotypus: **E**).

Caules 30–50 cm alti, 2·5–5·0 mm diam., fere albi, 8–14 sulcati; vaginae (dentibus exclusis) 5–7 mm, pallide viridi-griseae; dentes tot quot sulci, 2–costati, tenues, acuti, marginibus latis pallide brunneis scariosis lateraliter inter se adhaerentibus: cavitas centralis $\frac{1}{3}$–$\frac{1}{2}$ caulis diam. Ramuli patentes, tenues regulariter verticillati, iterum ramosi, plerumque tetragoni vivide sed pallide virides; costae biangulatae; vaginae pallidae, dentibus triangularibus-acuminatis patulis minute nigro-apiculatis. Strobilus c. 1·2 cm longus; sporae abortivae.

Stems 30–50 cm or more, erect, thick, 2·5–5·0 mm in diameter; main stem internodes somewhat fleshy, mostly very pale green, nearly white in the lower part of the stem, minutely rough; grooves 8–14, numerous, fairly deep, ridges ± rounded, sheaths long, 5·0–7·0 mm (excluding teeth), ± appressed, pale greenish-grey, sometimes blackish above and below; teeth numerous, as many as the grooves, 2-ribbed, of variable length, mostly 4·0–6·0 mm long, slender, acute, their central portions deep brown, mostly straight, their margins broad, pale brown and scarious; the teeth often adhering laterally by their margins in 2s—4s for their full length; central hollow about $\frac{1}{3}$–$\frac{1}{2}$ diameter of stem. Branches numerous, long (up to c. 7·5 cm), in regular and numerous whorls, spreading widely all around the shoot and drooping at their tips, very slender, mostly 4-angled, bright pale green, almost all bearing sparse to numerous long secondary branches of similar form and colour; branch sheaths pale greenish-brown, teeth triangular-acuminate, green and dark-tipped, somewhat spreading; branchlet ochreolae conspicuous, chaffy, pale golden brown; branch internode with narrowly grooved (biangulate) ridges and shallowly rounded furrows.

Cones, when present, borne from the tops of shoots of generally similar form to the vegetative ones but the shoots thicker (mostly 5 mm diam.), with larger, looser, leafier sheaths to 2 cm long; the cones ovoid, c. 1·2 cm long, dark, hardly rising out of the uppermost sheath, their sporangia poorly-filled, the spores abortive.

The vegetative and cone-bearing shoots of this hybrid are both strikingly intermediate in size and morphology between those of *E. telmateia* and *E. sylvaticum*. The vegetative shoots differ from those of *E. sylvaticum* in their slightly larger size, and thicker and more succulent stems, and especially in the long, narrow, dark-centred teeth to their sheaths, the paleness of their main stem internodes (especially on the lower parts of the stem), and branches with ± biangulate internodal ridges and of bright pale green colour, forming the dominant colour of the plant. They differ from *E. telmateia* in the much more slender main stem, with long nodding tip, the slenderness of the branches which are themselves drooping at the tips and copiously branched, and roughness of the main stem internodes and the depth of their grooves, and the conspicuous brown scarious margins to the main stem teeth which are broad and tend to adhere laterally with each other, forming broad lobes. The stem in section has a central hollow, and the number of carinal and vallecular canals (about 8–14) is intermediate between those of the parents. The length of the first internode of the branches is also intermediate between the short, first internode of *E. telmateia* and the long, first internode of *E. sylvaticum*.

The intermediate form of the fertile (cone-bearing) shoots is also striking. These are semi-dimorphic, with thick, somewhat succulent shoots, shorter than those of *E. sylvaticum*, and much larger chaffier and looser sheaths than in *E. sylvaticum*, sparse whorls of branched green branches, and a cone like that of *E. telmateia* in shape but similar to that of *E. sylvaticum* in size.

The sporangia of the cone of *E.* × *bowmanii* contain numerous but poorly-formed spores, which appear to be 100% abortive. These include about 95% of very small, generally irregularly rounded, misshapen or wholly shrivelled, nearly colourless spores, each with a shrunken and nearly colourless cytoplasm and only very rudimentary and scarcely-formed elaters; and about 5% of varyingly larger spores of imperfectly rounded form, but with varyingly pale green-coloured chloroplasts, and fairly well-formed but inoperative elaters.

The spore evidence thus wholly supports the conclusion that this plant is of hybrid origin, whilst its very distinctive morphology, which is almost exactly intermediate between that of two native horsetail species in a large number of distinct characters, enables its parentage to be deduced with a very high degree of certainty. These features also readily distinguish this hybrid from both parents and from *E.* × *mildeanum* (see below), which shares *E. sylvaticum* as a common parent, as well as from other hybrids in *Equisetum* (Page 1972, 1982).

DISTRIBUTION AND ECOLOGY

This hybrid was found by R. P. Bowman in July 1986 in a single colony spreading over heathland road banks, grass verges and in adjacent short turf on wet clay soil near the A337 Minstead Road, Minstead, New Forest, S. Hants., v.c. 11 (GR 41/296.105). Plants occur in open sites where they are more slender and rather stunted and subject to grazing by ponies, except where they emerge in the shelter of low *Rubus fruticosus*, *Ulex*, *Prunus spinosa* and *Pteridium aquilinum*, with some *Quercus robur* seedlings. Other associates include *Mentha aquatica*, *Cirsium palustre*, *Senecio aquaticus*, *Betonica officinalis*, *Prunella vulgare*, *Galium palustre*, *Lysimachia nemorum* and *Juncus conglomeratus*. *Equisetum arvense* occurs nearby on the same road banks. On the periphery of the site is a light cover of medium-aged *Quercus robur*, *Fagus sylvatica* and *Pinus sylvestris*, with an open understorey of stunted *Ilex aquifolium*. It is possible that a few trees were earlier removed during the construction of the new section of road. The site dips slightly to the west and the road ditches drain into a main ditch, in turn draining an open grazed sward. The altitude of the site is approximately 35 m. On the southern side of the road, shoots of the hybrid occur along approximately 30 m of verge, whilst on the northern side, they extend along at least 50 m of road bank. The clay exposure is that of the Barton Clay of the Eocene.

There are four recorded sites for *Equisetum sylvaticum* in the area, all situated along the same watercourse: Fleet Water, Minstead, on flushed slope in deciduous woodland; below mill pond outfall (GR 41/295.100), 500 m distant from the hybrid site; Fleet Water, Newtown, Minstead, side of damp ride in bushy plantation (GR 41/278.107), 1800 m distant; Stoney Cross, wet flush in pasture (GR 41/260.117), 3650 m distant; and near Bartley Water, Busketts Lawn Inclosure, damp sides of ditch draining into stream (GR 41/314.103), 1750 m distant.

Recorded but unlocalized sites for *Equisetum telmateia* exist at Minstead (GR 41/26.10) and Canterton (GR 41/26.12), both about 3 km away, west and north-west of the hybrid site. In Busketts Lawn Inclosure (GR 41/314.103), there is a local population of *E. telmateia* along ditch banks on clay only 10 m from the very small population of *E. sylvaticum* described above. The habitat of this site is beech and oak plantation, but the presence of *Sorbus torminalis* is indicative of a former ancient woodland. Here *E. telmateia* grows mainly where the clay is exposed, whilst *E. sylvaticum* prefers the damp slightly flushed ground, where some *Sphagnum* is present.

EQUISETUM × *MILDEANUM*

Equisetum × **mildeanum** Rothm. (*E. pratense* Ehrh. × *E. sylvaticum* L.).
Stems 10–35 cm, erect, slender, 0·8–1·5 mm in diameter; main stem internodes very pale green, conspicuously and minutely rough with perpendicular setose spicules; grooves 8–15, numerous, fairly deep, the ridges angular; sheaths long, 3·0–4·5 mm (excluding teeth), somewhat loose, pale greenish-grey, sometimes pale brown to blackish above; teeth numerous, as many as the grooves, 1-ribbed, 2·0–3·0 mm long, slender, acute, their central portions deep brown above, grey-green at the base, straight or, when paired, bent laterally mostly only at the base, their margins scarious, mostly pale brown, narrow near the tips of the teeth, but broadening rapidly downwards, adjacent teeth mostly adhering laterally by their margins in 2s–3s for their full length; central hollow about ½ diameter of stem. Branches numerous, up to c. 5·5 cm long, whorled but becoming somewhat asymmetrically arranged to give the shoot an often slightly bilaterally compressed appearance, spreading and drooping at their tips, very slender, all 3-angled, mid-green, each usually bearing a small number of regular, short, spreading secondary branches of similar form and colour; branch sheaths pale green, teeth triangular-acuminate, green throughout, ± straight or only slightly spreading; branchlet ochreolae chaffy, pale brown; branch internodes with very prominent acute, uniangulate ridges and deep, flat-sided V-shaped furrows each with a narrow, lengthwise basal channel.

Vegetative shoots of this hybrid are strikingly intermediate in morphology between those of *E. pratense* and *E. sylvaticum*. They differ from *E. pratense* most clearly in having, in most specimens, secondarily branched branches throughout all or much of the length of the shoots, somewhat looser main stem sheaths which bear fewer teeth with broader, whitish to pale brown margins which also typically adhere together laterally by their margins in 2s and 3s. It differs from its other parent, *E. sylvaticum*, principally in the more bilaterally compressed (and hence not quite radially symmetric) habit of the overall shoot, its shorter, somewhat fewer, branchlets to the branches, the paler ochreolae at the branchlet bases, the generally non-spreading and concolorously green habit of the branch node teeth, the more numerous, more acute angles of the main stem internodes, and the straighter, darker-centred, more acutely tapering teeth of the main stem sheaths. Its sheaths are also generally tighter and typically somewhat less cup-shaped than are those of *E. sylvaticum*. Cone-bearing shoots have not, as yet, been found, but overall, the slender, pale green, somewhat compressed shoots of *E.* × *mildeanum*, combined with main stem sheaths with long dark teeth adhering together by broad scarious margins, and branches which are themselves mostly sparsely but regularly secondarily branched, leave little doubt about its identity, and produce a horsetail of distinctive and delicate appearance. The combination of these characters distinguishes this hybrid from both parents and from *E.* × *bowmanii*, which shares *E. sylvaticum* as a common parent, as well as from other hybrids in *Equisetum* (Page 1972, 1982).

DISTRIBUTION AND ECOLOGY IN BRITAIN

Three British stations for *E.* × *mildeanum* are known:

Perthshire, Ben Lawers, between large tumbled boulders on west-facing, slightly flushed damp, grassy slope, c. 2050 ft (625 m), with both parents; July 1985, *C. N. Page & D. Marden*, det. C. N. Page.

Perthshire, Caenlochan, in scree, 2900 ft (860 m); 10 July 1986, *H. McHaffie*, conf. C. N. Page.

Perthshire. Glenshee: Glas Choire, 26 August 1986, E. Birse, comm. P. I. Rothwell, conf. C. N. Page.

All three montane locations are in sites where both parents occur in the general vicinity or in the immediate neighbourhood of the hybrids. All are in fairly base-flushed (and in one site, wet) habitats over mica-schist rocks, and two of the sites are amongst boulders or on scree. In its Glas Choire locality, the rather small shoots of the plant grow with *Carex nigra*, *C. echinata* and *Sphagnum recurvum*. In the other two localities, plants grow in sites where, in addition to both parents, other pteridophytes of upland, basic screes are frequent, including *Dryopteris expansa*, *Polystichum aculeatum* and *P. lonchitis*.

DISCUSSION

Both hybrids reported here have *Equisetum sylvaticum* as one parent, and are the first two hybrids involving this parent known in the British flora.

Equisetum × *bowmanii* is a hybrid hitherto unknown anywhere, and its two, rather dissimilar-looking parents are, elsewhere, often widely separated geographically. In Europe as a whole, *E. sylvaticum* is generally northern and montane, and *E. telmateia* southern and lowland (Jalas & Suominen 1972). The ranges of two parent species thus mostly overlap only in middle latitudes in Europe, where they are often further separated by habitat differences (Page 1982, 1988). Even in Britain, their geographical overlap is not large (Jermy *et al.* 1978), and the New Forest locality for this hybrid is in one of the few regions of Britain where the two parents seem to occur near to each other in some quantity.

Here, the habitat of *E.* × *bowmanii* in many ways represents an abutment of habitats each more typical of the parent species locally: *E. telmateia* on damp clay banks and *E. sylvaticum* in damp acid heathy woodland. Further, the bulk of the habitat of *E.* × *bowmanii* occurs along a section of road which was constructed anew as part of a road realignment 13 years before (1973) the date of the first find of this plant, with the area of the hybrid closely coincident with that of roadside clay originally disturbed. It is not known whether the hybrid was present before the road widening event, but it seems probable that its formation may be a direct result of the soil disturbance resulting from this activity, the road construction creating new damp clay verge sites initially free of competition from established vegetation and suitable for gametophyte growth. It is by no means impossible that the whole of the present population area, including plants on both sides of the road, is a single clone.

The only other hybrid involving *E. telmateia* in the British Isles is *E.* × *font-queri* Rothm. (*E. telmateia* Ehrh. × *E. palustre* L.) known from the Isle of Skye (Page 1973) and from two lowland English sites (Roberts & Page 1979; Page & Busby 1985). The damp, clay substrate of *E.* × *bowmanii* and its roadside situation is strongly reminiscent of some of the sites for *E.* × *font-queri* in Skye. The only other known hybrid involving *E. sylvaticum* in the British Isles (or, indeed anywhere) is *E.* × *mildeanum* Rothm. (*E. sylvaticum* L. × *E. pratense* Ehrh.), reported and described here. *E.* × *bowmanii* is thus significant not only in its unusual appearance and in being a hybrid between two species of very different morphology and ecology, but also in having two parents neither of which seems to enter into many natural hybrid combinations.

Equisetum × *mildeanum* was described by Rothmaler (1944) from a number of localities in central and northern Europe, viz. "Hassia, Holsatia, Saxonia, Prussia, Silesia, Rossia". I have examined and confirmed the identity of Rothmaler's type (at Jena, **J**), and the match of these British specimens to it. Through central and northern Europe and Asia, the two parents of this hybrid have, indeed, very widely sympatric ranges, and their ecology is such that the two species probably frequently meet. It is of interest that all three known British stations for *E.* × *mildeanum* reported here are in Perthshire, thus all within the sympatric portions of their parental ranges (cf. Page & Barker 1985), and indeed, Scotland is probably the only part of the British Isles in which *E. pratense* occurs in any great abundance. Only one other hybrid involving *E. pratense* in its parentage is known in the literature. This is *E.* × *montellii* Hiitonen (*E. arvense* L. × *E. pratense* Ehrh.), reported from Finland, Sweden and the Canadian arctic (Duckett & Page 1975), and which could also yet be found in the British Isles. These two finds now bring to eight the total number of native

British horsetail hybrids (Page 1982), and update the information and further emphasize the ecological conclusions drawn in Page & Barker (1985).

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The spread of *Epilobium ciliatum* Raf. in the British Isles

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ABSTRACT

Epilobium ciliatum Raf. (*E. adenocaulon* Hausskn.) was first collected in Britain at Cropston Reservoir, Leicester, in 1891, and by 1894 it was well-established there. It was gathered in a further five vice-counties before 1930, but not correctly identified until the 1930s when G. M. Ash realized that it was naturalized in Surrey. Thereafter it spread rapidly, reaching Wales by 1942, Scotland by 1957 and Ireland by 1958. This spread is illustrated by a series of distribution maps; some of the problems it poses are discussed, and the possible reasons for the success of *E. ciliatum* as a weed are briefly reviewed.

INTRODUCTION

Of the many thousands of plant species which have been deliberately or accidentally introduced into the British Isles, relatively few have become widely naturalized. Some of these, notably certain arable weeds, were introduced in prehistoric times, so long ago that they are difficult to distinguish from native species. *Silene alba*, probably introduced with crops in the Neolithic (Baker 1947; Godwin 1976), provides one such example. Other species spread in historic times. These include plants, such as *Acer pseudoplatanus*, which were so widespread before systematic recording began that their spread cannot be reconstructed from botanical records. Such records have, however, been used to study the spread of those naturalized aliens which were introduced more recently. These include *Cardaria draba* (Scurfield 1962), *Elodea* spp. (Simpson 1984), *Polygonum* and *Reynoutria* spp. (Conolly 1977), *Senecio squalidus* (Kent 1956 *et seq.*) and *Veronica filiformis* (Bangerter & Kent 1957, 1962). This paper documents the spread in the British Isles of *Epilobium ciliatum* Raf. (*E. adenocaulon* Hausskn.), American Willow-herb, which is now one of the more widespread weeds of alien origin.

Epilobium ciliatum is native to North America, from Newfoundland and Alaska south to Baja California, Sonora, New Mexico and Virginia. In this area the name *E. ciliatum* covers a complex which "is far from resolved taxonomically" (Raven & Raven 1976). It is an established alien on the European mainland and in Australasia: the early records from these areas are reviewed by Lawalrée & Reichling (1961) and Raven & Raven (1976) respectively.

The biology of *E. ciliatum* has been studied by Myerscough & Whitehead (1966, 1967). The seeds can retain viability for several years. Seeds which germinate in autumn give rise to plants which overwinter as rosettes and produce flowering shoots in spring in response to increasing day length. Seeds germinating in early summer can flower within 5·5 weeks. The flowers are automatically self-pollinated, and the fruit capsules dehisce about 4 weeks after pollination. The seeds possess a tuft of silky hairs, and are wind-dispersed. Plants perennate by means of leafy rosettes, which develop at the base of the stem and produce their own adventitious root systems independent of the parent plant. Despite this ability to perennate, Raven & Raven (1976) have noted that *E. ciliatum* often behaves as an annual, relying on its abundant seed production for survival.

SOURCE OF RECORDS

This study is based on records held by the Biological Records Centre, Monks Wood Experimental Station. In order to ensure that these are as complete as possible I have extracted records from the following herbaria: **ABRN**, **BM**, **CGE**, **E**, **GL**, **K**, **LIV**, **LTR**, **NMW**, **RNG**, **OXF**. I have also searched appropriate literature sources, including the *Proceedings of the Botanical Society and Exchange Club of the British Isles* (from 1935), the *B.S.B.I. Year Book*, the *Proceedings of the B.S.B.I.*, *Watsonia* and many county and local Floras published up to the end of 1986.

THE SPREAD OF *EPILOBIUM CILIATUM*

In describing the spread of *Epilobium ciliatum* it is convenient to consider four arbitrarily chosen time spans: 1891–1929, 1930–1949, 1950–1969 and 1970–1986.

1891–1929

The presence of *Epilobium ciliatum* in Britain was not announced until 1934, but subsequent investigation has unearthed a number of earlier herbarium specimens which were not correctly identified at the time of their collection. All the specimens cited below have been determined by G. M. Ash.

The species was first collected by the Rev. T. A. Preston on 20 July 1891 at Cropston Reservoir, Leics., v.c. 55 (**BM**). Preston collected the plant again in 1894 (**BM**, **CGE**, **NMW**). Both gatherings were named as the hybrid *E. obscurum* × *E. roseum*, an identification "confirmed" by the Rev. E. S. Marshall, then the British expert on the genus. Fortunately a detailed description of the habitat of *E. ciliatum* at Cropston in 1894 is available (Mott 1895): "On the muddy shores left dry by the receding water of Cropstone Reservoir . . . sprang up vast beds of plants, sometimes a belt of one genus followed lower down by a belt of a quite different genus. One of these was an *Epilobium* belt. The species were *hirsutum*, *parviflorum*, *montanum*, *obscurum* and *roseum*, but hybrid forms occupied by far the largest area, the individuals of the pure type being comparatively rare. Among the hybrids, what appears to be *obscurum* × *roseum* [i.e. *E. ciliatum*] was perhaps most conspicuous. This belt being rather high on the sloping banks has probably been exposed for at least two summers, so that it is possible the hybridizing may have taken place on the spot." A. R. Horwood collected *E. ciliatum* at Cropston in 1905 (**CGE**, **NMW**), noting that it "continues to flourish on the silty ground . . . growing in great profusion, and reaching a height of 3–4 feet".

S. H. Bickham and R. F. Towndrow collected *E. ciliatum* at a second locality on 31 July 1905, a timber yard at Malvern Link, Worcs., v.c. 37 (**CGE**). This collection was again named *E. obscurum* × *E. roseum*, with the assent of E. S. Marshall. The next record was also from a timber yard, at Woodchester, W. Gloucs., v.c. 34, where H. J. Riddelsdell found it in 1920 (**NMW**, **OXF**). In 1921 J. Fraser gathered it on heaths north of Woking (**K**) and in 1927 E. C. Wallace found it at Ballards Plantation near Croydon (**RNG**); both localities are in Surrey, v.c. 17. Two more collections were made in 1928, from Coleman's Moor, Berks., v.c. 22 (*G. C. Druce*, **OXF**) and from a wood near Meopham Green, Kent, v.c. 16 (*A. R. Horwood*, **K**). This wood may have been Ryarsh Wood, as in 1929 Horwood collected *E. ciliatum* there. It seems to have been well-established, as there are 15 plants on the seven sheets at **K** gathered by Horwood in 1929.

Records of *E. ciliatum* made up to 1929 are plotted in Fig. 1.

1930–1949

G. M. Ash first collected *Epilobium ciliatum* in 1931. By the time that the plant was identified and its discovery published, it was clear that the species was well-established in Surrey. During the period 1930–1934 there are records of *E. ciliatum* from seven 10-km squares in that county; it was also recorded from five of the six neighbouring vice-counties, v. cc. 12, 13, 14, 16 and 22. Ash (1934) described it as abundant in south-western Surrey, and "as common as any other *Epilobium* about Witley, Godalming and Eashing". It grew in a range of habitats: "damp woods, copses and along stream-sides far from houses, as well as on railway-banks and in gardens, timber yards and waste places" (Ash & Sandwith 1935).

During the next five years, 1935–1939, *E. ciliatum* was recorded from a further six vice-counties in south-eastern England, v. cc. 11, 15, 18, 20, 23 and 24. In addition it was found further west, in v. cc. 6, 33 and 34, and further north, in v. cc. 31 and 39. G. M. Ash and J. F. G. Chapple also revisited the original British locality, Cropston Reservoir, and found that *E. ciliatum* still persisted there and also occurred at the nearby Swithland Reservoir.

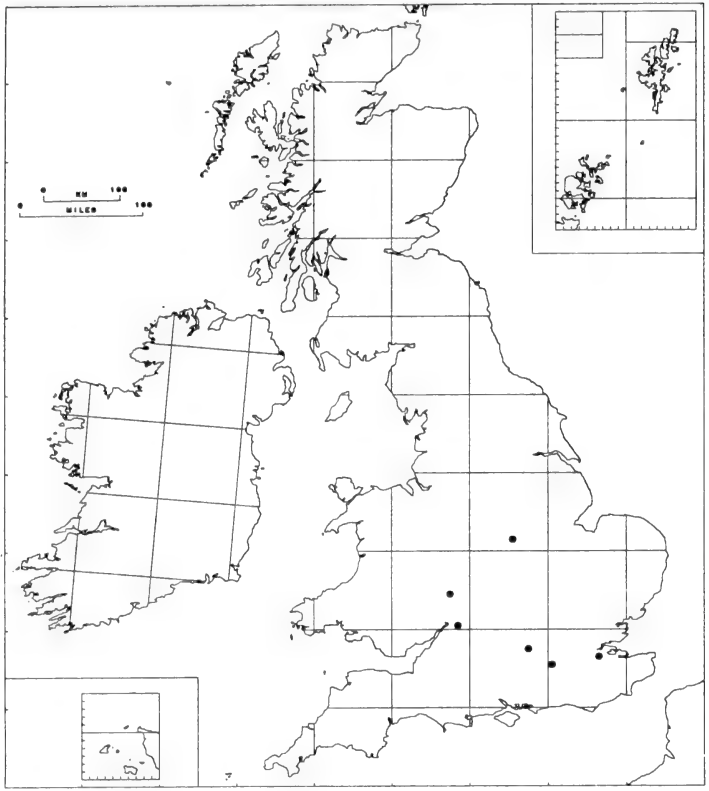

FIGURE 1. Records of *Epilobium ciliatum* up to 1929. Records are plotted in 10-km squares of the British and Irish national grids.

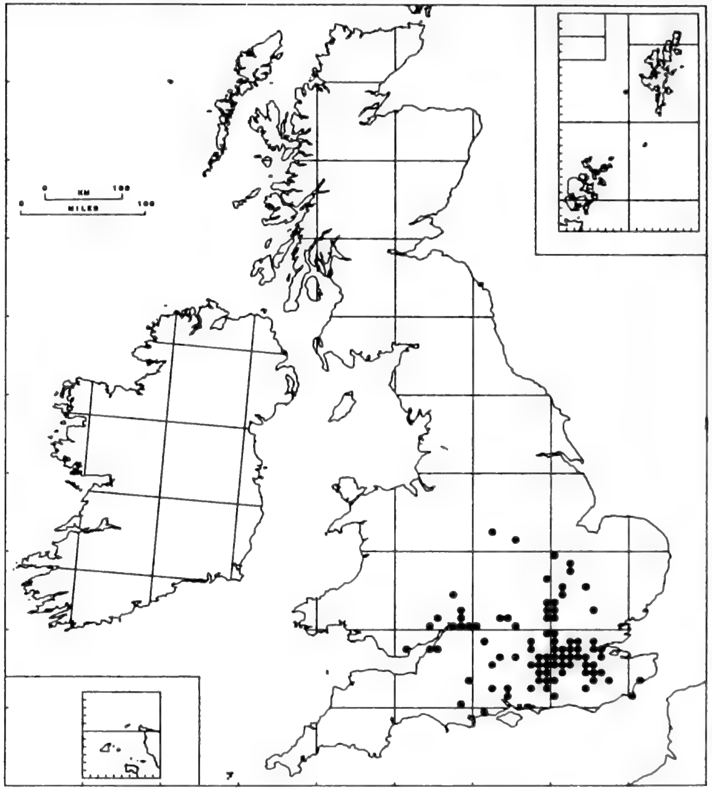

FIGURE 2. Records of *Epilobium ciliatum* up to 1949.

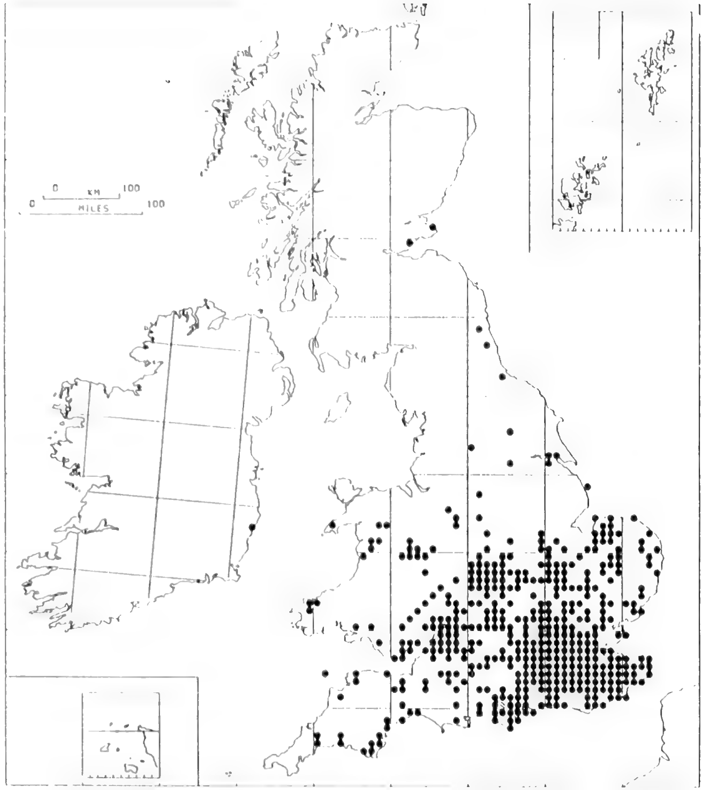

FIGURE 3. Records of *Epilobium ciliatum* up to 1959.

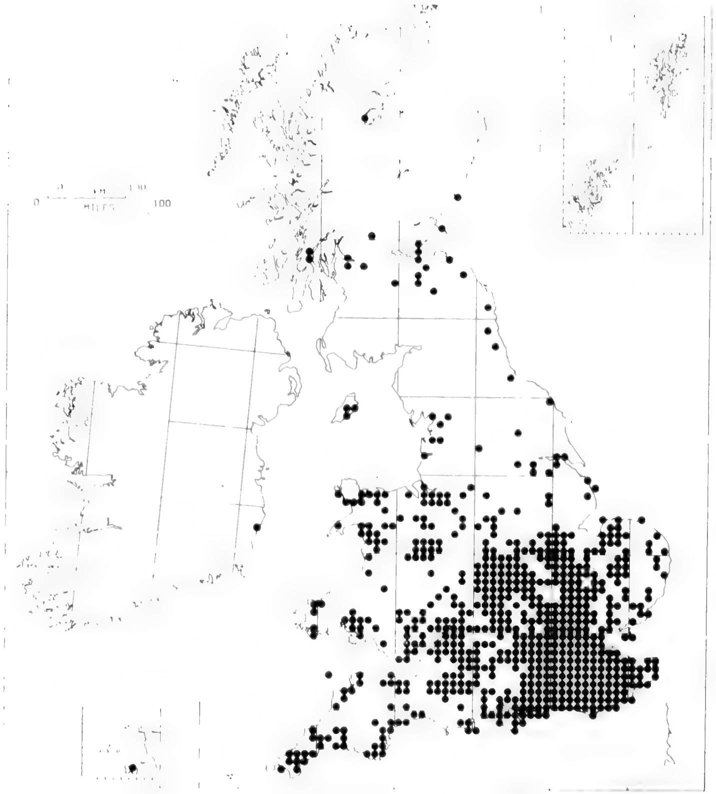

FIGURE 4. Records of *Epilobium ciliatum* up to 1969.

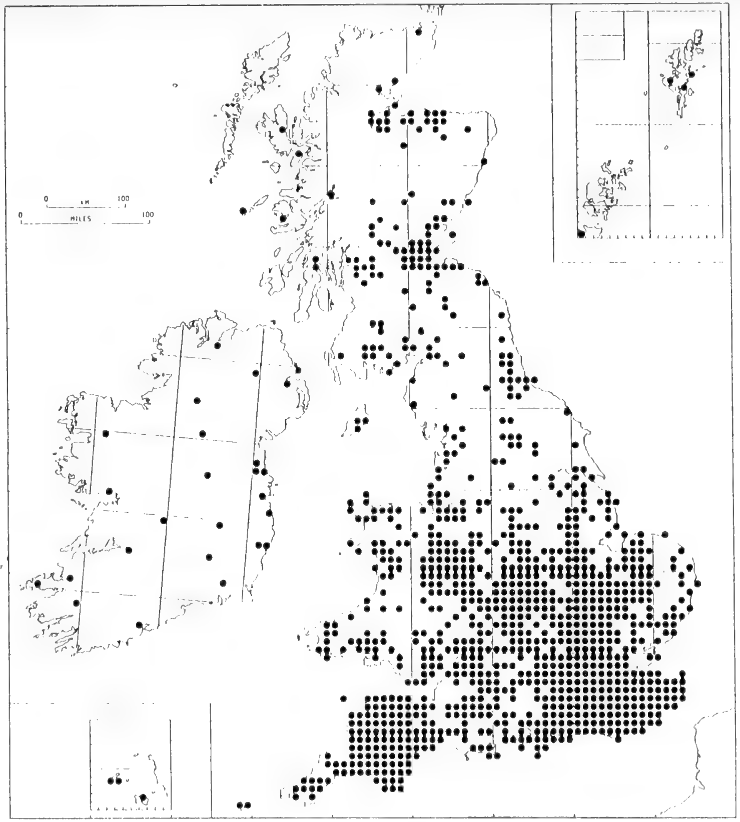

FIGURE 5. Records of *Epilobium ciliatum* up to 1986.

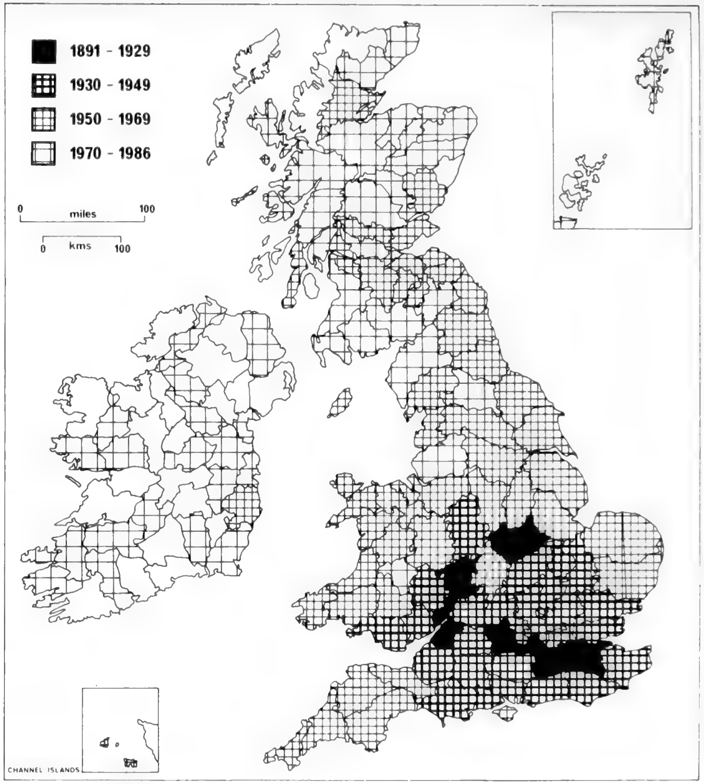

FIGURE 6. The date of the first record of *Epilobium ciliatum* in the vice-counties from which it has been recorded. Unshaded vice-counties are those in which the species has not yet been found.

E. ciliatum continued to spread during the next decade, 1940–1949. It was first recorded in Wales at Rookwood Hospital, Llandaff, v.c. 41, in 1942 and by 1947 it was established in Cardiff (Wallace 1949). All records up to 1949 are plotted in Fig. 2. The concentration of records around Surrey is still apparent, and in 1946 J. P. M. Brenan commented that it was "as yet rare in Oxfordshire" (Brenan 1948). The westernmost records mapped in Fig. 2 are in Dorset, v.c. 9, and Glamorgan, v.c. 41, but a specimen collected at Torrington in Devon, v.c. 4, in 1935 (*J. F. G. Chapple et al.*, **OXF**) was determined as *E. ciliatum* × *E. obscurum* by G. M. Ash (Hall 1936). Ash commented: "on the whole I consider the plants very convincing and I shall want much argument before I believe that *Ep. adenocaulon* is not to be found near Torrington".

There is no evidence that the spread of *E. ciliatum* was favoured by the wartime bombing of London and other major cities. Lousley (1944, 1946) does not list it as a colonist of the bombed sites in central London which he investigated in 1942 and 1944, nor is it referred to by Salisbury (1945). Lousley did, however, collect it from three bombed sites in 1945. These were the first records of the species from Middlesex, v.c. 21 – surprisingly, as it was known from all the surrounding counties by 1937.

Epilobium species hybridize readily, and by 1949 hybrids of *E. ciliatum* with all the native lowland species had been recorded (Stace 1975).

1950–1969

The dramatic spread of *E. ciliatum* in this period is shown by the accompanying maps (Figs 2–4). At the start it was still a relatively local species, albeit frequent in some areas of south-eastern England. By 1969 it was frequent throughout most of southern and midland England and in many areas of Wales, and there were scattered records in northern England and Scotland. The first Scottish record was made in 1957 by Dr M. Dunn, by a wooded stream at Kenley, Fife, v.c. 85; the second was of a population in "overgrown open woodland" on the banks of a stream at the Raith estate, Fife, where it was discovered by G. H. Ballantyne in 1959. Between 1950 and 1969 it was also found on several islands, including Lundy (1952), the Isle of Man (1958), Anglesey (1964) and Jersey, Channel Islands (1968). In 1958 it was collected by J. G. and C. M. Dony at Arklow, Co. Wicklow, v.c. H20, the first Irish record.

1970–1986

In Great Britain the spread of *E. ciliatum* continued during this period (Fig. 5). The species was recorded for the first time in many Scottish vice-counties, and reached the Hebridean islands of Skye (1976), Ulva (1982) and Tiree (1982).

Although it was first recorded in Ireland in 1958, there were few records before 1980. The hybrid *E. ciliatum* × *palustre* was collected in Co. Down, v.c. H38, in 1969 and there is a 1971 field record of *E. ciliatum* itself on an island in Lough Neagh, Co. Antrim, v.c. H39. In 1978 *E. ciliatum* was found in a garden at Aughrim, Co. Wicklow, v.c. H20, where it grew with *E. lanceolatum*, and in a nearby nursery (Walters 1979). In the next few years there were numerous records from all parts of Ireland, and in some areas the species spread explosively (Doogue *et al.* 1985).

In south-eastern England, where it was first recognized as a naturalized plant, *E. ciliatum* was very abundant by the 1970s. In Surrey it was "almost ubiquitous" and Lousley (1976) described it as "by far our commonest willowherb". It was "the commonest willow-herb in London" (Burton 1983) and "much the commoner of the small willowherbs" in Kent (Philp 1982); in both these areas, as in Bedfordshire (Dony 1976), it was recorded in 70–78% of tetrads (2 × 2 km squares). In Hertfordshire (Dony 1967) and Sussex (Hall 1980) it is known in 62% and 64% of tetrads, but further north and west the percentage is smaller: 47% in Devon (Ivimey-Cook 1984), 43% in Rutland (Messenger 1971) and only 22% in Shropshire (Sinker *et al.* 1985).

ERRONEOUS RECORDS

In compiling the records of *Epilobium ciliatum* I have rejected a number as erroneous. The following published records are sufficiently important for the reason for their rejection to be put on record.

Cadbury *et al.* (1971) report as the first Warwickshire record a specimen in **herb. J. E. Bagnall** collected by Bagnall in a wood near Gannaway Gate in 1889. If substantiated this would be the first British record, but the specimen cannot be traced in Bagnall's herbarium at **BIRA**, nor are the details known to Mrs P. Copson, the vice-county recorder. It seems likely that the reference is an error introduced in the compilation of the Flora. The earliest acceptable record from Warwickshire known to me is dated 1952.

The first Sussex record is given by Wolley-Dod (1937) as Lurgashall, 1930, det. G. M. Ash, but Ash & Sandwith (1935) cite "Lurgashall, 1934" as the only Sussex record. There are no Lurgashall specimens in **BM**, where both herb. Wolley-Dod and herb. Ash are lodged. I prefer to follow Ash & Sandwith, and to regard Wolley-Dod's date as a misprint.

Epilobium ciliatum was reported from the dried up bed of a loch at Gallanach Dunes, Coll, v.c. 103 (Harrison *et al.* 1941) and from the Bornish-Stoneybridge area, South Uist, v.c. 110 (Harrison 1941). Harrison's (1941) comment that *E. ciliatum* "is an American species and may not be a colonist in the Hebrides" suggested that it might be native at these sites. However these records have not been accepted by other botanists (e.g. Perring & Walters 1962).

DISCUSSION

HISTORY OF SPREAD IN THE BRITISH ISLES

The records of *Epilobium ciliatum* in Britain and Ireland are summarized above. The first question that needs to be considered is whether or not these accurately reflect its spread in the British Isles. The genus *Epilobium* is somewhat difficult and is sometimes ignored by field botanists. The smaller species cannot be distinguished without close scrutiny, and unusual plants can be explained away as hybrids. If *E. ciliatum* was overlooked for a considerable period or recognized by only a few botanists, the picture of its spread presented above might be misleading.

Until the early 1930s botanists were unaware that *E. ciliatum* occurred in Britain. A few specimens collected before then have been found, but it would be unwise to deduce too much from this fragmentary evidence. *E. ciliatum* was well-established at Cropston Reservoir by 1894. It is difficult to say whether it was established or casual at the other localities where it was collected before 1930, and the date when it became established in Surrey is not known. As Ash & Sandwith (1935) pointed out, the Rev. E. S. Marshall lived in the very area of Surrey in which *E. ciliatum* was well-established by the 1930s. Marshall was successively curate at Witley (1885–1890) and Vicar of Milford (1890–1900), and it was in this period that he carried out most of his work on *Epilobium* (Britten 1920). Although Marshall failed to recognize the pressed specimens of *E. ciliatum* that were submitted to him, it seems rather less likely that he would have overlooked the living plant and highly probable that he would have at least collected it in mistake for some other species or hybrid. It is tolerably certain, therefore, that *E. ciliatum* became established in Surrey between 1900 and 1930.

The first detailed account of *E. ciliatum* in Britain was published in 1935. Even after this there must have been some delay between the appearance of the plant in an area and its recognition by botanists, and no doubt this delay was greater in some regions than in others. Even the map of the current distribution (Fig. 5) shows some areas where the scarcity of records probably reflects a lack of recorders rather than any real scarcity of the plant. With these qualifications, it seems likely that the records available do provide a reasonably accurate picture of the spread in Great Britain of *E. ciliatum* after 1935. The extent to which Irish records reflect its spread there is discussed by Doogue *et al.* (1985).

A number of other questions can be asked about the origin of *E. ciliatum* in Britain. Did it arrive directly from North America? Were the scattered early records the results of separate introductions? Is the fact that two of its first three localities were timber yards significant, indicating that it may have been introduced or spread with timber?

Raven & Raven (1976) pointed out that *E. ciliatum* in Britain and New Zealand appears to be identical, despite the fact that they are drawn from a highly variable complex in N. America, and suggest that the New Zealand plant might have been introduced from Britain. *E. ciliatum* was first recorded in New Zealand in 1896. By 1905 it seems to have been widespread in North Island, and it was first recorded in South Island in 1912. Thus the species was found in Great Britain five years before it was collected in New Zealand, but appears to have spread more rapidly in New Zealand. The possibility that it was introduced from New Zealand to Britain, rather than vice versa, cannot be ruled out.

This raises perhaps the most mysterious question about the spread of *E. ciliatum* in Britain, first posed by Ash (1953) who wrote "Why has it made such rapid progress in recent years whilst remaining more or less static near Leicester for 50 years?" Although *E. ciliatum* was well-established and persistent at Cropston Reservoir there is no evidence to suggest that it spread beyond the immediate neighbourhood. It did not become a weed in T. G. Tutin's Leicester garden until 1965 (Tutin 1973). The distribution maps suggest that the populations near Cropston were engulfed by the advancing front of *E. ciliatum* from further south. It is tempting to suggest that the plants at Cropston had a different genotype from those which spread so rapidly, but this is only speculation.

After the initial scattered records, the spread of *E. ciliatum* in Britain appears to have been continuous rather than discontinuous. This is suggested by Fig. 6, which illustrates the date of the first record from each vice-county. This continuous spread presumably reflects a natural expansion of an established population, rather than introduction by man at different sites which then acted as foci for secondary expansion. The spread of *E. ciliatum* contrasts with that of *Senecio squalidus*, described by Salisbury (1961) as "markedly discontinuous with respect to the more remote infections, whilst at the same time spreading locally around each new station".

POSSIBLE REASONS FOR THE SUCCESS OF *E. CILIATUM* AS A WEED

Myerscough & Whitehead (1966, 1967) compared the germination behaviour and subsequent growth of *Epilobium ciliatum* with that of the native species *E. montanum*. Both species possess many of the attributes of successful weeds: considerable phenotypic plasticity which enables them to grow in a range of environmental conditions, efficient vegetative and sexual reproduction and seeds with the capacity to survive in a dormant state. However, the minimum period from germination to flowering is shorter in *E. ciliatum*, 5·5 weeks compared to 7, and its relative growth rate is greater. The overwintering rosettes of *E. ciliatum* are larger than those of *E. montanum*, which probably allows it to make more growth during the winter although it renders the plant more susceptible to adverse weather conditions. Flowering and fruiting plants of *E. ciliatum* are less leafy than those of *E. montanum*, and the green stems and capsules make a greater contribution to photosynthetic assimilation. Raven & Raven (1976) stress the "enormous seed production" of *E. ciliatum* as a factor in its spread in Europe and Australasia, but quantitative comparisons with other species have not been made.

It has recently been suggested that the evolution of resistance to the widely used persistent triazine herbicides such as simazine might be one factor responsible for the predominance of *E. ciliatum* in urban areas. S. M. Walters (pers. comm.) found that it was the only species which flourished on soil in an area of Grantchester churchyard, Cambs., which had been subjected to excessive applications of simazine, and resistance to pre-emergence treatments has been demonstrated experimentally (Bailey *et al.* 1982).

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I am grateful to the vice-county recorders and other B.S.B.I. members who have helped by providing records of *E. ciliatum*, to T. D. Pennington for examining a number of specimens, to Mrs D. M. Greene for much assistance including the production of the 10-km square distribution maps and to J. Clark for drawing the vice-county map. S. M. Walters and D. Briggs pointed out the possible importance of herbicide resistance in the *E. ciliatum* story, and J. R. Akeroyd, M. D. Hooper and T. C. G. Rich kindly commented on a draft of this paper.

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The taxonomic relationships and typification of *Festuca brevipila* Tracey and *F. lemanii* Bastard (Poaceae)

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ABSTRACT

Festuca brevipila Tracey (= *F. trachyphylla* (Hack.) Kraj.) and *F. lemanii* Bast. have long been a source of confusion for British botanists. The aim of this paper is to clarify the current taxonomic situation by distinguishing the two species on the basis of their morphology and anatomy, by reviewing the taxonomic history and nomenclature and by examining their taxonomic status. Some data are also presented on the geographical distribution and ecology of each species.

INTRODUCTION

The subject of this paper is two species of grass that have for long been collectively known in the British literature as *Festuca longifolia* Thuill. It was shown conclusively by Auquier (1973) that this application is wrong, and that *F. longifolia* is the correct name for the glaucous fescue found in East Anglia, to which the names *F. caesia* Smith and *F. glauca* Lam. had been applied. *F. caesia* correctly refers to that taxon (though a later synonym), but *F. glauca* is another misapplication, the true *F. glauca* not occurring in the wild in the British Isles.

The correct names of the two species to be discussed are *F. brevipila* Tracey and *F. lemanii* Bastard. The misapplication of the name *F. longifolia* to these seems to date from Howarth (1925), who was followed by Hubbard (1954), Dandy (1958) and Tutin (1952, 1962). These authors included both *F. brevipila* and *F. lemanii* as a single species, although the former is probably more closely related to *F. valesiaca* Schleicher ex Gaudin and the latter to *F. ovina* L. The drawing in Hubbard (1954) for the most part could refer to either species, but the leaf section is definitely that of *F. lemanii*.

The long list of differential characteristics which separate *F. lemanii* and the only slightly less variable *F. brevipila* (Table 1) suggests that the species are very well separated. However, Hackel

TABLE 1. CHARACTERS WHICH SEPARATE *F. LEMANII* AND *F. BREVIPILA*

Character	*F. brevipila*	*F. lemanii*
Panicle	usually nodding	usually erect
Awn length (mm)	1·4–2·5	0·3–1·8
Palea length (mm)	3·8–4·7	4·0–5·2
Leaf-blade scabridity	usually scabrid or scabrid distally	usually scabridulous distally
Number of adaxial leaf-blade furrows	4–6	2–4
Number of leaf-blade veins	(5–)7–9	5–7
Margins of leaf-blades	infolded	infolded or not
Sclerenchyma in leaf-blades	usually in three islets (sometimes semi-connected)	usually in ring or broken ring
Prickle length on adaxial surface of leaf-blade (μm)	(2·7–)5–13(–15)	(10·5–)23–46(–63·5)
Stomatal length (leaf) (μm)	(37·5–)41–50	38–42(–46)
Stomatal length (lemma) (μm)	31·5–37·5	29–33·5

(1882, p. 87) noted the existence of individuals intermediate between *F. ovina* subsp. *eu-ovina* var. *vulgaris* subvar. *firmula* Hack. (= *F. lemanii*) and *F. ovina* subsp. *eu-ovina* var. *duriuscula* subvar. *trachyphylla* Hack. (= *F. brevipila*). The present study has also uncovered a number of intermediate specimens, although completely intermediate individuals are rather rare and the taxa are generally easily separated when all differential characters are taken into consideration. We therefore consider them to be best recognised as distinct species.

FESTUCA LEMANII BASTARD

F. lemanii Bastard, *Essai Fl. Maine et Loire* 36 (1809). TYPE: France. Chinon. In sabulosis aridis. *E. H. Tourlet No. 12530* – ex herb. Hackel (Neotype: **W**, designated here).

F. cinerea sensu Desvaux, *Fl. Anjou* 61 (1827); sensu Moisan, *Fl. Nantaise* 185 (1839); non Vill. (1787).

F. duriuscula sensu Moisan, *Fl. Nantaise* 185 (1839); sensu Guépin, *Fl. Maine et Loire*, 3rd ed., 50 (1845); sensu Boreau in *Mém. Soc. Acad. Maine et Loire* **6**: 181 (1859); sensu Lloyd, *Fl. Ouest France*, 3rd ed., 372 (1876); sensu Corbière, *Nouv. Fl. Normandie* 645 (1893); sensu Desvaux, *Fl. Anjou* 61 (1927); sensu Huon in *Bot. Rhed.*, sér. A, **9**: 187 (1970); non L. (1753).

F. glauca sensu Moisan, *Fl. Nantaise* 185 (1839); non Lam. (1787).

F. duriuscula L. var. *hirsuta* sensu Hardouin, Renou & le Clerc, *Catal. Pl. vasc. Calvados* 307 (1848); sensu Tourlet, *Catal. rais. Pl. vasc. Indre et Loire* 583 (1908); non (Host) Gaudin (1828).

F. ovina subsp. *eu-ovina* var. *vulgaris* Koch subvar. *firmula* Hack. f. *lemanii* (Bast.) Hack., *Monogr. Fest. Europ.* 87 (1882); *F. ovina* subsp. *ovina* var. *firmula* (Hack.) Hegi f. *lemanii* (Bast.) Hack. in Stohr, *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg* **4**: 405 (1955).

F. hirsuta sensu Corbière, *Fl. Normandie* 645 (1893); non Host (1802).

F. ovina subsp. *eu-ovina* var. *lemanii* (Bast.) Aschers & Graebn., *Syn. Mitteleur. Fl.* **2**: 468 (1900).

F. longifolia sensu Howarth in *J. Linn. Soc. (Bot.)* **47**: 35 (1925), pro parte; sensu Hubbard, *Grasses* 111 (1954), pro parte; sensu Tutin, *Fl. Br. Isl.*, 2nd ed., 1129 (1962), pro parte; non Thuill. (1800).

F. ovina var. *firmula* (Hack.) Richt. subvar. *lemanii* (Bast.) Kraj. in *Acta Bot. Bohem.* **9**: 189, 193 (1955).

F. cinerea Vill. var. *trachyphylla* sensu Stohr in *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg* **4**: 732 (1960); sensu Auquier in *Bull. Jard. Bot. nat. Belg.* **39**: 97–118 (1969); non (Hack.) Stohr.

TAXONOMIC HISTORY

The type specimen of *F. lemanii* was described by Bastard as being collected from the area around Brissac and Saumur (Maine et Loire, France). The herbarium of Bastard is said to be mainly in Angers (**ANG**) with other specimens in Paris (**P**) and Manchester (**MANCH**). M. Kerguélen (in litt. 1984) examined the collections in **ANG** and **P** but failed to find either a type specimen or an authentic specimen which may become a neotype. Auquier (1974) reported having requested such material from **MANCH** and **ANG** but without success. M.J.W. visited **MANCH** but also failed to find a suitable specimen. In the apparent absence of a type specimen or of an authentic specimen to serve as a neotype, Kerguélen (in litt. 1984) suggested that an alternative neotype might be sought.

Hackel's (1882) concept of the epithet '*lemanii*' came from the examination of herbarium material collected from areas around Chinon (Indre et Loire, France) by E. H. Tourlet. Auquier (1974) examined one such specimen from Hackel's herbarium (**W**, No. 12530) collected by Tourlet from "Chinon in sabulosis aridis", and stated that it agrees well in the majority of characters with plants of the thermophilous calcareous grasslands in the region (and by implication with *F. lemanii*). He later suggested, in a note attached to the specimen, that this plant may provide a convenient neotype for *F. lemanii*. Kerguélen (in litt. 1984) agreed with this view.

We have observed *F. lemanii* growing on both calcareous and acidic soils and a detailed comparison of the two ecodemes covering 126 characters has revealed few differences between them. Traditionally important characters such as spikelet length, awn length and leaf-blade diameter were not found to differ between the two ecodemes, but minor differences were observed in both panicle length and culm height (Fig. 1). These differences are considered by us to be too small to warrant taxonomic distinction, since both characters were found to be highly unreliable under cultivation. Therefore, we feel that it is not inappropriate to use a specimen collected from

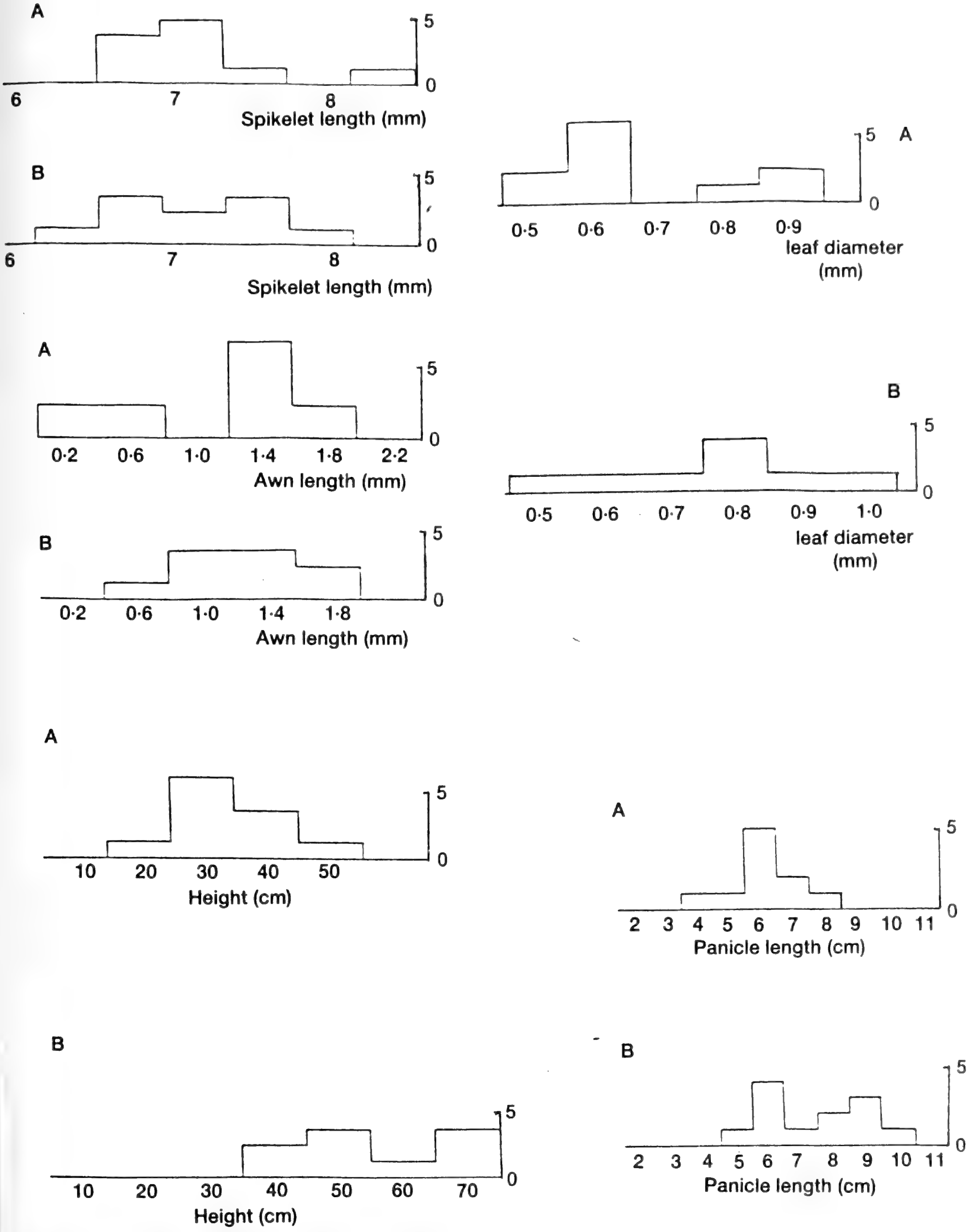

FIGURE 1. Variation in spikelet length, awn length, leaf-diameter, height and panicle length in two ecodemes of *F. lemanii*, A. calcifuge, B. calcicole. Vertical axes = no. of plants.

acid sands as a neotype for *F. lemanii*, even though the original plant was collected from an area of predominantly calcareous soils.

The Tourlet specimen was obtained on loan from **W** and examined. The characteristics of this specimen agree reasonably well with the descriptions of *F. lemanii* given by Auquier (1974), Markgraf-Dannenberg (1980) and Kerguélen (1983) (Table 2). Accordingly, we designate this specimen as the neotype of *F. lemanii*.

Hackel (1882, p. 87) included *F. lemanii* under *F. ovina* var. *vulgaris* subvar. *firmula*. Plants referable to *F. lemanii* were distinguished from others in the subvariety only by their hairy spikelets. However, the modern concept of *F. lemanii* encompasses plants with both hairy and glabrous spikelets and so is more accurately referable to the whole of Hackel's subvar. *firmula*.

TABLE 2. CHARACTERISTICS OF *F. LEMANII*

Character	Neotype (W–N.12530)	Auquier (1974)	Kerguélen (1983)	Markgraf-Dannenberg (1980)
Panicle length (cm)	(4·6–)5·7(–7·5)	(2–)5–7(–11)	(2–)5–7(–11)	(2–)4–7(–11)
Spikelet length (mm)	(6·3–)6·6(–7·2)	(5·6–)6·5–7·2(–8·3)	(5·6–)6·5–7·2(–8·3)	(5·6–)6·5–7·2(–8·3)
Lemma length (mm)	(3·8–)4·1(–4·5)	(3·6–)4·2–4·6(–5·5)	(3·6–)4·2–4·6(–5·5)	(3·6–)4·2–4·6(–5·5)
Awn length (mm)	(0·7–)1·5(–2·3)	(0·2–)0·8–1·6(–2·8)	—	<2·75
Upper glume length (mm)	(3·6–)3·8(–4·3)	(2·8–)3·5–4·0(–5·2)	—	(2·8–)3·5–4·0(–5·2)
Leaf-blade scabridity	scabridulous in distal third	usually scabridulous distally or at tip	scabrid only at tip	usually scabrid distally
Leaf-blade diameter	(0·59–)0·62 (–0·66)	(0·43–)0·62–0·79 (–1·14)	(0·45–)0·6–0·8(–1·14)	(0·43–)0·62–0·79 (–1·14)
No. of veins	5(–7)	(5–)7(–9)	(5–)7(–9)	(5–)7(–9)
No. of grooves	2(–4)	2–4(–6)	(2–)3–4	(2–)3–4
Sclerenchyma distribution	much broken ring	continuous or broken ring	continuous ring	continuous or broken ring

MORPHOLOGICAL VARIATION

Plants fairly densely to loosely tufted; vegetative shoots all intravaginal and retaining or shedding old leaves. Culms (19–)28–66 cm, erect, (0·32–)0·38–0·5(–0·55)mm wide below the first panicle node, generally smooth or scabridulous below the panicle, glabrous or hairy, grooved or weakly grooved distally; nodes 2–3, the uppermost not pruinose, visible beyond the subtending sheath or not, and reaching (3–)12–32(–37)% of the height of the plant.

Leaves green, usually not glaucous, subpruinose or not. Leaf-sheaths (1·3–)2·1–4·4(–4·7)cm, fused for (0–)15–36(–41)% of their length, smooth or scabridulous distally, glabrous or hairy; auricles short, usually minutely ciliate (rarely glabrous). Ligules short, usually minutely ciliate (rarely glabrous). Leaf-blades lank to robust, (4–)6–11(–17)cm, not acutely pointed, (9–)11–56(–79)% on each plant curved at the tip, usually scabrid at least in the upper half, occasionally scabridulous in the distal third or smooth, glabrous or hairy at the base.

Panicles usually erect but occasionally slightly nodding, 3·7–7·8(–8.6)cm, with (8–)16–24(–34) spikelets. Panicle branches subpruinose or not pruinose, not narrowing below the spikelets, smooth to scabrid, covered in hairs or prickles, rarely subglabrous; 1st and 2nd panicle nodes (1·1–)1·3–2·7(–3·2)cm apart. Spikelets subpruinose or not, (6·1–)6·5–7·5(–8·5)cm, with (2–)3–6(–8) florets (plus one sterile floret); pedicels (0·62–)1·45–2·35(–2·5)mm. Glumes unequal; the lower subulate to narrowly lanceolate, (2·15–)2·4–3·2(–3·52) × 0·58–0·82 mm, usually glabrous, but sometimes with a scabrid tip or rarely laxly hairy, 1-veined, with a ciliate margin; the upper narrowly lanceolate to lanceolate, (3·4–)3·5–4·6(–4·8) × (0·89–)1·05–1·2(–1·3)mm, usually glabrous or with a scabrid distal third, rarely laxly hairy, 3-veined with a ciliate margin or rarely glabrous. Lemmas lanceolate, (4·05–)4·1–4·85(–5·35) (excluding awn) × 1·5–1·83(–1·93)mm, green but often purple at the apex, with awns (0·3–)0·6–1·6(–1·9)mm long, 5-veined, scabrid in the distal half or hairy. Paleas linear-lanceolate, (3·9–)4·1–4·6(–5·2) × 0·68–0·9 mm. Anthers yellow or purple, 1·83–2·5mm. Pollen grains oblong, brown, 2·3–3·1 × 0·65–1·0mm.

Leaf-blade anatomy (Fig. 2): outline of leaf-blades usually oval or V-oval, occasionally V-form or circular-elliptical; margins usually not infolded; leaf-blade diameter (0·43–)0·59–0·85(–0·95)mm, diameter/thickness ratio (1·87–)2·1–2·4(–2·9); veins 5 (–7); sclerenchyma forming a complete or broken ring which may be thickened slightly at the margins and midrib, sometimes forming a much broken ring; 2–4 grooves and 1–4 ridges on the adaxial surface; adaxial midrib (0·09–)0·1–0·14(–0·15)mm wide and 0·035–0·08mm deep; adaxial epidermal cells usually of fairly uniform size, rarely individualized, lacking bulliform cells but with prickles (10·5–)23–46(–63·5)μm. Leaf-blade adaxial epidermis: stomata (31–)38–41·5(–45·8)μm, usually predominantly solitary or with an accompanying prickle-cell, (1-)8–74(–91)% solitary, (0–)23–88(–99)% with an accompanying silica-cell; prickles usually predominantly solitary, (28–)35–79(–100)% solitary, (0–)11–50(–57)% forming short rows of 2 or more prickle-cells, 0–15(–65)% with an accompanying silica-cell.

Leaf-blade abaxial epidermis: stomata absent; long-cells with sinuous walls, (75–)85–133(–143)μm; silica-cells and cork-cells present; prickles usually present.

FESTUCA BREVIPILA TRACEY

F. brevipila Tracey, *Plant Syst. Evol.* **128**: 287–292 (1977). TYPE: Niederösterreich, Waldviertel, Ampliendorf (nördlich von Schrems), in der Nähe des Houses Nr. 55; in sehr flachgründigen Rasen über Granit. 20 Mai 1977, *A. Weber* (Holotype: **WU**).

F. ovina L. var. *glaucescens* Link, *Hort. Berol.* **2**: 266 (1833), nom. ambig. sec. Stohr (1960, p. 398).

F. ovina subsp. *eu-ovina* var. *duriuscula* (L.) Koch subvar. *trachyphylla* Hack., *Monogr. Fest. Europ.* 91 (1882) (Lectotype: Prenzlau, *Grantzow*, ex herb. Hackel (**W**), designated here).

F. ovina subsp. *eu-ovina* var. *duriuscula* subvar. *pubescens* Hack., *Monogr. Fest. Europ.* 91 (1882).

F. duriuscula var. *trachyphylla* (Hack.) Richt., *Pl. Eur.* **1**: 94 (1890).

F. duriuscula subsp. *trachyphylla* (Hack.) Rohlena in *Vestn. Kral. ces. spol. Nauk* **24**: 4 (1900), sec. Rauschert (1960, p. 270).

F. ovina var. *trachyphylla* (Hack.) Druce, *List Br. Pl.* 83 (1908).

F. longifolia var. *trachyphylla* (Hack.) Howarth in *J. Linn. Soc.* (*Bot.*) **47**: 35 (1925).

F. trachyphylla (Hack.) Kraj. in *Acta Bot. Bohem.* **9**: 190, tab. 2, fig. 5, 6 (1930); non Hackel ex Druce (1915).

F. ovina subsp. *ovina* var. *duriuscula* subvar. *trachyphylla* (Hack.) Maire, *Fl. Afrique Nord* **3**: 126 (1955).

F. longifolia sensu Hubbard, *Grasses* 111 (1958), pro parte; sensu Tutin, *Fl. Br. Isl.*, 2nd ed., 1129 (1962), pro parte; non Thuill. (1800).

F. duvalii (St. Yves) Stohr in *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg* **4**: 232 (1955), pro parte quoad descr., excl. typ.

F. cinerea var. *trachyphylla* (Hack.) Stohr in *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg* **9**: 395, 402 (1960).

F. stricta Host subsp. *trachyphylla* (Hack.) Patzke in *Österr. Bot. Zeitschr.* **108**: 506 (1961).

TAXONOMIC HISTORY

Auquier (1973, pp. 270–272) pointed out that considerable confusion had arisen over Hackel's original concept of subvar. *trachyphylla*. Some authors had applied the epithet *trachyphylla* to fescues with a continuous ring of sclerenchyma (Stohr 1955, 1960; Korneck 1961; Huon 1970; Bidault 1966, 1968), whereas others applied the name to fescues with three islets of sclerenchyma tissue (e.g. Howarth 1925, 1948; Krajina 1930). Auquier (1973) outlined the principal arguments for each view. Evidence in favour of using the epithet to describe specimens with a continuous ring of sclerenchyma is as follows:

i) Hackel (1882, pp. 90) placed subvar. *trachyphylla* under var. *duriuscula* (L.) Koch, which he considered to have a continuous ring of sclerenchyma only rarely interrupted.

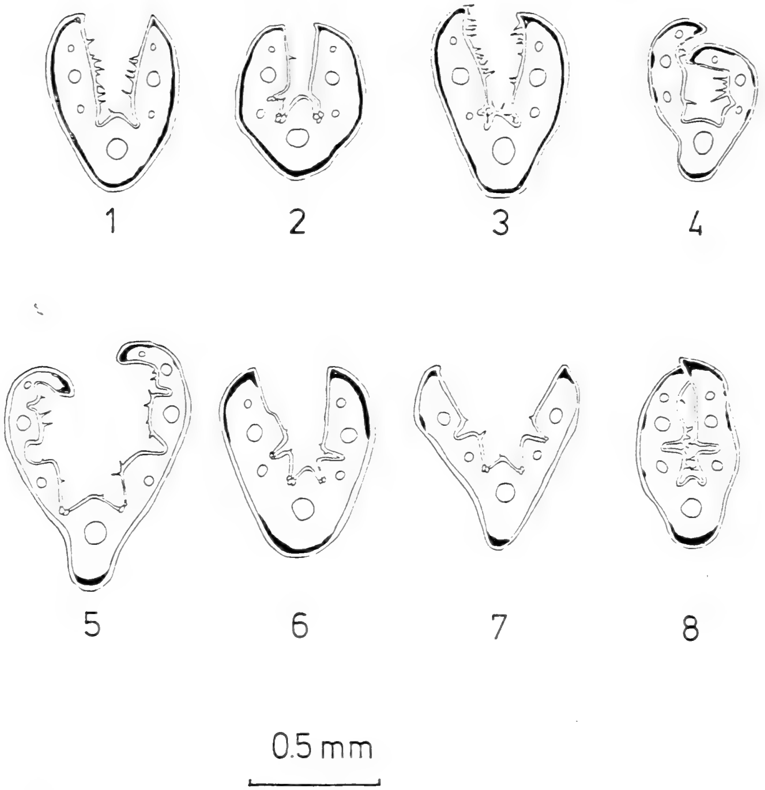

FIGURE 2 Leaf-blade sections of *F. lemanii* and *F. brevipila*.
1. *F. lemanii*, Seven Sisters, nr River Wye, Herefordshire, v.c 36 (**LTR**).
2. *F. lemanii*, Monks Dale, nr Tideswell, Derbyshire, v.c. 57 (**LTR**).
3. *F. lemanii*, Jezainville, Meurth-et-Moselle, France (**LTR**).
4. *F. lemanii*, (Neotype) Chinon, France (**W**).
5. *F. brevipila*, Lakenheath Warren, W. Suffolk, v.c. 26 (**LTR**).
6. *F. brevipila*, Wangford, W. Suffolk, v.c. 26 (**LTR**).
7. *F. brevipila*, nr Brandon, Suffolk (**LTR**).
8. *F. brevipila*, (Holotype), Niederosterreich, Austria (**WU**).

ii) Hackel determined and annotated specimens with a continuous ring of sclerenchyma under this name (cf., for example, St Yves (1913, pp. 63–64)).
iii) Hackel (1882) established a close affinity between subvar. *trachyphylla* and subvar. *firmula* of var. *vulgaris* Koch, the latter typically having a continuous ring of sclerenchyma.
iv) In Hackel's herbarium (**W**) specimens with a continuous ring of sclerenchyma are often classed under the epithet "*trachyphylla*".

Evidence in favour of the epithet being used to describe specimens with discontinuous sclerenchyma is as follows:
i) Hackel said of subvar. *trachyphylla* "vulgaris in Germania boreali . . . non vidi e Gallia, Hispanica". Auquier (1973) pointed out that this distribution agrees well with that of fescues with discontinuous sclerenchyma but differs strongly from those with a continuous ring.
ii) Hackel (1882, p. 105), in proposing a new taxon (*F. ovina* subsp. *sulcata* Hack. var. *genuina* Hack. subvar. *typica* Hack.) that typically has three sclerenchyma islets (cf. p. 104: "fasciculis sclerenchymaticis 3 crassiusculis") and five veins, distinguished it from subvar. *trachyphylla* as follows: "Laminae rarissime 7 nerves inveniuntur et planta tum a *F. ovina duriuscula trachyphylla*

vix distinguenda". Auquier (1973) concluded from the last point that it seemed that Hackel considered subvar. *trachyphylla* to have a discontinuous sclerenchyma as well.

Specimens of subvar. *trachyphylla* were obtained on loan from Hackel's herbarium in Vienna (**W**) in order to search for a possible lectotype. This search produced one specimen of relevance (**W**, No. 977). The main label of this specimen contains a description of the collection site signed by Grantzow (of which only the locality Prenzlau can be diciphered readily) and the determination "*F. ov.* var. *duriuscula* subv. *trachyphylla*" signed by Hackel. A pencil note contains measurements of the lemma, awn and leaf-diameter and the date 2.5. [18] 65. This predates Hackel's monograph (1882) in which the taxon is described. A note added by P. Auquier places Prenzlau 60 km north of Berlin, but a later note by C.A.S. corrects this to 90 km N.N.E. of Berlin in Brandenberg (E. Germany). Morphologically this specimen agrees fairly well with the modern concept of *F. trachyphylla* (*F. brevipila*) (Table 3) and it is accordingly selected as the lectotype.

TABLE 3. CHARACTERISTICS OF THE LECTOTYPE OF *F. OVINA* SUBVAR. *TRACHYPHYLLA* COMPARED WITH THOSE OF *F. BREVIPILA*

Character	*F. brevipila*	*F. ovina* subvar. *trachyphylla* (**W**–No.977)
Panicle length (cm)	(3·5–)4·2–8·8(–9·5)	(4·5–)5·8(–6·8)
Spikelet length (mm)	(6·1–)6·4–8·0(–8·5)	(6·9–)7·2(–7·5)
Lemma length (mm)	(3·9–)4·2–5·1(–5·5)	(3·9–)4·2(–4·4)
Awn length (mm)	(1·2–)1·4–2·3(–2·6)	(0·3–)1·6(–2·2)
Leaf-blade scabridity	scabrid or scabrid distally	scabrid distally
Leaf-blade shape in section	V-form or V-oval	V-form or V-oval
No. of leaf-blade veins	(5–)7–9	7
No. of adaxial leaf-blade furrows	4(–6)	4
Prickle length (μm)	(2·7–)5–13(–15)	(7·5–)11·6(–15)

Krajina (1930) was the first author to recognise subvar. *trachyphylla* Hackel at the species level. However, Hackel (ex Druce 1915) had previously used the name to describe a totally different taxon from South America. The one character (prickles on the glumes) used to distinguish it from *F. dumetorum* Phillippi non L. is sufficient to validate the name. Therefore, the later homonym *F. trachyphylla* (Hackel.) Kraj. must be rejected. This had earlier been realized by Dandy (1958) when erroneously placing *F. trachyphylla* as a synonym of *F. longifolia*, as pointed out to us by P. J. O. Trist (in litt. 1984). M. Kerguélen (in litt. 1984) drew our attention to the fact that Pils (1984) quoted *F. brevipila* Tracey as a synonym of *F. stricta* Host subsp. *trachyphylla* (Hack.) Patzke. Tracey (1977) distinguished *F. brevipila* from *F. trachyphylla* (Hack.) Kraj. by its shorter culms and leaves, its very shortened hairs on the leaves, its more variable stomatal length, its shortened panicles, and its relatively shorter spikelet lengths only encompassing the lower part of the range found in *F. trachyphylla*. The holotype and the isotype of *F. brevipila* were received on loan from **WU** and compared with the lectotype of *F. trachyphylla* (Hack.) Kraj. (Table 4). These specimens bear a remarkable resemblance to one another in all of Tracey's diagnostic characters, including the variability of stomatal length, and there seems little justification for their separation taxonomically. This being so, *F. brevipila* becomes the oldest legitimate name for the taxon at the species level and so replaces the illegitimate *F. trachyphylla* (Hack.) Kraj.

MORPHOLOGICAL VARIATION

Plants densely to loosely tufted; vegetative shoots all intravaginal and retaining or shedding old leaves. Culms (9–)30–47(–72)cm, erect, (0·3–)0·38–0·62(–0·74)mm wide below the first panicle node, smooth or scabrid distally, grooved; nodes 2(–3), the uppermost not pruinose, visible beyond subtending sheath or not, and reaching (8·5–)11–20(–32)% of the height of the plant.

Leaves green, occasionally glaucous, usually subpruinose. Leaf-sheaths (1·3–)1·7–4·2(–4·9)cm, fused for (6·5–)13–32(–39)% of their length, smooth or scabridulous in distal third, usually laxly hairy but sometimes glabrous; auricles short, minutely ciliate. Leaf-blades robust to fairly robust,

TABLE 4. COMPARISON OF TWO TYPE SPECIMENS OF *F. BREVIPILA* AND LECTOTYPE OF *F. OVINA* SUBVAR. *TRACHYPHYLLA*

Character	*F. brevipila* holotype	*F. brevipila* isotype	*F. ovina* subvar. *trachyphylla* lectotype
1. *Diagnostic characters*			
Culm height (cm)	(16–)30(–36)	(25–)32(–46)	(20–)26(–32)
Panicle length (cm)	(3·5–)6·0(–7·0)	(4·5–)6·5(–7·5)	(4·5–)6·0(–7·0)
No. of spikelets per panicle	(15–)21(–31)	(13–)21(–34)	(15–)20(–24)
Spikelet length (mm)	(7·0–)7·6(–8·2)	(6·3–)6·8(–7·1)	(6·9–)7·2(–7·5)
Leaf-blade length (cm)	(2·5–)5·5(–7·5)	(7·0–)9·0(–13·0)	(4·5–)6·0(–7·5)
Stomatal length (μm)	(42·5–)46·9(–50)	(42·5–)45(–48·8)	(33·75–)38(–42·5)
2. *Other important characters*			
Lemma length (mm)	(4·2–)4·9(–5·3)	(4·1–)4·4(–4·6)	(3·9–)4·2(–4·4)
Awn length (mm)	(0·6–)1·9(–3·0)	(1·1–)1·7(–2·3)	(0·3–)1·6(–2·2)
Sclerenchyma in leaf-blade	3 islets	3 islets	3 islets
No. of leaf-blade veins	7(–8)	7–8	7
No. of leaf-blade furrows	4(–6)	4	4

(3·7–)5·5–15(–19·2)cm, (6–)14–54(–89)% on each plant curved at the tip, scabrid at least in the upper third, usually hairy at base, but sometimes glabrous.

Panicles erect to nodding, (3·5–)4·2–8·8(–9·5) cm, with (10–)14–28(–39) spikelets. Panicle branches subpruinose or not pruinose, not narrowing below the spikelets, smooth to scabrid, covered in hairs or prickles, rarely subglabrous; 1st and 2nd panicle nodes (0·89–)1·3–2·6(–4·3)cm apart. Spikelets subpruinose or not, (6·1–)6·4–8·0(–8·5)mm, with (2–)3–6(–7) florets (plus one sterile floret); pedicels (1·2)1·5–2·6(2·8)mm. Glumes unequal; the lower subulate to narrowly lanceolate, (2–)2·5–3·1(–3·3) × (0·45–)0·58–0·8(–0·88)mm, usually glabrous or scabrid at tip but rarely weakly hairy, 1-veined, with a ciliate or serrate margin; the upper narrowly lanceolate to lanceolate, (3·3–)3·6–4·5(–4·7) × (1–)1·2–1·45(–1·6)mm, usually scabrid near apex but occasionally hairy or glabrous, 3-veined, with a ciliate margin. Lemmas lanceolate, (3·9–)4·2–5·1(–5·5) (excluding awn) × (1·5–)1·6–2·1(–2·5)mm, green but sometimes purple at apex, with awns (1·2–)1·45–2·3(–2·6)mm, 5-veined, usually hairy or scabrid on distal half, but occasionally glabrous. Paleas linear-lanceolate, (3·8–)4·1–5·0(–5·3) × (0·68–)0·8–0·9(–1·0)mm. Anthers yellow or purple, (1·9–)2·1–2·9 mm.

Leaf-blade anatomy (Fig. 2): outline of leaf-blades usually V-form but occasionally V-oval; margins not infolded; leaf-blade diameter (0·59–)0·74–0·93(–1·1)mm; diameter/thickness ratio 2·15–2·5(–2·75); veins (5–)7–9; sclerenchyma usually forming three tailing islets at midrib and margins, 1–4 cells thick, often with smaller islets opposite veins (1 cell thick), rarely forming a complete ring much thickened at margins and midrib; 4(–6) grooves and 3–5 ridges on the adaxial surface; adaxial midrib (0·85–)0·9–1·6(–1·8)mm wide and (0·03–)0·04–0·07mm deep; adaxial epidermal cells of fairly uniform size, usually lacking bulliform cells but occasionally with small bulliform cells in grooves, with prickles (2·7–)5–13(–15)μm.

Leaf-blade adaxial epidermis: stomata (37·8–)40·3–48·3(–50·5)μm, predominantly solitary, 52–80(–100)% solitary, (0–)3–16(–29)% with an accompanying prickle-cell, (0–)3–16(–29)% with an accompanying silica-cell; prickles predominantly solitary, (44–)53–97(–100)% solitary, 0–19(–53)% forming short rows of 2 or more prickle-cells, 0–35(–50%) with an accompanying silica-cell.

Leaf-blade abaxial epidermis: stomata absent; long-cells (101–)112–200(–212)μm; silica-cells and cork-cells present; prickles present or absent.

DISTRIBUTION

At present, we have relatively little information concerning the distribution of either *F. brevipila* or *F. lemanii*.

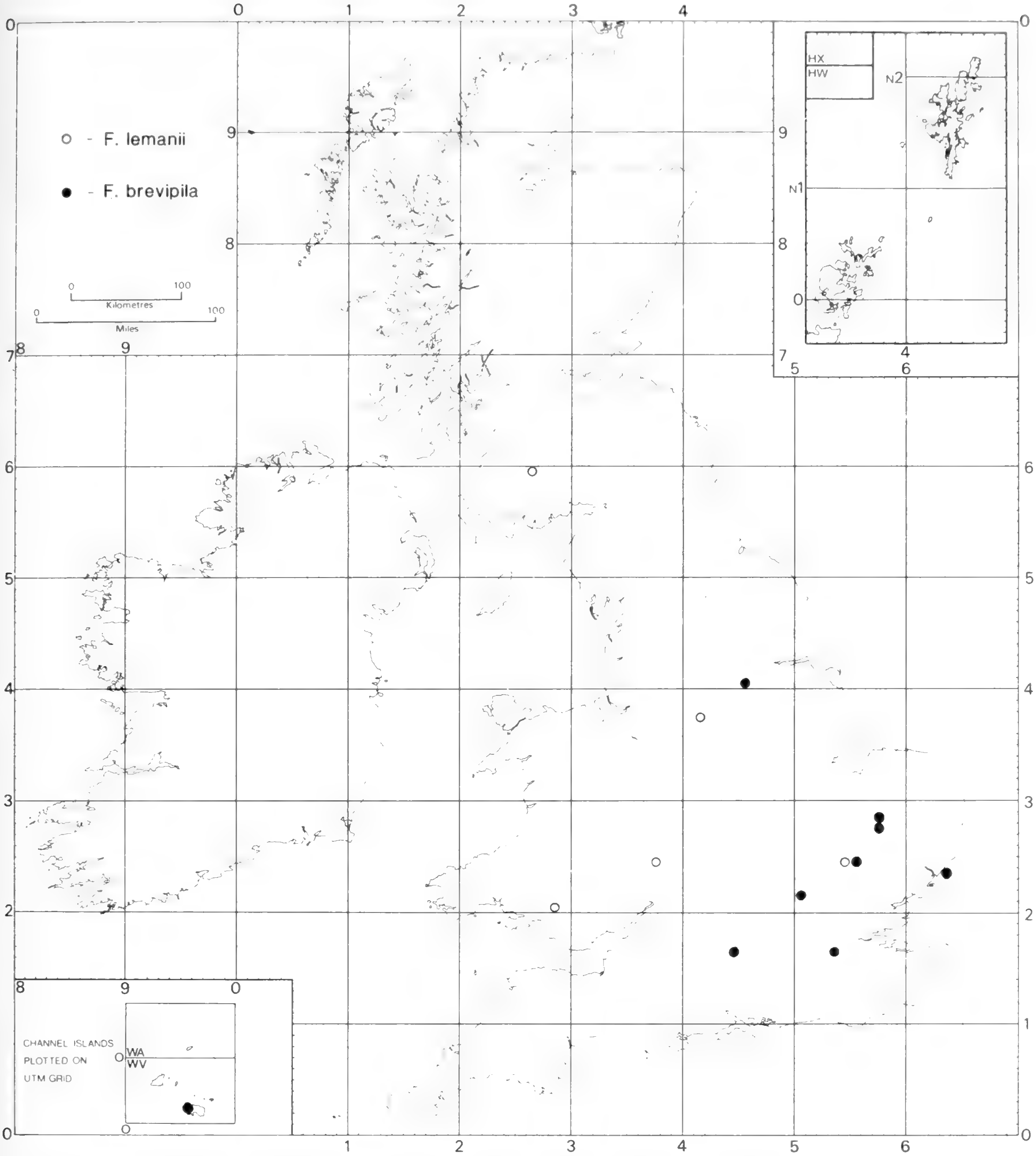

FIGURE 3. Geographical distribution of *Festuca lemanii* Bastard (○) and *F. brevipila* Tracey (●).

In Britain, *F. brevipila* appears to be most common in southern and central England, extending to South-West Yorkshire (v.c. 63) and westwards to Salop (v.c. 39). We have also collected a single specimen from a car-park in Jersey. Records have been made from the following vice-counties: 17, 19, 20, 21, 22, 25, 26, 28, 29, 30, 39, 55, 63. A distribution map is given in Fig. 3.

It is highly unlikely that *F. brevipila* is native to the British Isles. It has probably been introduced during the past 200 years as a commercial turf-grass species for roadside verges and railway embankments, and it is still available commercially as several cultivars of 'Hard Fescue'. It does not grow in its natural habitat in the British Isles. It is native to central Europe, but is also introduced in France and in much of Scandinavia.

Our records of *F. lemanii* are even less complete. Specimens have been observed from scattered sites in England, Scotland and Wales. Kirkcudbright, Scotland (v.c. 73) marks its northern limit and Glamorgan, Wales (v.c. 41) its western limit. Unlocalised specimens suggest that it may also be most common in southern and eastern England. It has been recorded with certainty from vice-counties 19, 37, 41, 57 and 73. A distribution map is given in Fig. 3.

F. lemanii is commonly found growing in more natural habitats, together with *F. ovina* subsp. *ovina*, subsp. *hirtula* (Hack. ex Travis) M. Wilkinson and/or subsp. *ophioliticola* (Kerguélen) M. Wilkinson, and it is likely to be native in the British Isles. It has a wide range of habitat preferences and has been found growing on both acidic and calcareous soils.

In Europe, *F. lemanii* extends through Belgium, France and Spain (Markgraf-Dannenberg 1980).

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Alopecurus × *plettkei* Mattfeld in Britain

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ABSTRACT

The hybrid *Alopecurus* × *plettkei* Mattfeld (*Alopecurus bulbosus* Gouan × *A. geniculatus* L.) is reported new to Britain. Its variation, distribution, habitat and growth performance are discussed.

INTRODUCTION

Alopecurus × *plettkei* Mattfeld, the sterile hybrid between *A. bulbosus* Gouan and *A. geniculatus* L., is known from Belgium, Germany and the Netherlands (Hubbard 1975). It was first found in Britain by Brian Wurzell on 27 May 1977, and confirmed by C. A. Stace, from marshes west of Glynde Reach, near Lewes, E. Sussex, v.c. 14, GR 51/465.094. It has subsequently been found at several sites in S. Hants. (v.c. 11), W. Kent (v.c. 16) and E. Suffolk (v.c. 25). The following account describes the morphology, anatomy, phenology, cytology and ecology of the British populations.

DESCRIPTION OF *ALOPECURUS* × *PLETTKEI*

Perennial, erect and densely tufted or sometimes forming mats of decumbent spreading culms, compactly tufted or occasionally solitary, frequently branched from nodal growth, with some internodes arcuate. Culms (15–)18–77(–93) cm, weak, with (2–)4–13 nodes at uneven intervals, from 5–15 cm below the panicle, over the entire length of the culm; lowest internode 1–33 × 1–6(–7·5) mm, very swollen to slightly swollen, extremely variable in shape, with a smooth or ridged surface, sometimes with one or two slightly bulbous swellings but generally straight sided. Basal leaves (8–) 15–20 (–38) cm; culm leaves hairless, 1·5–15 cm × 0·7–3·3 mm, finely pointed, flat or infolded, minutely scabrid on margins and veins; sheaths smooth, the uppermost often inflated; ligule 1·8–4·5 mm, broadly obtuse, membranous.

Panicles 1·4–4·5 (–6·3) cm × 2·5–5 mm; dense, narrowly cylindrical, spike-like, bluntly pointed. Pedicels 0·4–1 mm. Spikelets oblong, 2·5–3 mm, flattened, 1-flowered, falling entirely at maturity. Glumes equal, 2·5–3 mm, free to the base, narrowly oblong, broadly obtuse, exceeding lemma by (0·05–)0·1–0·4(–0·5) mm, 3-veined with uneven-length hairs on the keel and margins. Lemma 2–3 mm, keeled, smooth, narrowly oblong, membranous, 4–veined, sometimes weakly hairy in distal quarter, awned on the back c. 1 mm from the base; awns 3–5·6 mm, protruding 1·0–2·8 (–3·5) mm beyond the glumes. Anthers 1–1·5 mm, indehiscent, containing imperfect pollen 0(–4)% stainable in Muntzing's aceto-carmine, 20–28 μm in diameter.

Leaves in section: adaxial and abaxial epidermises with cells of irregular size and shape, with small bulliform-cells on the adaxial surface between veins; small islets of sub-epidermal sclerenchyma usually occur in association with the veins.

Abaxial epidermis with solitary stomata 35–49 μm long, in continuous or semi-continuous rows, 47–95 μm apart in continuous rows; short-cells (other than stomata) (0–)1–4(–6) per 100 μm^2, 27–73% being hook-cells or prickles; long-cells (60–)100–220 μm.

Adaxial epidermis with fewer stomata than abaxial epidermis but with (2–)4–10 non-stomatal short-cells per 100 μm^2; long-cells 90–380 μm long.

A comparison of *A.* × *plettkei* and its parental species is given in Table 1.

TABLE 1. A COMPARISON OF *A. BULBOSUS*, *A.* × *PLETTKEI* AND *A. GENICULATUS*

Character	*A. bulbosus*	*A.* × *plettkei*	*A. geniculatus*
Culm	erect	erect to spreading	spreading, geniculate
Culm length (cm)	11–29	(15–)18–77(–93)	15–38
No. of branches per culm	0	0–3(–7)	0–3(–5)
No. of nodes per culm	1–4(–5)	(2–)4–13	2–6(–8)
Rooting culm	absent	absent or present	absent or present
[a]Basal internode swelling (mm)	(1–)2–4·5(–6·0)	(0–)0·5–2·2	(–0·5–)0–1·0(–1·5)
Basal internode length (cm)	0·4–2	0·6–33	10–35
[b]'Twin' basal swollen internodes	present or absent	usually absent	absent
Cauline leaf width (mm)	0·5–3·5	0·7–4·5	0·7–5·0
Cauline leaf	infolded	usually flat	flat
Ligule (mm)	1·6–4·0	1·8–4·5	2·0–5·5
Panicle length (cm)	1·3–4·4(–5·4)	1·4–6·3	(2·0–)2·6–5·0
Spikelet length (mm)	2·5–3·3	2·5–3·0	2·0–3·0
Glumes	lanceolate, acute. Short hairs on keel and margins	lanceolate, acute to obtuse. Uneven long and short silky hairs on keel and margins	lanceolate, obtuse. Silky hairs on keel and shorter appressed hairs from middle to base of keel
Total awn length (mm)	(3·4–)4·0–5·3(–6·5)	(3·0–)4·5–5·5	3·0–4·5(–5·0)
Awns	exceeding glumes by 3–4 mm	exceeding glumes by 1·0–3·5 mm	exceeding glumes by 0·8–1·7 mm
Lemma	hairy at tip	hairs at tip present (often few) or absent	usually no hairs at tip
Anther length (mm)	1·2–2·2	1·0–1·5	0·8–1·7
Distance between glumes and lemmas (mm)	0·2–0·7(–0·9)	(0–)0·1–0·4(–0·5)	(0–)0·1–0·35(–0·55)
Chromosome no.	14, 21, 28	21	28

[a] Difference between basal internode width and stem width.

[b] Adjacent basal internodes swollen.

The hybrid is very variable morphologically and anatomically and cannot be reliably identified with any one character. Indeed, even pollen sterility can break down as a diagnostic character; specimens of both *A. bulbosus* and *A. geniculatus* have been recorded with highly sterile pollen (<1% stainable with Muntzing's aceto-carmine).

All hybrids were observed to contain at least some characteristics from both parents, although all were invariably much more similar to one parent than to the other. Whilst scatter diagrams can be used to show some degree of intermediacy (Fig. 1), overall intermediacy is best represented on a percentage hybrid index. Representatives of *A. bulbosus*, *A.* × *plettkei* and *A. geniculatus* were compared on a percentage hybrid index according to the scheme given in Appendix 1. A histogram constructed from the index (Fig. 2) shows that the individual plants fall into two relatively broad but distinct groups, corresponding to the index range of the two parental species. The score of the hybrids falls at the margins of the two parents and is in no case entirely intermediate between them. Hence, there are both '*A. geniculatus*-like' and '*A. bulbosus*-like' representatives of *A.* × *plettkei*, but apparently no nearly intermediate representatives.

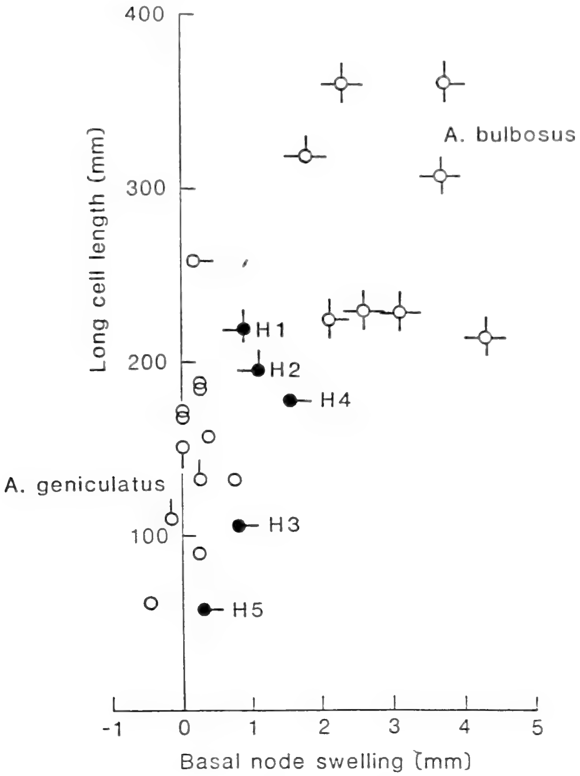

FIGURE 1. Scatter diagram showing specimens of *A. bulbosus*, *A. geniculatus* and some representatives of the hybrid between them, *A.* × *plettkei* (H1–5).
KEY

○ <25% of short-cells are prickles/hook-cells (abaxial surface)
○- >25% of short-cells are prickles/hook-cells (abaxial surface)
○ glumes obtuse
⫯ glumes obtuse to acute
⫯ glumes acute
○ leaves flat
-○ leaves mostly infolded

○ rooting nodes absent
⫰ rooting nodes present
○ tetraploid or diploid
● triploid

Hybrid localities: H1, GR 63/505.074; H2, GR 50/514.994; H3, GR 41/362.144; H4, GR 51/465.094; H5, GR 40/170.918

The decumbent growth habit of the '*A. geniculatus*-like' hybrid makes it unlike either of its two parents. The panicle is often hidden under leaves or just turning up beyond the leaf-tips. The lengths of the stem, panicle, cauline and basal leaves and the widths of the panicle and cauline leaves are extremely variable. On open ground, decumbent stems readily develop from 4–5 nodes, producing branches which in total produce 15–50 leaves on a stem. This nodal branching is seen in *A. geniculatus* but with less leaf production. This hybrid is not a robust plant: its stems, unlike those of either parent, need support from surrounding vegetation.

Two features are significant for field recognition: the number of nodes and the number of leaves per culm, which both far exceed those of either of the parents.

The '*A. bulbosus*-like' hybrids are less distinctive in the field but may be identified by their intermediate internode swelling (0·5–2 mm), their variable glume-tip shape (obtuse to acute), their lemmas which are only weakly hairy in the distal third, their fairly erect culms, and their '*A. geniculatus*-like' awn length (3–4·4 mm).

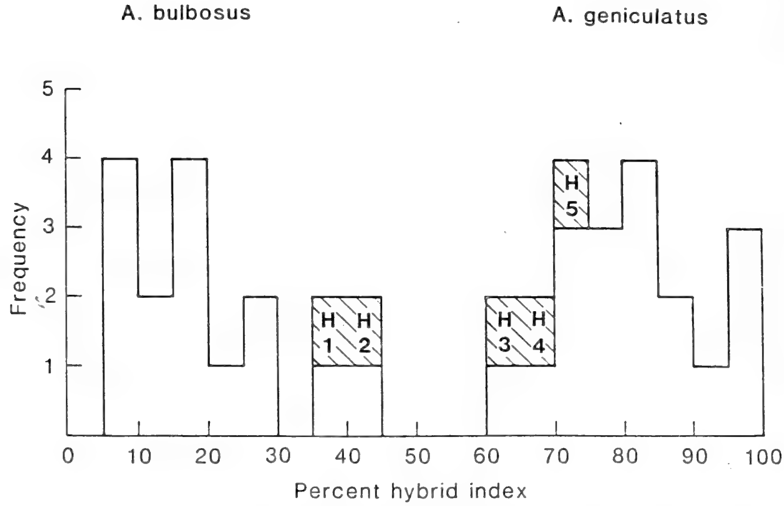

FIGURE 2. Percent hybrid index showing relationship between *A. bulbosus*, *A. geniculatus* and *A.* × *plettkei* (H) (see Fig. 1 for localities of the hybrids).

CHROMOSOME NUMBER

Given the close affinity shown by representatives of *A.* × *plettkei* to its parents, chromosome number can provide strong additional evidence for identification purposes.

Several authors have reported a chromosome complement of 2n=14 for *A. bulbosus* (e.g. Maude 1939; Sieber & Murray 1979, 1980) and of 2n=28 for *A. geniculatus* (e.g. Kattermann 1930; Sieber & Murray 1979). Sieber & Murray (1979) investigated chromosome numbers in *Alopecurus* species at several stations on the south coast of England. For *A. bulbosus* they recorded that, in addition to diploids, triploids and tetraploids were found growing together in a mixed population from Seasalter, E. Kent, v.c. 15. Of the eight plants studied three were diploid, three were triploid and two were tetraploid. The chromosome numbers were 2n=14, 21, and 28. In a subsequent work (Sieber & Murray 1980) it was concluded on the basis of pairing behaviour during meiosis that the triploid and tetraploid plants were autopolyploids.

The same authors (Sieber & Murray 1979) found 2n=28 in natural populations of *A. geniculatus* from Buxton, Derbys., v.c. 57. Their observations on the meiotic and mitotic behaviour of two tetraploid species of *Alopecurus* agree with those of Johnsson (1941) and support the suggestion that *A. pratensis* is an allotetraploid and *A. geniculatus* is an autotetraploid.

Dr P. E. Brandham of Kew has recently confirmed that material of *A.* × *plettkei* on the Stanpit South Marsh, Christchurch, S. Hants., v.c. 11, (Sept. 1985) is triploid (2n=21). We have also confirmed the following hybrids to be triploid: two specimens from Stanpit South Marsh, Christchurch, S. Hants, GR 40/170.918 and three specimens from Glynde Reach, nr. Lewes, E. Sussex, v.c. 14, GR 51/465.094. It is of some importance to remember that because specimens of *A. bulbosus* exist with chromosome numbers of 2n=21 and 2n=28, there may be specimens of *A.* × *plettkei* derived from such plants with chromosome numbers 2n=21–28. Therefore it is possible that there are tetraploid representatives of *A. bulbosus* and *A.* × *plettkei* as well as of *A. geniculatus*. Furthermore, although the possession of 21 chromosomes is strong additional evidence of hybrid status it is not a guarantee since triploid representatives of *A. bulbosus* also occur.

PHENOLOGY

In *A.* × *plettkei* the anthers are indehiscent and produce very little pollen; that produced is largely sterile. Presumably reproduction is almost entirely by vegetative means by growth from swollen stem bases (particularly in the '*A. bulbosus*-like' hybrids) and by rooting at culm nodes (particularly in the '*A. geniculatus*-like' hybrids). In cultivation, the decumbent culms of the '*A. geniculatus*-like' hybrids will develop 4–5 nodes which are quick to root and produce leaves 10–35 cm long within two weeks. This is also seen in the wild, where propagation has taken place on bare ground.

In cultivation, the autumn leaf growth of the hybrids survives a fairly severe winter up to mid-February. This growth then withers and is quickly followed by spring growth with culms appearing before the end of April. Panicles break from the sheath throughout May but their progress is slow; stems with partial panicle exsertion of ± 2·5 cm in mid-May can take a further 15 days for the panicle to break fully to a length of 4·5–5·8 cm. At this stage the plants are light green in colour with a slightly glaucous sheath as in *A. bulbosus*. All flowering is completed before the end of June, when the leaves start to wither. By early July new growth is developing, as the panicles of previous growth are breaking up.

This hybrid is vigorous and responds to management by grazing and cutting by extending its growing season. At Glynde Reach, E. Sussex, in 1986 the marsh had been cut for hay in July and on 8th August there was fresh *A.* × *plettkei* growth with panicles only half exserted. At Nursling N.R., S. Hants., v.c. 11, in late July, in an area grazed by cattle earlier in the year, *A.* × *plettkei* had regrown, with decumbent culms up to 77 cm long and with a considerable bulk of basal leaves. To consider the hybrid's capacity for propagation, three basal internodes of 2 cm in length were put into autumn cultivation, with subsequent production of 93 culms. Single internodes autumn-planted will produce 4–13 tillers by February.

THE DISTRIBUTION OF *ALOPECURUS* × *PLETTKEI* IN BRITAIN

1. South Hampshire, v.c. 11: marshes subject to occasional tidal overflow. Lower Test Nature Reserve, Nursling, GR 41/368.145 and 41/362.144, *R. P. Bowman*, 1978 (**CGE**, **K**, **herb. R.P.B.**, **herb. P.J.O.T.**). The Furlongs, Redbridge, GR 41/364.137, *R.P. Bowman*, 1978 (**CGE**, **K**, **herb. R.P.B.**, **herb. P.J.O.T.**). Unprotected coastal marshes, Stanpit South Marsh, Christchurch, GR 40/170.918, *S. R. Davey*, 1980 (**CGE**, **herb. R.P.B.**, **herb. P.J.O.T.**, **herb. R.M. Walls**). Derelict marsh subject to tidal inflow, Keyhaven, GR 40/305.916, *R.P. Bowman*, 1986 (**herb. R.P.B.**).
2. East Sussex, v.c. 14: managed grazing marshes, south-east of Decoy Wood and adjacent to Glynde Reach, near Lewes, GR 51/465.094, *B. Wurzell*, 1977 (**CGE**, **LTR**, **herb. P.J.O.T.**, **herb. B.W.**). Disturbed river wall-berm, east bank of R. Cuckmere, near Exceat bridge, Seaford, GR 50/514.994, *Lady R. FitzGerald*, 1987 (**herb. P.J.O.T.**, **herb. R.F.**).
3. West Kent, v.c. 16: wet track in rough grazing, upland of marsh level, Higham marshes, Church Street, near Higham, east of Gravesend, GR 51/713.742, *Lady R. FitzGerald*, 1987 (**herb. P.J.O.T.**, **herb. R.F.**).
4. East Suffolk, v.c. 25: managed grazing marshes, Castle Farm, Burgh Castle, GR 63/473.058, *R. P. Libbey*, 1980 (**LTR**). Humberstone marshes, south of Breydon Water near Great Yarmouth, GR 63/505.074, *P.J.O. Trist*, 1982 (**herb. P.J.O.T.**).

Specimens collected from Lewes and from Burgh Castle resemble *A. bulbosus* more closely than *A. geniculatus*. Specimens collected from the remaining sites show a stronger resemblance to *A. geniculatus*.

ECOLOGY

The habitat of *Alopecurus* × *plettkei* is coastal marsh that is inadequately protected from tidal water owing to an absence or a breakdown in sea defences. These areas are occasionally shallowly flooded for a few hours at periods of high spring and autumn tides, when tidal water runs up the ditches and overflows on the land. A saline deposit is built up in the soil, more particularly in the marsh depressions and in the furrows on marshes that were at one time under cultivation.

A. × *plettkei* thrives in a soil texture of organic loam with additions of alluvium. It has a lower salt tolerance than *A. bulbosus* and a preference for an open position at or slightly above marsh level. It will colonise the bare margin of a depression, but not the depression itself, showing its preference for drainage, as opposed to *A. bulbosus* which will thrive in the water-logged bed of a depression. At

Stanpit South Marsh, Christchurch, where there are old grips, and rills in adjacent saltings, the hybrid colonises the margin and not the bed of grips that support *Salicornia* spp., an indication of a high salt level (too high for *A. bulbosus*).

At Keyhaven in a small 0·5 ha marsh, *A.* × *plettkei* has been found only in two small colonies at the back of the marsh, just above the general level, so that a tide lapping near the area would rapidly run off. Here *A. bulbosus* is widespread but thinly spaced among *Glaux maritima*, *Puccinellia maritima* and some *Aster tripolium* in a soil with 0·5% NaCl. During the warm months of the year it is likely that this percentage is higher and that *A. bulbosus* is here at its limit of salt tolerance. At The Furlongs, Redbridge, there is a similar demonstration of the difference in saline tolerance of *A. bulbosus* and *A.* × *plettkei*. The sward, subject to fairly frequent tidal over-spills, is almost entirely a simple mixture of *Puccinellia maritima* and *Agrostis stolonifera* with some *Aster tripolium*. Soil samples taken contained a range of 0·4–0·5% NaCl, but the presence of *Aster tripolium* suggested a higher percentage in June–July. *A. bulbosus* was thinly distributed and only occasionally small, weak plants of *A.* × *plettkei* were found on low elevations of old ditch spoil where drainage would be rapid following tides.

The marshes on the Lower Test N.R. at Nursling have probably never been disturbed. The surface levels are therefore uneven, with isolated areas of halophytes demonstrating saline deposits from occasional flooding. In an unimproved marsh, *Eleocharis uniglumis*, *Festuca rubra*, *F. arundinacea*, *Agrostis stolonifera* and *Trifolium fragiferum* are common associates, but, where *A. bulbosus* is present in lower levels, these plants are supplemented by *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Ranunculus sceleratus* and *Triglochin maritima*. *A.* × *plettkei* would be found in open areas of *Agrostis-Festuca* but not, or rarely, in the lower and wetter areas of *A. bulbosus* and its associates.

On the Lower Test N.R. the limits of variation of salt content of soil samples taken in August at 15 cm depth were 0·08–0·48% NaCl. This range will vary with the temperature of the season when samples are taken, and seasonal factors diluting sea water. Both at Redbridge by Southampton Water and at Stanpit South Marsh by Christchurch, for instance, there is a complicated double tide which increases salinity on the one hand, and an outflow of fresh-water from the R. Test, Avon and Stour which diminishes salinity on the other.

The hybrid was abundant on the site where it was first recorded in 1977 (Glynde Reach, v.c. 14) and occupied wet areas over a large part of G.R. 51/46.09. No *Alopecurus bulbosus* was present in 1977; it was last recorded near the river bank in 1962 by B. Wurzell, C. A. Stace and others on a London Natural History Society field day. The site would have been in the area of a now derelict ditch below the high bank containing the river. Over-spills of saline water no longer occur. Sometime prior to 1975, a tidal flap and pump were installed on The Reach at the point just above the A27 road, preventing land flooding. The former wet state of the hybrid site is still witnessed by small grips crossing the marsh and connecting to boundary ditches. The marsh is now dry with a diminishing amount of *Alopecurus* × *plettkei*. A soil sample taken in August 1986 at 15 cm from the bed of a grip, where only a few plants of the hybrid were seen, contained 0·01% NaCl. There was no plant indicative of salinity in the sward or in the river which rejoiced with *Nuphar lutea* on its surface.

A. × *plettkei* would not make a constituent of a grass-seed mixture. It produces long decumbent stems which are weak and lie over the ground and would therefore be smothered by tall marsh grasses such as *Festuca arundinacea*, *Agrostis stolonifera* and *Elymus repens*. The *A. geniculatus* parent of the hybrid is common on most coastal marshes, but its other parent, *A. bulbosus*, is still comparatively rare, in spite of the fact that it has been removed from the Red Data lists (Perring & Farrell 1983). This hybrid is able to continue to occur where *A. bulbosus* is extinct, as on the marshes by Glynde Reach, but from observations of this taxon in cultivation we consider its perennial life is limited.

IS *A.* × *PLETTKEI* A THREAT TO THE SURVIVAL OF *A. BULBOSUS*?

It has been suggested that the spreading growth of *A.* × *plettkei* may have a smothering affect on *A. bulbosus* and may pose a threat to its survival. This is unlikely. The growth period of the two taxa does not overlap. *A. bulbosus* is fully developed and flowering by the last week in May to the first week in June, and, before the end of July, leaves and culms have died back when cattle-treading soon disperses the plant remains so that *A. bulbosus* is difficult to trace until the following year, except by exploration for the swollen stem bases (Trist 1981). *A.* × *plettkei* has an extended growing season and the plants which over-winter die back in July only to be immediately replaced by new growth which continues into September. Thus *A. bulbosus* has completed its growth in early summer while strong growth of the hybrid continues throughout July and August.

There is a significant difference in the habitat of the two taxa. The hybrid is seen on average mid-marsh level and not below, and preferably in a position of better drainage which is slightly above the average level. *A. bulbosus* prefers a reasonably constant moisture supply and has a tolerance to salinity of the order of 0·4–0·5% NaCl. It is found on the higher margin of saltings and often in the low areas and furrow depressions of marsh adjacent to tidal rivers, which gives an indication of tolerance or even preference for salinity. Although it can be cultivated for several years in the absence of salinity and a constant moisture supply, it eventually reverts to a poor state and dies. *A.* × *plettkei* behaves as a perennial but it is likely that it is short-lived.

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APPENDIX: SCORING SCHEME FOR HYBRID INDEX

	A. bulbosus	Intermediate	*A. geniculatus*
Score	0	1	2
Vegetative characters			
No. of nodes per culm	3	3–4	4
No. of branches per culm	0	N/A[a]	1
Rooting nodes	absent	N/A	absent
Basal node swelling (mm)	(1–)2–4·5(–6·0)	(0–)0·5–2·2	(–0·5–)0–1·0(–1·5)
'Twin' basal swollen internodes	present	N/A	absent
Basal leaves infolded	mostly infolded	N/A	mostly flat
Stem	erect	fairly erect or spreading	spreading, geniculate
Flag-leaf width (mm)	1–2	2·01–3	>3
Lower culm-leaf width (mm)	1–2	2·01–3	>3
Reproductive characters			
Panicle length (cm)	2·0–2·5	2·51–4·4	>4·4
Panicle width (cm)	<3·5	3·5–4·5	>4·5
Glume sharpness	acute	acute to obtuse	obtuse
Awn length (mm)	>5	4–5	<4
Hairs at top of lemma	present	sparse	absent
Distance between glume tips & lemma tip (mm)	>0·4	0·25–0·4	<0·25
Pollen diameter (μm)	<29·4	29·4–33·0	>33·0
Abaxial epidermis			
% short-cells being hooks/prickles	0–20	21–37	>37
Short-cell frequency (per 0·11 mm^2)	0	1–2	>2
Mean long-cell length (μm)	>200	180–200	<180
Presence of rows of short-cells	absent	N/A	present
Distance between stomata in continuous rows (μm)	>90	70–90	<70
Stomatal length (μm)	<38	38–41	>41
Adaxial epidermis			
Mean long-cell length (μm)	>210	190–210	<190
Short-cell frequency (per 0·11 mm^2)	<3	3–4	>4
Prickles above nerves	present	N/A	absent

[a] N/A: not applicable

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Potamogeton × *lanceolatus* Sm. in the British Isles

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ABSTRACT

Potamogeton × *lanceolatus* Sm., the sterile hybrid between *P. coloratus* Hornem. and *P. berchtoldii* Fieb., is known only from the British Isles. The names *P. lanceolatus* Sm. and its synonyms *P.* × *lanceolatus* var. *hibernicus* A. Benn. and *P.* × *perpygmaeus* Hagstr. ex Druce are lectotypified. The distribution of *P.* × *lanceolatus* is outlined and the history of its taxonomic treatment reviewed.

INTRODUCTION

Potamogeton × *lanceolatus* Sm. (*P. coloratus* Hornem. × *P. berchtoldii* Fieb.) is one of the few hybrids between the broad-leaved *Potamogeton* species in Sect. *Potamogeton* and the species with narrow, linear leaves in Sect. *Graminifolii.* It is a sterile plant, only known from the British Isles. Since its discovery in 1806 three names have been given to it: *P. lanceolatus* Sm., *P.* × *lanceolatus* var. *hibernicus* A. Benn. and *P.* × *perpygmaeus* Hagstr. ex Druce. The purpose of this paper is to outline the circumstances in which these names were published, to lectotypify them where necessary and to describe the taxonomic history and distribution of this rare hybrid in the British Isles.

POTAMOGETON × *LANCEOLATUS* SM.

Potamogeton × **lanceolatus** Sm. in Sowerby, *Engl. bot.* **28**: t. 1985 (1809) pro sp. ('*lanceolatum*').
Lectotype: North Wales, August 1808, *H. Davies*, herb. J. Sowerby, **BM**! Isolectotype in **BM**!.

The description of *P.* × *lanceolatus* in *English Botany* was written by J. E. Smith and illustrated by a plate drawn by J. Sowerby. Smith (Sowerby 1809) stated that the plants he described were sent to him by the Rev. H. Davies "from the lakes of North Wales". There is no reason to suppose that Smith saw the earliest specimen of *P.* × *lanceolatus*, collected by Davies in October 1806 (**BM**). There is, however, a specimen in Smith's herbarium (**LINN**, Savage manuscript catalogue 246.17) labelled in his own hand "Potamogeton lanceolatum Engl. Bot. t.1985. North Wales. *Rev. H. Davies* 1807". There are two specimens in J. Sowerby's herbarium (**BM**) labelled "Potamogeton lanceolatum nova spec. Received H. Davies. N. Wales. August 1808. E.B. t.1985". All these specimens were determined as *P.* × *lanceolatus* by J. E. Dandy and G. Taylor, and I agree that they all represent this taxon. All conform to Smith's description, and none is a better match than the others.

Both the specimen in Smith's herbarium (**LINN**) and those in Sowerby's (**BM**) must be regarded as syntypes. Those in Smith's herbarium were presumably used by him to draw up the description in *English Botany*. Sowerby's specimens were probably sent to him directly by Rev. H. Davies. The original drawings for *English Botany* are preserved in the British Museum (Natural History) and notes on them show that some, at least, were based on specimens sent directly to Sowerby (e.g. *Schoenus monoicus*). There is no such evidence on the original drawing of *Potamogeton* × *lanceolatus*, but as Sowerby notes that it was drawn from fresh specimens it seems likely that they came directly to him. The labelling of the specimens also suggests this. There is therefore no evidence that Smith saw them. Close comparison of the two sheets in Sowerby's herbarium with the original drawing show that one plant is so similar to the drawing that the conclusion that it is the plant actually drawn is inescapable. It is less easy to identify the plant drawn by comparing the specimen to the published plate as there are some differences between the original drawing and the published version, notably a young leaf at the apex of the stem on the drawing which appears on the plate as an inflorescence in bud.

Thus there are available for selection as lectotype two specimens closely related to the protologue, that studied by Smith who drew up the description and that drawn by Sowerby who illustrated it. J. E. Dandy and G. Taylor have labelled the specimen at **LINN** as the "type" and the sheet at **BM** which includes the plant illustrated in *English Botany* as the "lectotype" of *P.* × *lanceolatus*. This introduces a further complication. If one considers that the labelling of the **BM** specimen constitutes effective lectotypification then it must be accepted as the lectotype, as it could only be rejected if it seriously conflicts with the protologue. However if one considers that a lectotypification is only effective when published then there is a choice of lectotype, as Dandy and Taylor did not publish their selection. If I choose the specimen in Smith's herbarium as lectotype the actual lectotype of *P.* × *lanceolatus* will be left in doubt, as it would depend on one's view of what constitutes lectotypification. This would be undesirable, so I have decided to uphold Dandy and Taylor's choice and cite it above as lectotype. It is reproduced as Fig. 1.

It is unfortunate that the specimens available to Smith and Sowerby lacked broad floating leaves, one of the characteristic features of *P.* × *lanceolatus*. This was probably the reason for a number of erroneous nineteenth century records of *P.* × *lanceolatus*.

P. LANCEOLATUS VAR. *HIBERNICUS* A. BENN

Potamogeton lanceolatus var. **hibernicus** A. Benn. apud Praeger in *Irish Nat.* **5**: 243 (1896).
Lectotype: Clonbrock River, Co. Galway, June 1896, *R. L. Praeger*, **DBN**!
P. lanceolatus forma *hibernicus* A. Benn. apud Praeger in *Irish Nat.* **5**: 243 (1896), nom. provis.

R. L. Praeger collected *P.* × *lanceolatus* (as well as *P. coloratus*) from the Clonbrock River not far from the House on 21st June 1896, probably on a pre-breakfast ramble (McWeeney & Praeger 1896). Material from Clonbrock was submitted to Arthur Bennett who, after describing differences between it and plants from Anglesey and Cambridgeshire, stated "it might be called var. *hibernicus* (or f. *hibernicus*), characterized by its longer, and broader upper leaves, longer lower leaves, slightly longer flower-spikes and the structure of the leaves" (Praeger 1896). I follow J. E. Dandy and G. Taylor (in their unpublished monograph *British species of* Potamogeton *L.*) in regarding var. *hibernicus* as a validly published name, with f. *hibernicus* as a provisional name, not validly published at that rank. There is no material of Praeger's 1896 collection in Bennett's herbarium (**BM**). There are, however, two specimens in Praeger's herbarium (**DBN**). One is labelled "Potamogeton lanceolatus Smith var. hibernicus, A. Benn. in litt." and I have designated this as the lectotype. It is reproduced as Fig. 2.

There is some variation in the leaf shape of *Potamogeton* × *lanceolatus* (Figs. 2, 3). This appears to be correlated with the age of the plant and with environmental factors. The lower stem leaves are more or less linear and superficially resemble the leaves of *P. berchtoldii*, although they are broader and differ in venation. Sometimes such leaves occur all along the stem, even on a flowering plant. Other plants have broader upper leaves which are elliptical in shape and are more obviously intermediate between the putative parents. W. Wilson noticed that in Anglesey the broader leaves "are *always* found when the current is slow" (Hooker 1830). They are well developed in plants from Burwell which were collected from a ditch or cultivated in a small pond, but are not always found on plants collected in the swifter water of the Afon Lligwy or the Caher River. The type material of var. *hibernicus* only has more or less linear leaves. However I can see no difference between the leaf size and shape of these plants and that of some collections from the type locality of *P.* × *lanceolatus*, the Afon Lligwy (Table 1). I cannot understand why Bennett thought that the leaves of var. *hibernicus* were longer and broader than those of the type: there is no reason to regard them as broader, either in absolute terms or in relation to their length. The lacunae along the midrib, said by Bennett to be much less conspicuous in var. *hibernicus*, are similar to those of plants from Anglesey. I can

FIGURE 1. The lectotype of *Potamogeton lanceolatus* Sm. (**BM**). The plant on the lower right-hand side of the sheet is the one illustrated in *English Botany*, t. 1985 (Sowerby 1809).

FIGURE 2. The lectotype of *Potamogeton lanceolatus* var. *hibernicus* A. Benn. (**DBN**). The specimen is a good example of the form of *P.* × *lanceolatus* without broad upper leaves.

FIGURE 3. The lectotype of *Potamogeton* × *perpygmaeus* Hagstr. ex Druce (**OXF**). The specimen shows the broad upper leaves often produced by the hybrid *P. coloratus* × *berchtoldii*.

TABLE 1. COMPARISON OF *POTAMOGETON* × *LANCEOLATUS* SPECIMENS FOR CHARACTERS ON WHICH VAR. *HIBERNICUS* WAS BASED

Based on dried specimens in **BM** & **CGE** (Afon Lligwy & Caher River) and **DBN** (Clonbrock, the type material of var. *hibernicus*).

	Afon Lligwy	Clonbrock	Caher River
Lower leaves (mm)	23–75 × 2–5·5	(22–)40–72 × (2–)3–5	25–65 × 2–5
Involucral leaves (mm)	17–65 × 3·5–10	40–65 × 3–6	21–48 × 3–7
Peduncles (mm)	9–50	39–42	10–51
Width of midrib and adjacent lacunae (mm)	0·3–0·7	0·3–0·7	0·3–0·7

therefore see no reason to regard the Clonbrock plants as distinct from those from Anglesey, and support the reduction of var. *hibernicus* to synonymy.

POTAMOGETON × *PERPYGMAEUS* HAGSTR. EX DRUCE

Potamogeton × **perpygmaeus** Hagstr. ex Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **6**: 630 (1923).
Lectotype: Cahir River, Co. Clare, September 1921, *G. C. Druce*, **OXF**!, photograph in **BM**! Isolectotypes in **BM**!, **CGE**!, **E**!, **K**!, **OXF**! and probably elsewhere.
P. × *perpygmaeus* Hagstr. ex Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **6**: 580 (1922), *nom. nud.*

P. × *lanceolatus* was collected by P. B. O'Kelly in the Caher River in 1891, the first Irish record (Levinge 1891). In June 1909 G. C. Druce was taken by O'Kelly to see it, and noted that it did not strike him as identical to the Anglesey plant (Druce 1910). Later Druce submitted specimens to J. O. Hagström, who in 1919 suggested that they might be *P. coloratus* × *P. berchtoldii*, despite the fact that the former was not then known from the area (Hagström thought that *P.* × *lanceolatus* from Anglesey was *P. alpinus* × *P. berchtoldii*). In September 1921 Druce, making "a somewhat adventurous journey to Ireland just after the truce"[a], returned to the Caher River with Mrs M. L. Wedgwood. He found *P.* × *lanceolatus* "in profusion and in very much better condition than that obtained on my first visit", together with *P. coloratus* in some quantity (Druce 1923a, b). On examining the 1921 material Hagström suggested the name *P.* × *perpygmaeus* for plants from Ireland and Cambridgeshire, and promised to write a note on it in a book he was writing. At first Druce (1922) published *P.* × *perpygmaeus* as a *nomen nudum*, but he wrote a longer note about it after Hagström's death in 1922 (Druce 1923a). Although the second note does not contain a formal morphological description, Druce validated the name by his remark that "the reddish colour of *coloratus* is also present in *perpygmaeus* which thus differs from the beautiful grass-green of the Anglesey *lanceolatus*". (The fact that one would expect the Anglesey plant to have a reddish colour if it actually was *P. alpinus* × *P. berchtoldii* is not commented upon).

P. × *perpygmaeus* should be typified by a specimen from Druce's 1921 gathering, of which there are three sheets in his herbarium (**OXF**). I have selected one of these as the lectotype (Fig. 3). The extract from the B.E.C. Report in which Druce validated *P.* × *perpygmaeus* is attached to this sheet, as is a note from Hagström beginning "This hybrid which I ad int. [erim] names *P. perpygmaeus* is undoubtedly the most interesting plant Ireland owns . . .". This note from Hagström is dated 22nd July 1921, presumably an error as the material was not collected until September of that year.

Judging by herbarium specimens, the colour of *P.* × *lanceolatus* in Anglesey is no different from that of the populations in Ireland. Some Anglesey collections have clear green leaves but others – as Bennett (1924) pointed out – have a reddish brown tinge. Ironically this coloration is well developed in material collected by Druce himself in June 1900 (**CGE**). It is unfortunate that Hagström was

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[a] A truce between the Irish Republican Army and the forces of the British Crown had existed since 11th July 1921. The I.R.A. had retained their arms, and their units would have been in evidence at the time of Druce's visit.

unable to publish his reasons for separating the Irish and Cambridgeshire plants as *P.* × *perpygmaeus*. I can see no differences which would justify such a distinction, and therefore agree with the view that they represent a single taxon.

TAXONOMIC HISTORY OF *P.* × *LANCEOLATUS*

Most 19th century authors maintained *P. lanceolatus* as a species (W. J. Hooker 1830, Babington 1843, Sowerby 1869, J. D. Hooker 1870). Of the authors of the standard Floras only Bentham (1858), whose species concept in *Potamogeton* was extremely broad, included *P. lanceolatus* as a synonym of *P. lucens*. However, some of the specimens attributed to *P. lanceolatus* were erroneously identified and the concept of this taxon, not all that clearly defined by Smith, became even more blurred. Thus the fifth edition of Babington's *Manual of British Botany* (1862), the most critical of the more readily available Victorian Floras and one written by an author who had a special interest in *Potamogeton*, contained erroneous records of *P. lanceolatus* from Buttermere, Killarney and Antrim. Babington added a description of the fruit of *P. lanceolatus* to this edition of the *Manual*, but this was based on material which he later recognized as *P. polygonifolius*. J. T. Syme concluded that all except the Anglesey specimens had been erroneously identified, a conclusion which Babington accepted (Sowerby 1869, Babington 1872).

Babington was able to visit Anglesey in 1880, where he was shown *P. lanceolatus* by J. E. Griffith, author of *The Flora of Anglesey and Carnarvonshire*. In his account of his visit Babington (1881) stressed the fact that the fruit of *P. lanceolatus* was still unknown, despite the fact that he had visited the site at the end of August and Griffith returned in late October. "If it had not been for Mr. Bennett's discovery", Babington commented, "we might have thought that the plant of Anglesea was a barren form of some species, and that it propagated itself by offsets . . . but the discovery of exactly the same plant in the Fens renders this improbable". Bennett's discovery of *P.* × *lanceolatus* in Cambridgeshire stimulated interest in the plant, and with the publication of his paper in the *Journal of Botany* (Bennett 1881) an excellent drawing of *P.* × *lanceolatus*, accompanied by an accurate and detailed description, finally became available to British botanists.

Alfred Fryer was the first to suggest that *P.* × *lanceolatus* was a hybrid. In an early discussion of the possibility of hybridization in the genus (Fryer 1888) he called it "one of the best and most distinct species of *Potamogeton*", citing it to demonstrate that "barrenness is no proof of hybridity". He later came to realize that it was a hybrid between a broad-leaved and a narrow-leaved species, suggesting the parentage *P. gramineus* (as *P. heterophyllus*) × *P. berchtoldii* (as *P. pusillus* [auct.]) for the Anglesey plant and *P. gramineus* × *P. friesii* for Cambridgeshire material (Fryer 1894). Hagström (1916) considered that the Anglesey plant was *P. alpinus* × *P. berchtoldii*, and later suggested the parentage *P. coloratus* × *P. berchtoldii* for plants from Cambridgeshire and Ireland (see above). Bennett (1919, 1925) refused to accept that either *P. alpinus* or *P. coloratus* was the broad-leaved parent of *P.* × *lanceolatus*, still favouring *P. gramineus*. However *P. coloratus* × *P. berchtoldii* is now accepted as the parentage of *P.* × *lanceolatus* at all its localities (Dandy 1958, 1975).

DISTRIBUTION OF *P.* × *LANCEOLATUS* IN THE BRITISH ISLES

CAMBRIDGESHIRE (V.C. 29)

Bennett (1880) discovered *P.* × *lanceolatus* at Burwell Fen on 4th August 1880. The exact locality was a ditch on the right-hand side of Burwell Drove, going from Wicken to Burwell (**CGE**). In his first notice of the plant Bennett (1880) stated that it grew with *P. coloratus*; in a later paper he said that it grew with *P. gramineus* in a ditch lined with *Eleocharis acicularis* (Bennett 1925). It was in the later note that he argued for *P. gramineus* rather than *P. coloratus* as one of the parents of *P.* × *lanceolatus*! Specimens of both *P. coloratus* and *P. gramineus* collected by Bennett at Burwell on the day he discovered *P.* × *lanceolatus* were seen by J. E. Dandy and G. Taylor.

Alfred Fryer searched repeatedly for *P.* × *lanceolatus* at Bennett's locality, without success. He reported (1894) that the ditch in which it grew "has now closed up, and its aquatic vegetation is extinct". He was unable to discover it in nearby water-courses. As a plant relying entirely on vegetative reproduction for its survival. *P.* × *lanceolatus* is presumably ill-adapted to survive a period when its habitat becomes overgrown.

Bennett cultivated the Burwell plant in a small pond in his Croydon garden – it "flourished remarkably" and he was able to distribute 200 specimens of cultivated material (Bennett 1925). The plate in Fryer & Bennett (1915) is based upon Cambridgeshire material.

ANGLESEY (V.C. 52)
Despite the fact that Smith stated that the plants he described as *P.* × *lanceolatus* were sent to him by the Rev. H. Davies "from the lakes of North Wales" (Sowerby 1809), there is no doubt that they came from the Afon Lligwy, a stream in Anglesey. Davies (1813) himself cites the locality as "the rivulet between Bodafon and Lligwy" and the Afon Lligwy remains the only known Welsh locality for the hybrid. It was collected there repeatedly after its discovery by Davies. In 1875 C. Bailey found that it grew "in longish patches to the exclusion of anything else near it. In a few places where the stream is slower, and more water in, it simply fills it up, from the bed to the surface, so that ducks cannot comfortably paddle in it; in the swifter places it is in the middle of the brook, forming patches of two to three yards long by six to twelve inches broad" (Bennett 1881). Five years later Babington (1881) "found plenty of the plant growing in the quieter parts of the rather rapid stream, both above and below the bridge of Penrhos-lligwy". Many botanists saw it subsequently, most recently R. H. Roberts who recorded it in c. 1960 at grid reference 23/483.854 and in 1968 near the bridge where the A5025 road crosses the Afon Lligwy, at 23/488.862. On 1st August 1987 Ms V. Morgan and I attempted to refind the plant in the Afon Lligwy, but without success.

CO. CLARE (V.C. H9)
As in Anglesey, *P.* × *lanceolatus* has been regularly collected in the Caher River since its discovery by P. B. O'Kelly in 1891. Webb & Scannell (1983) describe it as "plentiful in the Caher R. over most of its course". On 26th June 1984 K.G. & J.O. Mountford recorded *Apium nodiflorum*, *Eleocharis palustris*, *Juncus articulatus*, *Mentha aquatica* and *Ranunculus flammula* as associates of *P.* × *lanceolatus* in the Caher River at grid reference M160.080.

N.E. GALWAY (V.C. H17)
Two localities for *P.* × *lanceolatus* are known in Co. Galway. It was discovered in the Clonbrock River by R. L. Praeger in 1896 and refound in the same river in 1952 at Clonbrock (*N. D. Simpson*, **BM**) and by Island Bridge near Ahascragh (*R. B. Drummond*, **K**). The other site is near Tuam, where it was discovered by R. L. Praeger in 1899. The most detailed specimen was collected on 13th July 1899 (**BM**) and is labelled "rapid shallow pebbly stream, Grange River, Barbersfort near Tuam".

OTHER EUROPEAN HYBRIDS BETWEEN SPECIES IN SECT. *POTAMOGETON* AND SECT. *GRAMINIFOLII*

Three more hybrids between Sect. *Potamogeton* and Sect. *Graminifolii* are known in Europe. Two are similar to *P.* × *lanceolatus*: *P.* × *rivularis* Gillot, *P. polygonifolius* × *P. berchtoldii*, which is known from France, and *P.* × *miguelensis* Dandy, *P. polygonifolius* × *P. pusillus*, described from the Azores (Dandy 1970, 1975). The third hybrid is *P.* × *variifolius* Thore, *P. natans* × *P. berchtoldii*, recorded in France and Ireland (Dandy & Taylor 1967). The identity of *P.* × *heslop-harrisonii* Clark, described from the Outer Hebrides, has yet to be elucidated. Clark originally reported this as *P. gramineus* × *P. berchtoldii*, later amending this to *P. gramineus* × *P. perfoliatus* × *P. berchtoldii* (Clark 1942, 1943). Heslop Harrison (1949) commented that the parentage *P. alpinus* × *P. berchtoldii* could not be excluded. According to Clark (1943) the type material was deposited in the herbarium of the Department of Botany, King's College, Newcastle upon Tyne (NCE), but I cannot find it there now, nor is it at **HAMU**, in Clark's personal herbarium (**BM**) nor at **K**.

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A reappraisal of the British and Irish dactylorchids, 3. The spotted-orchids

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ABSTRACT

52 morphological characters were recorded for ten individuals from each of 20 populations of *Dactylorhiza fuchsii* (Druce) Soó and 23 populations of *D. maculata* (L.) Soó. Multivariate analyses of data for both species demonstrate largely continuous morphological variation polarized into two independent trends representing vegetative vigour and degree of pigmentation. Both trends reach greater extremes in *D. fuchsii*. Possible causes of this variation, including environmental modification, are discussed. Univariate, bivariate and multivariate analyses demonstrate considerable overlap between existing and potential infraspecific taxa of both species. Revised diagnostic descriptions are provided for five British and Irish varieties of *D. fuchsii*: var. **fuchsii** (Druce) Bateman & Denholm, **comb. nov.**, var. **hebridensis** (Wilmott) Bateman & Denholm, **comb. nov.**, var. *cornubiensis* (Pugsley) Soó, var. **alpina** (Landwehr) Bateman & Denholm, **comb. et stat. nov.**, and var. **okellyi** (Druce) Bateman & Denholm, **comb. nov.** The morphological distinction of some taxa previously regarded as subspecies has been exaggerated due to insufficient or unrepresentative data and unsubstantiated assumptions regarding their population biology. Their distributions have been confused by a priori identifications of populations based on geographical locations rather than morphological criteria. No justifiable infraspecific taxa can be detected within *D. maculata*. Several long-standing taxonomic and nomenclatural controversies are resolved by detailed study of both the new data and past literature. Solutions to other problems, including the possible conspecificity of *D. fuchsii* and *D. maculata*, require comparable data from Continental spotted-orchid populations.

INTRODUCTION

The taxonomy and nomenclature of the spotted-orchids have evolved progressively but spasmodically since Linnaeus described *Orchis maculata* L. in 1753. *Dactylorhiza maculata* (L.) Soó (Heath Spotted-orchid) is now more clearly and narrowly delimited, and has been joined in the Subsection *Eumaculatae* Vermeulen by *D. fuchsii* (Druce) Soó (Common Spotted-orchid; Druce 1915) and the exclusively Continental *D. saccifera* (Brongniart) Soó (Brongniart 1832). Senghas (1968) and Landwehr (1975) disagreed with Vermeulen's (1947) surprising inclusion of the Madeiran endemic *D. foliosa* (Solander) Soó in this subsection. Some workers have advocated the amalgamation of *D. fuchsii* with *D. maculata* (e.g. Nelson 1976) and the splitting of *D. saccifera* (e.g. Baumann & Künkele 1982). However, this degree of taxonomic instability at the species level is greatly exceeded by a general lack of consensus over numerous infraspecific taxa, which reflects the difficulty of partitioning largely continuous ranges of morphological variation into satisfactory taxa (Prentice 1986). This problem requires detailed morphological studies capable of identifying and quantifying trends in variation that can be assessed for potential taxonomic value and interpreted in an evolutionary context.

This paper continues our morphometric studies on dactylorchids (Bateman & Denholm 1983, 1985), and concludes our survey of infraspecific morphological variation in British and Irish populations.

MATERIALS AND METHODS

20 populations of *D. fuchsii* and 23 of *D. maculata* were sampled between 1982 and 1986, including at least three populations of each of the subspecies listed by Heslop-Harrison (1954) and Clapham (1962). Details of these populations and the sample localities are presented in Tables 1 and 2.

52 morphological characters were recorded for each of ten flowering plants per population (twelve plants of *D. maculata* were measured at Kilmory). Details of these characters (and of ten indices (a–j) derived from them) largely follow Bateman & Denholm (1985), though an additional category (5 = ± solid blotch) was introduced for character 11 (type of labellum markings) and mean peripheral bract cell lengths (character 26) represent 30–100 cells, not 10–30 as was erroneously stated previously.

Tables listing mean values and standard deviations for all characters and indices of each study population are available from the authors on request.

Data were analyzed by univariate and multivariate methods using the Genstat computer program (Payne *et al.* 1987). Characters 46–51 were excluded from the multivariate analyses to avoid bias caused by a series of zero values reflecting the absence of a single feature (i.e. leaf markings), and indices were excluded to avoid duplication of their component characters. *D. fuchsii* and *D. maculata* were analyzed separately. After standardization to unit variance, each species yielded two similarity matrices (Gower 1971), the first using population means and the second using data for individual plants. Each matrix was used to link either populations or individuals by their maximum similarities to yield a minimum spanning tree (Gower & Ross 1969) and then compute principal coordinates (Gower 1966), compound vectors incorporating correlated characters of potential diagnostic value. The first two principal coordinates (PC1, PC2) from each analysis were plotted together to assess the degree of morphological separation of potential taxa in these dimensions (see Bateman & Denholm (1983, 1985) for further details of the application of these techniques to dactylorchids).

MAJOR TRENDS IN MORPHOLOGICAL VARIATION

The multivariate analyses of both populations and individuals demonstrated strikingly similar overall patterns of infraspecific variation in *D. fuchsii* and *D. maculata*. In each of the four analyses (Figs. 1–4), the first two principal coordinates largely represented variation in vegetative vigour and intensity of pigmentation; lower order coordinates consistently accounted for much smaller proportions of the variance than the second and were of little biological or taxonomic significance. For simplicity, we have used our revised classification of *D. fuchsii* into five varieties (shown in the left-hand column of Table 1) throughout this paper.

ANALYSES OF POPULATIONS

19 of the 46 characters used for multivariate analysis of *D. fuchsii* populations contributed appreciably to the first two principal coordinates, which together accounted for 50% of the total variance (Table 3). The second coordinate (PC2 on Fig. 1) largely represented characters determined by vegetative and floral anthocyanin pigments, and clearly separated four anthocyanin-low populations from the Burren (var. *okellyi*; PC2 values <−0·2) from eight anthocyanin-high populations (vars *hebridensis, cornubiensis* and *alpina*; PC2 values >0·1). The eight remaining populations (var. *fuchsii*) had intermediate values for PC2 but were widely dispersed along PC1, which represented characters such as stem, leaf, bract and inflorescence dimensions that determine vegetative vigour. Thus, Oldshore and Polin were the least vigorous and Oaklands and Parham were the most vigorous of the populations studied. Five populations of var. *fuchsii* showed greater overall vigour than all populations of the other varieties.

The superimposed minimum spanning tree resolved variation along these axes into five branches, radiating from the area occupied by less vigorous populations of var. *fuchsii* in the centre of the plot

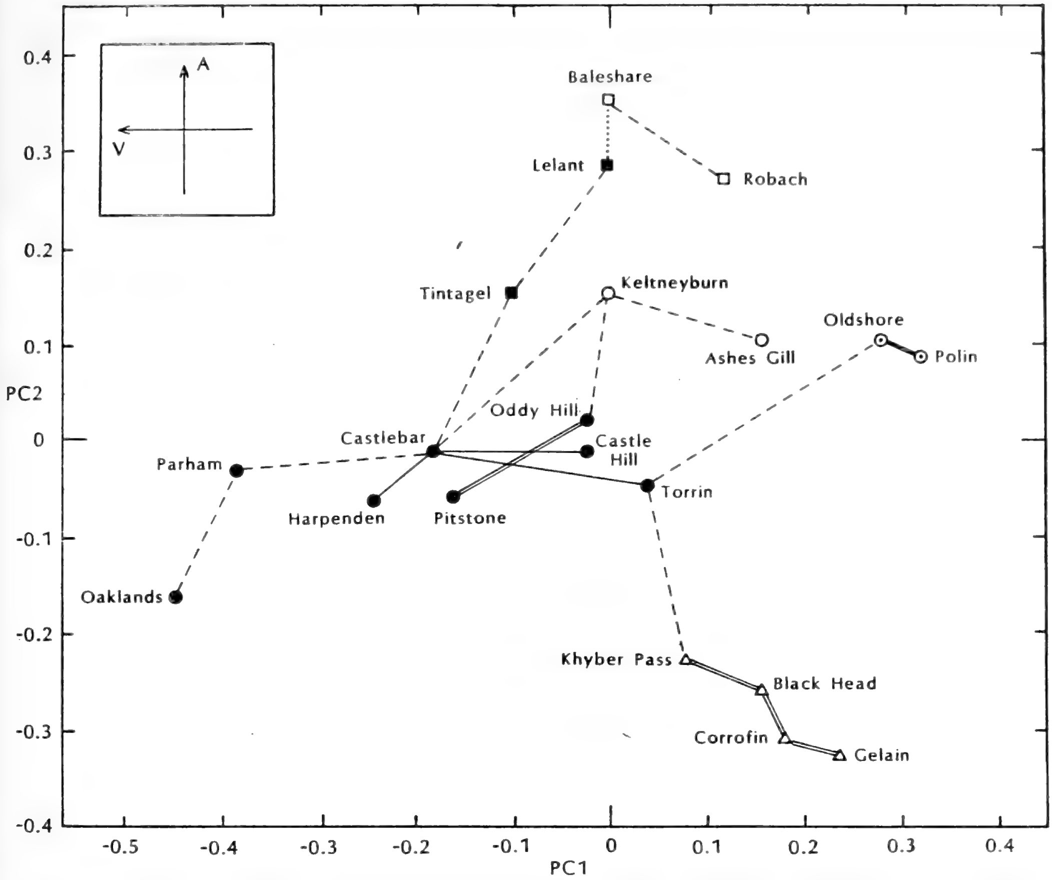

FIGURE 1. Principal coordinates plot of PC1:PC2 with superimposed minimum spanning tree. *D. fuchsii*, population means.
● var. *fuchsii* (◑ individuals lacking floral anthocyanins; Fig. 3)
□ var. *hebridensis*
■ var. *cornubiensis*
○ var. *alpina* (⊙ coastal habitats)
△ var. *okellyi* (◬ individuals lacking floral anthocyanins; Fig. 3)
Minimum spanning tree links: double line = similarity of populations >95%, single line = 92·6–95%, dashed line = 90–92·5%, dotted line = <90% Inset: Main trends of variation represented on the plot.
V = vegetative vigour
F = floral dimensions
A = anthocyanin pigments.

(Fig. 1). The eight anthocyanin-high populations formed three branches: (i) var. *hebridensis* (Baleshare, Robach) and var. *cornubiensis* (Tintagel, Lelant), (ii) upland populations of var. *alpina* (Keltneyburn, Ashes Gill), and (iii) coastal populations of var. *alpina* (Oldshore, Polin). The strongest links of the tree reflected a combination of geographical and ecological proximity; they occurred between the four populations of var. *okellyi* from the limestone pavements of the Burren, two adjacent populations of var. *alpina* from machair in Sutherland (Oldshore, Polin) and two populations of var. *fuchsii* from chalk soils near the Hertfordshire/Buckinghamshire border (Oddy Hill, Pitstone).

The first two coordinates for *D. maculata* populations incorporated 44% of the total variance, largely encompassed by 21 characters (Table 4). They resembled closely the corresponding

TABLE 1. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS: *D. FUCHSII*

Taxon[1]	Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H_2O)	Approx. no. of plants	Peak flowering period[2]	Presence (and frequency) of other dactylorchids[3]
var. *fuchsii*	Downland, CASTLE HILL, Folkstone, Kent, v.c. 15	61/213.380	125	Chalk	7·4	200	6/4	None
	Downland, ODDY HILL, Wigginton, Herts., v.c. 20	42/934.109	170	Chalk	7·5	100	6/2–3^5	F×MPr(vr)
	PITSTONE Fen, Marsworth, Bucks., v.c. 24	42/938.142	130	Chalk	7·7	5000	6/2–3^5	None
	OAKLANDS gravel pits, Colney Heath, Herts., v.c. 20	52/185.082	80	Till	7·0	10000	6/2–3^5	MPr(vr), F×MPr(o)
	Willow carr, PARHAM airfield, Suffolk, v.c. 25	62/333.609	35	Till	7·8	600	6/3–4^5	None
	Scrubby woodland, HARPENDEN Common, Herts., v.c. 20	52/139.131	120	Clay-with-flints/ Chalk	5·6	100	7/1–2	None
	Marshy meadow, CASTLEBAR, Co. Mayo, v.c. H26	11/165.897	40	Till/ Carboniferous limestone	7·7	50	7/1	None
	Damp meadow, TORRIN, Skye, N. Ebudes, v.c. 104	18/578.201	40	Carboniferous limestone	7·6	25	7/1	None
var. *okellyi*	Pavement, BLACK HEAD, Murroogh, Co. Clare, v.c. H9	12/150.116	30	Till/ Carboniferous limestone	7·3	100	6/4	MO(r)
	Grassy bank, KHYBER PASS, E. Murroogh, Co. Clare, v.c. H9	12/150.088	80	Thin peat/ Carboniferous limestone	6·0^4	200	7/1	Mc(f), II(vr), IP(r), MO(r), MT(vr), IP×MO(vr), F×Mc(vr), F×MO(vr)
	Pasture, W. Lough Baile, E. CORROFIN, Co. Clare, v.c. H9	11/324.920	15	Carboniferous limestone	7·9^4	50	6/4	Mc(o), ICr(r), MO(r)
	Pavement, Lough GELAIN, N. Corrofin, Co. Clare, v.c. H9	11/313.947	35	Till/ Carboniferous limestone	—	100	7/2^6	Mc(c), MP(o), Mc×F(r), Mc×MP(vr), F×MP(r)

var. *alpina*	Pasture, ASHES GILL, Ingleton, Mid-W. Yorks., v.c. 64	34/777.784	290	? Till/mica schist	6·1	200	6/4–7/1	Mc(f), MP(o), F×MP(vr)
	Pasture, KELTNEYBURN, Fortingall, Mid Perth, v.c. 88	27/772.496	165	Till/Cambrian limestone	6·7	350	7/1–2	None
	Machair, OLDSHORE More, W. Sutherland, v.c. 108	29/198.588	5	Blown sand/ Lewisian gneiss	7·7	5000	7/3	None
	Machair, POLIN, Oldshore Beg, W. Sutherland, v.c. 108	29/196.587	5	Blown sand/ Lewisian gneiss	6·9	5000	7/3	None
var. *hebridensis*	Machair, Teanamachar, BALESHARE, N. Uist, Outer Hebrides, v.c. 110	08/779.618	5	Blown sand/ Lewisian gneiss	7·7	30	7/2	IC(c), MP(f), F×MP(vr)
	Machair, ROBACH, Newtonferry, N. Uist, Outer Hebrides, v.c. 110	08/873.762	5	Blown sand/ Lewisian gneiss	7·9	100	7/1–2	IC(c), MP(f), F×MP(o)
var. *cornubiensis*	Stable dunes, LELANT, St Ives, W. Cornwall, v.c. 1	10/543.382	30	Blown sand/ Devonian slates	7·7	100	6/3	MPr(o), F×MPr(f)
	Rough grassland, Bossiney cliffs, TINTAGEL, E. Cornwall, v.c. 2	20/065.894	70	Dinantian tuffs/ lavas	5·9	20	6/2–3	None

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[1] See ‘Classification’ for revised nomenclature.

[2] Estimated value. The number before the oblique indicates the month, numbers after the weeks of that month.

[3] F = *D. fuchsii*
Mc = *D. maculata*
II = *D. incarnata* subsp. *incarnata*
IC = *D. incarnata* subsp. *coccinea*
ICr = *D. incarnata* subsp. *cruenta*
IP = *D. incarnata* subsp. *pulchella*
MO = *D. majalis* subsp. *occidentalis*
MP = *D. majalis* subsp. *purpurella*
MPr = *D. majalis* subsp. *praetermissa*
MT = *D. majalis* subsp. *traunsteinerioides*
‘c’ = common, ‘f’ = frequent, ‘o’ = occasional, ‘r’ = rare, ‘vr’ = very rare.

[4] Value approximate due to very large amounts of organic matter in sample.

[5] Measured during 1982, a particularly early season.

[6] Measured during 1985, a particularly late season.

TABLE 2. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS: *D. MACULATA*
See Table 1 for footnotes and explanation of abbreviations.

Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H_2O)	Approx. no. of plants	Peak flowering period[2]	Presence (and frequency) of other dactylorchids[3]
Heath, KYNANCE Cove, Lizard, Cornwall, v.c. 1	10/682.142	70	Peat/serpentinite	5·2	10000	6/2–3	None
Heath, PORLOCK Common, Exmoor, N. Devon, v.c. 4	21/846.462	410	Devonian phyllite	4·5	100	7/4[6]	None
MATLEY Bog, Denny Lodge, S. Hants., v.c. 11	41/333.073	20	Peat/Barton sands	5·1	1000	6/3–4	None
Bog, N. STEPHILL Bottom, Beaulieu, S. Hants., v.c. 11	41/360.061	20	Peat/Barton sands	4·5[4]	100	6/3–4	IP(f)
Heath, S. CROCKFORD Bottom, Boldre, S. Hants., v.c. 11	40/349.987	30	Plateau gravels	4·8	500	6/3	None
Bog, THURSLEY Common, Surrey, v.c. 17	41/904.416	55	Peat/Lower greensand	6·0[4]	50	6/3–4	IP(c)
Streamside marsh, STANMORE Common, Middlesex, v.c. 21	51/159.941	125	Claygate sands	6·6	17	6/4	None
Heath, BRICKETWOOD Common, Herts., v.c. 20	52/128.008	80	Till	5·6	100	6/2[5]	F(vr), Mc×F(vr)
Pasture, ASHES GILL, Ingleton, Mid-W. Yorks., v.c. 64	34/777.785	280	Thin peat/till/ Carboniferous limestone	5·0[4]	5000	6/4[6]	F(o), MP(o), Mc×F(r), Mc×MP(vr), F×MP(r)
Streamside marsh, WHITE NOOK, Conistone, Mid-W. Yorks., v.c. 64	34/984.661	205	Peat+alluvium/till/ Carboniferous limestone	5·8	80	6/2–3[5]	F(r), MT(r)
Damp moorland, LLANDEGFAN Common, Anglesey, v.c. 52	23/576.747	90	Till/Mona schists	—	200	7/1	MP(o), Mc×MP(r)

Maritime pavement, POULSALLAGH, W. Lisdoonvarna, Co. Clare, v.c. H9	12/086.018	25	Thin peat/ Carboniferous limestone	6·7	500	6/1	MO(vr), F(vr)
Pavement, BALLYRYAN, W. Lisdoonvarna, Co. Clare, v.c. H9	12/087.018	25	Thin peat/ Carboniferous limestone	6·1	100	6/1	None
Maritime pavement, MURROOGH, Black Head, Co. Clare, v.c. H9	12/143.103	25	Thin peat/ Carboniferous limestone	5·9	50	6/1–2	MO(vr), F(o)
Rough pasture, W. CLIFDEN, W. Galway, v.c. H16	02/651.503	15	Thin peat/Dalradian gneiss	5·6^{4}	500	7/1	MO(o), Mc×MO(vr)
Marsh, above LAWERS Burn, S.W. Kenmore, Mid-Perth, v.c. 88	27/677.411	360	Peat/till/mica schist	5·0	2000	6/4–7/1	None
Rough pasture, GLENCAIRN, S. Boat of Garten, S. Aberdeen, v.c. 92	28/941.163	220	Thin peat/ glaciofluvial sand/ schist	4·4	3000	6/4–7/1	None
Marsh, S. Cran Loch, CULBIN Forest, Nairn, v.c. 96b	28/946.588	8	Peat/blown sand/ glaciofluvial sand	5·9	30	7/1–2	MP(r), Mc×MP(vr)
Heath, N.E. shore Loch CLUANIE, Glen Moriston, Easterness, v.c. 96a	28/174.104	180	Thin peat/granite	5·5	50	7/1	None
Streamside marsh, N.E. ELGOL, Skye, N. Ebudes, v.c. 104	18/536.152	115	Peat/till/doleritic sill	6·1	500	7/1	None
Bog, upper KINLOCH Glen, Rhum, N. Ebudes, v.c. 104	18/369.001	110	Peat/Torridonian sandstone	4·6^{4}	50	7/1	None
Bog, upper KILMORY Glen, Rhum, N. Ebudes, v.c. 104	18/364.010	*c*.50	Peat/Torridonian sandstone	—	60	7/2–3	None
Machair, HARRIS Bay, Rhum, N. Ebudes, v.c. 104	18/335.958	*c*.65	Thin peat/raised beach sand/gabbro	5·9	1000	8/1	None

TABLE 3. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR *D. FUCHSII* POPULATION MEANS, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	27·1		23·1	
Variate name, and direction of increase in value of variate in relation to increase in value of vector (e.g. populations with the largest mean values for leaf width and other vigour characters tend to occur towards the left side of PC1 on Fig. 2).	Width of widest leaf	–	Labellum colour, 'y'	–
	Stem diameter	–	Labellum colour, reflectivity (Y)	–
	Inflorescence length	–	Presence of leaf markings	+
	Plant height	–	Stem anthocyanin	+
	Length of basal bracts	–	Bract anthocyanin	+
	Length of longest leaf	–	Labellum markings, contrast	+
	Position of longest leaf up stem	–	Labellum markings, distribution	+
	Number of non-sheathing leaves	–	Labellum markings, type	+
	Number of sheathing leaves	–		
	Number of flowers	–		
	Length of floral bracts	–		

TABLE 4. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR *D. MACULATA* POPULATION MEANS, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	29·2		15·1	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Stem diameter	–	Bract anthocyanin	+
	Length of basal bracts	–	Stem anthocyanin	+
	Length of floral bracts	–	Presence of leaf markings	+
	Number of flowers	–	Labellum markings, type	+
	Ovary length	–	Labellum markings, contrast	+
	Width of widest leaf	–	L.o.p.s[1], solid markings	+
	Spur, length	–	Labellum markings, distribution	+
	Labellum, width	–		
	Plant height	–		
	Inflorescence length	–		
	Length of longest leaf	–		
	Labellum, length to lateral lobe	–		
	Labellum, length to central lobe	–		
	Labellum, length to base of sinus	–		

[1] L.o.p.s = lateral outer perianth segments.

coordinates for *D. fuchsii* populations; PC1 again represented vegetative vigour (though supplemented with some floral dimension characters) and PC2 represented pigmentation. At the extremes of PC1 were the stunted, late-flowering populations from Harris and Porlock, and the especially vigorous populations from marshes at Thursley and Llandegfan (Fig. 2). Separation of populations along PC2 according to degree of pigmentation was less clearly defined than for *D. fuchsii*. The five anthocyanin-low populations from Carboniferous limestone habitats (PC2 values $<-0{\cdot}15$) differed considerably in vigour, and consequently formed three separate branches of the minimum spanning tree: Ashes Gill (Yorkshire, hay-meadow), Poulsallagh, Murroogh, Ballyryan (Burren, limestone pavements), and White Nook (Yorkshire, upland pasture). No populations of *D. maculata* were as anthocyanin-rich as the extreme populations of *D. fuchsii*. The Burren populations, and those from New Forest heathlands (Matley, Stephill, Crockford), formed two clusters, but the three populations from the Isle of Rhum (Kilmory, Kinloch, Harris) did not associate closely.

ANALYSES OF INDIVIDUAL PLANTS

Both principal coordinates plots for individual plants (Figs. 3 & 4) represented more characters but much less of the total variance than the equivalent ordinations of population means (Tables 5 & 6). Characters reflecting floral dimensions made more important contributions to plots for individuals than to those for populations.

Pigmentation replaced vigour as the strongest coordinate (PC1) in the plot of *D. fuchsii* individuals (Fig. 3), which revealed almost complete overlap of the three dark-flowered varieties (vars *hebridensis*, *cornubiensis* and *alpina*) and considerable overlap between them and the supposedly predominantly pale-flowered var. *okellyi*. Var. *fuchsii* again tended to have intermediate values for the pigmentation coordinate (PC1), and included numerous vigorous plants that dominated the positive end of PC2. The apparent discontinuity between anthocyanin-deficient plants (PC1 values <−0·15) and the remainder was exaggerated by zero scores for three characters representing a single feature (absence of labellum markings) and was much less evident when the data were re-analyzed without these characters. The anthocyanin-deficient plants were mostly var.

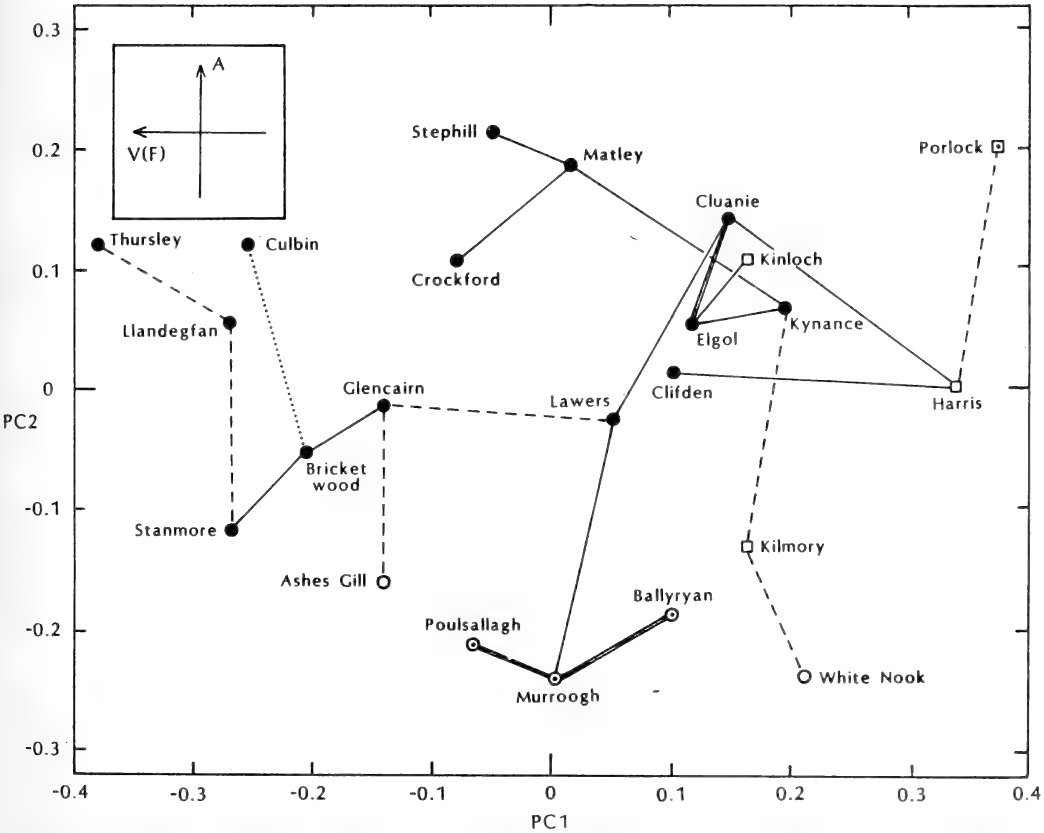

FIGURE 2. Principal coordinates plot of PC1:PC2 with superimposed minimum spanning tree. *D. maculata*, population means.
⊙ Burren
○ Other Carboniferous limestone regions (◑ individuals lacking floral anthocyanins; Fig. 4)
☐ Rhum
⊡ Porlock
● residuum
See Fig. 1 for strengths of minimum spanning tree links.
Inset: Main trends of variation represented on the plot (see Fig. 1).

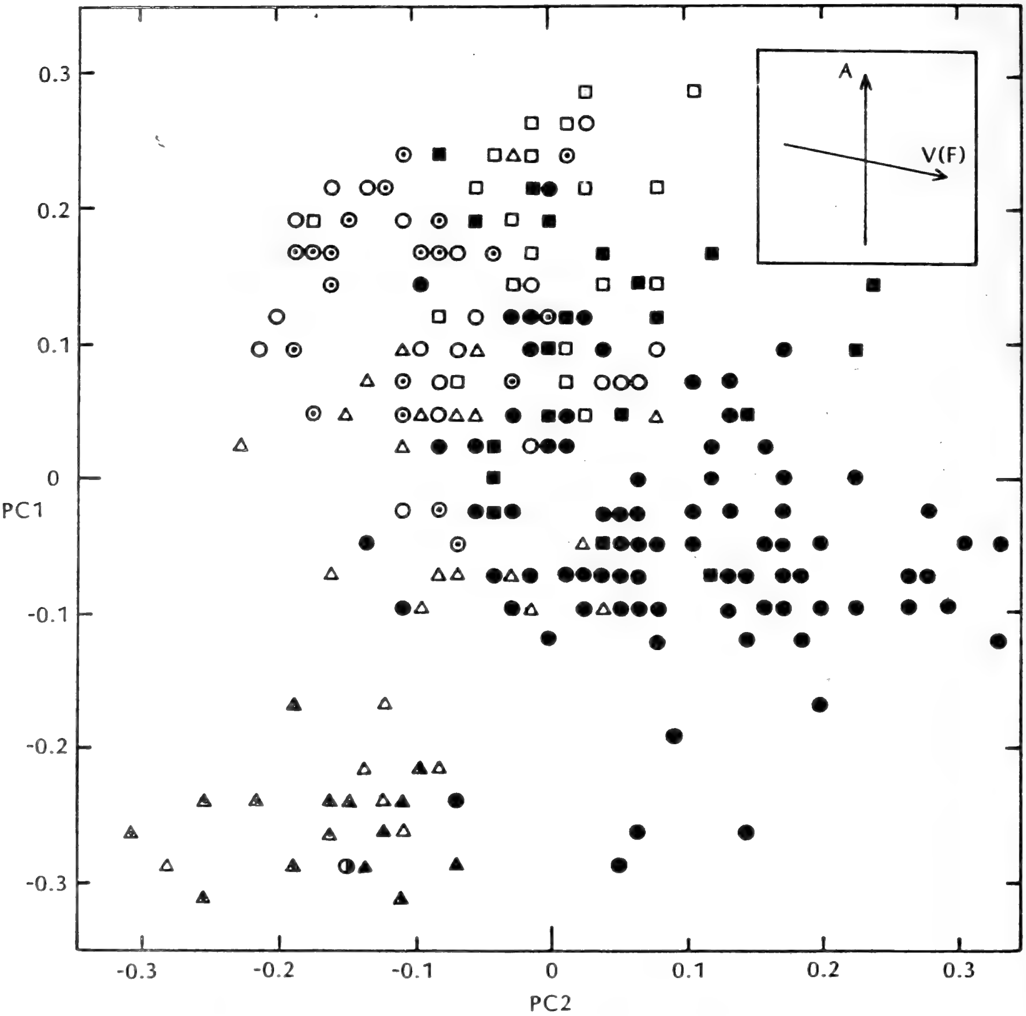

FIGURE 3. Principal coordinates plot of PC1:PC2. *D. fuchsii*, all individuals.
Inset: Main trends of variation represented on the plot.
See Fig. 1 for explanation of symbols.

okellyi, but also included some individuals of var. *fuchsii*. Some plants of both varieties lacked all floral pigments (Fig. 3, Table 8).

The ordination of *D. maculata* individuals was generally similar to that for *D. fuchsii*, though the vigour coordinate remained slightly stronger than the pigmentation coordinate and the subordinate trend in flower size did not parallel the trend in vegetative vigour (Table 8, Fig. 4 (inset)). The morphological extremes on Fig. 4 were anthocyanin-less plants from Carboniferous limestone habitats in the Burren and Yorkshire (bottom), small, late-flowering plants from Porlock and Harris (left) and large, marsh-dwelling plants from Thursley, Llandegfan, Stanmore and Culbin (top right). However, geographically- and/or ecologically-related populations (including those from Rhum) were widely dispersed on the plot, which showed considerable morphological overlap of any potential infraspecific taxa that could be delimited using these criteria.

Thus, variation in both species of spotted-orchid is polarized into two major trends of approximately equal importance: vigour and pigmentation. Each trend represents a group of consistently correlated characters but the trends themselves are uncorrelated, so that most combinations of intensity of pigmentation and degree of vigour can be encountered within the species as a whole. Extensive intra-population variation further obscures resolution of the populations into clearly delimited intraspecific taxa. *D. fuchsii* achieves greater vigour and more intense pigmentation than *D. maculata*, thus presenting a broader morphological range that offers greater scope for taxonomic subdivision.

INTERPRETATION OF VARIATION IN THE SPOTTED-ORCHIDS

The major trends of variation in vigour and pigmentation obscure some interesting subordinate trends, and could represent several causal factors. In this and the following section we examine in greater detail the nature and taxonomic implications of the patterns of variation shown by the spotted-orchids, and speculate on possible underlying mechanisms.

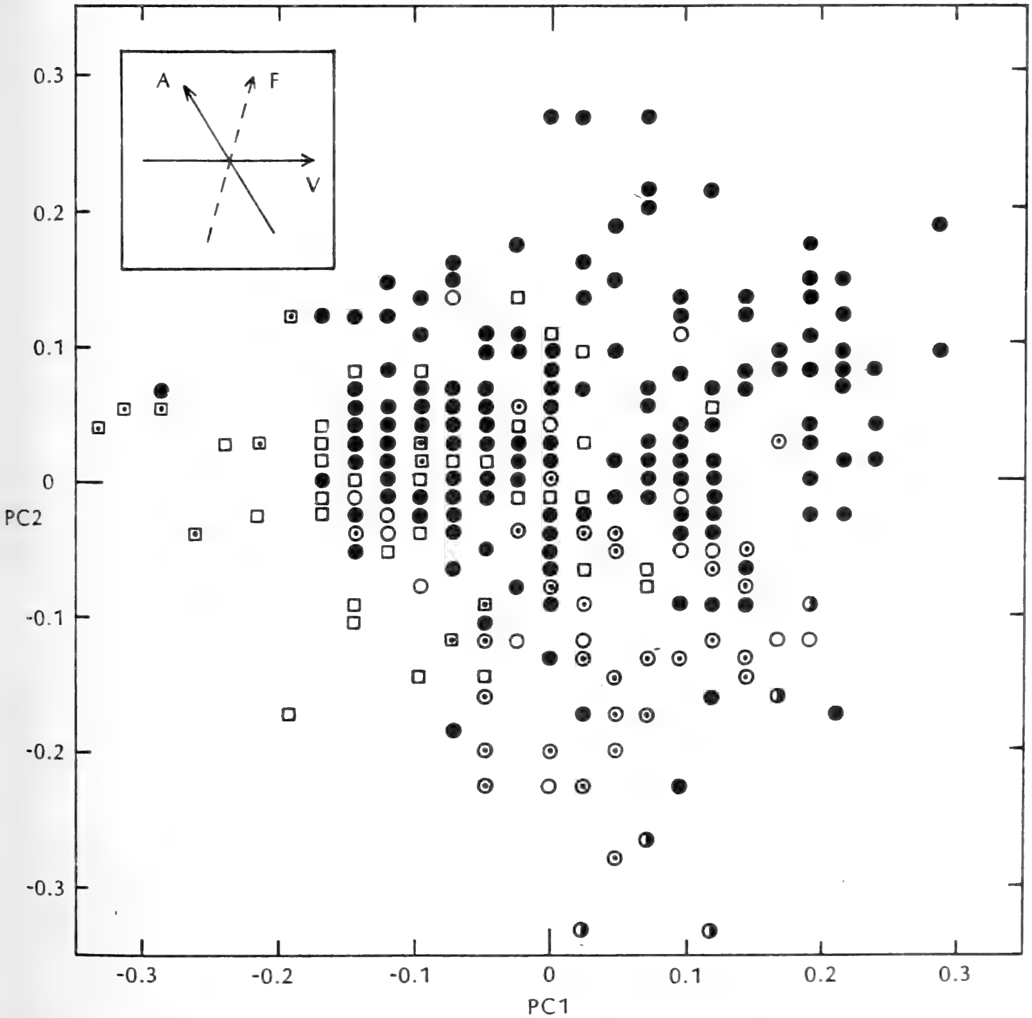

FIGURE 4. Principal coordinates plot of PC1:PC2. *D. maculata*, all individuals.
Inset: Main trends of variation represented on the plot.
See Fig. 2 for explanation of symbols.

TABLE 5. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS OF *D. FUCHSII*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	17·0		13·0	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Bract anthocyanin	+	Width of widest leaf	+
	Stem anthocyanin	+	Stem diameter	+
	Labellum colour, reflectivity (Y)	−	Plant height	+
	Labellum colour, 'y'	−	Length of basal bracts	+
	Labellum markings, contrast	+	Inflorescence length	+
	Labellum markings, distribution	+	Length of longest leaf	+
	Presence of leaf markings	+	Number of flowers	+
	Labellum markings, type	+	Position of longest leaf up stem	+
	L.o.p.s[1], solid markings	+	Labellum, length to lateral lobe	+
	Labellum colour, 'x'	−	Length of floral bracts	+
	Plant height	−	Number of sheathing leaves	+
	Length of longest leaf	−	Spur, length	+
	Labellum, lateral lobe indentations	+	Labellum, length to central lobe	+
	Inflorescence length	−	Spur, median width	+
	Number of flowers	−	Labellum, length to base of sinus	+
	Number of sheathing leaves	−	Labellum, width	+

[1] L.o.p.s = lateral outer perianth segments.

TABLE 6. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS OF *D. MACULATA*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	14·1		10·7	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Length of basal bracts	+	Presence of leaf markings	+
	Stem diameter	+	Labellum, length to base of sinus	+
	Number of flowers	+	Labellum markings, type	
	Width of widest leaf	+	Labellum, length to central lobe	+
	Bract anthocyanin	−	L.o.p.s[1], solid markings	+
	Length of floral bracts	+	Labellum markings, contrast	+
	Inflorescence length	+	Labellum, length to lateral lobe	+
	Labellum colour, reflectivity (Y)	+	Plant height	+
	Plant height	+	Labellum, width	+
	Labellum colour, 'y'	+	Length of longest leaf	+
	Labellum, width	+	Bract anthocyanin	+
	Labellum, length to lateral lobe	+	Spur, length	+
	Stem anthocyanin	−	Labellum markings,	+
	Ovary length	+	distribution	+
	Spur length	+	Stem diameter	+
	Labellum, length to central lobe	+	Stem anthocyanin	+

[1] L.o.p.s = lateral outer perianth segments.

VIGOUR

Stephenson & Stephenson (1920), Summerhayes (1951) and Ettlinger (1976) noted that *D. fuchsii* from clay woodlands tend to be unusually tall and 'leafy'. Harpenden, our only population from a clay wood, had tall (mean height 43 cm) but not especially broad stems (the inflorescence, which was not especially long, was consequently a small proportion (mean value 0.13) of the total stem length)

TABLE 7. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES FOR ALL INDIVIDUALS FROM DARK-FLOWERED POPULATIONS OF *D. FUCHSII*, LISTED IN ORDER OF DECREASING IMPORTANCE

Principal coordinate	PC1		PC2	
Percentage of variance accounted for	15·0		11·1	
Variate name, and direction of increase in value of variate in relation to increase in value of vector.	Labellum, width	–	Labellum, lateral lobe indentations	+
	Labellum, length to lateral lobe	–	Labellum markings, distribution	+
	Labellum, length to central lobe	–	Presence of basal leaf	–
	Width of widest leaf	–	Length anthocyanin	–
	Inflorescence length	–	Bract anthocyanin	+
	Labellum, length to base of sinus	–	Leaf colour	+
	Spur, median width	–	L.o.p.s[1], position	–
	Length of basal bracts	–		–
	Number of flowers	–		
	Spur, width at entrance	–		
	Stem diameter	–		
	Number of sheathing leaves	–		
	Spur, length	–		

[1] L.o.p.s = lateral outer perianth segments.

and many long but not particularly broad sheathing leaves that were widely spaced along the stem. These characteristics of lengthening of structures without concomitant increases in width were shared by the population growing in an overgrown meadow at Castlebar, and probably represent a compensation response to low light intensities rather than exceptional vigour per se.

Genuinely vigorous *D. fuchsii* had stems that were unusually broad as well as tall, their leaves were broad as well as long, and they had many (4–6) non-sheathing as well as sheathing leaves. They also had long (>7 cm), many-flowered inflorescences and uppermost sheathing leaves that were broadest well above the base. These increases in overall sizes rather than just lengths of structures were exhibited by the Oaklands and Parham populations from flooded gravel-pits, and those individuals from Pitstone that occupied the marshy floor of the chalk quarry rather than its dry grassy margins. Thus, true vigour in *D. fuchsii* appears to be strongly correlated with high soil moisture content, again suggesting a phenotypic response to environmental (in this case edaphic) factors. Intriguingly, at least some of these marsh-dwelling *D. fuchsii* possessed hollow stems, a feature that is supposedly confined to marsh-orchids.

Two populations of *D. maculata* (Thursley, Llandegfan), collected from amongst tall vegetation in wet habitats, exhibited many of the vigour characteristics shown by the Oaklands and Parham populations of *D. fuchsii*. They had tall, broad stems, long, many-flowered inflorescences, long, broad (though not particularly numerous) leaves widely distributed along the stem and long basal bracts. Three other populations (Culbin, Stanmore, Bricketwood) from *Juncus*-rich marshes showed extreme values for various combinations of these characters, and all five populations possessed rather long spurs.

Populations of both species exhibiting the smallest values for vigour characters grew among short vegetation in exposed coastal (Oldshore and Polin populations of *D. fuchsii*, Harris population of *D. maculata*) or upland (White Nook and Porlock populations of *D. maculata*) habitats, and were probably environmentally dwarfed.

Thus, size variation in vegetative characters may primarily reflect an interaction between the ontogeny of spotted-orchids and environmental factors such as light intensity, soil moisture and exposure (particularly to wind). The resulting effects on the phenotype, which are more readily discerned in *D. fuchsii* than *D. maculata*, obscure any independent geographical trends such as the latitudinal cline in leaf number suggested by Heslop-Harrison (1951).

PIGMENTATION

The eight populations of *D. fuchsii* with mean labellum reflectivities below 40% (Fig. 6) also tended to have the lowest standard deviations for this character (all but Tintagel <10%), suggesting that

TABLE 8. GEOGRAPHICAL AND ECOLOGICAL VARIATION IN FREQUENCIES OF ANTHOCYANIN DEFICIENCIES IN *D. FUCHSII* AND *D. MACULATA*

		D. FUCHSII				*D. MACULATA*			
	Percentage of plants lacking:	All populations	Carboniferous limestone: Burren	Carboniferous limestone: Yorks.	Non-Carboniferous limestone	All populations	Carboniferous limestone: Burren	Carboniferous limestone: Yorks.	Non-Carboniferous limestone
Vegetative anthocyanins	Stem anthocyanins	*51*	70	10	48	*64*	90	90	56
	Bract anthocyanins	*46*	68	10	43	*39*	67	70	31
	Leaf markings	*13*	43	20	9	*15*	53	25	8
Floral anthocyanins	L.o.p.s[1], markings	*40*	68	40	32	*10*	10	35	7
	Labellum markings	*15*	48	0	5	*5*	0	35	2
	Labellum anthocyanins	*12*	48	0	3	*25*	3	35	27
	All floral anthocyanins	*8*	35	0	2	*3*	0	30	0
	All floral and vegetative anthocyanins (i.e. albinos)	*6*	25	0	1	*1*	0	10	0
	(Total number of plants)	(*200*)	(40)	(10)	(150)	(*232*)	(30)	(20)	(182)

[1] L.o.p.s = lateral outer perianth segments.

they constitute a distinct and consistent anthocyanin-high facies of *D. fuchsii*. This was supported by the frequent occurrence of bract and stem anthocyanins in these populations, though leaf and labellum markings were not especially large or bold. However, this group was very heterogenous in other respects, notably labellum size, and included both the largest- and smallest-flowered populations of *D. fuchsii* (Fig. 6). Marked bimodality in labellum dimensions (particularly width) distinguished the large-flowered vars. *hebridensis* and *cornubiensis* from the small-flowered var. *alpina*. As labellum dimensions were only minor contributors to the first two principal coordinates for all *D. fuchsii* individuals (Table 5), this distinction was not apparent in that plot (Fig. 3). When the analysis was repeated using only individuals of dark-flowered populations, PC1 largely separated var. *alpina* from vars *hebridensis* and *cornubiensis* (Fig. 5) using floral dimensions (Table 7). PC2 gave an equal degree of separation of vars. *hebridensis* and *cornubiensis*, but using a more diverse set of unrelated characters that are less easily interpreted (Table 7). Hence, this dark-flowered facies comprised three groups of populations showing approximately equal levels of morphological and ecological differentiation.

Two populations of *D. maculata* (Harris, Rhum; Porlock, Exmoor) resembled the dark-flowered facies of *D. fuchsii* in having mean labellum reflectivities of less than 40%. They were also distinguished by their late flowering (August; Table 2), narrow stems and small number of narrow leaves. However, they were not especially rich in vegetative anthocyanins and do not appear to form a cohesive morphological unit (see ‘Classification’).

Neither species of spotted-orchid included a distinct pale-flowered facies that could be distinguished by differences in population means for labellum reflectivity, but both included populations with unusually high frequencies of individuals lacking floral and/or vegetative anthocyanins. Anthocyanin-deficient plants of *D. fuchsii* were most frequent in the Carboniferous limestone habitats of the Burren but, contrary to popular belief, comprised a minority of plants in all four study populations (Table 8); these Burren populations even included plants that matched typical individuals of vars *hebridensis*, *cornubiensis* and *alpina* in intensity of floral pigments. Ashes Gill, Yorkshire, the only other study population of *D. fuchsii* from Carboniferous limestone, was attributed to the dark-flowered var. *alpina*. In contrast, *D. maculata* populations with the highest frequencies of plants deficient in vegetative anthocyanins were associated with Carboniferous limestone habitats in both the Burren and Yorkshire (Table 8). Floral pigments were also unusually infrequent in *D. maculata* populations from Yorkshire but, surprisingly, not in those from the Burren; most Burren plants of *D. maculata* possessed diffuse anthocyanins in their labella, albeit at

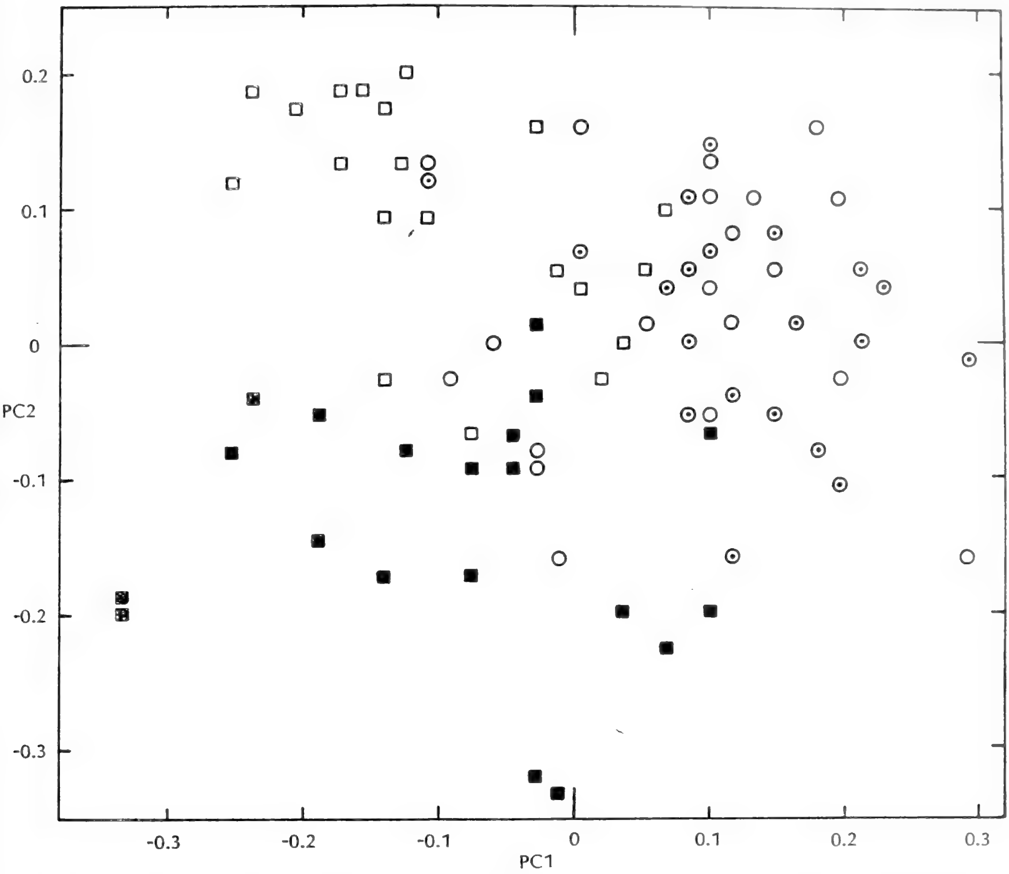

FIGURE 5. Principal coordinates plot of PC1:PC2. *D. fuchsii*, individuals of dark-flowered populations. See Fig. 1 for explanation of symbols.

very low concentrations (over half had reflectivities >70%) and often in very pale hues of red-purple rather than the purple more characteristic of this species. All four anthocyanin-less plants of *D. maculata* that we measured were from Yorkshire (Ashes Gill and White Nook).

Overall, the two species showed similar frequencies of vegetative anthocyanins, but plants lacking all anthocyanins (i.e. true albinos) were more frequent in *D. fuchsii* (Table 8). Labella of *D. fuchsii* more often lacked markings but less often lacked diffuse (i.e. background) anthocyanins than those of *D. maculata*. Approximately 2% of individuals of both species possessed annular leaf markings, a character much more common in marsh-orchids (notably *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *occidentalis* (Pugsley) P. D. Sell) but evidently not confined to them (Stephenson & Stephenson 1920; Godfery 1933; Helsop-Harrison 1948; Wiefelspütz 1976).

TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

The delimitation of spotted-orchid taxa and the ranks awarded to them should reflect available knowledge of the nature and causes of their variation: whether the variation is continuous or discontinuous, whether it exhibits geographically- and/or ecologically-related patterns, and to what extent the phenotypic patterns reflect genetic and environmental influences.

Our multivariate analyses demonstrated that each spotted-orchid species constitutes a morpholo-

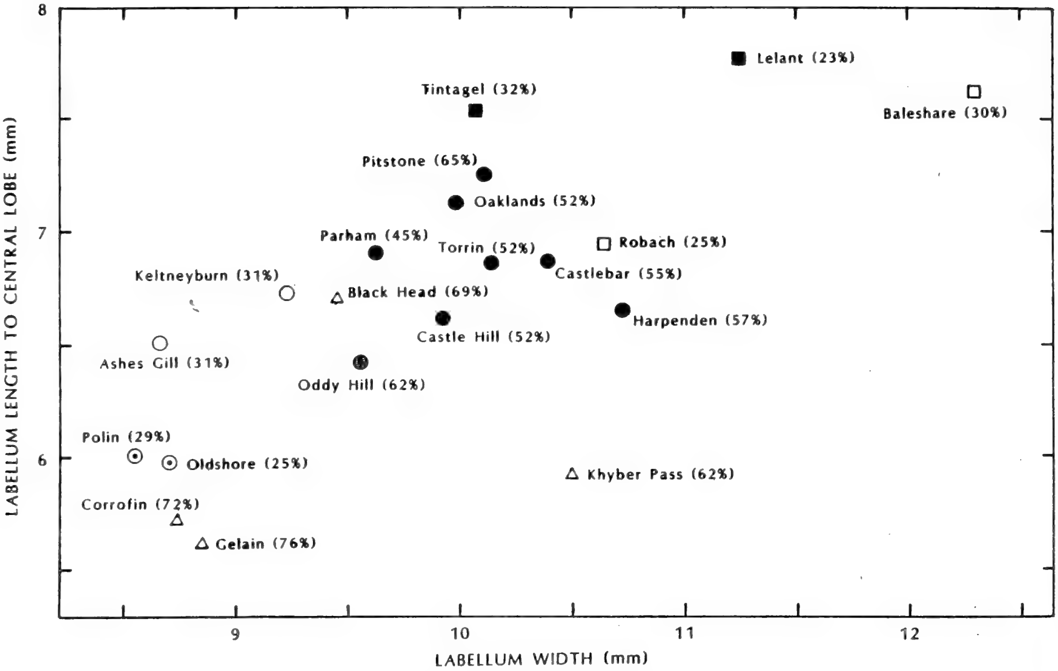

FIGURE 6. Bivariate plot of mean labellum dimensions for *D. fuchsii* populations. Percentages denote mean reflectivities of labella, the best measure of densities of floral anthocyanin pigments. See Fig. 1 for explanation of symbols.

gical continuum in which all potential infraspecific taxa show considerable overlap. Moreover, much of the variation in both species is polarized into two trends (sets of inter-related characters) representing vigour and pigmentation. This contrasts with the more complex associations of often unrelated characters observed in marsh-orchids, whose variation is also continuous but has strong geographical and/or ecological components and can be resolved into subspecies showing only limited morphological overlap (Bateman & Denholm 1983, 1985). Thus, no group of spotted-orchid populations is sufficiently differentiated to merit subspecific status, and those considered worthy of any taxonomic separation have been treated as varieties. We regard the subspecies and the variety as essentially similar concepts; both describe geographically- or ecologically-related groups of populations, but varieties show less morphological differentiation and are separated by fewer, generally less predictive characters. The *D. fuchsii* segregates assigned to this rank are relatively homogeneous and possess distinguishing characters (see 'Classification') that are unlikely to show substantial environmental modification. Var. *fuchsii* remains a comparatively heterogeneous taxon, but further subdivision on the basis of differences in vigour, which may be largely environmentally determined, seems unwise. We have not recognized any infraspecific taxa of *D. maculata*, whose overall range of variation is narrower and even less readily partitioned than that of *D. fuchsii*.

Our treatment of *D. fuchsii* taxa as varieties rather than subspecies contradicts most classifications published during the last 40 years. However, we believe that the taxonomic importance of the two most widely accepted 'subspecies' of *D. fuchsii* (*hebridensis* and *okellyi*) has been inflated by exaggeration of their morphological distinctness, failure to identify optimal diagnostic character states, tautological arguments concerning their identification and speculative assumptions regarding their evolution.

D. fuchsii subsp. *hebridensis* was well described from the Hebrides, initially qualitatively by Wilmott (1939) and later quantitatively by Heslop-Harrison (1948, 1952, 1954), but it soon became entrenched as a geographically and ecologically restricted taxon with dark flowers that occupied machair along the western seaboard of the British Isles (Heslop-Harrison 1952, 1954, 1968). Var.

TABLE 9. TREATMENT OF SELECTED INTRASPECIFIC TAXA OF *D. MACULATA* BY (a) BRITISH AND (b) CONTINENTAL WORKERS

– = taxon not mentioned (0 = taxon not yet described); √ = considered to occur in Britain; × = not considered British; abbreviations = taxon considered synonymous with subsp. *maculata* (ma), *elodes* (el), *ericetorum* (er); ? = authors' intentions unclear.

(a)

Taxon	Druce (1915, 1918, 1924b, 1925)	Bennett (1921)	Stephenson & Stephenson (1921)	Godfery (1921, 1933)	Summerhayes (1951)	Heslop-Harrison (1951, 1954)	Clapham (1952, 1962)	Hunt & Summerhayes (1965)	Ettlinger (1976)	Lang (1980)	Davies *et al.* (1983)
maculata	√	–	√	×	–	×	×	–	–	–	?
ericetorum	ma	√	?ma	el	√	√	√	√	√	√	√
elodes	ma	er	×	√	?er	?er	?er	–	er	er	?
praecox	ma	–	ma	el	–	er	–	–	–	–	–
rhoumensis	0	0	0	0	–	–	√	√	√	–	√

(b)

Taxon	Camus & Camus (1929)	Vermeulen (1947)	Soó (1960)	Senghas (1968)	Nelson (1976)	Wiefelspütz (1976)	Landwehr (1977)	Soó (1980)	Sundermann (1980)	Delforge & Tyteca (1984)
maculata	√	?	√	?	er	?	√	√	√	√
ericetorum	el	√	√	el	√	√	√	ma	ma	√
elodes	√	?	×	√	er	×	√	√	ma	×
praecox	el	el	er	–	–	er	er	–	–	–
rhoumensis	0	0	√	√	–	–	–	–	–	–

cornubiensis and coastal populations of var. *alpina*, which were also dark-flowered and conformed to these distributional criteria, were included in *hebridensis* without supporting morphological data (e.g. Perring & Sell 1968) while inland populations of var. *alpina* were excluded. Consequently, *hebridensis* became a morphologically heterogeneous taxon whose individuals could not be identified without knowledge of their geographical location (Heslop-Harrison 1968, p. 23). Its morphological distinction was exaggerated by insufficient knowledge of the broad morphological range encompassed by var. *fuchsii* and failure to recognize the small- and dark-flowered taxon that we have named var. *alpina*.

The recorded (predominantly western) distribution of subsp. *okellyi* resembles that of subsp.

hebridensis (Perring & Sell 1968) and also covers a restricted range of habitats, typically limestone pavements. It therefore received the same distributional 'positive feedback' as subsp. *hebridensis*, and progressed from "an indistinct recessive colour race" (Stephenson & Stephenson 1921) to a subspecies exhibiting a typical Atlantic distribution (Heslop-Harrison 1954; Perring & Sell 1968). However, *okellyi* differs from *hebridensis* in having been poorly described in its original diagnosis (Druce 1909), which greatly exaggerated its anthocyanin deficiency. Our data show that flowers from populations of var. *okellyi* in the Burren (its type locality) are not especially pale (their mean labellum reflectivities resemble those of chalk populations of var. *fuchsii* at Oddy Hill and Pitstone), nor are they unusually deficient in bract and stem anthocyanins. Anthocyanin-deficient plants are a subordinate component of most populations of *D. fuchsii* in the Burren, including all four that we studied, and the Burren populations are even less readily distinguished by other supposedly diagnostic characters such as smaller labella and spurs, and narrower stems and leaves. Furthermore, anthocyanin-less *D. fuchsii* from the Burren cannot be distinguished from similar plants growing in other regions and habitats (Fig. 3). Hence, var. *okellyi* is much less differentiated from var. *fuchsii* then has generally been assumed, and differs mainly in the higher frequency of individuals deficient in floral and/or vegetative anthocyanins. It coexists in the Burren with an analogous anthocyanin-low variant of *D. maculata* (see 'Classification').

A third British spotted-orchid subspecies, *D. maculata* subsp. *rhoumensis*, has not received such general acceptance. This enigmatic Rhum endemic reputedly has pale purple flowers, bold labellum markings, blooms in August and is diploid (Heslop-Harrison 1948). Our three study populations from Rhum differed appreciably in morphology and phenology both from each other and from the original diagnosis of *rhoumensis* (see 'Classification'), but not from populations of *D. maculata* elsewhere in the British Isles. We cannot therefore identify any cohesive infraspecific taxon peculiar to, or present on, Rhum.

The infraspecific taxonomy of the spotted-orchids has also been strongly influenced in the past by speculative interpretations of their population biology. Heslop-Harrison (1952, 1954, 1968) justified subspecific status for *hebridensis* and *okellyi* by arguing that in their "extreme" forms both approach ecologically and morphologically well-defined races, probably of monophyletic origin, that are largely reproductively isolated from the type due to their disjunct geographical ranges. However, he also noted that vars. *hebridensis* and *okellyi* intergrade extensively with var. *fuchsii*, both by extensive geographical clines and by 'hybridization' at sites where two taxa occur (Heslop-Harrison 1948, 1949, 1951, 1952, 1954; Allen 1971; Wiefelspütz 1976). Our observations suggest that populations of *D. fuchsii* are not as differentiated as the above argument implies, and we do not believe that taxonomic decisions should be based solely on geographical and morphological extremes. It seems more appropriate to regard *D. fuchsii* as a variable species whose populations differ locally in 'mean morphology' in response to prevailing edaphic and climatic factors, both through adaptive shifts in gene frequencies and environmental modification of phenotypes. We believe that morphological continuity in both species probably reflects potentially unrestricted gene flow within and between the poorly-differentiated groups of populations; if so, terms such as 'intergradation' and 'hybridization' are inapplicable in this context. However, neither hypothesis can be substantiated without non-morphological data and new insights into the control and adaptive significance of particular morphological traits.

POSSIBLE CONSPECIFICITY OF THE SPOTTED-ORCHIDS

Most British workers have regarded *D. fuchsii* and *D. maculata* as separate species, distinguished by consistent differences in morphology (principally labellum shape) and chromosome number. The supposed cytological discontinuity dates from a few chromosome counts by Hagerup (1938) of $2n=40$ (diploid) for *D. fuchsii* and $2n=80$ (tetraploid) for *D. maculata* subsp. *maculata* and subsp. *elodes*. Much emphasis has been placed on this apparent discontinuity by subsequent authors, including ourselves. However, in the same year, Heusser (1938) demonstrated the presence in Switzerland of diploid and tetraploid populations that were both assignable to *D. fuchsii* on morphological criteria, and the potential taxonomic significance of this observation was quickly realized by Pugsley (1939). Hagerup (1944) then described *D. fuchsii* embryos with $2n=20$ and $2n=60$, and a few *D. maculata* embryos with $2n=40$. Heslop-Harrison (1948) reported $2n=40$ for *D.*

maculata subsp. *rhoumensis* from Rhum. Populations of *D. fuchsii* in Austria may be $2n=40$, 60 or 80 without showing significant morphological differences (Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980), and Averyanov (1977) reported *D. maculata* near Leningrad with $2n=60$. Thus, both spotted-orchid species appear to be capable of maintaining cytologically stable populations that are diploid, triploid or tetraploid, and previous assumptions of chromosome number based on extrapolation from morphology may have been rash.

When Druce (1915) first separated *D. fuchsii* from *D. maculata* he speculated that the morphological differences between the two species may simply reflect differences in the soils that they inhabit. Stephenson & Stephenson (1921) and Godfery (1921) questioned this hypothesis, noting that the two species remained morphologically distinct in mixed colonies. Heslop-Harrison (1948) compared soil pH from several populations of *D. fuchsii* and *D. maculata* in the Hebrides, and concluded that the former occupied soils of pH less than 5·5 and the latter soils of pH greater than 5·0. He subsequently repeated these figures as generally characteristic of the habitats of the two species (Heslop-Harrison 1951, 1954). However, 11 of our 23 study populations of *D. maculata* occupied soils of pH greater than 5·5 (Table 2), and four populations grew in neutral soils (pH >6). *D. fuchsii* is almost confined to neutral or alkaline soils, though our study population of *D. fuchsii* that most closely resembled *D. maculata* (Harpenden) occupied a slightly acidic soil (pH 5·8; Table 1). Its labella had relatively shallow sinuses and central lobes that equalled or only slightly exceeded the laterals, resulting in a small labellum shape index (1·23) similar to that of the Harris population of *D. maculata* (1·24). Furthermore, the Harpenden *D. fuchsii* had unusually broken labellum markings and a small value for mean leaf shape index (0·11) more typical of *D. maculata*. Four populations of *D. maculata* had appreciably larger mean values for the labellum shape index than the remainder; two were from isolated southern populations in only mildly acidic soils (Bricketwood and Stanmore) and two were environmentally-stunted (Harris and White Nook). Plants from Bricketwood and Harris also had central labellum lobes that considerably exceeded the laterals, approaching *D. fuchsii* in this respect (e.g. Stephenson & Stephenson 1921). Thus, spotted-orchid populations showing intermediate characteristics tend to occupy intermediate habitats, and an edaphic influence on their morphology is possible.

Biometric studies on spotted-orchid populations from mainland Europe (Heslop-Harrison 1951; Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980; Reinhard 1985) indicate that *D. fuchsii* and *D. maculata* are less distinct on the Continent than in the British Isles (see also Summerhayes 1951, p. 273). Thus, Continental workers (e.g. Vermeulen 1949; Landwehr 1977; Soó 1980) have attempted to partition a more restricted range of variation, and have consequently created a large number of poorly-defined and often overlapping infraspecific spotted-orchid taxa. This observation also explains why *D. fuchsii* was first described as a species by a British worker (Druce) as late as 1915; during the previous 80 years, Continental workers, including several who were content to treat apparently much more trivial entities as species, had recognized *D. fuchsii* under several different names at varietal and formal rank (see 'Classification'). If *D. fuchsii* and *D. maculata* prove to be both morphologically and cytologically indistinct on the Continent, there is a strong argument for following Nelson (1976) and Sundermann (1980), and relegating *D. fuchsii* to *D. maculata* (L.) Soó subsp. *fuchsii* (Druce) Hylander.

CLASSIFICATION

The classification and diagnostic descriptions that follow are based on our principal coordinates (Figs. 1–5, Tables 3–7), minimum spanning trees, analyses of population means, and ranges for individual characters. Published data on British plants (Heslop-Harrison 1948, 1951, 1954) and on Continental plants (Heslop-Harrison 1951; Groll 1965, 1968; Voth 1978; Voth & Greilhuber 1980; Reinhard 1985) have also been considered.

The following terms are used to describe the frequencies of character states in taxa: rarely, less than 20% of individuals; occasionally, 20–50%; often, 51–80%; usually, greater than 80%. Frequencies of the best diagnostic characters (italicized) show most discontinuity between varieties. Some terms used in the descriptions are qualitative but are derived from quantitative measurements:

Density of inflorescence: dense, index 'f' value greater than 7. Depth of labellum sinuses: very deep,

index 'b' value greater than 1.5 (the term 'labellum shape index' refers exclusively to index 'b'). Roundness of labellum: broad, index 'a' value less than 0.4. Position of lateral outer perianth segments: ± horizontal, categories 1 and 2 on our scale.
Soil pH: acid, <6; neutral, 6–7; alkaline, >7.

Genus *Dactylorhiza* Necker ex Nevski, *Acta hort. bot. Acad. sci. URSS* **4**: 332 (1937).
Sect. *Maculatae* (Parlatore) Vermeulen, *Stud. Dactyl.* 65 (1947).
Subsect. *Eumaculatae* Vermeulen, *Stud. Dactyl.* 68 (1947).

1. **Dactylorhiza fuchsii** (Druce) Soó, *Nom. nov. gen.* Dactylorhiza 8 (1962).
Orchis fuchsii Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **4**: 105 (1915).
O. maculata L. var. *trilobata* Brébisson, *Fl. Normandie* 313 (1835).
O. maculata L. var. *meyeri* Reichenbach f., *Icon. Fl. Germ.* 67 (1851).
O. maculata L. subsp. *meyeri* (Reichenbach f.) Camus, *Mon. Orch. Eur.* 193 (1908).
O. maculata L. var. *obscura* Neuman in *Bot. Notiser 1909*: 153 (1909).
O. fuchsii Druce subvar. *albiflora* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **5**: 167 (1918).
Dactylorchis fuchsii (Druce) Vermeulen, *Stud. Dactyl.* 147 (1947).
D. fuchsii (Druce) Vermeulen var. *meyeri* (Reichenbach f.) Vermeulen, *Stud. Dactyl.* 146 (1947).
Dactylorhiza fuchsii (Druce) Soó var. *meyeri* (Reichenbach f.) Soó, *Nom. nov. gen.* Dactylorhiza 8 (1962).

Stem 7–50(–70) cm, 1·5–7·5(–11) mm in diameter, often lacking anthocyanins. Basal 1f or sheath 0–1, broadest at or above middle; sheathing 1vs (2–)3–6(–7), usually strongly crowded towards base of stem, usually recurved, narrowly to broadly lanceolate, usually broadest well above base, longest 1f usually above widest, 4·5–16·5 cm long, widest 1f 0·5–4(–5·5) cm wide, width/length ratio of 1vs decreasing up stem, usually bright to dark green, tips rarely distinctly hooded; non-sheathing 1vs (1–)2–6(–9), narrow, broadest at base; 1vs usually sparsely to densely marked on upper surface only, markings usually solid (very rarely annular), usually ± evenly distributed and transversely elongated, usually 1·5–6 mm in mean diameter. Inflorescence 1·5–10(–22) cm, 8–30% of stem length, fls 8–60(–95), fairly lax to dense (3·5–10(–13) fls/cm). Basal bracts 7·5–23(–38) mm, 1·5–2·5 times the length of the ovaries, floral bracts 5–12 mm, approximately equalling the ovaries, often suffused with anthocyanins; peripheral bract cells (40–)55–135(–170) μm long, barrel-shaped to triangular. Labellum width exceeding length (usually considerably), 4·5–8·5(–9·5) × 7–12(–13·5) mm, widest ± at middle or above (obtriangular), base colour varying densities (reflectivity 10–89%) of purple or less frequently white; markings pale to bold dashes and/or loops, occasionally dots and dashes, rarely absent or a solid blotch, often covering about two-thirds of the labellum, occasionally more or less; sinuses present (labellum three-lobed), usually deep, central lobe often exceeding lateral lobes by >1 mm, labellum shape index usually >1.25; lateral lobes usually indented, slightly deflexed to moderately reflexed; lateral outer perianth segments usually nearer horizontal than vertical, often with solid (rarely annular) markings; median outer perianth segment and inner perianth segments connivent; spur straight to moderately decurved, 3·5–8 × 1–2·5 mm at entrance, 0·8–2·3 mm halfway along (2–3.7 mm at entrance, 1·6–3·2 mm halfway along in var. *cornubiensis*), usually slightly tapering, half as long to as long as the ovary. $2n=?40$. Flowering mid-June to late July. Frequent and locally common throughout most of the British Isles, local in northeast Scotland and the southwest. Neutral to alkaline (rarely slightly acid) soils.

Most early classifications recognized only a single species of spotted-orchid, *Orchis maculata* (Linnaeus 1753). However, towards the end of the 19th Century, some workers began to realize that two distinct taxa occurred in the British Isles. One had oval, planar lower leaves, deeply and subequally three-lobed labella with the central lobe projecting beyond the laterals, and fairly narrow, tapering spurs (*D. fuchsii*). It inhabited calcareous and neutral soils. The second had lanceolate, keeled lower leaves, shallowly three-lobed labella with the lateral lobes equalling the central lobe in length and considerably exceeding it in area, and very narrow, parallel-sided spurs (*D. maculata*). It inhabited acid soils. Early attempts to recognize this taxonomic distinction were made at infraspecific levels within *D. maculata*. *D. fuchsii* was regarded as *O. maculata sensu stricto* and therefore treated as the type, and what we now call *D. maculata* was the segregate. Webster's

(1886) *O. maculata* var. *praecox* was a restricted and unusual taxon, but Linton (1900) provided a much more generally applicable description of British *D. maculata* as *O. maculata* subsp. *ericetorum* Linton, a name that is still in general use in Britain (Table 9; see also discussion of *D. maculata*).

Few short papers can have initiated more taxonomic and nomenclatural controversy than that of Druce (1915), which segregated the calcicolous spotted-orchids as a new species, *Orchis fuchsii*, and treated the calcifuge as Linnaeus' *O. maculata*. He was repeatedly obliged to justify this decision (Druce 1915, 1918, 1924a, b, 1925) in barbed exchanges with Godfery (1921, 1923, 1924, 1933), who believed that *O. maculata* was the calcicolous species. The debate was eventually settled in Druce's favour by Vermeulen (1947, 1968) and Heslop-Harrison (1951), who demonstrated that Linnaeus' type specimen of *O. maculata* was the calcifuge taxon.

The evolution of spotted-orchid nomenclature on the Continent resembles that in Britain. Early workers included a broad morphological range in *O. maculata*, but this was progressively subdivided at subspecific or, more often, varietal level. *D. fuchsii* was repeatedly segregated from *D. maculata*, most notably as *O. maculata* var. *trilobata* Brébisson (1836), var. *meyeri* Reichenbach f. (1851) and var. *obscura* Neuman (1909) (Heslop-Harrison 1951). Most Continental workers now include these taxa in *D. fuchsii*, but few are willing to treat *D. fuchsii* as a full species.

One notable exception is Holub (1983), who argued that *D. fuchsii* is a junior synonym of *D. longebracteata* (F. W. Schmid) Holub, based on *Orchis longebracteata* F. W. Schmid (1791). However, Jagietto (1986) convincingly demonstrated that the original description of *longebracteata*, although ambiguous, is clearly discordant with *D. fuchsii*.

Extremes of pigmentation

About 20% of the *D. fuchsii* individuals at Oddy Hill occurred as an anthocyanin-rich form with labellum markings more-or-less fused into a solid blotch and the upper surface of the sheathing leaves with at least 50% areal coverage of large (mean diameter >6 mm) markings or entirely covered with diffuse anthocyanins. Such plants also frequently possess spotted bracts and dashes on their stems and ovaries, resembling some plants of var. *hebridensis*. This variant has also been recorded in other chalk grassland populations at Beacon Hill, N. Hants. (D. M. T. Ettlinger pers. comm. 1985; A. R. G. Mundell pers. comm. 1987), Mickleham, Surrey and Barton-le-Clay, Beds. (R. M. Bateman), and "near Winchester" (Godfery 1933, p. 206 and Plate 50/22, 25), from limestone grassland near Buxton, Derbyshire (D. M. T. Ettlinger pers. comm. 1987) and from mildly acid coastal grassland at Armadale, Skye (R. M. Bateman). Nelson (1976, p. 100 and Plate 70c, d) illustrated similar plants from Scandinavia. Analogous variants occur in *D. maculata* (q.v.), *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó (near Hartlepool) and *D. ?incarnata* (L.) Soó (near Southampton) (D. M. T. Ettlinger pers. comm. 1986).

Anthocyanin-less individuals have white or very pale cream-coloured flowers and have been called subvar. *albiflora* Druce (1918). They form a small proportion of many populations of var. *fuchsii* (e.g. Pitstone) and a much larger proportion of populations of var. *okellyi*.

a. var. **fuchsii** (Druce) Bateman & Denholm, **comb. nov.**
Orchis fuchsii Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **4**: 105 (1915).
Dactylorchis fuchsii (Druce) Vermeulen subsp. *typica* Vermeulen, *Stud. Dactyl.* 148 (1947).
Dactylorhiza fuchsii (Druce) Soó subsp. *fuchsii* (Druce) Soó, *Nom. nov. gen.* Dactylorhiza 8 (1962).

Stem usually >20 cm, often >3·5 mm in diameter, occasionally suffused with anthocyanins (rarely densely). Sheathing lvs usually 4 or more, longest lf often >9 cm long, widest lf often >2 cm wide; non-sheathing lvs often 4 or more; markings usually present, often covering >10% of the upper surface. Inflorescence often >4 cm, occasionally >20% of stem length, occasionally dense, fls often more than 25. *Floral bracts often >8 mm, occasionally suffused with anthocyanins* (rarely densely); peripheral bract cells occasionally angular. Labellum often >6·7 mm long to apex of central lobe, often >5·5 mm to apex of lateral lobe, occasionally >4 mm to base of sinus, often >9·5 mm wide, occasionally broad, sinuses occasionally very deep; *reflectivity of base colour often >40%* (rarely >80%); markings usually present; lateral outer perianth segments often ± horizontal, markings often present (rarely annular); spur occasionally >2 mm wide at entrance, >1·8 mm halfway along. Flowering June/early July. Throughout the range of the species.

Var. *fuchsii* is a very heterogeneous taxon, encompassing considerable variation in vigour and pigmentation (see 'Major trends in morphological variation').

b. var. **hebridensis** (Wilmott) Bateman & Denholm, **comb. nov.**
Orchis hebridensis Wilmott in *J. Bot., Lond.* **77**: 192 (1939).
O. fuchsii Druce var. *hebridensis* (Wilmott) Heslop-Harrison p. in *Vasculum* **25**: 111 (1940).
O. fuchsii Druce subsp. *hebridensis* (Wilmott) Clapham, *Fl. Br. Isl.* 1317 (1952).
Dactylorchis maculata (L.) Vermeulen subsp. *hebridensis* (Wilmott) Vermeulen, *Stud. Dactyl.* 141 (1947).
D. fuchsii (Druce) Vermeulen subsp. *hebridensis* (Wilmott) Heslop-Harrison f. in *Ber. geobot. Forsch. Inst. Rübel* **1953**: 55 (1954).
Dactylorhiza fuchsii (Druce) Soó subsp. *hebridensis* (Wilmott) Nelson, *Mon. Ikon. Orchid. Gatt.* Dactylorhiza 102 (1976).
D. maculata (L.) Soó subsp. *hebridensis* (Wilmott) Nelson, *Mon. Ikon. Orchid. Gatt.* Dactylorhiza 102 (1976).
D. hebridensis (Wilmott) Averyanov in *Bot. Zhurn.* **71**: 92 (1986).

Stem rarely >20 cm, occasionally >3·5 mm in diameter, usually suffused with anthocyanins (often densely). Sheathing lvs often 4 or more, longest lf rarely >9 cm long, widest lf occasionally >2 cm wide; non-sheathing lvs rarely 4 or more; markings usually present, usually covering >10% of the upper surface. Inflorescence rarely >4 cm, rarely >20% of stem length, *usually dense*, fls occasionally more than 25. Floral bracts rarely >8 mm, usually suffused with anthocyanins (often densely); *peripheral bract cells usually angular.* Labellum usually >6·7 mm long to apex of central lobe, usually >5·5 mm to apex of lateral lobe, occasionally >4 mm to base of sinus, usually >9·5 mm wide, *usually broad*, sinuses occasionally very deep; reflectivity of base colour rarely >40%; markings usually present; *lateral outer perianth segments usually ± horizontal*, markings often present (occasionally annular); spur occasionally >2 mm wide at entrance, >1·8 mm halfway along. Flowering late June/July. Hebrides and western Ireland.

Many authors (Summerhayes 1951; Clapham 1952; Akeroyd & Curtis 1980; Lang 1980; Davies *et al.* 1983; Webb & Scannell 1983) have argued that var. *hebridensis* is merely an environmentally dwarfed ecotype of *D. fuchsii* with unusually dark flowers. However, Wilmott's (1939) original description of *Orchis hebridensis* stipulates unusually broad labella, and its large labellum and spur were demonstrated biometrically by Heslop-Harrison (1954); see also Clapham (1962) and Ettlinger (1976). Our data indicate strong bimodality in flower size that distinguishes dark-flowered populations along the coasts of Cornwall, western Ireland and the Outer Hebrides from those further east with similarly coloured but much smaller flowers (usually <6·7 × 9·5 mm; Fig. 6). The larger-flowered populations also tend to have less prominent central labellum lobes (and therefore smaller values (<1·5) for the labellum shape index), broader spurs (often >2·0 mm at the mouth), and greater proportions of plants with annular lateral outer perianth segment markings (though there are exceptions to all these criteria). We have therefore segregated the smaller-flowered plants as var. *alpina* (q.v.), which includes some populations along the west coast of the Inner Hebrides and Scottish mainland that have traditionally been regarded as var. *hebridensis* (e.g. Oldshore).

Populations of *D. fuchsii* with dark flowers and large labella occur in three areas (Heslop-Harrison 1954; Perring & Sell 1968): the Outer Hebrides (Wilmott 1939; Heslop-Harrison 1948, 1951), western Ireland (Brenan & Simpson 1949; Heslop-Harrison 1949, 1950, 1951, 1952; Akeroyd & Curtis 1980; Webb & Scannell 1983) and Cornwall (Pugsley 1940; Heslop-Harrison 1951, 1954; Margetts & David 1981). Most of the populations occupy coastal machair (or machair-like) habitats. The Cornish populations have been separated as var. *cornubiensis* Pugsley (q.v.).

Other characters that reputedly distinguish var. *hebridensis* from var. *fuchsii* are as follows: shorter (c. 10 cm) stems (Lang 1980; Davies *et al.* 1983) bearing fewer, narrower leaves (Summerhayes 1951; Lang 1980; Davies *et al.* 1983) that are less heavily spotted (Lang 1980; Davies *et al.* 1983) or more heavily spotted (Summerhayes 1951), a denser inflorescence (Akeroyd & Curtis 1980; Davies *et al.* 1983), labella with more broken markings (Wiefelspütz 1976; Lang 1980) and a more prominent central lobe (Ettlinger 1976), and spurs more than 7 mm long (Heslop-Harrison 1954, p. 71) but narrow (Wiefelspütz 1976), c. 1 mm wide (Clapham 1952). However, the Baleshare and Robach populations resembled many populations of var. *fuchsii* in all these respects. Vermeulen's (1947) suggestions that var. *hebridensis* is later flowering than var. *fuchsii* and tetraploid are incorrect (Heslop-Harrison 1952). A population of var. *hebridensis* in Co. Galway had taller stems and longer spurs than any of our study populations (Heslop-Harrison 1954), and white-flowered plants may occur rarely in the Outer Hebrides (Wiefelspütz 1976). Heslop-Harrison (1948, 1954) thoroughly described var. *hebridensis*, but exaggerated its distinctness from var. *fuchsii* as his data on the latter encompassed an unrealistically narrow range of morphological variation.

c. var. **cornubiensis** (Pugsley) Soó, *Nom. nov. gen.* Dactylorhiza 8 (1962).
Orchis maculata var. *cornubiensis* Pugsley in *J. Bot., Lond.* **78**: 180 (1940).
O. fuchsii Druce var. *cornubiensis* (Pugsley) Clapham, *Fl. Br. Isl.* 1317 (1952).

Stem rarely >20 cm, rarely >3·5 mm in diameter, often suffused with anthocyanins (occasionally densely). Sheathing lvs often 4 or more, longest lf occasionally >9 cm long, widest lf rarely >2 cm wide; non-sheathing lvs occasionally 4 or more; markings usually present, usually covering >10% of the upper surface. Inflorescence occasionally >4 cm, often >20% of stem length, rarely dense, fls rarely more than 25. *Floral bracts often >8 mm*, usually suffused with anthocyanins (occasionally densely); peripheral bract cells rarely angular. Labellum usually >6·7 mm long to apex of central lobe, often >5·5 mm to apex of lateral lobe, *usually >4 mm to base of sinus*, usually >9·5 mm wide, *rarely broad*, sinuses rarely very deep; reflectivity of base colour rarely >40%; markings usually present; *lateral outer perianth segments rarely ± horizontal*, markings often present (occasionally annular); *spur usually >2 mm wide at entrance, >1·8 mm halfway along*. Flowering June. Cornwall.

The Cornish populations were first described by Pugsley (1940) as *Orchis maculata* var. *cornubiensis*, and incorporated into *Dactylorchis fuchsii* subsp. *hebridensis* by Heslop-Harrison (1954). The long obscure type locality, "a cliff-top near St Ives", may have been refound recently (M. Jenkinson pers. comm. 1987). Otherwise, the only known populations of var. *cornubiensis* are those we studied on a cliff-top at Tintagel and stabilized dunes at Lelant (Perring & Sell 1968; Margetts & David 1981). However, Pugsley's (1940) description of the St Ives plants is consistent with these other Cornish populations, which tend to have wider spurs (median width >2 mm), more lax inflorescences (<6 fls/cm) and longer leaves (longest lf >8 cm) than those in the Hebrides. Wiefelspütz (1976) over-simplified when describing var. *cornubiensis* as intermediate to var. *hebridensis* and var. *fuchsii*.

Many populations of var. *hebridensis* and var. *cornubiensis* have acquired unusual characteristics, perhaps as a consequence of geographical isolation. The large mean labellum width of the Baleshare population (12·3 mm) exceeds those of all populations of *D. majalis* described by Bateman & Denholm (1983). Similarly, the spur widths of the Lelant population (mean value for median width 2·5 mm) match those of the smaller-flowered populations of *D. majalis* (Bateman & Denholm 1983), *D. incarnata* (Bateman & Denholm 1985) and *D. saccifera* (e.g. Nelson 1976), and the stems of the Tintagel plants are as broad (mean diameter 4·6 mm) as those of marsh-orchid populations of similar stature, suggesting that they may be hollow. As in the type population of var. *hebridensis* on Barra (Wilmott 1939), a small proportion of the Robach plants have spots on the undersides of the leaves and bracts, and dashes on the stems and ovaries, features otherwise confined in British orchids to the most anthocyanin-rich individuals of *D. incarnata* subsp. *cruenta* (O. F. Müller) P. D. Sell and *Neotinea maculata* (Desfontaines) Stearn. In contrast, many of the plants in a population of var. *hebridensis* from Co. Donegal lacked leaf markings (Heslop-Harrison 1949).

d. var. **alpina** (Landwehr) Bateman & Denholm, **comb. et stat. nov.**
Dactylorhiza fuchsii (Druce) Soó f. *alpina* Landwehr in *Orchideeën* **37**: 78 (1975).

Stem occasionally >20 cm, rarely >3·5 mm in diameter, usually suffused with anthocyanins (occasionally densely). Sheathing lvs occasionally 4 or more, longest lf rarely >9 cm long, widest lf rarely >2 cm wide; non-sheathing lvs occasionally 4 or more; markings usually present, often covering >10% of the upper surface. Inflorescence rarely >4 cm, occasionally >20% of stem length, rarely dense, fls rarely more than 25. Floral bracts rarely >8 mm, usually suffused with anthocyanins (often densely); peripheral bract cells rarely angular. Labellum occasionally >6·7 mm long to apex of central lobe, *rarely >5·5 mm to apex of lateral lobe*, rarely >4 mm to base of sinus, rarely >9·5 mm wide, occasionally broad, sinuses often very deep; reflectivity of base colour rarely >40%; markings usually present; lateral outer perianth segments occasionally ± horizontal, markings often present (rarely annular); spur rarely >2 mm wide at entrance, >1·8 mm halfway along. Flowering late June/July. Scotland and northern England, possibly also Wales and Ireland.

Landwehr (1977) described and illustrated slender plants with small, dark flowers from the Austrian Alps as *D. fuchsii* f. *alpina*. His original diagnosis fits well the populations of small, dark-flowered plants that we have measured, though the maximum stem height of 25 cm would have to be increased to allow the inclusion of the taller plants from Keltneyburn and Ashes Gill. Figure 40.8 of Landwehr (1977) shows unusually large leaf markings on a plant of f. *alpina* taken into cultivation, but they are not mentioned in his diagnosis. We have therefore adopted this name for fairly homogeneous British populations of *D. fuchsii* with small, dark flowers. As these populations are as distinct from var. *fuchsii* as are vars. *hebridensis* and *cornubiensis*, we have raised *alpina* to varietal status. The populations from inland meadows at Keltneyburn and Ashes Gill attain a stature (mean height 23 and 30 cm respectively typical of var. *fuchsii* in such habitats, but the Oldshore and Polin populations (mean height c. 10 cm) are from exposed coastal habitats and consequently environmentally-dwarfed. This taxon was recognized (though not named) by Clapham (1952, p. 1317): "northern forms [of *D. fuchsii*] are commonly smaller with narrower basal lvs, stem purplish above, and smaller fls, often pale reddish-violet in colour".

When first describing *D. fuchsii*, Druce (1915) cited the French taxon *O. maculata* var. *trilobata* Brébisson (1836, p. 313) as its earliest possible synonym, but regarded the brief original description as ambiguous: "epi grêle; fl. petites; labelle à trois lobes profonds presque égaux" (inflorescence lax; flowers small; labellum with three deep, subequal lobes). He later described var. *trilobata* as "very close to [the white-flowered] *o'kellyi*, but it has spotted leaves and tinted flowers", a statement followed by several British records for this taxon (Druce 1918, p. 167). Since flower colour is not mentioned in the original diagnosis of *trilobata*, Druce's logic eludes us, but it is a recurring theme in subsequent treatments of *trilobata*. Godfery (1933, p. 206) applied the name to typical populations of *D. fuchsii* occupying limestone grassland, which he regarded as having paler labella with shorter central lobes than woodland populations. A similar morphological distinction between these "habitat races" was described by Summerhayes (1951), but it is not supported by our data.

A second school regards *trilobata* as a small, dark-flowered form that is probably our *D. fuchsii* var. *alpina*; indeed, records of *trilobata* from "Kenmore, Mid-Perth" (Druce 1916) and "near Aberfeldy, Perthshire" (Wiefelspütz 1976) may both refer to our study population of var. *alpina* at Keltneyburn. Similarly dark-flowered plants, with exceptionally reduced lateral labellum lobes, were illustrated as *D. fuchsii* f. *trilobata* (Brébisson) Landwehr (a combination that does not appear to have been validly published) by Landwehr (1977, Plate 43.5, 6). As flower colour was omitted from the original diagnosis of var. *trilobata*, and the stipulation for small flowers was probably intended to distinguish var. *trilobata* from *D. maculata* rather than other infraspecific taxa of *D. fuchsii*, we reject use of this epithet for both pale-flowered calcicolous populations and dark-flowered populations occupying neutral or slightly acid soils.

e. var. **okellyi** (Druce) Bateman & Denholm, **comb. nov.**
Orchis maculata L. var. *okellyi* Druce in *Irish Nat.* **9**: 211 (1909).
O. okellyi (Druce) Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **4**: 108 (1915).
O. maculata L. subsp. *okellyi* (Druce) Druce, in Hayward, *Bot. Pocket-book, 15th ed.* 277 (1917).
Dactylorchis fuchsii (Druce) Vermeulen subsp. *okellyi* (Druce) Vermeulen, *Stud. Dactyl.* 149 (1947).
Dactylorhiza fuchsii (Druce) Soó subsp. *okellyi* (Druce) Soó, *Nom. nov. gen.* Dactylorhiza 8 (1962).

Stem rarely >20 cm, rarely >3·5 mm in diameter, occasionally suffused with anthocyanins (rarely densely). Sheathing lvs often 4 or more, longest lf rarely >9 cm long, widest lf rarely >2 cm wide; non-sheathing lvs occasionally 4 or more; markings often present, occasionally covering >10% of the upper surface. Inflorescence rarely >4 cm, occasionally >20% of stem length, occasionally dense, fls occasionally more than 25. Floral bracts rarely >8 mm, *occasionally suffused with* *anthocyanins* (rarely densely); peripheral bract cells occasionally angular. Labellum rarely >6·7 mm long to apex of central lobe, *rarely >5·5 mm to apex of lateral lobe*, rarely >4 mm to base of sinus, occasionally >9·5 mm wide, often broad, sinuses occasionally very deep; *reflectivity of base colour usually >40%* (occasionally >80%); markings often present; lateral outer perianth segments occasionally ± horizontal, markings occasionally present (rarely annular); spur rarely >2 mm wide at entrance, >1·8 mm halfway along. Flowering June/early July. Western Ireland, western Scotland, Isle of Man.

Although discussion of var. *okellyi* usually centres on its type locality in the Burren, it was probably first reported from Sutherland by E. S. Marshall in 1908 (as *Orchis scotica*). Several other populations have since been located in western Scotland (Druce 1915, 1918; Heslop-Harrison 1954; Perring & Sell 1968; Summerhayes 1968; Lang 1980) and the Isle of Man (Perring & Sell 1968; Allen 1963, 1971, 1986), leading to its description as an "Irish-Hebridean race" (Allen 1971) with "a wide distribution exhibiting . . . a neat Atlantic pattern" (D. E. Allen pers. comm. 1987).

The origin of the epithet is confused. Druce was shown non-flowering plants of *Orchis immaculata* in the Burren by P. B. O'Kelly, who subsequently supplied the type material (also in a non-flowering state according to Praeger (1934)) described by Druce (1909). It proved to be a white-flowered variant of *D. fuchsii*, though Praeger (1934) claimed that the plants were selected by O'Kelly in error for the white-flowered form of *D. maculata*, which is also unusually frequent in the Burren. Wiefelspütz's (1976) statement that *okellyi* was originally described as a variant of *Orchis mascula* L. is undoubtedly incorrect.

Previous authors have disagreed over the range of pigmentation encompassed by var. *okellyi*. The most stringent do not allow any floral or vegetative anthocyanins (McKechnie 1918; Stephenson & Stephenson 1920, 1924; Godfery *et al.* 1924; Camus & Camus 1929; Godfery 1933; Clapham 1952; Keane 1980), others permit labellum markings only (Druce 1909, 1915, 1918; Stelfox 1924; Vermeulen 1947; Ettlinger 1976; Webb & Scannell 1983), and the most liberal accept a *minority* of individuals with both labellum and leaf markings (Summerhayes 1951; Heslop-Harrison 1954; Clapham 1962; Allen 1971; Wiefelspütz 1976; Landwehr 1977; Lang 1980; Davies *et al.* 1983). Druce caused much of the confusion by (1) precluding all pigmentation from *O. fuchsii* var. *okellyi* in his original diagnosis (Druce 1909) and in its redescription as a full species, *O. okellyi* (Druce 1915), but adding in the latter paper that some plants have labellum markings, and (2) including a misprint in the original diagnosis, which should have read "leaves . . . unspotted" rather than "leaves . . . spotted". Summerhayes (1951) provided the most accurate description: "Flowers are very frequently almost white . . . with very faint pink or lilac markings on the lip, but in some populations there may be quite a high proportion of plants with more heavily and brightly marked lips". In fact, pigmented plants predominated in all the populations that we measured. Taxonomic recognition of *okellyi* at the population level therefore requires diagnostic characters other than those dependent on pigmentation.

D. fuchsii var. *okellyi* supposedly has smaller flowers (Druce 1909, 1915, 1918; Camus & Camus 1929; Summerhayes 1951; Allen 1971; Wiefelspütz 1976; Lang 1980; Davies *et al.* 1983) whose labella have "more rounded" lateral lobes (Allen 1971; Ettlinger 1976) with crenate margins (Stelfox 1924), and less prominent central lobes (Druce 1909; Allen 1971; Wiefelspütz 1976; Lang 1980), resulting in a smaller labellum shape index (Heslop-Harrison 1954). Thus, the labella and spurs should be intermediate in shape between those of *D. fuchsii* var. *fuchsii* and *D. maculata* subsp. *ericetorum*. Our data (which are consistent with the single data set for Burren *okellyi* published by Heslop-Harrison (1954)) reveal considerable variation between populations of var. *okellyi* in flower size and shape. Black Head plants have similar labellum dimensions (means 6·7 × 9·5 mm) to var. *fuchsii* (Fig. 6). Khyber Pass differs from all other populations in having wide but short labella, resulting in very small mean values for labellum roundness (0.37), labellum shape index (1.32) and central lobe prominence (0.6 mm). Corrofin and Gelain have small labella (mean values c. 5·7 × 8·8 mm) of similar size to *D. fuchsii* var. *alpina*. Only one population (Gelain) had unusually short (<5 mm), narrow (median width <1·5 mm) spurs.

Var. *okellyi* is also supposed to have short (Allen 1971), slender (Druce 1915, 1918; Godfery *et al.* 1924; Summerhayes 1951; Allen 1971) stems with few (Ettlinger 1976; Wiefelspütz 1976), slender leaves (Druce 1909; Camus & Camus 1929; Godfery 1933; Summerhayes 1951; Allen 1971; Ettlinger 1976; Wiefelspütz 1976; Lang 1980) and a narrow (Vermeulen 1947), dense (Druce 1909), cylindrical/flat-topped inflorescence (Druce 1909, 1915; Camus & Camus 1929; Godfrey 1933; Lang 1980; Davies *et al.* 1983). However, our data show that its stem height and diameter are not unusually small, nor are its leaves unusually short. Its leaves are fairly narrow (means 13–17 mm) but are matched by populations of *D. fuchsii* var. *hebridensis*, var. *cornubiensis* and var. *alpina*. Inflorescence shape is not a useful taxonomic character; it reflects the length of the inflorescence and the proportion of flowers open, and therefore changes during anthesis. We have also been unable to detect the strong changes during anthesis. We have also been unable to detect the strong fragrance attributed to *okellyi* by Stelfox (1924), Godfery (1933). Clapham (1962), Landwehr (1977), Lang (1980) and Davies *et al.* (1983), and there is little evidence to support the claim by Wiefelspütz (1976) that it can flower as early as April. Thus, populations of *D. fuchsii* var. *okellyi* are much less distinct from var. *fuchsii* than has been suggested.

It is therefore tempting to regard var. *okellyi* as anthocyanin-less individuals rather than populations, but it is equally difficult to distinguish Burren anthocyanin-less individuals from those elsewhere in the British Isles. Druce (1915, 1918), subsequently supported by McKechnie (1918, p. 185), Stelfox (1924), Summerhayes (1951, p. 271) and Lang (1980), argued that this was possible, but at the same time he described white-flowered plants from several sites in Yorkshire as var. *okellyi* (Druce 1916). Similarly, Godfery (1933) listed numerous records for var. *okellyi* from throughout the British Isles. Stelfox's (1924) argument that var. *okellyi* always has yellow pollinia while other white-flowered individuals of *D. fuchsii* have pink pollinia is void, as both pollinia colour morphs occur throughout the range of *D. fuchsii*. Heslop-Harrison (1949, p. 293) stated that plants of *D. fuchsii* in Co. Donegal with white flowers and unmarked leaves "are simply aberrant forms of the natural population; the white [*D. fuchsii*] races of north Clare [i.e. var. *okellyi* on the Burren] are more worthy of critical examination". However, three years later he wrote more cautiously "In *O. fuchsii* populations elsewhere [i.e. outside the Burren] albino individuals occur which agree with the type diagnosis of ssp. *okellyi*, but this does not remove the necessity for recognising as a distinct taxonomic entity the race which occurs in Clare and Sutherlandshire" (Heslop-Harrison 1952, p. 105). We agree; anthocyanin-less individuals of *D. fuchsii* from the Burren cannot be reliably distinguished from those elsewhere in the British Isles, and the name *okellyi* is best retained at varietal level to describe heterogeneous, anthocyanin-low populations of *D. fuchsii* along the western coasts of the British Isles.

D. E. Allen (pers. comm. 1986) argued that anthocyanin-low populations of *D. fuchsii* on the Isle of Man that have been attributed to var. *okellyi* (Allen 1963, 1971, 1986; Perring & Sell 1968) are more distinct from var. *fuchsii* than those in the Burren, having very small labella with three subequal lobes and showing different geographical and ecological distributions from the type. If these observations can be supported by biometric data, the Manx populations lie outside the range of variation encompassed by var. *okellyi* and represent a new infraspecific taxon.

We cannot detect any characters in descriptions of the diploid Hungarian 'endemic' *D. fuchsii* subsp. *sooiana* (Borsos) Borsos (Borsos 1959, 1961; Landwehr 1977; Soó 1980) that justify its separation from plants of var. *okellyi* with pigmented but unmarked labella.

2. **Dactylorhiza maculata** (L.) Soó, *Nom. nov. gen.* Dactylorhiza 7 (1962).
Orchis maculata L., *Sp. Pl.* 942 (1753).
Dactylorchis maculata (L.) Vermeulen, *Stud. Dactyl.* 130 (1947).
Orchis candidissima Krocker, *Fl. Silesiaca* **3**: 16 & tab. 2 (1814).
O. elodes Grisebach, *Über. Bild. Torfs Emsm.* 25 (1846).
O. maculata L. var. *helodes* (Grisebach) Reichenbach f., *Icon Fl. Germ. Helv.* 67 (1851).
O. maculata L. var. *praecox* Webster, *Brit. Orchid.* 54 (1886).
O. maculata L. f. *candidissima* (Krocker) Schulze, *Orchid. Deutsch., Deutsch. Schweiz* (1894).
O. maculata L. subsp. *ericetorum* Linton, *Fl. Bournemouth* 208 (1900).
O. maculata L. subsp. *elodes* (Grisebach) Camus, *Mon. Orch. Eur.* 192 (1908).
O. ericetorum (Linton) Marshall in *Rep. botl Soc. Exch. Club Br. Isl.* **3**: 127 (1912).
O. maculata subvar. *leucantha* Druce in *Rep. botl Soc. Exch. Club Br. Isl.* **8**: 213 (1916).
O. maculata L. f. *ericetorum* (Linton) Hagerup in *Dansk. Bot. Ark.* **11**: 3 (1944).
Dactylorchis maculata (L.) Vermeulen subsp. *ericetorum* (Linton) Vermeulen, *Stud. Dactyl.* 69 (1947).

D. maculata (L.) Vermeulen subsp. *typica* Vermeulen, *Stud. Dactyl.* 131 (1947).
D. elodes (Grisebach) Vermeulen, *Stud. Dactyl.* 137 (1947).
Orchis fuchsii Druce subsp. *rhoumensis* Heslop-Harrison f. in *Trans. Proc. bot. Soc. Edinb.* **35**: 53 (1948).
Dactylorchis maculata (L.) Vermeulen subsp. *elodes* (Grisebach) Vermeulen in *Ned. Kruidk. Archf.* **56**: 235 (1949).
D. maculata (L.) Vermeulen var. *candidissima* (Krocker) Vermeulen in *Ned. Kruidk. Archf.* **56**: 235 (1949).
D. maculata (L.) Vermeulen subsp. *rhoumensis* (Heslop-Harrison f.) Heslop-Harrison f. in Watsonia **4**: 48 (1957).
D. maculata (L.) Vermeulen var. *ericetorum* (Linton) Vermeulen, in *Fl. Neerlandica* (1958).
D. fuchsii (Druce) Vermeulen subsp. *rhoumensis* (Heslop-Harrison f.) Clapham, *Fl. Br. Isl.*, 2nd ed. 1046 (1962).
Dactylorhiza maculata (L.) Soó subsp. *rhoumensis* (Heslop-Harrison f.) Soó, *Nom. nov. gen.* Dactylorhiza 7 (1962).
D. maculata (L.) Soó subsp. *elodes* (Grisebach) Soó, *Nom. nov. gen.* Dactylorhiza 7 (1962).
D. maculata (L.) Soó var. *praecox* (Webster) Soó, *Nom. nov. gen.* Dactylorhiza 7 (1962).
D. maculata (L.) Soó subsp. *ericetorum* (Linton) P. F. Hunt & Summerhayes in *Watsonia* **6**: 132 (1965).
D. maculata (L.) Soó f. *candidissima* (Krocker) Landwehr in *Orchideeën* **37**: 79 (1975).

Stem 4–40(–50) cm, 1·3–5·5(–8·5) mm in diameter, often lacking anthocyanins. Basal 1f or sheath 0–1, broadest at or above middle; sheathing 1vs (1–)2–4(–5), usually strongly crowded towards base of stem, usually recurved, narrowly lanceolate, usually broadest well above base, longest 1f often also widest, 4–16(–19) cm long, widest 1f 0·5–2(–2·5) cm wide, width/length ratio of 1vs decreasing up stem, usually bright to dark green, tips occasionally distinctly hooded; non-sheathing 1vs (1–)2–5(–7), narrow, broadest at base; 1vs usually sparsely to densely marked on upper surface only, markings usually solid (very rarely annular), ± evenly distributed or concentrated towards tips, ± round to tranversely elongated, usually 1–3 mm in mean diameter. Inflorescence 1–8(–10) cm, 8–35% of stem length, fls 5–50(–60), lax to dense (2–10(–12) fls/cm). Basal bracts 6–20(–25) mm, 1·5–2 times the length of the ovaries, floral bracts 4–12(–15) mm, approximately equalling the ovaries, often suffused with anthocyanins; peripheral bract cells 55–120(–150) μm long, barrel-shaped to triangular. Labellum width usually exceeding length (often considerably), (4–)5–9·5(–11) × (5·5–)6·5–13(–15) mm, widest ± at middle or less frequently above (obtriangular), base colour varying densities (reflectivity (10–)25–89%) of purple, less frequently red-purple or white; markings pale to bold, ranging from dots to dashes and loops (rarely absent or only loops), often covering about two-thirds of the labellum, occasionally more or less; sinuses present (labellum three-lobed), usually shallow, central lobe rarely exceeding lateral lobes by >1 mm, labellum shape index rarely >1·25; lateral lobes often indented, slightly deflexed to moderately reflexed; lateral outer perianth segments usually nearer horizontal than vertical, usually with solid (rarely annular) markings; median outer perianth segment and inner perianth segments connivent; spur straight to moderately decurved, (2·5–)3·5–8(–9·5) × 0·6–2·2 mm at entrance, 0·5–2 mm halfway along, cylindrical or slightly tapering, half as long to as long as the ovary. $2n=?80$. Flowering mid-June to late July (rarely August in the west). Frequent and locally common in the north and west, local in central and eastern England and Ireland. Neutral to moderately acid soils.

Five noteworthy intraspecific taxa of *D. maculata* have been recognized in the British Isles (Table 9). Subsp. *rhoumensis*, a relatively recent segregate confined to Rhum, is discussed later. No author has chosen to recognize *Orchis maculata* var. *praecox* since its original description (Webster 1886; Druce 1912), but there is considerable disagreement concerning which of the other three subspecies encompass(es) British and Irish populations of *D. maculata*. Most British authors (e.g. Bennett 1921; Summerhayes 1951; Heslop-Harrison 1951, 1954; Ettlinger 1976; Lang 1980) have only recognized one subspecies, subsp. *ericetorum*, and have regarded Grisebach's (1846) *Orchis elodes* as a synonym of *ericetorum* and subsp. *maculata* as exclusively Continental. Godfery (1921, 1923, 1933) dissented on a nomenclatural point, arguing that subsp. *elodes* is synonymous with, and has priority over, subsp. *ericetorum*. In contrast, most Continental workers believe that subsp. *maculata* occurs in Britain, together with a second subspecies. This may be subsp. *ericetorum*, with *elodes* treated as a separate, exclusively Continental subspecies (Soó 1960; Wiefelspütz 1976; Delforge & Tyteca 1984), or it may be subsp. *elodes*, with *ericetorum* treated as a synonym of *elodes* (Camus & Camus 1929; Senghas 1968) or of subsp. *maculata* (Soó 1980). Alternatively, all three subspecies may occur in the British Isles (Vermeulen 1947; Landwehr 1977). The complex reasons for this lack of consensus are a microcosm of taxonomic problems in general, and will be discussed in detail elsewhere.

D. MACULATA SUBSP. *RHOUMENSIS*

D. maculata subsp. *rhoumensis* was originally described as a subspecies of *D. fuchsii* endemic to Rhum by Heslop-Harrison (1948). He initially attributed it to *D. fuchsii* due to its apparently diploid karyotype, but later transferred it to *D. maculata*, which it more closely resembled in morphology (Heslop-Harrison 1957). Clapham (1952, 1962) and Perring & Sell (1968) considered it morphologically indistinguishable from *D. maculata* subsp. *ericetorum*, though Ettlinger (1976) and Davies *et al.* (1983) stated that it has unusually bold, looped labellum markings. The exceptionally late flowering period (August) attributed to *rhoumensis* by Heslop-Harrison has been overlooked by most subsequent authors, whilst most Continental workers have overlooked this taxon completely (Table 9b).

Our three study populations from Rhum spanned a wide flowering period from early July (Kinloch) to early August (Harris). Each population deviated considerably from the original diagnosis of *rhoumensis*. Kinloch was the closest in overall morphology, but it flowered much too early and had leaf markings that were much too dense (mean areal coverage 25%). Kilmory also flowered too early, and had pale flowers (mean reflectivity 72·6%) with broken labellum markings of only low to moderate contrast. Harris flowered at the prescribed time for subsp. *rhoumensis* and had the stipulated dark flower colour (mean reflectivity 40%), but the plants were too short (mean height 6·9 cm), had a large mean labellum shape index (1·24) intermediate to typical values for *D. fuchsii* and *D. maculata*, and was tetraploid ($2n$ = c. 80; A. Karp pers. comm. 1985). Furthermore, Heslop-Harrison (1948, p. 53) specifically excluded from subsp. *rhoumensis* the populations of *D. maculata* occupying the Harris machair.

Thus, none of our three study populations fulfilled the morphological criteria in the original diagnosis of subsp. *rhoumensis*. Since Rhum populations of *D. maculata* are very variable, and overlap almost completely populations elsewhere in the British Isles, we conclude that *rhoumensis* is not a convincing taxon.

OTHER INFRASPECIFIC TAXA

Nonetheless, the August-flowering population from Harris provided an interesting comparison with Porlock, an August-flowering population from Exmoor (Table 1). These two populations were much the darkest-flowered of those studied (mean reflectivities <40%) and had narrow (c. 2 mm) stems bearing few (c. 3), narrow (c. 7 mm) sheathing leaves. However, they differed from each other considerably in several other characters. The shorter stem, shorter, more basally concentrated leaves and proportionately longer inflorescences of the Harris plants may merely reflect environmental dwarfing, but this is unlikely to explain their more sparse leaf markings, much shorter (c. 4 mm) spurs and more prominent (c. 1 mm) central labellum lobes. It would therefore be unwise to unite these populations as an infraspecific taxon.

None of the plants measured approached the 18 mm labellum width of Druce's (1920, p. 579) *D. maculata* var. *macroglossa*, which was probably a hybrid, but several exceeded the 12·5 mm labellum width required for *D. maculata* f. *grandiflora* (Vermeulen) Soó (Landwehr 1977). However, we see no merit in perpetuating a taxon diagnosed by a single size character.

The tall, relatively slender Llandegfan plants resembled *D. maculata* var. *traunsteinerifolia* (Harz) Soó (see Landwehr (1977, p. 37)). Other morphologically distinct populations were Stanmore, with an unusually large number of non-sheathing leaves, and Thursley, with unusually reflexed lateral labellum lobes more characteristic of *D. incarnata* (Bateman & Denholm 1985). Some British and Irish populations of *D. maculata*, particularly those growing in exposed habitats, resemble Scandinavian endemics described by Landwehr (1975, 1977): *D. maculata* subspp. *deflexa* Landwehr, *montellii* (Vermeulen) Landwehr and *elodes* var. *darnalensis* Landwehr. The latter closely resembles the late-flowering Porlock population. Comparative studies of British and Scandinavian populations are desirable to investigate these relationships.

EXTREMES OF PIGMENTATION

Stephenson & Stephenson (1921, p. 123) described a plant of *D. maculata* subsp. *ericetorum* with "the whole centre of the lip taken up by a patch of bright magenta". This anthocyanin-rich form of *D. maculata*, analogous to that already described for *D. fuchsii*, has also been reported from the Continent. It was named *Dactylorchis maculata* var. *concolor* Vermeulen (1949, p. 232), later demoted to *Dactylorhiza maculata* f. *concolor* (Vermeulen) Landwehr (1975, p. 79).

The well-known anthocyanin-low mode of *D. fuchsii* in the Burren (var. *okellyi*) occurs with a similar but less distinct mode of *D. maculata* which includes a few anthocyanin-less individuals (Druce 1915, 1918) that may have been confused with albino *D. fuchsii* (Praeger 1934; Heslop-Harrison 1952, 1954). Burren *D. maculata* also have labella that are on average unusually broad relative to their length (index 'a' means 0·40–0·42) and wide spurs (means 1·4–1·7 mm for median width) resembling those of *D. fuchsii*, though we could not detect the fragrance attributed to them by Clapham (1952, 1962). Anthocyanin-low populations of *D. maculata* occur in other limestone districts (Heslop-Harrison 1954); all four anthocyanin-less plants that we measured were found at Ashes Gill and White Nook, populations from the Carboniferous limestone of Yorkshire. However, even here the frequency of albinos has been exaggerated due to lack of close scrutiny; Marshall (1912) described white-flowered *D. maculata* as "not uncommon" in Yorkshire, but qualified this by stating that they were "seldom quite *pure* white"!

Interestingly, the epithet *candidissima* (currently *D. maculata* f. *candidissima* (Krocker) Landwehr (1975, p. 79)) is usually applied solely to albinos (e.g. Heslop-Harrison 1954). The original description of *Orchis candidissima* (Krocker 1814, p. 16 & Plate 2) is sufficiently detailed to show that it is indeed a variant of *D. maculata* (Druce 1925; Vermeulen 1947) but also that it is not a suitable basionym for a taxon composed of anthocyanin-less individuals; Krocker specified lightly spotted leaves, a pigmented spur and purple pollinia for *candidissima*. As Druce was aware of this (Druce 1925, p. 139), it is surprising that he suggested synonymy of *candidissima* with his *Orchis maculata* subvar. *leucantha* Druce (1916) (see also Godfery (1933)).

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Short Notes

OBSERVATIONS ON INLAND POPULATIONS OF *VIOLA CANINA* L. IN SOUTH-EASTERN SCOTLAND AND NORTH-WESTERN ENGLAND

Viola canina is a rare inland species in southern Scotland and northern England. It is virtually restricted to coastal habitats. Recently I discovered several small inland colonies in the Tweed valley of south-eastern Scotland where it was previously unknown, and rediscovered several inland sites, mainly in Cumbria in north-western England.

In 1983, colonies of *V. canina* were found by the River Yarrow in Selkirks., v.c. 79, and their identification confirmed by Prof. D. H. Valentine. Since then further colonies have been found by the Rivers Yarrow, Ettrick and Tima Water in Selkirks., and by the River Tweed in Roxburghs., v.c. 80. Grassland sites near Ancrum in Roxburghs., and Peel Hospital in Selkirks. also support small colonies. The altitudes of the localities vary from 45–252 m. In 1985 *V. canina* was refound on the shores of Ullswater in both Westmorland, v.c. 69, and Cumberland, v.c. 70, where it was first discovered at the end of the last century (Hodgson 1898; Wilson 1936). However it appears to have gone from the rocky islands of Ullswater (G. Halliday pers. comm.). Small populations still occur on the western bank of the River Lune west of Sedburgh in Westmorland and on the eastern bank in N. W. Yorks., v.c. 65. I found an additional riverside colony by the River Eden in the Baronswood gorge in Cumberland. The two grassland sites known to me are on Wan Fell near Penrith.

The riverside habitats consist of rock outcrops, which extend into the beds of the rivers and which are inundated only by the most severe floods. The Selkirks. rock habitats and those by the River Lune are composed of hard, fine grained and relatively basic Silurian strata. Those by the River Tweed are Carboniferous basalts, and the Ullswater rocks are of the Borrowdale volcanic series which are basic in places. Although the Permian sandstones by the River Eden are acid, the riverside rocks support a calcicolous flora from flushing with lime-laden water and silt deposition. *V. canina* grows on niches and ledges on these open rock outcrops, which support a flora that includes *Antennaria dioica*, *Campanula rotundifolia*, *Galium boreale*, *Leontodon autumnalis*, *L. hispidus*, *Scabiosa columbaria*, *Solidaga virgaurea* and *Thymus praecox*.

The grassland habitat in Roxburghs. is on the shallow soil overlying an outcrop of basalt, which also supports *Dianthus deltoides*. It is of interest, and possibly relevant, that this outcrop also supports the rare maritime lichen *Ramalina polymorpha* (Corner 1981). The Selkirks. grassland site consists of a relatively basic, stony glacial till with *Leontodon hispidus*, *Polygala vulgaris*, *Ranunculus bulbosus*, *Rhinanthus minor* and, more locally, *Ophioglossum vulgare*. Vigorous colonies of the hybrid *V. canina* × *riviniana* occur at the former site and further colonies of this hybrid have been found in Roxburghs. in dry shallow grassland from which *V. canina* is absent. There are few documented accounts of this hybrid in Scotland. The two Cumberland grassland sites are on light sandy soil overlying the Permian sandstone. Although *Calluna* is extensive, there are more basic areas which can be heavily grazed by rabbits. Here *V. canina* is associated with *Centaurium erythraea*, *Conopodium majus*, *Echium vulgare*, *Galium verum*, *Gentianella campestris*, *Leontodon taraxacoides*, *Lotus corniculatus*, *Myosotis ramosissima* and *Viola riviniana*. The hybrid *V. canina* × *riviniana* is common at one site and distributed on roadside verges in the surrounding district, where it is known from five sites.

The British habitat of *Viola canina* is given as "heathy places preferring sandy soils" (Druce 1932), and "heaths, dry grassland, dunes and fens" (Moore 1987). However in Scotland and Ireland it is not infrequently found on lakeshores. Buchanan White (1898) gives its habitat as "shingly margins of rivers and lakes . . .". Hadley (1985) mentions "stony loch shores, etc." and A. McG. Stirling (pers. comm.) states that in Dunbarton, v.c. 99, it is confined to the stony or rocky shores of the mainland or islands of the southern part of Loch Lomond. In Ireland there are references to the lakeshore habitat by Scully (1916), Praeger (1934), Stewart & Corry (1938) and Webb & Scannell (1983).

It is well known that *V. canina* is intolerant of shade. It seems likely that these specialized open waterside habits, and possibly the grassland ones also, have provided refugia for small relict populations. With the abundance of open habitats and unleached soil available in the early post glacial period, *V. canina* was probably a widespread species in Britain and Ireland. Indeed in Iceland I have seen it associated with *Alchemilla alpina*, *Galium boreale*, *Salix herbacea* and *Vaccinium uliginosum*. Godwin (1975) records it from glacial deposits in the Isle of Man dated at 10,000 years old, with tentative earlier records from the Lea Valley arctic plant beds in Essex as well as from Bronze and Iron age sites. With the expansion of the forest in the Boreal period, *V. canina* would have suffered widespread elimination. In the more northern and western parts of Britain and in Ireland, the growth of peat and leaching of soils during the wetter Atlantic period would have reduced the available habitats still further. It is now only able to exist as a relict in these open relatively basic inland sites which probably never carried closed woodland even during the post glacial forest maximum (Pigott & Walters 1954). Unfortunately these small populations are vulnerable to habitat change and their future is uncertain.

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SOME EARLY NOTICES OF ANTHOCYANIN-RICH VARIANTS OF COMMON BRITISH PLANTS

The *Lacnunga* (British Museum MS. Harley 585; edited by Cockayne (1866) and Grattan & Singer (1952)) is an Old English (Anglo-Saxon) magico-medical commonplace book dated at around 1000 A.D. but compiled from earlier sources. Much of the *Lacnunga* is adapted from Latin herbals (Cameron 1983a), although Christian as well as Saxon and Celtic pagan elements are represented. The book takes the form of herbal recipes supplemented by charms: 194 entries in all. A class of professional medical men (leeches) practised medicine at this level and had the task of trying to alleviate the common ailments of the period: particularly "spring fever" (endemic benign tertian malaria), dysentery (infection with *Entamoeba histolytica*) and abscesses caused by sheep liver fluke infestation (Cameron 1983b). As befits learned men, some able to read Latin, many Latin plant names are used. Nevertheless, roughly 50% of the *Lacnunga* plant names are Saxon in origin and an interesting source of information about our Saxon folk taxonomy. This will be discussed elsewhere, but it is notable that colours are rarely used to distinguish or denote plants.

Of some 200 plant names in the *Lacnunga* only eleven are associated with colour, such as: yelodwyrt (*Blackstonia perfoliata* (L.) Huds., yellow-wort) from the bright yellow flowers; brunwyrt (*Scrophularia aquatica* L., brownwort) from the colour of the stem; hwit cudu (white cud), and Hwitmæring (white ?mastic) both probably referring to the white gum resin of *Pistachia lentiscus* L., imported into Britain from the Mediterranean region during Saxon times. There is also hwæwen hnydele (hued nettle), said by Grattan & Singer (1952) to refer to *Lamium purpureum* L. This seems to be the only case in Saxon folk-taxonomy of a plant species being distinguished from another by a colour qualifier. However, no less than six of these eleven plants are associated with the colour red (read).

1) reade yearuwe (red yarrow – I have avoided Anglo-Saxon letters in transliterations and use appropriate modern equivalents where possible). *Achillea millefolium* L. (yarrow) is an important ingredient in Saxon leechcraft and wortcunning, being called for in seven recipes of the *Lacnunga*. One of these recipes, however (63 in Grattan & Singer's enumeration), called for reade yearuwe (red yarrow) specifically (i.e. *Achillea millefolium* forma *rosea* Desf. (Hegi 1928, p. 570)), a variant mentioned in Gerarde (1597), "common Yarrowe . . . the flowers whereof are either white or purple, which being rubbed do yeelde a strong smell, but unpleasant . . .", Lyte's (1578) translation of Dodoens, "the floures most commonly all white, sometimes also in this countrey of a purplish colour" and Bock's (1552) *De Stirpium*. Simples in *Lacnunga* recipe 63 are in alliterative pairs, and reade yearuwe has the happy property of alliterating with rædic (*Raphanus sativus* L., radish) and ribbe (*Plantago lanceolata* L., ribwort). Gerarde (1597), using Tabernaemontanus' plates, also illustrates a European species of *Achillea* of uncertain identity "the second kinde of Milfoile or Yarrow, hath stalkes, leaves, and roots like unto the former [*Achillea millefolium*], saving that his spokie tufts are of an excellent faire red or crimson colour, and being a little rubbed in the hand, is of a reasonable good savour . . . The first groweth every where in drie pastures and medowes: red Milfoile groweth in a field by Sutton in Kent, called Holly Deane [Holy-Deane in 2nd edition], from whence I brought those plants that do grow in my garden; but it is not common every where as the other is." This may be a Continental red yarrow introduced for medicinal purposes.

2) reade wuducerfille (red woodchervil). The Anglo-Saxon "cerfille", from the Latin *cerefolium*, refers to *Anthriscus cerefolium* (L.) Hoffm. (chervil), and it is not surprising that a Latin rather than Germanic name is used for a plant not native in Britain or northern Europe; rather more surprising, however, is that wuducerfille [wudufille] should be used instead of the Saxon name (now lost to us) for *Anthriscus sylvestris* (L.) Hoffm. Five entries in the *Lacnunga* call for wuducerfille and two of these (90 & 127) call for reade wuducerfille specifically (although entry 90 has "reade fille" which is probably a short form of reade wuducerfille). This variant has purple pigmentation at the nodes, or sometimes througout the whole stem and even the leaves. Extreme variants with purple-black spring leaves (Hegi 1926, p. 1020), i.e. *Anthriscus sylvestris* var. *nigra* Murr, are sometimes found growing amongst the typical morph (Gray 1863). The anthocyanin polymorphism was familiar to Johnson (in Gerarde 1636): "It hath a whitish wooddy root, from which arise round red and hairy stalkes . . . The leaves are . . . of a dark greene or else reddish colour."

3) reade hofe (red hove). The Saxons called *Glechoma hederacea* L. hove or hofe, which survives in the name alehoof. Two entries in the *Lacnunga* call for it, one (31) specifically for reade hofe which conveniently alliterates with ribbe (*Plantago lanceolata*). Plants of hove with purple stems and young leaves (*G. hederacea* forma *purpurascens* Otruba) are frequently found. Gerarde (1597) describes *Glechoma hederacea* as having "manie stalkes, of an uncertaine length, slender, and like those of the vine, something cornered, and sometimes reddish".

4) reade netele (red nettle). Netele, in five entries of the *Lacnunga*, refers to *Urtica dioica* L. However, three of these entries (49, 98 & 134) call for reade netele. Entry 134 further specifies "red nettle that groweth through into a house" ("seo reade netele the thurh ærn inwyxth"). A variant version (Meaney 1984) of entry 98 (for smallpox) occurs in Bald's *Leechbook* (entry 1.xxxix.2 in Cockayne (1865)); both clearly derive from the same earlier source and both specify red nettle, as does the next entry in Bald's *Leechbook* (1.xl, also for smallpox) which specifies: "the crop [flowering top] of red nettle". Many stinging-nettles have anthocyanin pigmentation on the ridges of their stems and petioles, and some have the entire stems dark purple and the young leaves suffused purple. An extreme variant with the leaves "suffused with violet-purple" has been described (*U. dioica* forma *purpurascens* Druce (1920)). Tabernaemontanus (1590) illustrates both variants: *Urtica maior, sive sylvestris asperior* (Groß Nettel/Brennend Nettel) and *Urtica rubra* (Rot Nettel).

Gerarde (1597) using these plates also describes them, of the second saying: "our common red Nettle, is knowne better to some than desired, and therefore needeth no description". Johnson, in his 1636 edition of Gerarde lumps the two, as does Lyte's (1578) translation of Dodoens, where he notes: ". . . our common great Nettell . . . The leaves . . . most commonly of a swarte greene colour, & sometimes reddish".

5) reade seales (red sallows). Sallow bark is required in entry 31, but in entry 155 leaf of red sallow ("reades seales leaf") is required. Several *Salices* have anthocyanin pigmentation to varying degrees, but notably *Salix purpurea* L., which has the anthers, and in some plants the twigs and buds, tinged purple. Of this species Gilbert-Carter (1936) notes "The bark is very bitter from the presence of salicin . . . which was much used in medicine before it was supplanted by . . . aspirin . . . It is an important osier, and its twigs are often boiled to strip off the bark, and to impart a red colour to the wood".

6) mugcwyrt (mugwort). The importance of colour is continued in entry 178: "If one is to have mugwort for a remedy, then let one take the red for the cure of a male and the green for the cure of a female" ("yif man scyle mugcwyrt to læcedome habban, thonne nime man tha readen wæpnedmen & tha grenan wifmen to læcecræfte" which Cockayne (1866) translates as: "If a man must have mugwort for a leechdom, then let him take the red males and the green females for a leechcraft"). Mugwort (*Artemisia vulgaris* L.) is an important item in leechcraft, used in six entries. The purple-stemmed variant of mugwort is a common plant, the most abundant in some areas according to Salmon (1931), who calls it *Artemisia vulgaris* var. *coarctata* Forselle. Others distinguish this variety on purely morphological grounds without regard to colour: contracted inflorescence and linear-lanceolate leaf segments (Hegi 1928, p. 639).

The purple mugwort variant is a familiar one. Fuchs (1542) says: "There are three Artemisias in Dioscorides and commonly found today. The first is platyphyllos which may be called in Latin *Artemisia latifolia*. This one is now simply called *Artemisia* however. Of this there are again two types contrasting in colour only: one with red stems and flowers is called in German Rotbucken or Rotbeyfüß[ss]: the other with a white stem and true yellow flowers is called by the Germans Weißbucken." Bock (1552) gives a similar account and Lyte's (1578) translation of Dodoens has: "Mugworte . . . Of this herbe there be twoo kindes moe [sic], differing onley in colour . . . The one hath redde branches & floures and is called redde Mugworte. The other hath greenish branches, changing towardes white, and is called white Mugworte, in all things els like one to an other". Gerarde (1636) has: "The second kinde of Mugwort hath a great thicke and wooddy root, from whence arise sundry branches of a reddish colour . . .", the editor, Johnson, adds: "I know not how this differeth from the former, but only in the colour of the stalke and flours, which are red or purplish; whereas the former is more whitish". Gerarde uses the woodcuts in Tabernaemontanus (1590) in which two mugworts are illustrated, viz. *Artemisia rubra*, Roter Beyfuß and *Artemisia alba*, Weißer Beyfuß.

Thus all the 'red' plants in the *Lacnunga* are unequivocally anthocyanin-rich variants, flushed with purple in their stems, leaves or flowers. It is interesting that the word 'red' is used, as Anglo-Saxons sometimes reserved this word for yellowish-red (Barley 1974). Laxity in colour description is continued today in the use of the name "copper beech" for the anthocyanin-rich variant of *Fagus sylvatica* L. The classically derived term 'purple' is based on the important colour reference point of Tyrrhenian purple, the dye derived from *Murex* spp. (in fact crimson (Stearn 1973)), which may not have been familiar in tenth century Britain.

As red variants are biochemically different from green ones, a pharmacological basis for the preference in leechcraft cannot be ruled out. The origin is more likely to lie in Roman sympathetic colour magic, however. The *Lacnunga* entries which call for red plants are almost all from the Latin and Christian sources (a & c of Grattan & Singer (1952)), while none come from the Saxon pagan source (b of Grattan & Singer (1952)). A passage of Marcellus Empiricus quoted by Grattan & Singer illustrates the importance of colour: "cut open the crop of a swallow. Little stones, both white and black will be found. Placed in a golden locket they will permanently avert all eye pain and, if wrapped in a yellow cloth or flaxen sac and hung around the neck, they avail against fevers". Another case is provided in the *Lacnunga* itself (entry 7) in which there are instructions for an eye-salve to be dripped into the eye through a flax-blue ("linhæwenne") cloth. It is possible that the red colour conveyed more power (mana of the anthropologists); indeed the symbolic significance of red persists today. These instances underline the fact that although the study of anthocyanin polymorphism is neglected today, these red variants were observed and used by our remote ancestors.

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DACTYLORHIZA TRAUNSTEINERI (SAUTER) SOÓ: VARIANTS IN NORTH-EAST YORKSHIRE

Examples of albino *D. traunsteineri* (Sauter) Soó are apparently very rare in the British Isles but records of single plants have been cited for two British localities (Roberts 1985). In June 1986 I found three such plants growing within a large colony of typical *D. traunsteineri* in N. E. Yorks., v.c. 62. All the albino plants grew within 3 m of each other and had pure white flowers with unmarked labella; the leaves were light green and also unmarked, whilst the upper stem and bracts lacked the anthocyanin staining typical of this taxon. Other than as described above, they resembled normal *D. traunsteineri* in habit, lax-flowered appearance and labellum shape and size, the plants being 10–14 cm tall, with 5–11 flowers, three or four sheathing leaves, one non-sheathing leaf, and with a maximum leaf width of 8·5–12 mm.

In the immediate area of these albino plants was a single plant of *D. traunsteineri* whose six flowers were coloured an extremely pale, delicate pink, with markedly tri-lobed labella sparingly spotted and loop-marked in bright red. This unusual and very attractive plant, whose flower colour lies well outside the normal range for *D. traunsteineri*, apart from having a greater maximum leaf width, exhibited a marked resemblance to descriptions and illustrations of *Orchis francis-drucei* recorded for W. Ross, v.c. 105, by Wilmott (1936) and Landwehr (1977), and recently interpreted as *D. traunsteineri* (Lowe, Tennant & Kenneth 1986).

In a second colony of *D. traunsteineri* in N. E. Yorks., c. 4 km from the above, a single pseudopeloric variant was found in June 1987. This had flowers whose labella were generally completely undifferentiated, although in a few instances an extremely short (1–2 mm) vestigial spur was present. All labella were narrow, sepal-like, and forward-pointing, of typical colour but completely lacking any form of dot- or loop-markings. In each flower both lateral sepals were spread horizontally (laterally), whilst the remainder were invariably arched forward in a closed configuration. The plant was 30 cm tall and had 24 flowers, both these characters being much in excess of those found for local *D. traunsteineri*. Pseudopeloria in British orchids was reviewed by Bateman (1985) but appears to be previously unrecorded for *D. traunsteineri*.

Colour photographs of all the plants described are retained by myself.

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THE BRITISH ROSE SURVEY OF 1952–54

The British Rose Survey was organized under the auspices of the Systematics Association by the late Professor P. C. Sylvester-Bradley, a paleontologist at Sheffield University with a keen interest in botany, in collaboration with Dr R. Melville of the Royal Botanic Gardens, Kew. Very little information about the survey appears in print; it was the subject of an exhibit at the B.S.B.I's exhibition meeting of 1952 (Sylvester-Bradley 1953) in which the results of a trial run conducted that summer and autumn were presented, and the strategy of the main survey for 1953 outlined. The plan was to sample 30–50 bushes from randomly selected populations and to score each individual for 38 characters relating to habit, foliage, armature, flowers and fruits (an example of a data-sheet was illustrated in *B.S.B.I. News* (Gornall 1988)); the data were later to be encoded on punched cards for statistical and taxonomic analysis. It was hoped that the results would "elucidate the nature of [rose] 'species' and the degree of reticulation present" (Sylvester-Bradley 1953; Lousley 1953). After the trial survey of 1952, extensive field work was carried out in 1953, involving 192 registered observers, 64 of whom sent in returns that year relating to 2764 bushes in 96 localities. Work, however, then rapidly tailed off over the following two seasons; the results were never analysed, and the survey was more or less forgotten.

It came as some surprise, therefore, when a total cache of 941 pressed *Rosa* specimens were exhumed from the basement of the herbarium at **K** and Mrs J. Sylvester-Bradley's garage in Leicester in the summer of 1987. These proved to represent an unknown proportion of the total gathered during the dry run of 1952 and the main survey of 1953. There was also documentation and a card index which connected the specimens with collectors and the localities visited.

A total of 213 individuals or organizations were registered as observers (many of them B.S.B.I. members) and they apparently visited 140 localities altogether, although the surviving specimens originate from only 54 of these; Fig. 1 shows the 10-km squares containing the survey sites.

Most of the specimens collected by Sylvester-Bradley had been identified but the rest (c. 800) were without names. One of us (A.L.P.) has now made determinations where possible, although it must be said that about half of the specimens were too poorly pressed, too poorly preserved, too

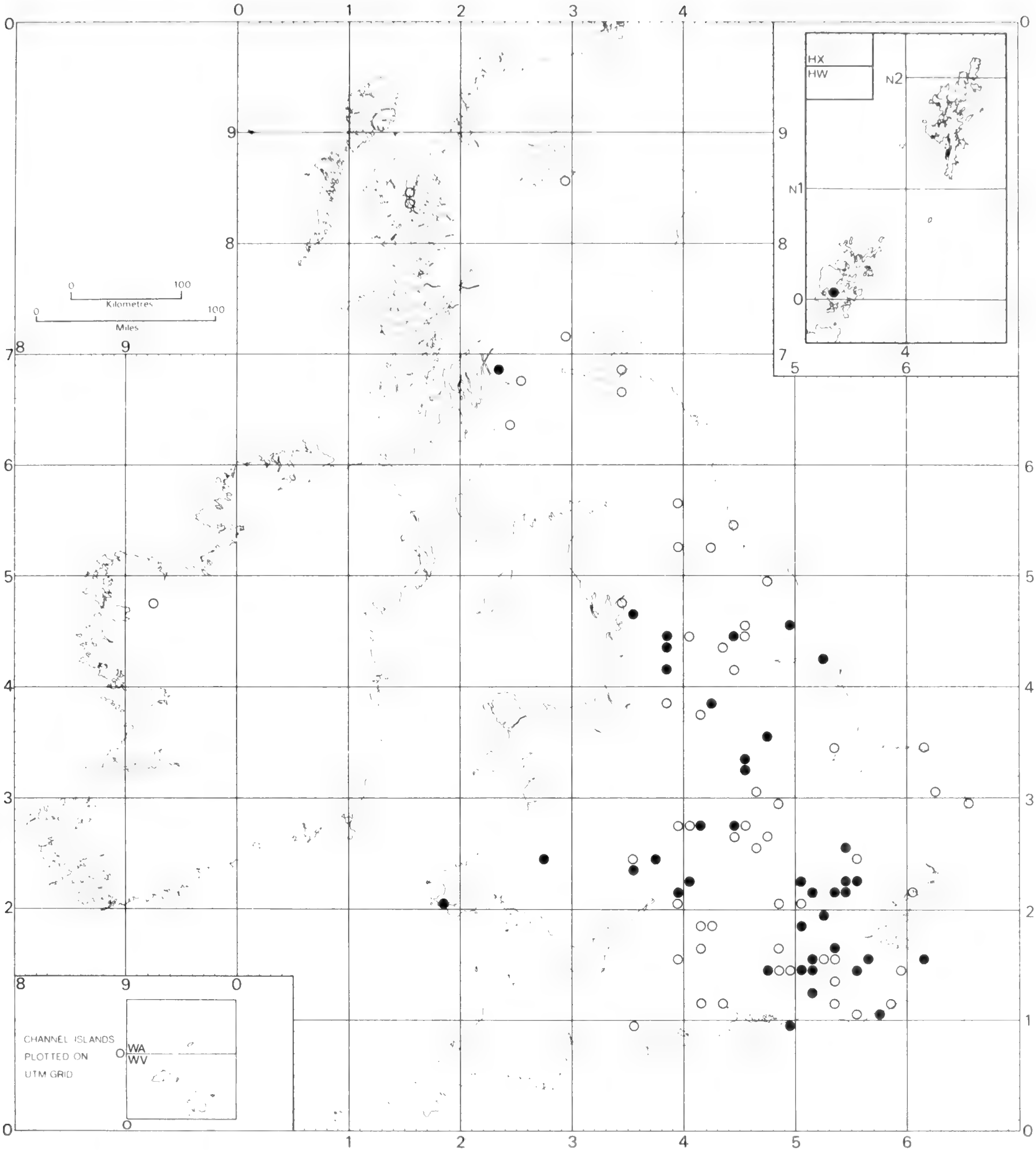

FIGURE 1. Distribution of 10-km squares containing one or more survey sites; ● with herbarium specimens, ○ without herbarium specimens.

immature or otherwise inadequate to allow identification. A taxonomic summary is presented in Table 1.

The Survey was, in our opinion, doomed to failure from the start partly because the organizers had bitten off more than they could chew; their intention was to transfer the vast amount of data to punched cards but this was never done. It is also clear from the surviving instructions and the printed data-sheets that the field-work was time-consuming and uninteresting, and the B.S.B.I. distribution maps scheme was beginning to compete successfully for the volunteer labour force.

The principal mistake which the organizers made was to confine the Survey to very small areas

TABLE 1.-TAXONOMIC SUMMARY OF THE DATA FROM THE BRITISH ROSE SURVEY OF 1952–54

Species/Hybrid*	No. specimens	No. localities
R. afzeliana	36	5
R. afzeliana × *canina*	20	7
R. arvensis	101	12
R. arvensis × *canina*	1	1
R. caesia × *canina*	9	2
R. canina	232	25
R. canina × *obtusifolia*	2	2
R. canina × *stylosa*	8	1
R. canina × *tomentosa*	2	1
R. dumetorum	10	4
R. micrantha	8	3
R. mollis	52	6
R. obtusifolia	5	5
R. rubiginosa	2	2
R. sherardii	22	3
R. stylosa	11	3
R. tomentosa	1	1
Indeterminate	418	43

* Parents of hybrids are given in alphabetical order.

containing a large stand of rose bushes. Such sites often contain only the commonest local taxon. Thus the specimens from the island of Hoy in the Orkneys are nearly all *R. mollis* Sm.; collections from the Midlands are often nothing else but *R. canina* L.; those from the south are often *R. canina* or *R. stylosa* Desv. In all the hundreds of specimens there are only eight of *R. micrantha* Borrer ex Sm., five of *R. obtusifolia* Desv., two of *R. rubiginosa* L., one of *R. tomentosa* Sm. and none at all of *R. pimpinellifolia* L., *R. caesia* Sm., *R. agrestis* Savi and *R. elliptica* Tausch (the occurrence of the last of which in Britain is now considered to be doubtful) (Table 1). The supreme example of this strategic mistake is the collection number 86/A. This was made by field-workers from the Juniper Hall Field Centre. With classic rose sites in the vicinity, such as Box Hill or even the immediate neighbourhood of Juniper Hall itself, the field-workers chose a ruderal site (the spoil-heap of a lime-works) and collected 40 specimens of *R. canina* and nothing else. It would have been far more informative from a taxonomic point of view if the field-workers had been instructed to examine a few individuals in as many localities and habitats as possible.

Nevertheless, the data do confirm our knowledge of the geographical distributions of some *Rosa* species. For example, all the specimens of *R. mollis* came from the north; all specimens of *R. stylosa* came from the south; and those of *R. arvensis* decline in frequency the more northerly the locality.

We have examined all the specimens with care and discarded all those which, for various reasons, are unidentifiable. The remainder have been divided into sets, with the top one housed at **LTR**; a subsidiary set has been sent to **NMW**, together with the documentation, data-sheets and the reference card index.

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A NEW *VACCINIUM* IN THE BRITISH FLORA?

A dwarf, prostrate, small-leaved *Vaccinium uliginosum* L. collected in 1968 by one of us (W.S.S.) on Roga Field, Shetland (GR 411/3.8) has proved to have a chromosome number of 2n=39. Typical *V. uliginosum* subsp. *uliginosum* from other British localities, e.g. Unity Bog, Cumbria (GR 35/528.591) and Hermaness, Shetland (GR 412/606.176), has 2n=48 in agreement with other European counts (Moore 1982). The more northerly subsp. *microphyllum* Lange from arctic and sub-arctic Europe is reported as having 2n=24 (Moore 1982). It has never been recorded from the British Isles. A hybrid between these two subspecies would be expected to have 2n=36.

Although the chromosomes are very small and difficult to count, consistent counts of 2n=39 have been made on the Roga Field plant. There are three possible explanations. Firstly it might be a first generation hybrid (F_1) with accessory chromosomes (2n=36+3B), though no differences in size or appearance could be detected in the chromosome set. Alternatively it might be a second (F_2) or third (F_3) generation hybrid resulting from a backcross to the tetraploid parent (subsp. *uliginosum*). Both diploids and tetraploids are probably self-incompatible (Vander Kloet 1977), so an F_2 is unlikely to have resulted from a self-fertilization, and the chance of there being two F_1 hybrid plants in the same area is probably low. Thirdly, as the Roga Field plant is similar in appearance to subsp. *microphyllum*, it might be derived solely from the subspecies through non-reduction of some chromosomes at meiosis in either pollen or ovule production.

We suggest, then, that the Roga Field area and other exposed summits and hillsides in the Shetland Isles should be searched for small-leaved, prostrate, strongly rhizomatous plants of *V. uliginosum* as they might prove to be the diploid subsp. *microphyllum*. The plant can easily be propagated at any time of year from small pieces of twig (preferably young) with attached rhizome wrapped in damp moss.

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NARTHECIUM OSSIFRAGUM L. IN THE BURREN, COUNTY CLARE

Webb & Scannell (1983) provided distribution data for plants in the Burren, Co. Clare, v.c. H9, and therein noted that *Narthecium ossifragum* L. occurred only in districts 1 (The Clare Shales) and 3 (The Burren Lowlands). District 2 (The Burren Hills) is not notable for extensive peat deposits yet, enigmatically, it does not have an exclusively calcicolous flora; plants such as *Calluna vulgaris* L., *Erica cinerea* L. and *Eriophorum* spp. abound in the region, colonizing the small hummocks of peat that rest on the limestone rocks, and the pockets of soil which are maintained in a perpetually damp state solely by rain water. However, plants characteristic of the wettest parts of raised bogs – for example *Erica tetralix* L. and *Myrica gale* L. – are absent from this region, or at least have not yet been reported. Hitherto *N. ossifragum* was included among the absentees.

During field studies in The Burren Hills at the beginning of August 1987, I found *N. ossifragum* in several places on the higher slopes of the western hills. The first sighting was near the summit of Dobhach Bhrainin, at about 270 m, in a damp, peaty area facing north-west. About 100 flowering spikes were visible in the colony which covered less than 100 m^2 (herbarium specimens collected 1

August 1987 are in **DBN**). On the succeeding three days, other populations were noted on the north-eastern slopes and summit plateau of Cappanawalla, and on the northern slopes of Gleninagh Mountain; these colonies were substantial and much more extensive than the original one on Dobhach Bhrainin.

What is the reason for the absence of earlier reports of this species in the Burren? It is not an abundant plant, but it is certainly not rare – anyone walking on the higher slopes of the Burren hills during the summer is likely to encounter it in blossom. Perhaps the silence of earlier botanists is explained by the fact that the bright yellow flower-spikes of *N. ossifragum* can be mistaken, at a distance, for those of *Galium verum* L. or *Solidago virgaurea* L.; even at close range there is a confusing similarity between the inflorescences of *N. ossifragum* and the diminutive variant of *S. virgaurea* that inhabits the Burren.

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NOTES ON THE ECOLOGY OF *BLYSMUS RUFUS* (HUDS.) LINK IN NORTH-EASTERN FIFE

Blysmus rufus (Huds.) Link is one of the few species considered to be a northern element in the British saltmarsh flora (Ratcliffe 1977; Adam 1978). In Scotland, *B. rufus* is found predominantly on the western coast, having a more fragmented distribution in the east (Perring & Walters 1982). It is therefore of interest that, during a coastal vegetation survey in Fife, v.c. 85 (Leach & Phillipson 1985), *B. rufus* was found to occur on 15 saltmarshes. The following observations were part of an investigation of the factors controlling the distribution of *B. rufus* in Fife (Penford 1982).

In Fife, *B. rufus* occurs on grazed beach-head saltmarshes, usually on raised beaches with a gravelly substrate. Stands are small (less than 10 m^2), and are found along the strand line at the transition zone between base-rich fen communities and *Juncus gerardii*-dominated saltmarsh. *B. rufus* often occurs as mono-dominant stands, although associates may include *Eleocharis quinqueflora* (occasionally co-dominant), *Triglochin maritima*, *T. palustris*, *Agrostis stolonifera*, *Festuca rubra*, *Glaux maritima* and *Plantago maritima*. Its confinement to the top of saltmarshes suggests that *B. rufus* is an obligate halophyte, but is unable to withstand prolonged exposure to strongly saline conditions. Soil analyses of sodium along transects (Table 1) confirmed that salinity increased

TABLE 1. CALCIUM AND SODIUM CONCENTRATIONS IN SOIL SAMPLES FROM THREE POINTS ALONG SALTMARSH TRANSECTS 8 M LONG

Figures are means ± s.e.; n = sample size

	Transect point		
	Fen zone 0 m	*Blysmus* zone 2 m	Saltmarsh zone 8 m
[Na] ppm	1011±284 n=7	1082±213 n=9	4703±1948 n=8
[Ca] $\log_{10}$ppm	4·03±0·14 n=7	4·16±0·15 n=10	3·69±0·21 n=8

sharply immediately to the seaward side of *B. rufus* stands ($t=1{\cdot}85$, $p<0{\cdot}10$) and decreased less sharply from the *B. rufus* zone to the glycophytic fen zone further up the marsh ($t=0{\cdot}20$, n.s.).

The proximity of *B. rufus* stands to fen communities containing predominantly basiphilic species, including *Carex otrubae*, *C. hostiana*, *C. disticha*, *Glyceria maxima*, *Lychnis flos-cuculi*, *Caltha palustris* and *Equisetum arvense*, suggests that *B. rufus* is subject to base-rich flushing. Soil analyses (Table 1) showed that mean levels of calcium increased slightly between the fen zone and the *B. rufus* zone ($t=0{\cdot}61$, n.s.) and decreased sharply ($t=1{\cdot}83$, $p<0{\cdot}05$) where more markedly halophytic vegetation became dominant. Thus the seaward boundary of *B. rufus* stands appeared to be influenced by a pronounced increase in salinity and a decrease in calcium.

The influence of calcium on the distribution of *B. rufus* in Fife may be significant due to the ability of calcium to ameliorate the effects of salinity. This occurs by affecting the selective ion transport mechanism at the root cells (Jennings 1976) and also by reducing the availability of sodium in cation exchange within soils (Waisel 1972). In this way, Ranwell (1972) suggests that high levels of calcium could exert a profound effect on the species composition of saltmarsh vegetation.

The similiarities in species composition between the beach-head saltmarshes of Fife that support *B. rufus* and the marshes of the western Scottish sea lochs, where it is more widespread, has been remarked on by Leach & Phillipson (1985). It is likely that, in Fife, *B. rufus* is confined to sites where a combination of factors produce conditions similar to those where this species commonly occurs. Low salinity is a feature of sea-loch marshes on the western coast and, whilst salinity is likely to be higher on Fife saltmarshes, the influence of base-rich flushing, coupled with a gravelly substrate to reduce the retention of sodium, may enable *B. rufus* to persist in localized habitats within an otherwise unsuitable area.

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TYPIFICATION OF *POTAMOGETON SPARGANIFOLIUS* LAEST. EX FR. AND *P. NATANS* SUBSP. *KIRKII* HOOKER FIL.

The hybrid between *Potamogeton natans* L. and *P. gramineus* L. is relatively frequent in northern Europe and is widespread, but very local, in the British Isles (Dandy 1975; Perring & Sell 1968). It is a variable plant, usually resembling *P. natans* but with laminar rather than phyllodal submersed leaves. The correct name for the hybrid is believed to be *P.* × *sparganifolius* Laest. ex Fr.; a later synonym is *P.* × *kirkii* (Hooker fil.) Syme ex Hooker fil., based on *P. natans* subsp. *kirkii* Hooker fil. The purpose of this note is to typify these names.

Potamogeton sparganifolius Laest. ex Fr., *Novit. fl. suec. mant. prima* 9 (1832). Holotype: Fluv. Torn. Muonionissa, *L. L. Laestadius* (**UPS**).

P. sparganifolius was described by Fries (1832) on the basis of material collected by L. L. Laestadius "in fluviis profundissimis ad Karesuando Lapponiae". The epithet *sparganifolius* had been applied to the plant by Laestadius, but not published by him. There is in Fries' herbarium (**UPS**) a specimen labelled "Potamogeton sparganifolius Laest. Fluv. Torn. Muonionissa L. L. Laestad.", i.e. collected from the R. Torneälven at Muonio, 75 km south-east of Karesuando. There is no material annotated by Fries at **S**, where Laestadius' herbarium is deposited (F. Björkbäck, in litt. 1988). The specimen at **UPS** therefore appears to be the holotype of *P. sparganifolius*, and I have labelled it as such. If further type material is ever located, the specimen at **UPS** would almost certainly be the most appropriate choice of lectotype. It conforms to Fries' description of *P. sparganifolius* and with the current concept of the hybrid *P. natans* × *gramineus*.

Potamogeton natans subsp. **kirkii** Hooker fil., *Student Fl. Brit. Isl.* 371 (1870). Lectotype: Ballinabrack River, Lough Corrib, 7 September 1853, *T. Kirk* (herb. W. Borrer, **K**), designated here.
P. kirkii Syme in Sowerby, *Engl. bot.*, 3rd ed., **9**: 31 (1869), nom. synon.
P. polygonifolius var. *kirkii* (Hooker fil.) H. Watson, *Lond. cat.*, 7th ed., 21 (1874).
P. kirkii (Hooker fil.) Syme ex Hooker fil., *Student Fl. Br. Isl.*, 3rd ed., 535 (1884).
P. × *sparganifolius* forma *kirkii* (Hooker fil.) Hagstr. ex Pearsall in *Rep. botl Soc. Exch. Club Br. Isl.* **11**: 186 (1936).

In September 1853 Thomas Kirk collected an interesting *Potamogeton* from "deep water by the bridge against Maam Hotel, Ballinabrack River, Lough Corrib, Galway". He identified it as *P. longifolius* Gay (a taxon now regarded as synonymous with *P. lucens* L.) and distributed numerous specimens under that name. Amongst those who received these were W. Borrer and C. C. Babington. Borrer (1854) published the record of *P. longifolius* but Babington realized that this was a misidentification. He was able to compare Kirk's plant with authentic material of *P. sparganifolius* which he had been sent by Fries himself. By January 1854 he had concluded that Kirk's collection was referable to *P. sparganifolius*, as the two plants agreed "in every particular that the respective specimens afford the opportunity of contrasting" (Babington to Borrer, letter in herb. Borrer, **K**). He included it under this name in all subsequent editions of his *Manual of British Botany*, tentatively in the 4th edition (Babington 1856) but emphatically from the 5th edition (Babington 1862) onwards. Babington's opinion has been supported by recent students of the genus, including Hagström (1916), Pearsall (1931) and Dandy (1975).

Babington's contemporaries, however, did not accept that Kirk's plant was *P. sparganifolius*. J. T. Syme gave an illustrated account of it in his edition of *English Botany* (Sowerby 1869). In discussing it he specifically mentioned the only flowering specimen he had seen – a specimen in Borrer's herbarium. He was uncertain of the identity of Kirk's plant, concluding "I have seen too little of the Irish plant to venture to affirm it to be specifically distinct from *P. polygonifolius*, so that, though convinced it is not the *P. sparganifolius* of Lästadius, I keep it under this name for the present, though much tempted to designate it *P. Kirkii*, after its discoverer". He also included the name "P. Kirkii, *mihi*, MS" in this synonymy of the species. This name was taken up by J. D. Hooker of Kew, who validly published it as *P. natans* subsp. *kirkii* in his *Student's Flora* (1870). In the third edition of this *Flora*, Hooker (1884) raised it to specific rank. It was described and illustrated as *P. kirkii* in Fryer & Bennett's (1915) monograph *The Potamogetons (Pond Weeds) of the British Isles*.

As far as I am aware there has been no attempt to lectotypify the name *P. natans* subsp. *kirkii* Hooker fil. There is no material in the general herbarium at Kew which could be selected as a lectotype. However, the three sheets in the herbarium of W. Borrer of the plant distributed as *P. longifolius* by Kirk would have been available to Hooker, as Borrer's herbarium was bequeathed to Kew in 1862. Although Hooker did not annotate the sheets, which had been labelled as *P. kirkii* by

Borrer, there can be no doubt that he saw them. In the preface to the *Student's Flora* Hooker (1870) emphasized that his descriptions were derived from specimens rather than copied from books, and we know he used Borrer's herbarium in writing the account of *Potamogeton* as a specimen in it is cited under *P. obtusifolius*. As the flowering plant of *P. sparganifolius* in Borrer's collection was mentioned twice by Syme it is reasonable to conclude that Hooker would have examined it. I have therefore selected this sheet as the lectotype. The flowering plant drawn in *English Botany* (t. 1903) matches the specimen and is clearly based upon it. The detached floating leaves illustrated must, however, have come from another specimen.

P. × *sparganifolius* is a variable hybrid, variation occurring both within and between populations. The extent to which this variation is genetic rather than phenotypic has not been tested by cultivation experiments. I do not see any reason to recognize individual populations, such as that at Maam, as distinct taxa, and therefore support the reduction of *P. kirkii* to a synonym of *P.* × *sparganifolius*.

ACKNOWLEDGMENTS

I am grateful to R. Moberg (**UPS**) and F. Björkbäck (**S**) for searching for type material of *P.* × *sparganifolius*, to Lyn Nichol (**CGE**) for arranging the loan of the holotype, to D. A. Simpson for help during visits to Kew and to P. D. Sell for comments on a draft of the manuscript.

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EARLIEST RECORDS FOR TWO × *FESTULPIA* COMBINATIONS

While checking herbarium specimens in folders labelled *Festuca rubra* we have recently come across two specimens of × *Festulpia* that in each case constitute the first known record anywhere of that particular hybrid combination. Both are also new vice-county records.

1. *Festuca rubra* L. agg. × *Vulpia bromoides* (L.) S. F. Gray. Ashley Hill, W. Gloucs., v.c. 34., May 1928, *C. Alden*, ex herb. Gibbons & Bell (**LTR**). The plant was labelled "*F. rubra* var. *grandiflora* ?viviparous". Several of the spikelets are indeed proliferating, a feature we have often encountered in × *Festulpia* specimens and in other hybrid *Festuca* plants.

The measurements of this plant fall partly outside the ranges given by Ainscough *et al.* (1986), as shown in Table 1; in general the parts are somewhat larger, but the glume ratio is not exceptional.

2. *Festuca rubra* L. agg. × *Vulpia myuros* (L.) C. C. Gmelin. By railway line at Mitchell Troy, 2

TABLE 1. DIAGNOSTIC MEASUREMENTS OF TWO × *FESTULPIA* SPECIMENS

	F. rubra agg. × *V. bromoides*, v.c. 34	*F. rubra* agg. × *V. myuros*, v.c. 35
Lower glume length (mm)	3·0–4·0	1·6–2·1
Upper glume length (mm)	5·5–7·2	3·7–4·7
Glume ratio	0·5–0·58	0·47–0·64
Lemma length (mm)	6·2–7·5	4·2–5·0
Awn length (mm)	1·7–4·0	3·7–5·9
Anther length (mm)	1·1–2·2	1·0–1·4

miles S.W. of Monmouth, Mons., v.c. 35., 16th June 1951, *E. Nelmes 973* (**K**). The plant was determined by C. E. Hubbard (undated) as "*F. rubra* ssp. *commutata*" (= *F. nigrescens*).

In this case the measurements are typical of those given by Ainscough *et al*. (1986) (Table 1).

Neither of the specimens shows any sign of rhizomes; the *Festuca* parent might be *F. rubra* subsp. *rubra* or *F. nigrescens* Lam. in each case. In both cases virtually all the pollen is empty, and the anthers indehiscent.

The earliest record of *F. rubra* × *V. fasciculata* known to us is the specimen collected by J. Gosselin in Guernsey, probably between 1788 and 1791 (**STPCM**). However, there is also an undated specimen in **BM**, collected as *Festuca cambrica* Hudson and cultivated in William Curtis's garden (Curtis died in 1799), that might pre-date it.

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CRATAEGUS × *MEDIA* BECHST. IN MIDDLESEX HEDGEROWS

Studies of hedgerow *Crataegus* in Middlesex, v.c. 21, suggest that *Crataegus* × *media* Bechst. (*C. laevigata* × *monogyna*) may be more common than is suggested in some local Floras. A survey of surviving agricultural hedgerows in the London Borough of Brent (Kingsbury, Wembley and Willesden) and a small adjacent part of the London Borough of Barnet was undertaken from 1983 to 1987, using a method for locating hedgerows discussed by Williams & McLauchlin (in press). The study area was between approximately 7 and 18 km north-west of central London and covered an area of about 46 km^2, 45 of which were accounted for by Brent. Much of Brent was still farmland until the suburban expansion of London in the 1920–30s. Only two enclaves of countryside remain, Fryent Country Park and, to a lesser extent, the area around the Welsh Harp Reservoir. In the south, much of Willesden could be described as inner-city.

For the main part of the study, *Crataegus* specimens were identified in the field, using the main lateral vein curvature and leaf shape as the chief identification criteria (Byatt 1975, 1976; Williams 1986). (Slight differences in stone shape were noted between the species: *C. monogyna* had a stone with a pointed apex and *C. laevigata* had blunter stones, but this may simply be due to species differences in style and stone numbers). The survey found 548 former hedgerows or remnants (520 in Brent) and *Crataegus* was present in 257 (47%) of these. *C. monogyna* occurred in 213 hedges, *C.* × *media* in 134 and *C. laevigata* in 18 hedges. A few *Crataegus* in 13 of the hedges remained unidentified due to access or other survey problems. At Fryent Country Park, a hedgerow planted in recent decades contained *C. monogyna* only, older hedges had both this species and *C.* × *media*, while some hedges planted before c. 1547 and others originating from assarts (woodland clearance) contained all three.

The survey area fell within 21 tetrads, though only four of these were fully within the study area. Comparisons were made with the flora of London (Burton 1983) which included *Crataegus* from all habitats and obviously from other Boroughs in the peripheral Brent tetrads (Table 1). Though the Brent study was only recording *Crataegus* from former agricultural hedges, *C. monogyna* and *C. laevigata* were found in a similar number of tetrads to those in Burton (1983), but for *C. laevigata* the two studies only agreed in five tetrads. *C.* × *media*, however, was found to be much more widespread than Burton (1983) suggested. Forty-three of the 66 monads (1-km squares) partly or wholly within the study area had hedgerow *Crataegus*. Forty-one of these had *C. monogyna*, 14 had *C. laevigata* and 36 had *C.* × *media*. While some of the discrepancies between the two studies may be due to the more comprehensive search of the hedgerow study, it is suspected that *C.* × *media* is under-recorded in the London flora. *C.* × *media* may be unfamiliar to many recorders or easily confused (Jermyn 1974) and is probably commoner than local Floras indicate. As explained by Bradshaw (1975), *C.* × *media* has a range of characteristics intermediate between those of the two parents, and such is the degree of hybridization that Byatt (1975) considered the concept of the two species *C. monogyna* and *C. laevigata* to be largely irrelevant in south-eastern England. Main lateral vein curvature, when used with other characters, does, however, appear to be a useful aid for the identification of *Crataegus* in the field and may show *C.* × *media* to be more widespread in other counties.

TABLE 1. *CRATAEGUS* RECORDS FROM 21 TETRADS IN MIDDLESEX

	Brent hedgerow survey	Burton (1983)
Crataegus monogyna	18	19
Crataegus × *media*	14	3
Crataegus laevigata	9	10

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Book Reviews

Mordecai Cubbitt Cooke. Victorian naturalist, mycologist, teacher and eccentric. M. P. English. Pp. xviii + 357, with numerous illustrations in black & white. Biopress Ltd., The Orchard, Clanage Road, Bristol BS3 2JX. 1987. Price £18.00 (ISBN 0–948–737–02–6).

It is a shame this book touches too marginally on the vascular plants of the British Isles to warrant more than a brief review in these pages, for it must surely be one of the best biographies of a botanist ever written. The product of an immense amount of research, taken to the point of tracing descendants in many parts of the world (and even interviewing one of them in Kenya), it is at the same time highly readable.

Socially unsure, tactlessly over-forthright, a crusty reactionary in a bushy red beard, 'M.C.' – as he liked to be called (he abominated his first name of Mordecai) – was one of those archetypal Victorian figures of almost superhuman energy who hardly seem to have stopped writing for a minute. Author of innumerable popular books and articles, some so ephemeral that even the indefatigable Dr English has been unable to run them to earth, he was driven all his life by a missionary fervour to spread to one and all the gospel of natural history. He was employed initially as an elementary schoolteacher and then, in a succession of humble posts sadly beneath his abilities, in the exhibiting of plant products in museums. He early found that his real love was mycology, a subject on which he also published prolifically, in which he was entirely self-taught and in which he achieved a place second only in Britain to the revered and incomparable Berkeley. In addition, he was the founder, in 1862, of the short-lived Society of Amateur Botanists, which met in Hardwicke's bookshop in Piccadilly and which included Trimen, Dyer, Newbould and Britten among its members, with the trend-setting *Flora of Middlesex* as its indirect product. The still-flourishing Quekett Microscopical Club is the offspring of that body. Hardwicke and Cooke subsequently strengthened their partnership with that fascinating miscellany, *Science Gossip*, of which Cooke acted as editor for its first seven years.

Not content with all that, Cooke also coped in secret with a family life of stunning bizarreness and complexity. With some brilliant detective work Dr English has uncovered the extraordinary fact that his children were not his wife's, as the world was led to suppose – but, most unexpectedly, her grandchildren. Cooke turns out to have had a series of illegitimate children by his stepdaughter and for long stretches of his life dwelt in what seems to have been a perfectly amicable *ménage à trois*. Truly, the more we learn of the Victorians, the more amazing they become.

D. E. ALLEN

Aroids. D. Bown. Pp. 266, with 24 colour plates and 44 line illustrations. Century Hutchinson Ltd., London. 1988. Price £25.00 (ISBN 0–7126–1822–8).

The Araceae are, without doubt, amongst the most commonly cultivated indoor plants, so it is surprising that there has been until recently a lack of books written for the non-specialist. Deni Bown's book more than adequately fills the need for an introduction to the family.

The book is divided into chapters that lead the reader from the elementary aspects of aroid identification through pollination, ecology, morphology, edible aroids and medicinal uses. To cover so many aspects of the family may seem daunting, but the way in which the information is presented is so readable that even most complex aspects are clear.

The Araceae are introduced in 'Variations on a theme'. The distinguishing floral features, vegetative architecture, distribution, position relative to other plant families and evolution are all covered in great detail. Here also habitats are briefly discussed as a precursor to the later chapters devoted to them. With these basics covered the text moves on to look in detail at individual aspects of the family.

A full account of the pollination biology of the Araceae could easily fill several volumes, and so the chapter concerned with reproduction ('Of tails and traps and the underworld') is, of necessity, simplified. However, this in no way implies that it is superficial; in fact, every pollination mechanism employed by the family is covered in detail.

Most of the book is concerned with the varied habitats in which aroids are found. The chapter titles give the setting (e.g. 'Woodlanders', 'Aquatics and amphibians', 'A place in the sun', 'In the shadows' and 'Towards the light'), and the text describes the aroid inhabitants by genus (e.g. *Arisaema*, *Cryptocoryne*, *Biarum*, *Aglaonema* and *Monstera* respectively). Within these chapters almost all the major genera are covered, together with many poorly known taxa.

The giant tuberous aroids are allotted their own chapter, appropriately entitled 'The Titans'. The greater part of the text is devoted to the Sumatran *Amorphophallus titanum*, a plant which has fascinated both the public and the biologist alike since its discovery over a century ago. However, this is by no means the only giant in the Araceae, and I am pleased to see that *Dracontium* and *Anchomanes*, which both contain very substantial species, are not overlooked.

The chapters concerned with the edible aroids ('An acquired taste') and chemistry and medicinal uses ('Acids and crystals') contain a wealth of information, much of it drawn from scattered sources and skillfully synthesized into a more readily accessible form. As much has been gathered from obscure sources, this volume provides information that would otherwise be difficult to find.

Aroids is generously illustrated with superb photographs taken by the author as well as numerous line drawings, although I feel that the latter could have been of higher quality. The book ends with a very useful 'Check list of Aroid genera', selected bibliography, detailed glossary and an exhaustive reference section. This book, with its wealth of information and beautiful illustrations, will be an essential part of a plant-lover's library.

P. Boyce

Wild flowers of Majorca, Minorca and Ibiza – with keys to the flora of the Balearic Islands. Elspeth Becket. Pp. 221 with 8 colour plates. A. A. Balkema, Rotterdam and Brookfield. 1988. Price £28.50 (ISBN 906–191–634–8).

There can be little doubt that there is ample room for a concise guide to the flora of the Balearic Islands that goes beyond basic picture books to provide a satisfying resource for the serious naturalist. When I first visited Majorca some 35 years ago, friends responded with puzzled comments like "Where on earth is that"? However, since then, with the immense development of cheap package holidays, countless botanists must have cut their teeth on the Mediterranean flora through visits to these islands. Does this book then meet the needs of the present-day botanical tourist? It is essentially a compilation of keys based very closely on those in *Flora Europaea*, and, as such, it should provide an effective means for identification, at least for those reasonably experienced in the use of Floras. The keys are clearly set out, but contain redundant abbreviations, e.g. Annl, bnnl and usu, which are irritating and save no space at all. Distributions are indicated by Ma, Mi and I for the three large islands, generally without any further information. Each family has an introductory section describing its features, sometimes accompanied by supplementary matter of general interest. Vernacular names are given in English, German, French, Spanish and Catalan. Eight composite colour plates are provided which may help beginners, who will probably find the keys hard going, but the large number of species depicted (71 on Plate 5) inevitably means that their utility is rather limited. A general introduction explains the use of keys and very properly urges the need for the conservation of this flora, which is under considerable pressure as a result of the tourist trade. The section on classification betrays such a state of mental confusion about the basics of nomenclature that we can only be heartily thankful that the text rests so firmly on the foundation of *Flora Europaea*. What then is lacking? Some introductory information on habitats and biogeography would have been most welcome, especially with regard to the very interesting endemic element. The space devoted to vernacular names would have been better allocated to more detailed distributional data, as there are hardly any indications as to whether species are abundant on every roadside or restricted to a few remote localities. The book is elegantly presented with high quality printing, but a clearer typographical distinction between family and generic names would have been an improvement.

I wish I could feel more enthusiastic about this book, which does seek to meet a real need. At £28.50 it is very expensive for the information it contains, and it would have been much better if its *de luxe* format had been bypassed in favour of a cheap, compact field guide that would have fitted into the pocket and cost half the price or less.

J. F. M. Cannon

Key works to the fauna and flora of the British Isles and north-western Europe. Edited by R. W. Sims, P. Freeman & D. L. Hawksworth. Fifth edition. Pp. xii + 312. The Systematics Association Special Volume No. 33, Oxford. 1988. Price £35.00 (ISBN 0–19–857706–0).

This work provides references to books and papers which are considered key works for identifying living organisms in the British Isles and north-western Europe. Apart from a great deal of updating, it differs conspicuously from the fourth edition (1978) in having a new and admirably clear layout, each entry starting with the title on the left and ending with the author's name in bold on the right. It is arranged taxonomically, with no index, and under, for example, Spermatophyta, the entries are arranged under countries in a Geographic section ('Britain' includes Ireland), under Trees and Shrubs, Water Plants, Sedges and Grasses, and Orchids in a Monographs of Special Groups section, and under Bibliography, History, Glossary, Anatomy and Morphology, and Pollen and Spores Identification. It is this part, and the Pteridophyta, that should be of chief concern to *Watsonia* readers, but it must be said that the flowering plants are poorly served in comparison with most of the other groups for which I am familiar with the literature.

A number of entries are very out-of-date. For example, W. Keble Martin, *The concise British flora in colour* (1969) is given rather than *The new concise British flora* (1982), J. Lid, *Norsk og Svensk flora* ed. 4 (1963) is given rather than *Norsk, Svensk, Finsk flora* ed. 5 (1985), and W. Rothmaler, *Excursionsflora* ed. 3 (1962–63) is given rather than ed. 12 (1984). No Floras of either Spitsbergen or the Faeroes are included. It would have been more helpful to give Á. Löve, *Flora of Iceland* (1983) in English rather than the Icelandic equivalent *Íslenzk – Ferðaflóra* ed. 2 (1977, erroneously given as 1983).

The taxonomic coverage of flowering plants is very uneven and poor in comparison with that for, say, bryophytes or many animal groups. Although P. F. Yeo's 1978 revision of *Euphrasia* and A. J. Richards's *Taraxacum* Flora of 1972 are included, there is nothing at all on *Hieracium*, and C. A. Stace & M. Ingrouille on *Limonium* are omitted. W. C. R. Watson, *Handbook of the Rubi* (1958) is included, but not H. E. Weber's works on the genus which are superior in almost all respects. No choice of Floras and field guides will suit everyone, but it is difficult to see why J. D. Hooker, *The student's flora of the British Isles* ed. 3 (1937) and E. Step, *Wayside and woodland ferns* new ed. (1949) are included; admirable though they once were, they have now been so totally superseded that they are positively misleading. The inclusion of G. C. Druce, *Hayward's botanist's pocket-book* ed. 19 (1948) is slightly more justifiable for its wealth of infraspecific taxa. It is a pity that works on galls seem to have been excluded, except for incidental mentions under some of the causers, and there are no works on seeds or seedlings although pollen and spores are well covered.

There are numerous errors in titles. The B.S.B.I. Handbook *Sedges of the British Isles* ed. 2 (1982) confusingly retains the title of ed. 1. Although in the headings, names such as Orchids are given their Latin equivalents, the *Docks and Knotweeds* Handbook lacks them which is unhelpful, at least to non-English users.

It is much to be hoped that in the next edition the section on flowering plants will be brought up to the standard of the rest of the book. It is unlikely to be of much use to B.S.B.I. members for this section, but (and this is not, I think, just the reviewer's perspective) it can be warmly recommended to members wishing to extend their knowledge to other groups of plants and animals.

A. O. CHATER

Wildlife conservation in churchyards. Pp. 16. Norfolk Naturalists Trust and Diocese of Norwich, Norwich. 1988. Price £3.00 incl. p. & p. Obtainable from Norfolk Naturalists Trust, 72 Cathedral Close, Norwich, NR1 4DF.

The increasing awareness in recent years of the importance of churchyards in conservation, stimulated to a large extent by the B.S.B.I. and R.S.N.C. churchyards survey, has led to the production of a number of booklets on the management of churchyards. Most of these have been done on a county basis, and the one under review, arising out of the Norfolk Naturalists Trust Churchyard Conservation Scheme started in 1981, is one of the most practical, detailed and helpful that I have seen. It explains the ecological and floristic value of churchyards, including the remarkable fact that six species characteristic of old meadows (*Conopodium majus*, *Pimpinella saxifraga*, *Primula veris*, *Saxifraga granulata*, *Leucanthemum vulgare* and *Galium verum*) now have about 50% of their Norfolk populations in churchyards. It gives advice on grass cutting, grazing, hedging, tree planting, clearance of overgrown churchyards, renovating and repointing stonework, management for lichens, birds and bats, the importance of ivy and many other matters. A one-page summary of the recommendations is an especially helpful feature, and it is attractively illustrated.

Although tailored to Norfolk, most of the booklet's advice is of very widespread applicability. It is strongly recommended to everyone interested in churchyards, and could profitably be taken as a model by anyone intending to produce a similar booklet for their own area.

A. O. CHATER

Flowers of Cyprus – Plants of medicine, vols. 1 & 2. C. C. Georgiades. Vol. 1: pp. 103 + 89 colour plates; vol. 2: pp. 103 + 91 colour plates. Cosmos Press Ltd, Nicosia. 1987. Price not stated (ISBN 9963–7540–1–5, vol. 1; 9963–7540–2–3, vol. 2).

Mediterranean people have tended to take a pragmatic approach to plants and animals in the country around them; indeed they can often ill afford the 'luxury' of sentimentality when competing for the land. By concentrating in a wide brief on the medicinal plants of Cyprus, Christos Georgiades has performed a service in showing the large number of species (180 illustrated) which are 'useful' in this context.

The third largest island in the Mediterranean (area – 9144 sq. km), Cyprus can boast some 1500 species of flowering plants, 75 of which are endemics. Its unique position has not only made it of strategic importance throughout its history but a botanical crossroads too. The isolation from neighbouring land masses for a significant time-span has enabled endemics to evolve, and the varied geology and wide range of habitat types has ensured floral diversity. Botanically the island can prove confusing since popular floras on the Mediterranean area are only partially relevant.

Though not claiming to be exhaustive, these two volumes cover a wide range of plants not illustrated elsewhere with a text that is clearly written and highly informative. On the whole, the illustrations are good for a work of this sort; anyone who has selected slides for plates will know that the pressure to publish necessitates one or two compromise shots having to be used. The blockmakers have done a good job in combatting the shrinkage of paper that bedevils the printing of colour in hot climes and only a few of the plates are 'out of register'.

For the serious student of the island's flora there is no recourse but to invest in light-weight clothing and use the baggage allowance for R. D. Meikle's incomparable two-volume *Flora of Cyprus*. However, for an acquaintance with the likes of the endemic *Crocus cyprius* and *C. hartmannianus*, unusual plants in the Troodos massif such as *Smyrnium connatum* (Perfoliate Alexanders) and *Phytolacca pruinosa* (Red Ink plant) or the merits of herbal tea 'Spazia' (pronounced Spacha) made from shade-grown leaves of *Salvia fruticosa* (syn. *S. cypria*) these volumes are certainly a worthwhile holiday purchase.

P. H. & J. A. DAVIES

Supplement to the Wild Flowers of Guernsey. D. McClintock. Pp. 54. La Société Guernésiaise, Candie Museum & Art Gallery, St Peter Port, Guernsey. 1987. Price £4.40 incl. p. & p.

The Flora to which this is a supplement was published by Collins in 1975, and was reviewed in *Watsonia* **11**: 83 (1976). Subsequent field work by members of the Société, together with numerous records submitted by visiting botanists, yielded much of the information in this tersely presented booklet. The five-page introduction updates the preliminary pages of the Flora with additional historical information, but fails to remedy the principal weakness of the earlier work with its scanty treatment of the vegetational history and ecology of the northern Channel Isles.

The information in the Supplement is cross-referenced to the Flora by page numbers in bold type. Taxonomic novelties are highlighted in three footnotes: *Hedera helix* subsp. *hibernica* (based on Kirchner's var. *hibernica*), *Elymus repens* var. *aristatus* (transferred from *Agropyron repens* var. *aristatus*), and × *Agropyron* [sic] *robinsonii*, which should read × *Agropogon robinsonii* as stated in the text. This hybrid between *Agrostis stolonifera* and *Polypogon viridis* has nothing to do with *Agropyron*.

Where taxonomic changes have been published elsewhere, such as Ingrouille's revision of the *Limonium binervosum* group, particulars are included. The author delights in alluding to obscure observations, such as in *Calluna* where he first dismisses a monographer's record of var. *hirsuta* from the Channel Islands and then pops in a reference to an aphid recorded from Guernsey on heather. Some of the information in this booklet verges on the whimsical ("four tons of Primroses were sent to England in connection with the inauguration of the memorial to Lord Beaconsfield on 16 April 1893"), but the underlying intention to stress the economic importance of cultivated plants to the Channel Islands is commendable.

J. R. EDMONDSON

An introduction to the flowering plants and ferns of Lochbroom & Assynt. C. Scouller, Pp. 33 with map. Lochbroom Field Club, 1988. Price £1.50 incl. p. & p. from P. Harrison, Leckmelm, Ullapool, Ross-shire.

This booklet is a botanical guide to two of the largest parishes in the British Isles, covering nearly 1000 sq. km. The introduction deals mainly with the history of botanical exploration in the area and the factors influencing plant distribution. Climate is given little coverage, but the geology is well treated although some of the geological terms may be unfamiliar to botanists.

The largest part of the book is a description of the special plants of the region, divided into ecological groupings of moorland, mountains, woodland, wetland and coastal plants, with a special mention of orchids. Arctic-alpines are identified throughout the text by the letters "AA" after their name.

The guide is intended to be used in conjunction with a field guide or flora with the key features of local subspecies and varieties described. This is a very useful feature, although the description of *Empetrum nigrum* subsp. *hermaphroditum* would lead you to think that it was monoecious.

A weak point of the booklet is the rather curious usage of some English plant names and terms, referring to Cyperaceae such as cotton grasses as "sedges" or calling *Ophioglossum vulgatum* a "fern ally". A more serious reservation is the lack of a contents page or index.

Regional guides may seem to be part of an old-fashioned tradition which has been squeezed out by general field guides on the one hand and local nature trail guides on the other, but as an introduction to the area, or as a useful souvenir of a visit, it can be recommended.

A. S. GUNN

Molecules and morphology in evolution: conflict or compromise? Edited by C. Patterson. Pp. x + 229. Cambridge University Press. 1987. Price £22.50 boards (ISBN 0–521–32271–5), £9.50 paperback (ISBN 0–521–33860–3).

Anyone who attended the systematic sessions at the recent XIV Botanical Congress in Berlin would have been astounded at the phenomenal rise in the number of people now working on the molecular aspects of evolution. A symposium entitled "Molecules versus morphology" was held at the Third International Congress of Systematic Biology, Sussex University, July 1985, to assess this burgeoning mass of molecular data. It produced a wide-ranging debate on a variety of animal groups. There were no plants considered at all, but any reader of *Watsonia* interested in the history of life will find an enormous amount of information about general principles and broad patterns of relationships achieved by modern methods.

This is one of the most interesting and digestible books to have been produced on a very complex subject. Buying it for Patterson's very lucid introduction alone provides an instant *entrée* for those readers who, like me, tend to skip the fine print of molecular evolution.

C. J. HUMPHRIES

The Fauna and Flora of Exmoor National Park. A provisional Check-List. Compiled by members of the Exmoor Natural History Society. Pp. 272, incl. 4 maps. Exmoor Natural History Society, Minehead. 1988. Available from the Exmoor National Park Office, Exmoor House, Dulverton, Somerset. Price £7.00, post free. (ISBN 0–9512893–0–6).

Exmoor National Park, established in 1954, embraces an area of 686 sq. km., comprising moorland, woodland and sea coast, much of which is between 360 and 580 m above sea level. The biological survey made was extensive and detailed, and the resultant check-list covers all branches of the plant and animal kingdoms. The account of the flowering plants, ferns and fern allies, which number over 900 taxa has been compiled by our member Caroline Giddens and occupies pages 60 to 115. These are arranged in the system of Holmes, *Outline of Plant Classification* (1986) and scientific names are based on those given in Clapham, Tutin and Warburg, *Excursion Flora of the British Isles*, ed. 3 (1980). English names follow Dony *et al.*, *English Names of Wild Flowers*, ed. 2 (1986). The list is supplemented by frequency data, habitat preferences and in a few instances locations.

D. H. KENT

The Natural History of the Chew Valley. K. Allen *et al.* Pp. 80. 1987. Available from 143 High Street, Pensford, Avon, BS18 4BH. Price £3.90, post free.

The Chew Valley lies some 11 km S. of Bristol in North Somerset (now Avon), and this account of its natural history by Keith Allen and 24 other contributors, including our members Clive Lovatt and Ron Payne, as well as that great authority on trees, Alan Mitchell, is unlike any local account that I have read before. Aimed not only at naturalists, it features walks and cycle rides in the area, chapters on local characters past and present, and information on orchards, geology and habitats. Several chapters are devoted to vascular cryptogams and a detailed list of species recorded from the valley is given.

This is a delightful and very readable pot-pourri of biological data presented in an unusual manner, and its profits are designated to the Avon Wildlife Trust, Friends of the Earth and the World Wildlife Fund.

D. H. KENT

Natural Science Collections in Scotland (Botany, Geology, Zoology). H. E. Stace, C. W. A. Pettitt, C. D. Waterston. Pp. xxvi–xxvii–xxx + 373 + 8 microfiches. National Museums of Scotland, Edinburgh. 1988. Price £25.00 (ISBN 0–948636–08–4).

Data on the natural science collections held at 286 Scottish institutions are given, as well as information on collections in the hands of 180 private individuals.

The list of institutions surveyed is arranged alphabetically by location, followed by a combined arrangement of institutions and individuals with details of the collections. Some biographical data are provided, but for botanical collectors it is patchy and very inadequate, and many years of birth and death which could have been easily ascertained are omitted.

A short series of microfiches covers subject indices to botany, geology and zoology and literature references. They are excellent for institutions with the necessary reading equipment, but are of little use to private individuals like the reviewer who lack that facility.

The book offers an insight into Scottish natural history collections, but with more skilful editing it could have been greatly improved.

D. H. Kent

The correspondence of Charles Darwin, Vol. 3, 1844–1846. Edited by F. Burkhardt and S. Smith. Pp. xxix + 523. Cambridge University Press, Cambridge. 1987. Price £30.00 (ISBN 0–521–25589–9).

This volume commences with the 35-year-old Darwin married and ensconced at Down House. 381 pages provide us with a clear insight into his preoccupations during the two years the book encompasses. An additional 142 pages include appendices which explain translations (13 pp.), chronology (4 pp.), Darwin's notes arising from conversations with Hooker (4 pp.) and his interest in breeding captive animals (2 pp.), together with comments on the manuscripts (18 pp.), a bibliography (25 pp.), a biographical register (36 pp.) and an index (35 pp.).

During the two years concerned, Darwin was evidently still digesting the results of his voyage aboard *Beagle*. He published his *Volcanic Islands* (1844) and *Geological Observations on South America* (1846), whilst also bringing forth the much-revised second edition of his *Journal of Researches* (1845) and a number of papers relating to the *Beagle* collections.

The impression has not infrequently been given that, once he settled at Down, Darwin became a hypochondriac recluse. The correspondence published here shows such a view to be far from the truth. He was a member and, at times, an officer of the Geological, Royal Geographical and Royal Societies of London, regularly travelling to the capital to attend their meetings. He maintained his lively correspondence with Forbes, Henslow, Lyell, Owen and Waterhouse, seen in the earlier volumes of this series, but the emergence of the young Hooker as confidant and 'sparring partner' begins to become clear here, with an exchange of no less than 107 letters.

In 1843 Joseph Dalton Hooker returned from his four-year voyage with James Clark Ross, who took *Erebus* and *Terror* into and around the southern oceans. Hooker, a botanist, was exercised by the relationship between the plants of the austral continents, and his perceptive Introductory Essay to the *Flora of Tasmania* is still required reading for students of these affinities. Henslow, who was originally charged with identifying Darwin's *Beagle* plants, found that his East Anglian responsibilities made this virtually impossible. Hooker took on this task, and the *Beagle* plants are dealt with in his mammoth *Botany of the Antarctic Voyage*. In the volume under review the exploitation by Darwin of Hooker's botanical knowledge is seen to be gradually transformed into an increasingly close friendship. Darwin was assembling his notes and mulling over his ideas on evolution, and, increasingly, he used Hooker as his 'sounding board'. It is interesting to read that he was also considering his mortality. Should he die, he wrote to his wife, his preliminary essay should be published. Possible editors of his essay were Lyell, Henslow, Forbes, Londsdale, Strickland or, perhaps, Owen; various emendations to this list resulted in his final choice – Hooker. The sum to be devoted to the publication was £400! Think on that!

As I have said before in relation to the previous two volumes of this *Correspondence* (*Watsonia*

16(2), **17**(1)), this is a book to be read and savoured; a review is inadequate. The high scholarship involved is maintained, the presentation is excellent, the price acceptable.

D. M. Moore

The flora and vegetation of County Durham. G. G. Graham. Pp. vi + 526. The Durham Flora Committee and Durham County Conservation Trust. 1988. Price £30.00 (ISBN 0–905362–02–0).

This book is divided broadly into three main parts. Firstly, an introduction (64 pp.) covers such matters as climate, soils, geomorphology and topography, as well as lists of recorders, abbreviations and herbaria consulted. Secondly, there is a list of all plants (263 pp.), from bryophytes and lichens to angiosperms. For each species are given other names by which it has been known in literature dealing with Durham, its status (native, introduced etc.), the phytogeographical element to which it pertains, its frequency and abundance, and up to eight records, including the first; most species are mapped by their occurrence in 2 km × 2 km tetrads. Thirdly, an account of the vegetation (149 pp.) in which, grouped under general structural/habitat headings, are listed the phytosociological associations, together with the relevés on which they are based. The text is adorned by line drawings of the major vegetation-types, prepared at the Sunderland Polytechnic. A bibliography (19 pp.), a gazetteer (7 pp.) and an index to plant names (21 pp.) complete the book.

In the British Isles there is a long and distinguished tradition of producing local Floras; in giving us the volume under review, Gordon Graham and his associates have added a jewel to this record – it must be a model for all future ventures of this sort. The organizational flair required to co-ordinate the activities of the numerous people and groups who contributed to the programme must be remarkable, while acknowledged financial support for the project reflects personal, regional and national commitment to, and affection for, the County Palatine.

Born and brought up in Barnard Castle, I spent the first 18 years of my life exploring the scenic, geological and biological riches of Teesdale, not to mention the search for fat brown trout in the river. During the next six years, as a student at Durham, I was introduced to the 'lowlands' of the eastern part of the County. Whilst I am not exactly languishing in the Thames valley, Graham's Flora has afforded me innumerable opportunities to return to the land of my youth. The vegetation described is recognizable, the plants listed recall memories of many happy days in the field, while the maps and places names bring a lump to the throat. The colour paintings of *Gentiana verna* and *Epipactis atrorubens*, by Derek Hall, are stunning.

As a botanist I like this Flora, and as a Durham patriot I am proud of it. I was intrigued to see that *Phalaris arundinacea*, amongst others, grows on the banks of 'rivulets'; are they only called becks amongst we of the hill-tribes in the west of the County? David Bellamy's Foreword is well worth a read in its own right.

The book's publication was delayed by problems with a vital component of the computer-printing system. The wait was worthwhile; the Flora is well-produced and attractively packaged. The price is very competitive and I commend this volume to anyone with an interest in, or love for, the plants and landscape of part of the land once controlled by the Prince-Bishops of Durham.

D. M. Moore

The genus Cyclamen (A *Kew Magazine* monograph). C. Grey-Wilson. Pp. 147, 12 colour plates. London; Royal Botanic Gardens, Kew, in association with Christopher Helm & Timber Press, Portland, Oregon. 1988. Price £13.95. (ISBN 0–7470–1221–0).

Cyclamen (Primulaceae) is not native in Britain and Ireland but it is a popular garden plant; several species are naturalized in woodland gardens (*C. hederifolium* and *C. coum*, in particular), and *C. persicum* in the guise of its various, over-blown cultivars is ubiquitous as a pot-plant. The natural habitats of the 19 species recognized by Dr Grey-Wilson range from southern France eastwards through southern Europe into Asia Minor and northern Iran, with outlying populations in the Balearic islands, north Africa and, as has recently been discovered, the Horn of Africa.

This *Kew Magazine* monograph, illustrated with full colour portraits of species (and some garden variants) by Mary Grierson and line drawings by Judith Gauden, follows the pattern established in the first one which treated *Paphiopedilum* (Orchidaceae). Species are the primary concern; each is described in detail, its history is discussed, and natural variation patterns are noted. *Cyclamen* is a notoriously difficult genus to understand, and many wild populations do not readily fit into a neat, 'pigeon-hole' taxonomic system. The long horticultural history of *Cyclamen*, the numerous garden hybrids and minor intraspecific variants recognized and named by gardeners, add to the confusion. Chris Grey-Wilson discusses these problems and defines a number of new taxa in his monograph.

As it is the second book in the *Kew Magazine* series, I compared it with the first one (*Paphiopedilum*) and was not favourably impressed. While the text is printed clearly, the colour plates are reproduced on such poor, thin paper that the image of the *Cyclamen* on the reverse of each sheet, as well as the text opposite that, are visible through the page; this is most distracting. The line drawings of *Cyclamen* are not as expertly executed nor as crisply printed as those of *Paphiopedilum*. It is a pity that the quality of the production has deteriorated, and I hope that this trend will be arrested promptly.

The *Cyclamen* volume includes blank pages at the end – instead of wasting paper, could the series editors not have included information on the sources of the plants depicted? In such a taxonomically perplexing genus the provenance of illustrated materials is of considerable significance. Moreover properly documented plates would greatly enhance the scientific and historical content of these otherwise excellent books.

For the numerous gardeners with a passion for *Cyclamen*, this book will be more than welcome as it contains substantial information about the cultivation of species and cultivars. For botanists it is an excellent introduction to the genus.

E. C. NELSON

Plant Crib. Compiled by T. C. G. Rich & M. D. B. Rich with the editorial assistance of F. H. Perring. Pp. (vii +) 141: numerous line drawings. B.S.B.I. Publications, 24 Glapthorn Road, Oundle, Peterborough PE8 4JQ. 1988. Price £8.00, post paid (ISBN 0–901158–17–8).

This latest spin-off from the Monitoring Scheme appeared in time for the second season of field recording. The book is an aid to the identification of some of the more tricky British flowering plants. It is largely based on Wigginton & Graham's *Guide to the identification of some of the more difficult vascular plant species*, published by the Nature Conservancy Council in 1981, which despite its original terms of reference has proved so useful nationally. In addition to making corrections and additions to 'Wigginton & Graham' (which remains indispensible, since the satisfactory accounts are cross-referenced and indexed, but not reprinted), the chief virtue of the *Plant Crib* is in making available in one place a vast range of previously scattered material from published and as yet unpublished sources and from a wealth of anecdotal field-knowledge.

One of the commonest sources used has been the various publications of the B.S.B.I.; reprinting of these has occasionally led to overlooking changes of mind on the part of the author (e.g. in *Gentianella*). Some of the sources, however, are less easily available and the re-publication of relevant details is a useful service (e.g. the interesting account of *Erophila*).

Summaries of much new information are given in Clapham, Tutin & Moore's *Flora of the British Isles* (3rd edition), but the *Plant Crib* makes this information more generally available. Accounts vary in style and content, from the lavish 10 pages allotted to the Water Buttercups to the simple drawings of leaf-shapes of the 'London Pride' Saxifrages. The many excellent thumb-nail sketches of diagnostic characters make the *Plant Crib* especially useful.

The large, traditional 'critical' groups are generally omitted, though there are useful new keys to *Rosa* and to the sections of *Taraxacum*. Four main types of plant group are concentrated on: introduced species (e.g. *Spiraea*, *Doronicum*), hybrids (e.g. *Reynoutria*), infraspecific taxa and what may be termed 'old chestnuts' (e.g. vegetative *Littorella*/*Isoetes*/*Subularia*/*Lobelia*).

My one reservation is the inclusion of so many infraspecific taxa (an extreme example of which may be seen in the key to *Fumaria*, which largely reverts to the excellent, but dated, work of Pugsley of 1912). They are perhaps inappropriate in what is intended primarily as an aid for field recording. Too many of the subspecies and varieties are not clear-cut enough to be recorded without collecting vouchers on which any serious study will always rely.

The usefulness of the Crib will only emerge from extensive testing in the field, and I hope that botanists will exploit it to the full. It is exactly the sort of floristic work that the B.S.B.I. should be publishing – flexible in format, practical and affordable. If your favourite nasty group (*Callitriche* for instance) has not been adequately covered, then I am sure the editors would welcome additions and amendments. Such a work should be frequently updated and reprinted, if it is to remain useful – as implied in the Introduction.

H. J. Noltie

The Flowering Plants and Ferns of the Shetland Islands. W. Scott & R. Palmer. Pp. 468 + ix, with 16 colour plates. The Shetland Times Ltd., Lerwick. Price £20.00 (ISBN 0–900662–56–5).

The authors of this book have been collaborating on its production for over thirty years and the result is a well written, meticulously researched work of fine scholarship. In all aspects it meets the authors' hopes that it represents a considerable advance over previous Shetland Floras. The present Flora begins with a 'General Account of Shetland' which describes the general environment. It is followed by 'An Outline of Shetland Plant Habitats' which introduces the most important ecological and floristic features of the fifteen main types of plant community recognized by the authors. The third chapter is on 'The Changing Vegetation of Shetland' which emphasizes the recent pressures on the flora. These are so severe that the authors sadly conclude "The meagre flora of our islands has been severely depleted, our rarities have now become even rarer; we cannot afford to lose much more". There follows 'A Botanical Itinerary through Shetland' which will be of great use to the visitor and can conveniently be used in conjunction with the 1:100,000 map of the Shetland Islands which is bound in the book's centre. The maps show the boundaries of the thirty-nine 10-km squares which the authors used as the basis for their distribution records.

There follows an 'Analysis of the Flora' which discusses generally the status and geographical affinities of the Shetland plants including some intriguing contrasts and similarities with the Orkney and Faeroe Islands. There is a final introductory Chapter on the 'History of Botanical Exploration in Shetland'.

Most of the book concerns detailed accounts of the Shetland taxa and includes a full treatment of critical general such as *Hieracium* and *Taraxacum*. It is good to read in depth about outstanding Shetland rarities such as *Arenaria norvegica* subsp. *norvegica* and the endemic *Cerastium nigrescens* subsp. *nigrescens*. The authors give excellent taxonomic criticisms on many Shetland taxa. For example they reject Druce's *Plantago edmondstonii* but favour renewed investigations into the taxonomic status of the Shetland sea-cliff *Silene dioica*. Many of the descriptions are entertaining: I would like to know the reasons why (for *Trientalis europaea*) "women seem particularly successful at finding it."!

I have little on the negative side to say about this book. I missed any attempt to deal with the non-vascular cryptogamic flora of Sheltand. More details of the Quaternary history of the Shetland flora would have been welcome along with some speculation on its source. I noticed only one factual error: fertiliser addition and surface seeding began in 1966 on the Keen of Hamar – not 1967 as implied on p. 30.

This book is essential for all naturalists who plan to visit Shetland. Its pleasing production and high quality colour photographs, combined with its clear and informative text will make it a desideratum for most botanical bookshelves. It is a pity that so much of the delight I found in the book was tempered by the sombre messages of the third chapter which reveals the great and continuing threats to the Shetland flora.

J. Proctor

The naturalist's garden. John Feltwell. Pp. 160, with numerous black & white and colour plates. Ebury Press, London. 1987. Price £12.95 (ISBN 0–85223–661–1).

There have been histories of gardening written from various viewpoints, e.g. landscape, cultivation, plant introduction; but I know of no previous works that have considered the gardeners and garden makers as naturalists. This new and revealing point of view has enabled the author to show, for example, not only that the Moorish gardens of southern Spain reflect an interest in the ambient plants and animals by their mediaeval designers, but that famous gardens of our own day, such as Christopher Lloyd's at Great Dixter, East Sussex, often betray an interest in local wild life. His 'wild lawn' in famous, and he favours mixed borders rather than beds of roses, for instance, as having the advantages of natural communities, attracting varied wild life and reducing attacks of diseases and pests.

The book is attractively written and illustrated, giving a good general history of gardens and gardeners as well as the abovementioned emphasis on their natural history interests. The historical sequence is interrupted by chapters on relevant but tangential subjects, such as 'Birds in the garden', 'North American explorers,' 'The parson-naturalists' and 'Encouraging wild flowers', all of which combine to make this book most useful as well as decorative. B.S.B.I. members, in particular those who have hitherto confined their interests to truly wild plants, should read it in order to see how many aspects of natural history (other than distribution, of course) can be studied in a garden.

N. K. B. Robson

The heritage of Clonmacnoise. Edited by M. Tubridy. Pp. 136. Environmental Sciences Unit, Trinity College [Dublin] in association with County Offaly Vocational Educational Committee. 1987. Price not stated (ISBN 0–9512627–0–X, hardback; 0–9512627–1–8, softback).

Clonmacnoise, along the River Shannon, is right in the middle of Ireland in the Central Lowlands. It is the site of a combination of conservation interests – Mongan Bog, one of the few remaining raised bogs left in Western Europe; The Callow, a flat area adjacent to the river which regularly floods in winter and occasionally in summer; eskers, formed in rivers 20,000 years ago, which now commonly support species-rich grasslands and a number of interesting esker woods; a small lake, Fin Lough, which is surrounded by a variety of vegetation types including fen and a distinct community associated with lime-rich spring water; and areas of outcropping limestone. As well as this considerable diversity of vegetation, the bird life is similarly rich and varied.

This book represents an attempt to bring together a number of experts, a team from Trinity College, Dublin, to record their observations on the Clonmacnoise region. This has been combined with fascinating accounts of the early history of the area including the very famous monastery and an insight into farming in the area since the 1830s. The result is a most readable work, full of detail, illustrations, photographs (some in colour) and maps which form an excellent guide to the history and conservation interest of the region and which will become an indispensible guide for any visitor. It should serve as a model for any inter-disciplinary approach to conservation areas and the authors and sponsors are to be congratulated on a fine combined effort.

B. S. Rushton

The difficult and critical plants of the Lizard District of Cornwall. L. J. Margetts, assisted by A. J. Byfield, R. W. David & P. L. Smith. Pp. x + 77, with 16 b/w plates, 88 distribution maps & transparent overlay. Grenfell Publications Ltd., Bristol. 1988. Price £7.95 (ISBN 0–948715–01–4).

Much as the Lizard acts as a magnet, it is usually the rare 'specials' that attract botanists, with most of Britain's clovers present, masses of *Erica vagans* (Cornish Heath) and many other taxa of extreme rarity in the British Isles. Some of the observations in this neatly presented and closely written book are evocative: Polypody "makes a more or less continuous fringe at shoulder height" (for the specialist, both *Polypodium interjectum* and *P. vulgare* are meant); the Prickly Sedge, *Carex* *muricata* subsp. *lamprocarpa*, grows "where the cows are still driven for milking and lightly graze the hedges as they pass", hedges in Cornwall being solid banks.

This approach means that other books will be needed for identification, despite the clear and succinct descriptions. These include *Rubus stanneus*, with "deeply toothed, overlapping leaflets" very characteristic of this bramble, and a one-line description of the leaf, flower and odour of *Mentha* × *piperita*. The 1-km square dot-maps show the amount of work achieved by the University of Bristol's Lizard Project, from which this book stems; they have researched the Lizard vascular flora with great intensity.

The presentation of the book is stylish, the writing is excellent, and it should inspire readers to take (or further) an interest in critical groups. The Lizard itself scarcely needs to be commended to botanists.

K. L. Spurgin

The flora of Lough Neagh. J. Harron and B. Rushton. Pp. iii + 270 with 1 colour plate, 3 figures and 334 plant distribution maps. Irish Naturalists Journal Committee, Belfast and University of Ulster, Coleraine. 1986. Price £5.00 (ISBN 0–901229–82–2).

Tansley in 1939 observed that L. Neagh fenlands were "probably the most extensive in the British Isles still remaining comparatively unspoilt". Unfortunately, even as Tansley was writing, Shephard was 'improving' the discharge of the R. Lower Bann and regulating lough levels; subsequent lowerings of lough levels by 1·5 m markedly reduced the fenlands and, by 30%, the open water area of the small macrophyte-rich L. Beg.

Nearly 50 years after Tansley's 'probably' and 'comparatively' comes this excellent volume actually recording what is there, a modern stock-taking of the wetland flora associated with L. Neagh. Its Introduction concisely reports on the topography and geology of the area, reviews the limited evidence of the pre- and post-glacial history of the vegetation and gives a synopsis of the drainage activities. The characteristics of the present vegetation (comprising some 700 species) are outlined in an Irish context; much of the flora is characteristic of much of lowland Ireland, although several species are of particular local significance, such as *Ranunculus fluitans* which has its only known Irish site in the Six Mile Water and *Spiranthes romanzoffiana* subsp. *stricta* which is also beautifully illustrated in Piper's coloured frontispiece, while for others L. Neagh appears to be the centre of their Irish distribution. The regrettable disappearance of half-a-dozen species including *Carex buxbaumii* and *Thelypteris palustris* is confirmed.

Some 200 pages of the book are devoted to the species records based on but authoritatively updating three previous and separate floras of the North-East of Ireland, Tyrone, and Armagh published in 1888, 1893 and 1942 respectively. There is a most helpful list of field workers, their publications and active periods, a clear map of the basin, and a good index.

The flora is the botanical offspring of a happy marriage of John Harron's amateur (in the loving sense of that oft-misused term) skills and enthusiasm for plants and Brian Rushton's equal but more professional academic talents. Bridesmaids and groomsmen come from a circle of colleagues, principally the Belfast Naturalists' Field Club, the Ulster Museum and the Irish Naturalists Journal.

Merely to say that the Flora is welcome would be a gross understatement. It comes at a time of increasing conservation activity in Ulster's post-Balfour era and must help in that. At £5.00 (machine type-set) it is a bargain even if the contents will last much longer than the soft covers. This – with the soon-to-appear revision of Stewart and Corry – will serve local botanists well.

R. B. Wood

Obituaries

IRENE MANTON
(1904—1988)

Professor Irene Manton, born at the turn of the century and who died on 31 May 1988, was one of the most remarkable botanists of our time. As a girl she was originally destined to be a musician but, by her own account, public appearances as solo violinist at school concerts were traumatic experiences. Although she abandoned the idea of music as a career, she remained an accomplished performer throughout her life and often relaxed by playing in a quartet. In her latter years at school she became a convert to science after reading Newton's Laws of Motion, which struck her forcibly by their elegant simplicity. Her interests were specifically channelled towards cytology by reading E. B. Wilson's book on *The Cell* (1902), but having won a scholarship to Cambridge she was disappointed to find that her undergraduate years there (1923–26) did nothing towards realising her ambition of studying chromosomes. However, the award by her College of a postgraduate studentship of £150 per annum enabled her to travel to Stockholm to work in Prof. Rosenberg's laboratory (and incidentally to become fluent in Swedish in a very short time!). At this period the study of chromosomes involved the lengthy and tedious process of embedding, sectioning and staining root tips. This formed the basis of her doctoral thesis, involving a study of 250 species of Cruciferae. Her external examiner pointed out a discrepancy between the text and drawings which was to have an important effect later on, namely that watercress was described as having $2n = 32$ but figured with $2n = 48$. Fresh material was hastily gathered and processed to determine how the discrepancy arose and this proved to have $2n = 64$! This was her introduction to a wild polyploid series and their sterile hybrid. It was also a portent in that thereby she added a new species to the flora by discovering its chromosomes first – a pattern that was to be repeated many times by herself and her students in various parts of the world.

Irene Manton went to the University of Manchester in 1929 as an assistant lecturer on the staff of Prof. W. H. Lang, co-author with R. Kidston of the famous series of papers on the Rhynie fossils. At this time Lang was interested in the mechanism of aposporously produced plants of the Royal Fern, *Osmunda regalis*, and asked her to look at them cytologically. From this work arose the classic papers on chromosome structure, together with the autoploid series of diploid, triploid and tetraploid plants which provided such excellent teaching material for future generations of cytologists.

During a short visit to Egypt, Dr J. Philp at the Cotton Research Institute showed her some slides of meiotic cells prepared by McClintock's method. This consisted of staining in aceto-carmine and placing a coverslip on top – the weight of the coverslip slightly flattening the soft cells. She took up this new technique with enthusiasm and greatly improved it by applying heavy manual pressure to the coverslip. This produced perfectly flat cells in which all the chromosomes could be seen in one plane and made possible the accurate counting of the high numbers found in the ferns – something that had defeated previous cytologists.

World War II brought restrictions on printing and Irene Manton had accumulated at Manchester such a wealth of material on the entire British fern flora that to publish it piecemeal when restrictions were lifted would have taken an unacceptable length of time and the decision was taken to incorporate it all in book form. In the meantime she had been appointed to the Chair of Botany at Leeds in 1946. Here, her incredible energy not only enabled her to run and re-equip the Department (delegation was not in vogue in those days!), but also rapidly to build up a very flourishing research school, and take on a full teaching load. Nevertheless at the end of each day she would settle down to do up to nine hours research. Weekends were an added bonus only interrupted by the necessity of a few hours sleep and snatched meals. One outcome of all this workload was the streamlining of the mechanics of research by using photographic methods wherever possible in order to eliminate much of the traditional drawing. This was of critical importance and set new standards, since she adopted as her maxim 'what cannot be photographed cannot be used in evidence'.

The book, *Problems of cytology and evolution in the Pteridophyta*, was published in 1950 and proved to be a landmark of much wider importance than its title might suggest. Not only were many problems in the British fern flora resolved, but it effectively disposed of the view held by many European flowering plant cytologists that polyploidy was a direct outcome of the cold experienced during the Ice Age. This was reinforced by the joint publication with W. A. Sledge in 1954 of the cytological survey of the ferns of Ceylon which showed an even higher percentage of polyploidy in this tropical island. The advent of the book stimulated research all over the world with the result that the ferns are now one of the best known groups of plants cytologically, despite the late start.

The frontispiece of the book depicts a fern spermatozoid as seen under the ultra-violet microscope at a magnification of ×3000. In this some of the cilia can be seen to have disintegrated into their fibrillar components and the observation led to the next great phase of her research which was to occupy Irene Manton for the rest of her life, namely the fine structure of cells and their components. Following what was literally a flying visit to the Rockefeller Institute in New York to work with an electron microscope, she soon established at Leeds the first electron microscope laboratory in the world devoted to the fine structure of plants. Initially work was concentrated on the structure of cilia in motile plant cells such as spermatozoids and zoospores. The structure of two central strands surrounded by nine outer ones was demonstrated to be common to all groups of plants with such motile cells. The quality of the photographic proof and the manner of presentation were, as always, of the highest standard and I well remember the whole audience giving her a standing ovation after her lecture at the International Botanical Congress in Paris in 1954. This work continued with investigations into other organelles such as plastids, vacuoles, and Golgi apparatus and much of what is now student textbook knowledge dates from this work.

The algae had always been a great interest of hers and much of the early scanning electron microscopy was based on these plants, some of it done in collaboration with Mary Parkes at the Marine Laboratory, Plymouth. The remarkable scale structures seen in the Chrysophyceae linked up with another of her passions, and the walls of Botany House were covered with SEM micrographs alternating with prints of modern abstract art without one feeling any sense of incongruity. During her time at Leeds, Irene Manton amassed a large and valuable collection of Chinese and modern abstract art – both prints and originals – and she delighted in staging exhibitions of these, the last one being at Lancaster University earlier this year.

Retirement in effect meant the shedding of administrative and teaching duties in order to devote herself fulltime to research and her other interests. Much of this period was taken up with a study of the structure and distribution of nanoplankton, taking her on collecting trips to Greenland, Hudson Bay and Resolute Bay, Alaska, South Africa and the Galapagos Islands. Many papers resulted from this, with one major paper a month being maintained over a number of years. Her style of writing was instantly recognizable and her accounts were often racy, but always models of clarity. The quality of her work was recognized by her election to the Royal Society and to the Presidency of the Linnean Society of London, together with the award of honorary degrees from several countries and other honours in the form of medals and citations.

From all this it will be gathered that Irene Manton was a person of enormous energy, a quality much in demand in Botany House at Leeds, where her office was on the first floor, the SEM and darkrooms in the basement and the optical bench on the first floor – to say nothing of the teaching laboratories being located in a different part of the University and the experimental gardens about a mile away! One of my abiding memories as a student is of trailing panting after her in an effort to keep up.

Her relationship with her research students was warm, and they were collectively always affectionately known to her as "The Young". It was as "The Young" that we remained despite the passage of the years and the acquisition of families of our own who were in their turn included in the fellowship.

T. G. Walker

CHARLES PLOWRIGHT PETCH
(1909—1987)

Charles Petch died suddenly at his home in Wolferton, Norfolk on 8 December 1987. Born and educated in the county, he was recording the local flora whilst still at school at Gresham's.

He was one of a party of six from the Universities of Oxford and Cambridge to visit the deserted island of St Kilda in 1931 (the inhabitants had been evacuated in 1930), and his paper on 'The vegetation of St Kilda' was published in *J. Ecol.* **21**: 92–100 (1933). After obtaining first class Honours in Natural Sciences from St John's College, Cambridge, he taught at Stowe. He then returned to his former college and from there went to St Thomas' Hospital, qualifying as a physician in 1939. During World War II he served as a Medical Officer in the R.A.F. In 1948 he was appointed consultant physician to St Hellier Hospital, Carshalton, a position he held until his retirement in 1975.

Whilst still at St Thomas', Charles married Margaret Stirling. She and their two sons would frequently accompany him in the field. A most hospitable family, they were always ready to entertain a grubby and noisy party of botanists to tea after a field meeting.

Charles joined the B.S.B.I. in 1952 and with the inception of the Mapping Scheme soon had his family out 'square bashing' in Norfolk. He was a meticulous recorder. In 1962, *West Norfolk plants today*, with E. L. Swann, was published as a supplement to *Proc. bot. Soc. Br. Isl.* **4** (1962). After his retirement Charles was appointed recorder for v.c. 28 and served on the Council of the B.S.B.I.

Although he lived and worked in Surrey, and Surrey botanists like to claim him as their own, his heart was in Norfolk, and it was there that he carried outt the major part of his botanical and ecological work, often in collaboration with Eric Swann. Every holiday and on many weekends, Charles, his family and his 'cello could be seen setting off in his old silver-grey Bentley in the direction of Norfolk, where he kept a caravan and a boat. He was a member of the Norfolk and Norwich Naturalists' Society, of which he was elected President for the year 1981–82. He contributed many papers on West Norfolk for the Society's *Transactions*, and to commemorate their centenary they published the *Flora of Norfolk* by C. P. Petch and E. L. Swann in 1968.

More recently he was a major contributor to the *Ecological Flora of Breckland*, edited by P. J. O. Trist, though he was critical of the random sampling method of recording, especially as it always seemed *just* to miss the rarities. He certainly knew the precise location of the interesting species in his neighbourhood. None of this "Well, it's along here somewhere": he knew exactly where to stop his car to point out to me the *Berberis* in the hedgerow or the rosettes of *Verbascum pulverulentum*. This was just as well if the weather was too appalling to open the car doors!

In Surrey Charles was a founder member of the Surrey Flora Committee in 1957, and a contributor to the *Flora of Surrey* (Lousley 1976). Following the sudden death of Ted Lousley in 1976, Charles Petch and Cecil Prime saw the *Flora* through to publication. Charles was elected to the S.F.C. in 1971, serving on it until his death. He was a very active member of the Committee, undertaking site recording and regularly attending field meetings. The area of Surrey that he chose to work in detail was the Lower Greensand around Leith Hill – perhaps because this was reminiscent of his native Norfolk, to which he later retired.

He was also a competent mycologist. This had been his father's profession. He led fungal forays in Surrey and Norfolk, and as his elder son writes, "the quality of our breakfasts was radically improved by his knowledge."

Charles was a reticent man, quick-tempered but with a pleasing sense of humour. "What has it to do with Norfolk County Council?", he inquired, when I referred to the N.C.C. at a Surrey meeting. I now realize that he must have had exceptional organizational ability. How else could he have managed a hospital consultancy, a private practice, beagling, sailing, walking, playing the 'cello, entertaining, and still contribute so much to the botanical and ecological knowledge of the counties of Surrey and Norfolk?

J. E. Smith

Watsonia, **17**, 382–383 (1988)

Report

ANNUAL GENERAL MEETING, 7 May 1988

Following the Presidential Address, the Annual General Meeting of the Society was held at 12.15 hrs in the Jodrell Laboratory Lecture Theatre, Royal Botanic Gardens, Kew, by kind permission of the Director. 120 members were present. Professor C. A. Stace, President, took the Chair, apologies for absence were read, and the Minutes of the 1987 Annual General Meeting, as published in *Watsonia* **17**: 119–120 (1988), were approved and signed by the President.

REPORT OF COUNCIL

The total of 4,760 survey cards sent in by B.S.B.I. members by the end of the first year of the Monitoring Scheme was added to the Report, and it was noted that the records were being entered on to the computer and copies of the cards were being returned to participants for the second year of field work. In the Conservation Committee report a sentence was amended to "letters had been sent supporting the opposition to three major conservation threats . . .". The adoption of the Report was then proposed by Mr E. Milne-Redhead, seconded by Mr R. G. Ellis and passed unanimously.

TREASURER'S REPORT AND ACCOUNTS

The Treasurer, proposing the adoption of his Report and Accounts, offered to clarify any points, but there were no queries. The adoption of the Report was seconded by Mr G. Ll. Lucas and unanimously approved.

RE-ELECTION OF HONORARY GENERAL SECRETARY AND HONORARY TREASURER

The President proposed Mrs M. Briggs and Mr M. Walpole for re-election as Honorary General Secretary and Honorary Treasurer, warmly thanking both for their major roles in the running of the Society. Their re-election was seconded by Dr T. C. G. Rich and carried by the meeting with applause.

ELECTION OF COUNCIL MEMBERS

In accordance with Rule 10, nominations had been received for Dr S. L. Jury, Dr P. S. Wyse Jackson and Mr N. F. Stewart; these were elected unanimously. The President then thanked all the Editors and Secretaries appointed by Council – their considerable work for the Society was very much appreciated; in particular Mr R. Smith, Field Secretary, the Secretaries of all the Committees, and the Editors of all the Society's publications. The achievements of the Society through the year were very largely due to the time and work given voluntarily by them to the Society.

ELECTION OF HONORARY MEMBER

Proposing Dr N. K. B. Robson from the Chair, the President referred to Dr Robson's 21 years of service as an Editor of *Watsonia*. The Society was exceedingly grateful for this very long term of service and Dr Robson would be one of our most deserving Honorary Members. In reply, Dr Robson wished the whole Editorial team to be included in the thanks, saying that his work as Editor had brought him much interest and enjoyment, and many contacts. He added that all aspects of the B.S.B.I. had been a pleasure to him since he first joined the Society.

RE-ELECTION OF HONORARY AUDITORS

The Chairman proposed the re-election of Grant Thornton, West Walk, Leicester, as Honorary Auditors, and the Treasurer, asking for a letter of thanks to be sent, said that the Society was fortunate to have a firm of international standing named below the Annual Accounts.

ANY OTHER BUSINESS

Mr E. Milne-Redhead asked if the Conservation Committee had considered his request for a recommendation to the Ministry of Transport on sowing wild flower seeds on motorway verges. Praising his County Council for their co-operation in sowing local wild flower seeds on minor roads, Mr Milne-Redhead said that in Suffolk they would welcome a similar policy for motorways and trunk roads. A lively discussion followed as Dr J. G. Dony reported a confusion of locally rare plants recorded after wild flower seed sowing. In Bedfordshire and Hampshire there was a strong feeling that no wild flower seeds should be sown, but that new verges should be left to natural colonization. Opinions from the floor were divided and the subject was referred to the Conservation Committee for discussion on the practicability of formulating a B.S.B.I. policy on this matter.

Mr R. M. Bateman asked whether both the date of receipt and of acceptance for publication could be recorded for papers published in *Watsonia*. This point was taken and referred to the Editors. Mr Bateman also asked if the general Editorial policy and aims for the journal could be stated in more detail than in the 'Instructions to Contributors' currently printed in *Watsonia*. The Editors replied that a longer statement on this was planned and will be published in *B.S.B.I. News*.

The meeting closed at 12.58 hrs.

M. BRIGGS

B.S.B.I. Conference Reports

*1. BRITISH FLOWERING PLANTS AND MODERN SYSTEMATIC METHODS
Ed. A. J. Wilmott, 1948, 104 pages, 18 plates. £5.25.
2. THE STUDY OF THE DISTRIBUTION OF BRITISH PLANTS.
Ed. J. E. Lousley, 1951. 128 pages, illustrations and maps.
3. THE CHANGING FLORA OF BRITAIN
Ed. J. E. Lousley, 1953. 203 pages, 9 plates, 25 text figs.
*4. SPECIES STUDIES IN THE BRITISH FLORA
Ed. J. E. Lousley, 1955. 189 pages, 2 plates and 23 text figs. £5.25.
*5. PROGRESS IN THE STUDY OF THE BRITISH FLORA
Ed. J. E. Lousley, 1957. 128 pages, 4 plates and 9 text figs. £5.25.
6. A DARWIN CENTENARY
Ed. P. J. Wanstall, 1961. 140 pages, 7 plates, 12 text figs.
7. LOCAL FLORAS
Ed. P. J. Wanstall, 1963. 118 pages, 1 plate (map), 9 text figs.
8. THE CONSERVATION OF THE BRITISH FLORA
Ed. E. Milne – Redhead, 1963. 90 pages.
9. REPRODUCTIVE BIOLOGY AND TAXONOMY OF VASCULAR PLANTS
Ed. J. G. Hawkes, 1966. 182 pages, 1 plate, 9 text figs.
10. MODERN METHODS IN PLANT TAXONOMY
Ed. V. H. Heywood, 1968. 312 pages, numerous text figs.
Held in association with the Linnean Society of London.
*11. THE FLORA OF A CHANGING BRITAIN
Ed. F. H. Perring, 1970. 158 pages, 21 text figs. £3.50 (1973 reprint).
12. TAXONOMY, PHYTOGEOGRAPHY AND EVOLUTION
Ed. D. H. Valentine, 1972. 431 pages, numerous text figs and tables. Held in association with The Linnean Society of London and the International Organisation of Plant Biosystematists.
*13. PLANTS WILD AND CULTIVATED
Ed. P. S. Green, 1973. 232 pages, 8 plates and 24 text figs. £3.20.
*14. THE OAK: ITS HISTORY AND NATURAL HISTORY
Ed. M. G. Morris & F. H. Perring, 1974. 376 pages, illustrations. £8.25
*15. EUROPEAN FLORISTIC AND TAXONOMIC STUDIES
Ed. S. M. Walters, with the assistance of C. J. King, 1975. 144 pages and 4 plates. Held in association with the Linnean Society of London. £3.80.
*16. THE POLLINATION OF FLOWERS BY INSECTS
Ed. A. J. Richards, 1978. 213 pages and 31 plates. Held in association with the Linnean Society of London. £45.
*17. THE BIOLOGICAL ASPECTS OF RARE PLANT CONSERVATION
Ed. H. Synge, 1981. 586 pages and numerous text figs. Held in association with the Linnean Society of London. £49.95.
*18. PLANT LORE STUDIES
Ed. R. Vickery, 1984. 260 pages. Held in association with the Folklore Society. £7.50.
*19. ARCHAEOLOGY AND THE FLORA OF THE BRITISH ISLES
Ed. M. Jones, 1987. 128 pages and numerous text figs. Held in association with the Association of Environmental Archaeologists. £15.
*20. THE LONG TRADITION
Ed. H. J. Noltie, 1987. 192 pages, 25 black and white illustrations. Held in association with the Botanical Society of Edinburgh and The Society for the History of Natural History. £21.50.

Items marked with an asterisk are in print and available from BSBI Publications, 24 Glapthorn Road, Oundle, Peterborough PE8 4JQ, at the prices stated (postage included).

INSTRUCTIONS TO CONTRIBUTORS

Papers and Short Notes concerning the systematics and distribution of British and European vascular plants as well as topics of a more general character are invited.

Manuscripts must be submitted in duplicate, typewritten on one side of the paper only, with wide margins and double-spaced throughout. They should follow recent issues of *Watsonia* in all matters of format, including abstracts, headings, tables, keys, figures, references and appendices. Note particularly use of capitals and italics. *Only underline where italics are required.*

Tables, appendices and captions to figures should be typed on separate sheets and attached at the end of the manuscript. Names of periodicals in the references should be abbreviated as in the *World list of scientific periodicals*, and herbaria as in Kent & Allen's *British and Irish herbaria*. Line drawings should be in Indian ink on good quality white card, blue-lined graph paper or tracing paper. They should be drawn at least twice the final size and they will normally occupy the full width of the page. Lettering should be done in Letraset or by high-quality stencilling, though graph axes and other more extensive labelling are best done in pencil and left to the printer. Photographs can be accepted only in exceptional cases.

Contributors are strongly advised to consult the editors before submission in any cases of doubt. 25 offprints are given free to authors of papers and Short Notes. Further copies may be purchased in multiples of 25 at the current price. The Society takes no responsibility for the views expressed by authors of articles.

Papers and Short Notes should be sent to Dr R. J. Gornall, Botany Department, The University, Leicester, LE1 7RH. Books for review should be sent to Dr J. R. Edmondson, Liverpool Museum, William Brown Street, Liverpool, L3 8EN. Plant records should be sent to the appropriate vice-county recorders. Reports of field meetings should be sent to Dr B. S. Rushton, Biology Department, The University of Ulster, Coleraine, Co. Londonderry, N. Ireland, BT52 1SA.

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