

Hybrids of *Epilobium brunnescens* (Cockayne) Raven & Engelhorn (Onagraceae) and their occurrence in the British Isles

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ABSTRACT

Data are presented on the occurrence of five new hybrids of *Epilobium brunnescens* (Cockayne) Raven & Engelhorn (Onagraceae) growing wild in the British Isles. Descriptions are given of *E. brunnescens* × *ciliatum*, *E. brunnescens* × *lanceolatum*, *E. brunnescens* × *montanum*, *E. brunnescens* × *obscurum* and *E. brunnescens* × *palustre*. These are named respectively as **Epilobium** × **brunnatum** Kitchener & McKean **hybr. nov.**, **E. × cornubiense** Kitchener & McKean **hybr. nov.**, **E. × confusilobum** Kitchener & McKean **hybr. nov.**, **E. × obscurescens** Kitchener & McKean **hybr. nov.** and **E. × chateri** Kitchener & McKean **hybr. nov.** Records of *E. brunnescens* × *ciliatum* and *E. brunnescens* × *montanum* in the British Isles are re-evaluated.

KEYWORDS: hybridization, willowherbs, New Zealand.

INTRODUCTION

Epilobium brunnescens (Cockayne) Raven & Engelhorn (New Zealand Willowherb) (Onagraceae) has long been naturalized in the British Isles. It was first recorded in 1904 at Craigmillar, Edinburgh, as a garden weed (Fraser 1905). It has been suggested that *E. brunnescens* was probably introduced into Britain for planting in rock gardens where it may have become a rampant weed. It was also brought in with wrappings and soil attached to other New Zealand plants. Its gradual spread accelerated from the 1930s (Davey 1953, 1961) and it now has a substantial presence in those parts of the British Isles whose high rainfall and humidity approximate best to its New Zealand habitats, where it is "especially common on shingly riverbeds in areas of high rainfall" (Webb *et al.* 1988). Its corresponding habitats in the British Isles are in the west and north or in upland areas: moist open areas, on gravel, gritty or stony soils, streamsides, ditches, paths, screes, damp stone walls and banks. Outside Britain, Ireland and its native home, *E. brunnescens* is also reported from Norway as a rarity and mainly as a garden weed. Although originally reported there in 1931 (Davy 1961) it has not become invasive as in Britain and Ireland. Although *Epilobium ciliatum*, *E. montanum*, *E. obscurum* and *E. parviflorum* (but not *E. lanceolatum* or *E. palustre*) have been, or are, found in New Zealand, only *E. ciliatum* has, as yet, been reported as having hybridized in the wild there with *E. brunnescens* (Raven & Raven 1976). The nomenclature used here follows that of Stace (1991) and Kent (1992).

ARTIFICIAL HYBRIDIZATION

Some data are available as to the synthesizing of hybrids between *E. brunnescens* and *Epilobium* species present in Britain. Brockie (1966) succeeded in crossing *E. brunnescens* (sub nomine *E. pedunculare*) with *E. ciliatum* (sub nomine *E. erectum*). From the progeny, an F₂ generation was raised. Brockie (1970) also reports an attempt by V. Thakur in the 1960s to cross *E. brunnescens*

(sub nomine *E. nerterioides*) with *E. montanum* in both directions, but with failure to set seed. It should not be assumed that this is evidence of a significant barrier against cross-fertilization, for it is not clear that enough attempts were made to effect good fertilization. Raven (1972) considered the failure of good seed set reported by Thakur and Brockie (1970) and concluded that there was no evidence for failure of good set as a barrier to hybridization between Australasian species of *Epilobium*. He also considered that there was no definite evidence for the operation of such a barrier between any two species of sect. *Epilobium* from anywhere in the world, with the possible exception of short styled small flowered species being incompatible with long styled large flowered species.

THE IRISH RECORDS

Northern Ireland accounts for the first records of *E. brunnescens* hybrids in the British Isles, but these have been the source of considerable confusion. Scannell & Synnott (1987) mention *E. brunnescens* × *ciliatum* and *E. brunnescens* × *montanum* as being present in v.c. H39. The former record is elaborated by Hackney (1992), who refers to *E. brunnescens* × *ciliatum* as being "abundant with both parents". The latter record relates to the specimen which resulted in "*E. brunnescens* × ?*E. montanum*" (sic) being credited to the flora of the British Isles by Stace (1991).

We have examined the relevant specimens (BEL) and it appears to us that the specimen determined as *E. brunnescens* × *ciliatum* is *E. brunnescens* × *obscurum*, together with a number of other plants (E) from the same location; the specimen determined as *E. brunnescens* × *montanum* is probably *E. brunnescens* × *ciliatum*.

All these records related to finds at the spoil tips of a quarry at Magheramorine, near the shore of Larne Lough in Co. Antrim (v.c. H39). A series of hybrid specimens were collected by D. Ledsham in 1980, and these now form three sheets held at E. Although sent for identification in 1981, they were unfortunately mislaid until 1994, when they were identified by one of us (D.R.M.) as *E. brunnescens* × *obscurum*, this being confirmed by T. D. Pennington.

Two subsequent collections were made from the same locality. The first, in 1981, was made by D. Ledsham and D. Getty, tentatively identified by C. A. Stace as *E. brunnescens* × *montanum* and so confirmed by P. H. Raven in 1982 (specimen held at BEL). An unqualified determination by Raven must carry considerable weight of authority, but this is difficult material. The flowers of such a cross may be expected to bear "confused" stigmas, i.e. almost clavate, but with traces of lobing (resulting from crosses between parents with four-lobed and clavate stigmas). The absence of these is not conclusive, because stigma-shape may vary on the same plant, but examination in 1996 of the most developed flower on this material (H8544) showed a clavate stigma. This suggests either *E. obscurum* or *E. ciliatum* as the other parent; the latter is more likely on the basis of stem and capsule hair characters.

Further evidence lies in the fact that *E. montanum* was altogether absent from the site, whereas *E. ciliatum* was frequent (fide D. Getty; P. Hackney, pers. comm., 1993). On the strength of this, *E. brunnescens* × *ciliatum* is given in the current local Flora (Hackney 1992), instead of *E. brunnescens* × *montanum*. The two different determinations of the same single specimen, however, have resulted in both hybrid taxa being recorded in Scannell & Synnott (1987).

The second collection (BEL) was made in 1983 by R. Piper and was, following the redetermination of the 1981 collection, tentatively determined by Getty and Hackney as *E. brunnescens* × *ciliatum*. The very limited presence of glandular hairs in the upper parts, however, points to this material being *E. brunnescens* × *obscurum*, as with the bulk of the specimens from this site.

A further Irish discovery of *E. brunnescens* × *obscurum* was made by J. McNeill (det. D.R.M.) in 1992. This is represented by a fragmentary specimen at E, part of a stem curving from a prostrate to semi-erect position. It was found in the Glenelly valley in the Sperrin mountains in Co. Tyrone (v.c. H36) in the company of *E. brunnescens*, *E. obscurum*, *E. montanum* and *E. palustre*.

THE BRITISH RECORDS

E. brunnescens × *ciliatum* was first recorded in Britain during 1995, in v.cc. 1, 2 and 44. In June 1995, A. O. Chater (pers. comm., 1995) noted about 100 plants on a gravelly and stony quarry slope

near Llansawel, Carms. (v.c. 44), three specimens from this population being confirmed as such by T. D. Pennington.

In July 1995, about 20 plants were located by D. T. Holyoak (pers. comm., 1995) on mine waste at Wheal Maid, near United Downs, West Cornwall (v.c. 1). A further plant was found by R. J. Murphy (pers. comm., 1995) and H. Meredith at the end of that month on china clay gravels at a disused tip at Goonamarris near Nanpean, East Cornwall (v.c. 2).

The United Downs locality was re-investigated by D. T. Holyoak (pers. comm., 1996) in July 1996, and while *E. brunnesens* × *ciliatum* was present in its usual small, red, semi-prostrate form, there were two near-erect plants, much larger and well branched. These are discussed in the comparison below. In the same month, he discovered six more specimens of this hybrid on mine spoil at Wheal Busy, West Cornwall (v.c. 1) – these have not been examined by us. Also in July 1996 one of us (G.D.K.) found six further plants, again on china clay gravels: three south of Burngullov Common, and the other three at Carclaze Downs pit, both locations being near St Austell, East Cornwall (v.c. 2).

E. brunnesens × *lanceolatum* was first discovered by D. T. Holyoak in July 1995 as a single small plant in the same United Downs location, being also in the company of *E. brunnesens*, *E. ciliatum*, *E. hirsutum*, *E. lanceolatum*, *E. montanum*, *E. obscurum*, *E. parviflorum*, *E. ciliatum* × *montanum* and *E. ciliatum* × *parviflorum*. The presence of *E. lanceolatum*, and hence its potential as a parent, was not recognised until the next year and so, unfortunately, this record was mistakenly published by one of us (Kitchener 1996) as *E. brunnesens* × *montanum*. The southern distribution of *E. lanceolatum* in Britain renders it unlikely that *E. brunnesens* × *lanceolatum* would be found other than in Cornwall, Devon or South Wales. A further specimen was located by D. T. Holyoak in July 1996, again at United Downs, West Cornwall (v.c. 1).

E. brunnesens × *montanum*, discounting the supposed Irish records mentioned above, was first found in the British Isles in July 1996 by one of us (G.D.K.) with R. J. Murphy and M. & A. Atkinson, growing on imported granite aggregate and rubble at Clicker quarry near Liskeard, East Cornwall (v.c. 2).

E. brunnesens × *obscurum* was first recorded in Britain in East Cornwall (v.c. 2), again from Clicker quarry, where R. J. Murphy discovered it on the occasion, and with the people, mentioned above (M. Atkinson having observed potential *E. brunnesens* hybrids there in the previous year). Also in July 1996 in v.c. 2, one of us (G.D.K.) found three plants on china clay gravels: two at Carclaze Downs pit, and a further one in a china clay pit north east of Stenalees.

E. brunnesens × *palustre* was first recorded in the British Isles by A. O. Chater in August 1995, growing on damp acidic shaley soil by a forestry road in a conifer forest near Hardro, Llyn Brianne, Cards. (v.c. 46). *E. palustre* was growing nearby, and the specimen has been confirmed by T. D. Pennington.

DESCRIPTIONS OF TAXA

Material from all the collections listed above has been examined by us in the compilation of the following descriptions unless otherwise stated.

Epilobium × *brunnatum* Kitchener & McKean, **hybr. nov.**

(*Epilobium brunnesens* (Cockayne) Raven & Engelhorn × *E. ciliatum* Raf.) (Fig. 1)

Hybrida inter *Epilobium brunnesens* (Cockayne) Raven & Engelhorn et *E. ciliatum* Raf., characteribus inter parentes variantibus; planta semi-prostrata, stigmatibus clavatis, seminibus praecipue sterilibus, eorum pagina plerumque tuberculato-costata, et in ovario pilis numerosis glandulis praeditis, aliquot pilorum ad pedicellum subtentum extensorum.

Herb with prostrate leafy runners, with stems much branched, curving up to an erect position, 8–20(–30) cm high and little branched above, except in cultivation, when growth habit is more erect and branched. Stems with two lines of short crisped hairs, descending from the nodes, and beginning between a pair of petioles and descending to the next node; the hairs become generally scattered on the stem upper parts and may be absent near the base. Leaves mainly opposite but largely alternate in the upper parts, green on younger growth, especially the upper surface; sessile or with petioles not exceeding 1.5 mm; cauline leaves (0.5–)0.8–1.2(–2.3) × (0.3–)0.4–0.6(–1.1) cm, average ratio of

length to breadth 1:0.4–0.5; ovate-lanceolate to elliptic with a few obscure teeth, glabrous except for marginal pubescence; leaves on runners similar, but tending to more elliptic shape. Sepals lanceolate, 2.5–3.0 × 0.7–1.2 mm, bearing crisped and glandular hairs. Flowers very pale pink, rarely darker c. 9 mm diameter, with petals 5–6 mm long. Four long stamens projecting to or just below top of stigma, their anthers being 0.55–0.85 mm long; four short stamens extending as far as stigma base. Ovary 0.7–1.8 cm, covered with dense patent glandular and crisped eglandular hairs, the glandular hairs extending to, but comparatively infrequent on, the pedicels. Stigma entire, clavate, 1.2–1.9 mm; style longer than stigma, erect, white, 1.3–2.8 mm. Capsules 1.2–3.0 cm long, with hairs as for ovary, sometimes twisted and shrivelled, mostly sterile, containing shrunken abortive seeds 0.34–0.47 mm long; also contained are a few larger seeds, either malformed (0.6–0.7 mm) or fully formed and fertile (0.8–0.9 mm) with rows of tubercles, often with the surface texture tending towards the ridged rows of *E. ciliatum*. The larger seeds may bear a short neck or appendage at the point of attachment of the coma.

HOLOTYPE: West Cornwall, v.c. 1, Wheal Maid, near United Downs, grid reference SW/745.420, on mine waste, alt. 100 m, 5 July 1995, *D. T. Holyoak* (E).

A wild population of this hybrid was seen by P. H. and T. E. Raven in 1969 or 1970 in New Zealand at the Whangaehu River, and they also note a collection from Canterbury, New Zealand in 1919 which is probably the same hybrid (Raven & Raven 1976).

Epilobium* × *cornubiense* Kitchener & McKean, *hybr. nov.

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. lanceolatum* Sebast. & Mauri)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. lanceolatum* Sebast. & Mauri, characteribus inter parentes variantibus; planta semi-prostrata stigmata lobis confusis ferens, caulibus pilis crispatis brevibus uniformiter obtectis, et floribus in colore ut minimum aliquot spectri colorum *E. lanceolati* exhibentibus.

Herb with stems curving up to erect position, 6.5–25 cm high, little branched above except for larger stems, and with a fairly uniform covering of short crisped hairs. Leaves opposite, largely alternate on inflorescence, reddish, sessile or with petioles not exceeding 1 mm; cauline leaves 0.5–1.1(–1.5) × 0.7(–0.9) cm, average ratio of length to breadth 1:0.57–0.63; basal leaves crowded; leaves ovate to broadly elliptic with a few obscure teeth, glabrous except for marginal pubescence and a few hairs on the underside midrib. Sepals lanceolate, 2.8–3.5 × 1.9–1.4 mm, bearing short crisped and patent glandular hairs. Flowers white, pale pink or very pale pink, and the colour may vary on the same plant, but not on the same flower; with petals c. 5 mm. Four long stamens extending to, or just below stigma, their anthers being c. 0.6 × 0.35 mm; four short stamens well below stigma. Ovary 1.2–1.9 cm, covered with many short crisped hairs and some patent glandular ones, a few of the latter descending to the pedicels; hair coverage of pedicels less dense than that of upper stem (in contrast to *E. × brunnatum*). Stigmas variable, with confused partial lobing 0.8–1.0 mm; style 3.5–4 mm. Capsule 2.2–3.1 cm, mostly sterile, containing shrunken abortive seeds 0.35–0.5 mm long, their surface with rows of platelets, sometimes reticulate; seeds occasionally fully formed, cylindrical, 0.65–0.95 mm with rows of tubercles.

HOLOTYPE: West Cornwall, v.c. 1, Wheal Maid, near United Downs, grid reference SW/745.420, on mine waste, alt. 100 m, 12 July 1995, *D. T. Holyoak* (E).

Epilobium* × *confusilobum* Kitchener & McKean, *hybr. nov.

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. montanum* L.)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. montanum* L., characteribus inter parentes variantibus; planta semi-prostrata, stigmata lobis confusis ferens, caulibus pilis crispatis brevibus uniformiter obtectis, et floribus coloris pallide purpureorosei.

Herb with stems branched at ground level, creeping at first, and then curving up to erect position, 5–10 cm high, scarcely branched above, and with a fairly uniform covering of short crisped hairs, diminishing in upper parts, and with occasional glandular hairs. Leaves opposite, largely alternate on inflorescence, pubescent petioles not exceeding 1(–1.5) mm; cauline leaves 0.5–1.0 × 0.25–0.5 cm, average ratio of length to breadth 1:0.45; basal leaves crowded; leaves ovate to broadly elliptic with a few obscure teeth; short crisped hairs on underside midrib and veins, with a light scattering elsewhere beneath, pubescent on margins; upper leaf surface varying from pubescent (especially on young growth) to glabrescent. Sepals lanceolate, 1.45–2.90 × 0.73–1.02 mm, with a scattering of

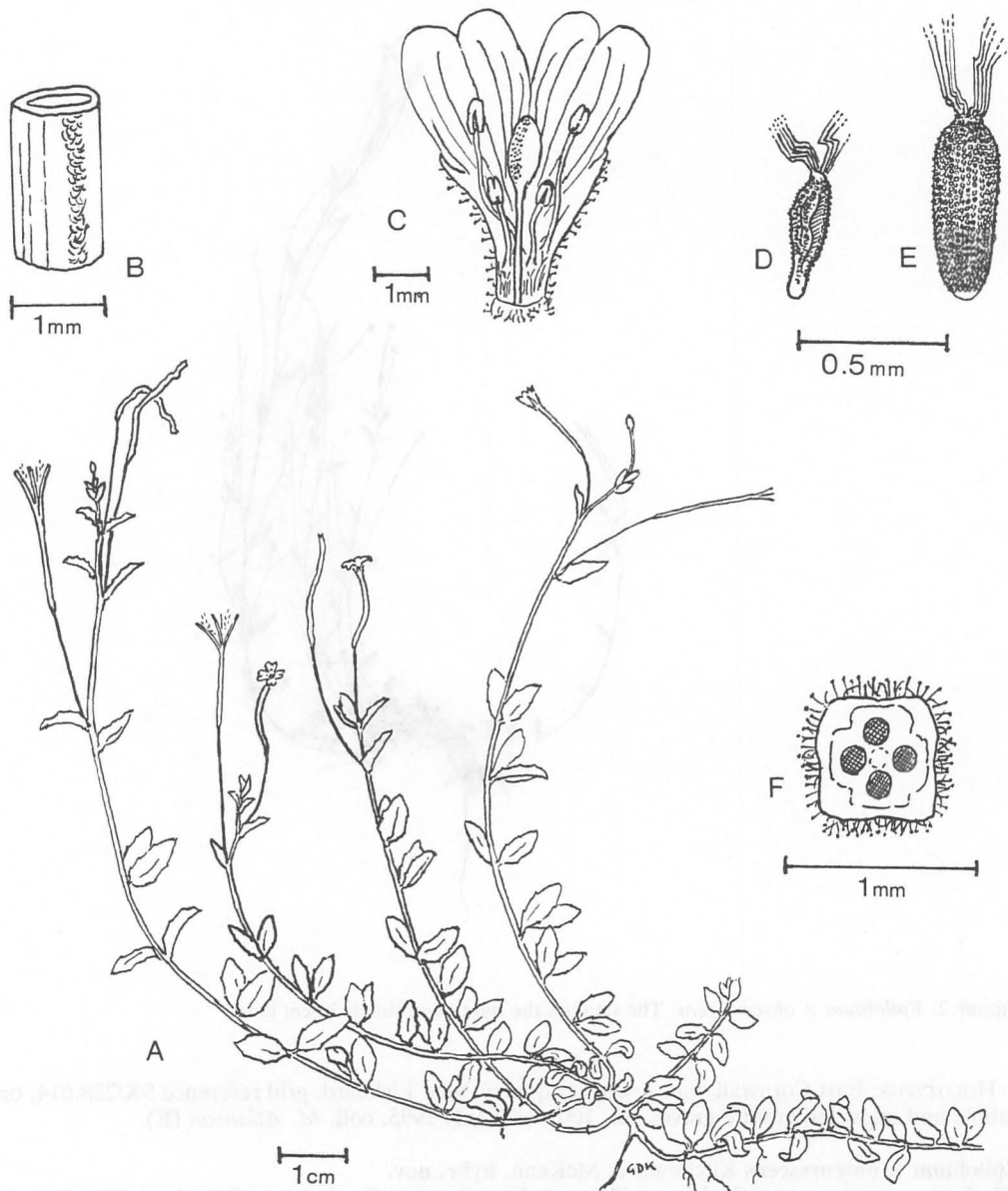


FIGURE 1. *Epilobium* × *brunnatum*. A. plant; B. mid-stem; C. flower (half cut away); D. sterile seed; E. fertile seed; F. transverse section of ovary.

glandular hairs. Flowers pale purplish pink, with petals c. 3.5 mm. Four long stamens projecting to top of stigma, their anthers being 0.4–0.5 × 0.3–0.35 mm; four short stamens extending to the mid-level or base of stigma. Ovary 0.7–1.25 cm, with lines of dense short glandular hairs, these hairs being scattered down the pedicel also. Stigma with confused partial lobing; style longer than the stigma. Capsule 1.6–2.6 cm, containing shrunken abortive seeds 0.35–0.45 mm long, surface flattish, marked in rows and sometimes bearing low tubercles; occasional larger seeds more fully formed, 0.65–0.95 mm, cylindrical with tubercular surface.

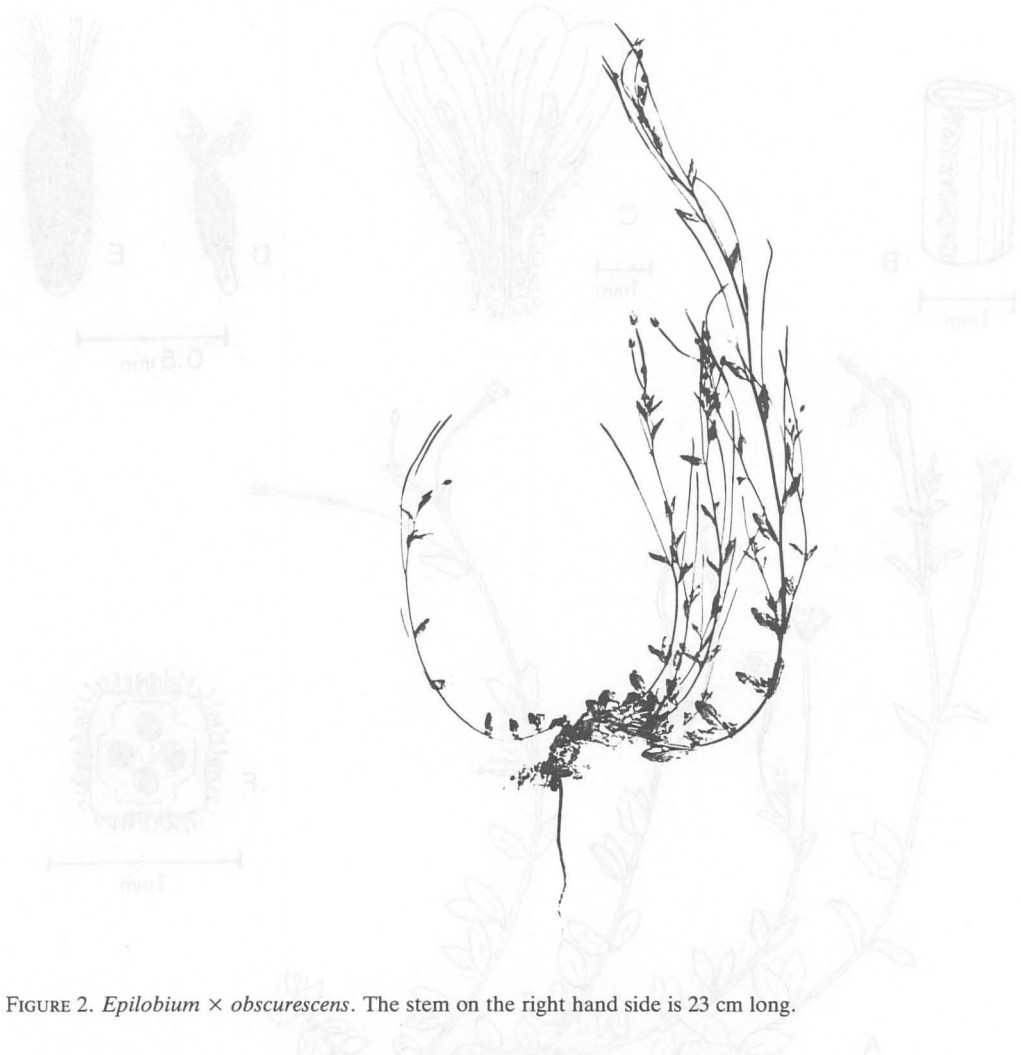


FIGURE 2. *Epilobium* × *obscurescens*. The stem on the right hand side is 23 cm long.

HOLOTYPUS: East Cornwall, v.c. 2, Clicker quarry, near Liskeard, grid reference SX/288.614, on rubble and imported granite gravel, alt. 100 m, 27 July 1995, coll. *M. Atkinson* (E).

Epilobium* × *obscurescens* Kitchener & McKean, *hybr. nov.

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. obscurum* Schreber) (Fig. 2)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. obscurum* Schreber, characteribus inter parentes variantibus; planta semi-prostrata, stigmatibus clavatis, et seminibus praecipue sterilibus, eorum pagina laevi et reticulatovenosa, et in ovario pilis nonnullis glandulosis praedito, eis ad pedicellos haud extensis.

Herb, conspicuously reddish, with stems well branched mainly at ground level, creeping at first and then curving up to erect position, 8–23 cm high, sharply quadrangular and with raised lines running from one node to the next, with fairly sparse short crisped hairs, more numerous in upper parts. Leaves mainly opposite, but largely alternate on upper part of stems, ovate-lanceolate to elliptic with a few, 2–3(–5) obscure teeth, glabrous except for short marginal pubescence, sessile or with petioles not exceeding 1(–2) mm; cauline leaves 0.6–1.5 × 0.3–0.65 cm, average ratio of length to width 1.042–0.44. Sepals 3–3.5 × 1 mm, bearing crisped hairs. Flowers very pale pink, petals 5–6

mm. Ovary 1.3–2.2 cm, with frequent crisped hairs and occasional patent glandular hairs, the latter not extending down to pedicel. Stigma entire, clavate. Capsules 1.5–3.1 cm, densely curly hairy; seeds mostly sterile, 0.6–0.8 mm long when fully formed but the sterile ones only averaging 0.32 mm, surface smooth but with reticulate veining.

HOLOTYPUS: Co. Antrim, v.c. H39, Magheramore, grid reference J/43.98–44.98, on spoil tips of quarry, 1 July 1980, *D. Ledsham*, s.n., bar-code no. 33089 (E); isotypus (BEL).

The specific name is spelt *obscurescens* rather than *obscurascens* because it is an epithet derived from part of each of the parental epithets.

Epilobium* × *chateri* Kitchener & McKean, *hybr. nov.

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. palustre* L.) (Fig. 3)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. palustre* L., characteribus inter parentes variantibus; planta semi-prostrata stigmatibus clavatis, et seminibus praecipue sterilibus sed interdum fertilibus tum plus quam 1 mm longis.

Herb with prostrate leafy runners, from which arise erect stems, 20–25 cm high and scarcely branched above, with 2 broad lines of short crisped hairs, descending from each node; the density of the hairs increasing in the upper parts of the stem. Leaves opposite, largely alternate on the flowering part of the stem, reddish, sessile or with petioles to 1 mm; cauline leaves 0.6–1.2 × 0.2–0.4 cm, average ratio of length to breadth 1.0:29; narrow, lanceolate with a few obscure teeth, glabrous except sometimes pubescent on margins or upper midrib. Leaves on runners similar, but smaller, up to 0.6 cm long, 0.2 cm wide and with more distinct petioles. Sepals c. 2.2 mm long, lanceolate and strigillose. Flowers very pale pink. Four long stamens projecting to lower part of stigma, their anthers being 0.43–0.50 mm long; four short stamens extending to style below. Ovary c. 1.3 cm, covered with short crisped and patent hairs, some glandular. Stigma entire, clavate, 0.95–1.76 mm long; style longer, erect, 1.42–2.37 mm. Capsules 1.5–3.3 cm long, with numerous crisped hairs and some patent glandular hairs; mostly sterile, containing shrivelled, abortive seeds 0.4 mm long; also contained are a few larger seeds 1.0–1.3 mm long with tubercled surface, generally part collapsed longitudinally, but occasionally fully formed and fertile. The larger seeds bear a neck or appendage at the point of attachment of the coma.

HOLOTYPUS: Cardiganshire, v.c. 46, south of Hadre, Llyn Brianne, grid reference SN/804.512, on damp, acidic shaley soil by Forestry Commission road, alt. 370 m, 7 August 1995, *A. O. Chater*, s.n. (E); isotypus (NMW).

COMPARISON OF TAXA

Virtually all wild specimens were noticeable in the field as having red stems and leaves. Growth began as prostrate, often spreading radially, with flowering stems curving up to an erect or semi-erect position. That growth habit is less conspicuous in cultivation. A specimen of *E. × brunnatum* was grown on by A. O. Chater and assumed a sprawling, multi-branched erect habit. This was replicated by one of us (G.D.K.) in growing on both *E. × brunnatum* and *E. × obscurescens*. A similar result arose from cultivation of experimental hybrids made by Brockie between *E. brunnescens* and *E. ciliatum*, it being reported by Raven & Raven (1976) that plants grew into large mounds about 1 m across, with very little about them to remind one of *E. brunnescens*. The cultivation by one of us (G.D.K.) of F₂ specimens of *E. × brunnatum* and *E. × chateri* also gave analogous results, with plants demonstrating extensive scrambling growth. Reddening generally only occurred at a late stage, when plants were transferred outdoors: it may derive from stress or exposure.

There have been a few instances where plants have been found in the wild with a more vigorous and nearly erect growth habit. One such was the 1981 Irish specimen mentioned above, to which the name of *E. brunnescens* × *montanum* was initially applied, but which appears to be *E. × brunnatum*. This is a well-branched green specimen rising to 20 cm. Others are the two 1996 West Cornish *E. × brunnatum* plants discovered by D. T. Holyoak. These rise to 24 and 28 cm, bear leaves over twice as large as are normally seen in such hybrids, and in general seem much closer to the erect parent. More favourable growth conditions may be suspected, although these latter plants were apparently growing in stony mine waste.

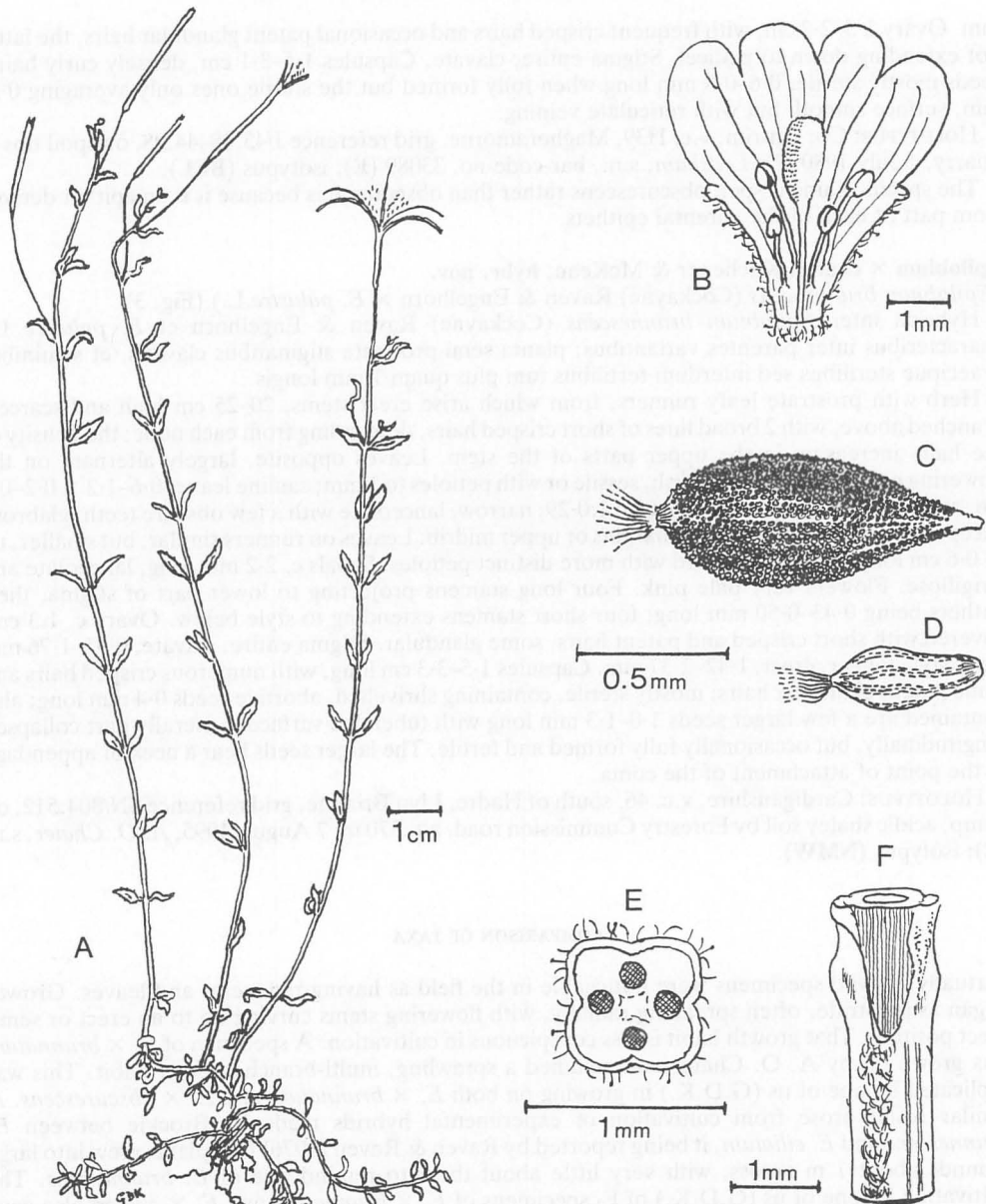


FIGURE 3. *Epilobium* × *chateri*. A. plant; B. flower; C. fertile seed; D. sterile seed; E. transverse section of ovary; F. mid-stem just below node.

The hybrids follow the erect species in bearing alternate leaves in the upper parts, instead of continuously opposite leaves with flowers borne individually in their axils, which is a characteristic peculiar to certain Australasian species of *Epilobium*, including *E. brunnescens* (Raven 1972). The wild specimens also show variable capsule length with very limited seed set, as is consistent with hybrid status. Their red colouring generally extends also to the sepals, which often bear an apical purple knob, as with *E. brunnescens*. The red sepals contrast with the greenish collar below. These sepal characteristics have not been repeated in each of the descriptions given above.

The morphological distinctness of prostrate *E. brunnescens* is so much greater than the differences between the various erect British species, however, that *E. brunnescens* is more readily identified as a parent than the other contributing species. In identifying the other parent, an analysis based on the species groupings put forward by Stace (1975) is of assistance. The initial grouping separates species with clavate stigmas and those with the stigmas four-lobed. As *E. brunnescens* has clavate stigmas, its hybrids with the former will carry similar stigmas, and its hybrids with the latter may be expected to bear variously intermediate stigmas (whose shapes are sometimes called "melted lobes" or "clenched fist").

The holotype specimens of *E. × cornubiense* and *E. × confusilobum* mentioned above indeed bear such intermediate stigmas. They are also distinct in carrying a fairly even spread of stem hairs which are short and crisped, representing the contribution of *E. montanum* or *E. lanceolatum*, as the case may be, and which are not conspicuously restricted to stem lines or bands. Some comment is perhaps due as regards the presence of glandular hairs on the upper parts of the specimens. Stace (1975) identifies *E. montanum* and *E. lanceolatum* as species which are not expected to contribute glandular hairs to a hybrid, and clearly they cannot be expected to do so to the same degree as, say, *E. ciliatum*. Many published descriptions do not mention glandular hairs in relation to these former species, although they do, nevertheless, occur. Exceptions are Stace (1991) and Haussknecht (1884): "Capsulis . . . junioribus tenuiter patentim glanduloso-pilosis" (*E. montanum*); and "Capsulis . . . pilis glandulosis brevissimis intermixtis obsitis; pedicellis glanduloso-puberulis" (*E. lanceolatum*).

The most apparent distinction between *E. × cornubiense* and *E. × confusilobum*, where (as with the Cornish mining or quarry sites) one hybrid combination cannot be ruled out by the absence of one of the potential parents, lies in the flower colour. The corollas of *E. lanceolatum* vary in the course of growth from white through to light and deep shell pink, each flower on a particular plant being a uniform colour, but perhaps differing from others on the same plant at that time. It appears that these colour characteristics can be inherited by *E. × cornubiense*. The 1995 specimen carries two flowers which were noted in the field as being white, as distinct from the very pale pink that characterizes most *E. brunnescens* hybrids so far found; and also as distinct from *E. × confusilobum*, whose corollas, on the material so far seen, are purplish pink. The 1996 specimens of *E. × cornubiense* carried several flowers which were noted in the field as ranging from pale pink to very pale pink, and that record of variability on one plant (while each flower was of uniform colour) is a valuable observation.

Hybrids with *E. palustre*, *E. ciliatum* and *E. obscurum* all involve parents with clavate stigmas. Distinguishing features are as follows:

E. × chateri is best recognised from leaf shape and (fertile) seed characteristics. *E. palustre* leaves are the narrowest of those of British species of *Epilobium*, and this character is not completely obscured by the broadly ovate to sub-orbicular leaf shape of *E. brunnescens*. The holotype hybrid specimen had a leaf length/breadth ratio of 1:0.29, significantly narrower than average measurements for material of *E. × brunnatum* (1:0.4–0.5), *E. × cornubiense* (1:0.57), *E. × confusilobum* (1:0.45) or *E. × obscurescens* (1:0.42–0.44). At the other end of the spectrum, the ratio for *E. brunnescens* is 1:0.7–0.85. *E. palustre* also has the largest seeds of British *Epilobium* species (1.6–1.8 mm), while *E. brunnescens* seeds, at 0.7 mm, are smaller than those of any of the native British species. The size of *E. palustre* seeds is reflected in the hybrid, whose fertile seeds (at 1.0–1.3 mm long) are longer than the fertile seeds of the other *E. brunnescens* crosses: *E. × brunnatum* (0.8–0.9 mm), *E. × cornubiense* (0.7–0.8 mm), *E. × confusilobum* (0.65–0.8 mm) and *E. × obscurescens* (0.6–0.8 mm). The fertile *E. × chateri* seeds also inherit beak characteristics from *E. palustre*, and bear a neck or appendage at the comal end.

E. × brunnatum and *E. × obscurescens* are very similar, but the former may be distinguished by the abundance of glandular hairs on the ovary deriving from *E. ciliatum* and descending at least down to the pedicels, such hairs being quite infrequent in the case of *E. × obscurescens*, and not present on the pedicels. The surface texture of the seeds also differs, with the sterile seeds of *E. × obscurescens* showing a pattern more reticulate than tuberculate (Fig. 4). It should be noted that the surface texture of fertile seeds is not necessarily the same as that of the sterile ones. That difference may perhaps be interpreted as a failure of the sterile seeds to develop fully their surface features, so presenting a somewhat desiccated effect. So the low ridging of sterile *E. × brunnatum* seeds (reflecting the ridged patterning of *E. ciliatum*) may become more prominent and tubercled in the fertile seeds. The reticulation of sterile *E. × obscurescens* seeds does not represent a reticulate

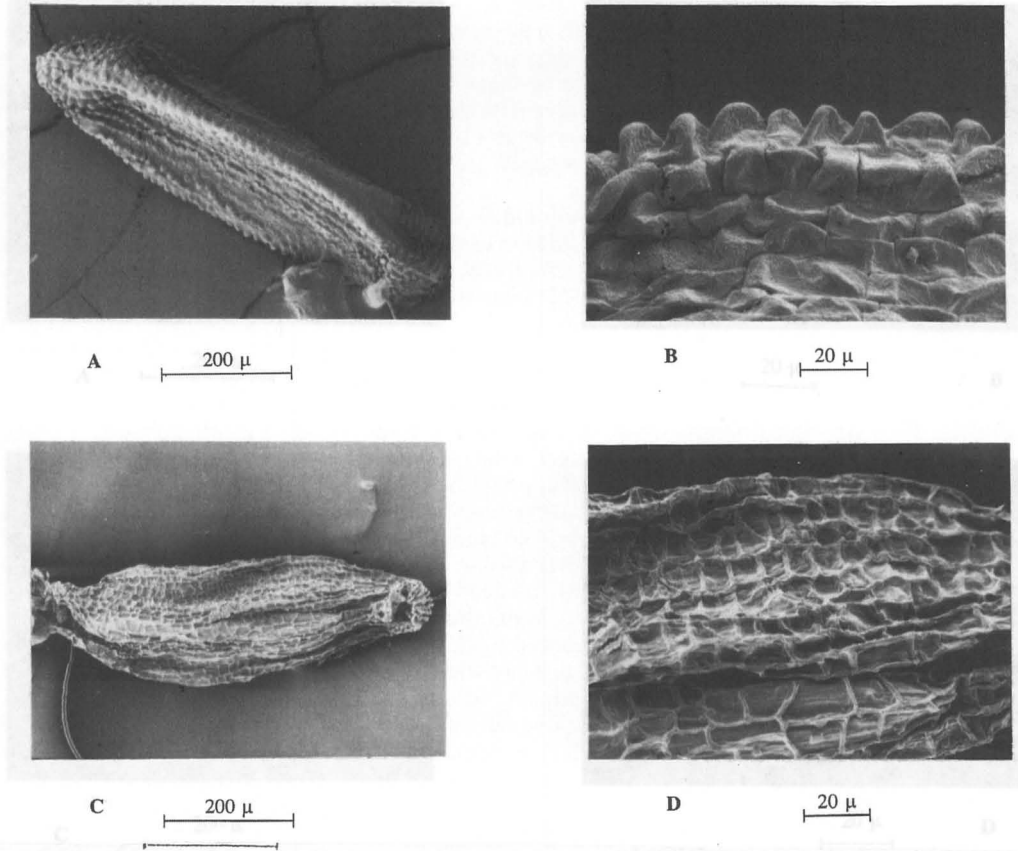


FIGURE 4. Scanning electron micrographs showing surface texture of sterile seeds of *E. × brunneatum* (A,B) and *E. × obscurescens* (C,D).

seeded parent. The surface of *E. obscurum* seeds is covered by narrow, wavy tubercles, and fertile *E. × obscurescens* seeds can repeat that appearance; so it seems likely that the reticulation of the sterile seeds also represents an undeveloped state of a tubercular surface. While it is often not easily observed, the presence of a short neck or appendage to the larger seeds, at the point of attachment of the coma, is an inheritance from *E. ciliatum*, and will clearly distinguish *E. × brunneatum* from *E. × obscurescens*.

STERILITY

Numerous hybrids were present at the recorded locations in v.cc. 1, 44 and H39. This opens the possibility of second or subsequent generations of hybrids, whether through back-crossing or self fertilisation. The presence of occasional seeds, either fully formed or only in part malformed (generally through longitudinal collapse of one side) has been noted in the specimens examined. A sample capsule from the v.c. 1 material of *E. × brunneatum* yielded 85 small abortive seeds and six larger ones. If fertile, the latter such seeds might account for at least some plants where hybrid populations exist.

Experimental sowing was undertaken in September 1995 using larger seeds taken from two of the v.c. 1 specimens of *E. × brunneatum*. Seeds were sown from each plant indoors, in small pots

containing a mixture of John Innes No. 3 and ballast sand; moisture was conserved by enclosing each in transparent plastic bags. Seeds were not covered, since Brockie (1966), working with New Zealand *Epilobium* hybrids, considered that light appears necessary to ensure good germination. From 18 seeds taken from one plant, nine seedlings germinated after 8 to 14 days. From 14 seeds taken from the other, five seedlings germinated over 14 to 39 days. The F₂ seedlings were transplanted into individual pots and, with some losses in cultivation, six plants survived successfully into the next year.

Germination of four F₂ seedlings was also achieved from material of *E.* × *chateri*.

The F₂ plants themselves set occasional apparently fertile seeds, as with the F₁ generation; one plant of *E.* × *brunnatum* was, however, apparently totally sterile, with collapsed, malformed stigmas. Apart from the general differences in cultivated material mentioned above, the F₂ plants showed a degree of variation which, if replicated in the wild, would render it even more difficult in some cases to identify what taxa were involved. The progeny of *E.* × *chateri*, for example, did not exhibit leaves quite as narrow as those from the original find (these wider leaved forms have been discounted in calculating the leaf length/breadth ratio given in the description of that hybrid).

DISTRIBUTION AND HABITAT

The occurrence of *E. brunnescens* hybrids in eleven localities in the British Isles up to 1996 (v.cc. 1, 2, 44, 46, H36, H39) provides limited scope for generalization. But data sufficient for mapping purposes have seldom been gathered in respect of any *Epilobium* hybrids – see Kitchener (1990), where it is concluded that “the real barrier to a fair assessment of the occurrence of willowherb hybrids has been lack of recognition, rather than scarcity”. Common to most of these localities, however, is an acid substrate, generally damp, open and of artificial origin; mining spoil appears particularly suitable.

The importance of open, disturbed habitats (e.g. quarries and wasteland) has been emphasised by Stace (1975) as affording a range of suitable opportunities for the establishment of *Epilobium* hybrids. But, in order for these opportunities to be taken up, there are at least two other relevant factors: the relative genetic compatibility of potential parents, and the availability of those parents themselves.

As regards the availability of the other parents, each of the species examined in this paper is readily to be found within the distributional range of *E. brunnescens*. As a limited measure of this – and taking into account the warning given that the data are not to be interpreted as showing comprehensive distribution – one may take the results of the B.S.B.I. sample survey under its Monitoring Scheme of 1987–8 (Palmer & Bratton 1995). *E. brunnescens* is recorded as present in 1987–8 in 125 of the sample squares, primarily in the damper western and northern parts and uplands of the British Isles. A high degree of coincidence is shown by the ubiquitous *E. montanum* (present in 90% of the same squares), by *E. palustre* (95%) and *E. obscurum* (82%).

The coincidence level of *E. ciliatum* is less (46%), as this species began its spread from the south-east, and has consolidated in the drier parts of the British Isles, from which *E. brunnescens* is largely absent. It has, however, been appearing increasingly within the range of *E. brunnescens*, as demonstrated by Preston (1989), with substantial spread in Wales and Cornwall occurring in the period 1959–69, and in Scotland and Ireland through to 1986. There is no reason to suppose that the spread of *E. ciliatum* has yet ceased; it has since appeared in vice-counties additional to those stated by Preston for the period up to 1986 (personal observation, and Palmer & Bratton 1995).

The increase of *E. ciliatum* may be relevant to the future occurrence of *E. brunnescens* hybrids if, as is possible, it is more ready to hybridize than other species, or such hybrids establish themselves with greater success. This is a matter for speculation, but some hybrid combinations of *Epilobium* are encountered more frequently in the field, and some species encountered more frequently as parents. Stace (1975) comments on this, and *E. ciliatum*, *E. montanum* and *E. obscurum* figure most prominently in the crosses which he regards as most frequently encountered. In our experience, within the range of *E. ciliatum*, it is the most frequently encountered parent in *Epilobium* hybrids. Further data are required before any assertion can be made about the relative frequency with which that species, in comparison with others, may hybridize with *E. brunnescens*.

CONCLUSION

It is perhaps surprising that these taxa have not been recognized until relatively recently in the British Isles, despite their potential occurrence having been publicised by Stace (1976). The confused history of the Irish records and the temporary loss of several specimens has not assisted that situation. It seems at least possible that, with further fieldwork, *E. brunnescens* hybrids may be found not to be so rare as the hitherto limited number of records suggests.

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