The distribution and habitat of *Potamogeton* × *suecicus* K. Richt. (*P. filiformis* Pers. × *P. pectinatus* L.) in the British Isles

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ABSTRACT

Recent studies of *Potamogeton* × *suecicus* K. Richt. (*P. filiformis* × *P. pectinatus*, Potamogetonaceae) have shown that the hybrid can be identified by morphological criteria and by isozyme analysis. The latter suggests that all plants studied are F_1 hybrids and does not provide any evidence for backcrossing to the parents. The hybrid is widespread in Britain in the area where both parents occur and also occurs in two rivers south of the current distribution of *P. filiformis*. In recent years it has been discovered at widely scattered localities in Ireland. The localities from which *P.* × *suecicus* has been recorded are listed, with records confirmed by isozyme analysis distinguished. In some rivers, streams and lakes it is the dominant macrophyte, growing in large, almost pure stands, whereas in other localities it is found as scattered plants in more open communities. The vegetation at the British sites is summarised from the results of 40 quadrats recorded at 21 sites. Sites where the hybrid may grow in the absence of one or even both parents are identified; they include rivers and shallow coastal lakes over sand. The history of the hybrid in Britain suggests that it is very easily over-looked; almost all records have been made in two periods (1940–1950, 1986–1998) when observers familiar with the plants were active on fieldwork. It is almost certainly still under-recorded in Scotland and Ireland.

KEYWORDS: Aquatic vegetation, hybridisation, isozyme analysis, orphaned hybrids.

INTRODUCTION

The detailed studies of the genus *Potamogeton* which J. E. Dandy and G. Taylor carried out between 1936 and 1976 did much to clarify the taxonomy and distribution of the British and Irish species and their hybrids. Indeed, it might be argued that Dandy & Taylor accomplished almost as much as one could hope to achieve using the traditional methods of herbarium taxonomy, leaving to their successors only the publication of a detailed account of the British and Irish taxa (which Dandy & Taylor never completed) and the tying up of the loose ends which are inevitably left at the end of any botanical career. However, the ever-increasing range of molecular techniques which have become available to plant taxonomists since the 1960s have allowed many aspects of the subject to advance beyond the restrictions hitherto imposed by traditional methods. This paper arises from a study of the distribution and ecology of the widespread and taxonomically difficult hybrid *Potamogeton* × *suecicus* which has combined traditional field and herbarium studies with the now well-established techniques of isozyme analysis.

Potamogeton × *suecicus* K. Richt. is the hybrid between the two species of *Potamogeton*

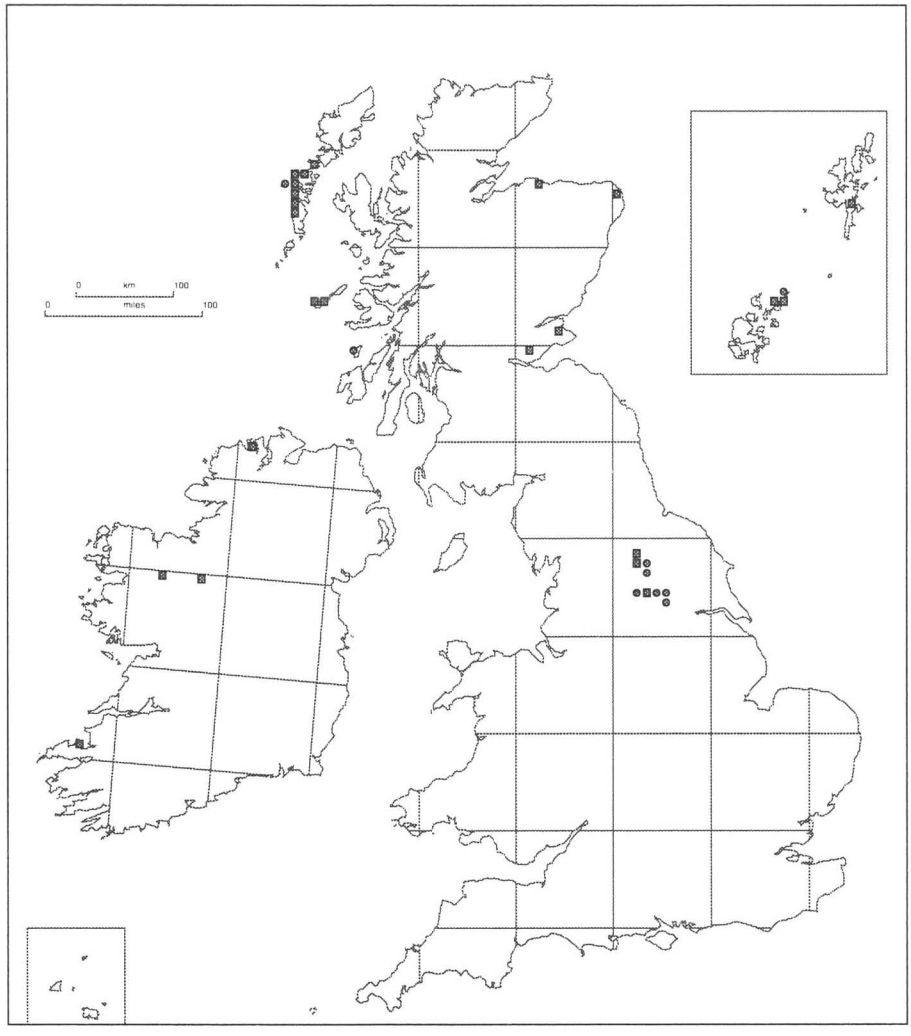

FIGURE 1. The distribution of *Potamogeton* × *suecicus* in the British Isles. Squares indicate 10-km grid squares where the hybrid has been seen from 1990 onwards; circles indicate squares where it was last seen before 1990.

Subgenus *Coleogeton* which occur in the British Isles, *P. filiformis* Pers. and *P. pectinatus* L. In general appearance it is closer to *P. pectinatus* than to *P. filiformis* but unlike *P. pectinatus* at least some of the leaf sheaths are tubular at the base. The stigmas may be borne on a distinct style (as in *P. pectinatus*) or be sessile (as in *P. filiformis*). Plants of *P.* × *suecicus* may flower freely from May to October but their pollen is sterile and they do not set fruit. Certain identification of the hybrid is not possible in the field, but under the binocular microscope the hybrid can be identified with some confidence using morphological characters alone. All three taxa are described and illustrated in Preston (1995) and an updated key, modified to take account of the presence of the similar hybrid *P.* × *bottnicus* Hagstr. in Britain, is provided by Preston *et al.* (1998).

The presence of *Potamogeton* × *suecicus* in the British Isles was first established by Dandy & Taylor (1940). They showed that earlier records of *P.* × *suecicus* in Britain were erroneous, but they

recognised the hybrid from a few herbarium specimens collected in Scotland in the 19th and early 20th centuries and from collections made in the Outer Hebrides by J. W. Campbell, W. A. Clark and A. J. Wilmott in 1938 and 1939. Further details of the Hebridean records, and additional records from the Hebrides and elsewhere, were published by Dandy & Taylor (1941, 1946), Clark (1943), Clark & Heslop Harrison (1940), Heslop Harrison (1941, 1949), Heslop Harrison & Clark (1941, 1942), Heslop Harrison & Heslop Harrison (1950) and Heslop Harrison *et al.* (1941, 1942). By 1950 *P.* × *suecicus* had been recorded in eight vice-counties, two (v.cc. 93 and 102) on the basis of old herbarium specimens and the rest (v.cc. 64, 65, 68, 81, 103 and 110) solely or in part on the basis of plants collected since 1940. Dandy & Taylor's (1946) records from the River Wharfe and River Ure in Yorkshire were supported by the anatomical studies of Bance (1946) and were especially significant. These rivers lie south of the known distribution of the rarer parent, *P. filiformis*, although subfossil fruits of *P. filiformis* have been found in Late Glacial deposits in southern England (Godwin 1975) and the species persisted in Anglesey until 1826 (Preston 1990).

Although many records of *P.* × *suecicus* were published between 1940 and 1950, there were very few additional discoveries during the next 35 years. The sites in the English rivers were often visited, and N. T. H. Holmes extended the distribution of the plant from the River Tweed into its tributary, the River Till (Holmes & Whitton 1975a, b). In Scotland M. McCallum Webster (1978) discovered the hybrid in Moray (v.c. 95) and U. K. Duncan (1969) rediscovered it at one of Heslop Harrison's localities on Tiree (v.c. 103). The hybrid was mapped by Perring & Sell (1968) and covered by Dandy's (1975) account of British and Irish *Potamogeton* hybrids.

Since 1985 there has been renewed interest in *P.* × *suecicus*. In 1986 C.D.P. began preparatory fieldwork for the B.S.B.I. handbook *Pondweeds of Great Britain and Ireland* (Preston 1995), and with N. F. Stewart refound *P.* × *suecicus* at several of the sites from which it had previously been recorded. In 1991 P.M.H. & R.J.G. began a detailed study of *P.* × *suecicus* and its parents, using isozyme analysis, in collaboration with C.D.P. (Hollingsworth *et al.* 1996a, b). As a direct or indirect result of this activity the hybrid has been rediscovered at most of its old localities, and several new sites discovered. These have included the first records from three vice-counties in Scotland, and the first records from Ireland. This paper draws together the recent records of the hybrid, documents the populations which have been identified on the basis of isozyme as well as morphological evidence, and describes the habitat of the hybrid in the British Isles.

Although recent work has confirmed the identity of many populations of *P.* × *suecicus*, it has also indicated that the material from the River Till and River Tweed differs in both morphological and isozyme characters from the other plants studied, and is apparently referable to the hybrid between *P. pectinatus* and *P. vaginatus* Turcz. (*P.* × *bottnicus* Hagstr.). As we have recently published a detailed account of these populations (Preston *et al.* 1998) they are not considered further in this paper.

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

The known sites for *P.* × *suecicus* are listed below, with the first record(s), any later records of particular interest and records made by us since 1986. The records are arranged by vice-county and site, with a site being taken as a single river or stream or as a lake together with its associated inflow and outflow streams and ditches. We have cited appropriate literature references or herbarium specimens to support all records; unpublished determinations by Dandy are cited from the "Dandy index", the card index of herbarium specimens compiled by Dandy and now at **BM**. Almost all records of *P.* × *suecicus* made since 1940 are supported by specimens determined by Dandy & Taylor or us; the main exceptions are literature references to sites in the Outer Hebrides in the works of J. W. Heslop Harrison and his colleagues, which we summarise after the accepted records for the vice-county. The records of *P.* × *suecicus* accepted below are mapped in Fig. 1.

The identity of some of the populations has been confirmed by isozyme analysis. Isozyme studies by Hollingsworth *et al.* (1996a, b) revealed consistent differences between the parent species in four enzyme systems, with *P.* × *suecicus* showing the additive inheritance which would be expected of the hybrid between them. Sites are marked with an double asterisk (**) if the isozyme results are described in detail by Hollingsworth *et al.* (1996a) or by a single asterisk (*) if the morphological identity is supported by unpublished results based on the diagnostic AAT and/or IDH enzyme systems.

MID-W. YORKS. (V.C. 64)

River Wharfe: near Pool, SE/2.4, 1868, *F. A. Lees* (Dandy & Taylor 1946); Linton Bridge, SE/3.4, 1880, *F. A. Lees* (Dandy & Taylor 1946); Wetherby, SE/4.4, 1881, *J. Jackson* (Dandy & Taylor 1946); Arthington, SE/2.4, undated but probably collected before 1890, *J. Abbot* (Dandy & Taylor 1946); Arthington, Leathley & Weeton, SE/2.4, Linton, Harewood & Netherby, SE/3.4, Wetherby, SE/4.4, Ozendyke, SE/5.3, and Ulleskelf, SE/5.4, 1940–1945, *G. Taylor* (Dandy & Taylor 1946); Harewood Bridge, SE/31.46, East Keswick, SE/34.46, Linton Bridge, SE/38.46, and Linton, SE/39.47, 1989–1996, *Mrs P. P. Abbott, P.M.H. & C.D.P.* (CGE**, **E**, **LTR**, **NMW**).

River Ure: Sharow, SE/3.7, 1875, *G. Nicholson* (Dandy index); Ripon, SE/3.7, 1881, *H. H. Slater* (Dandy & Taylor 1946); Littlethorpe, SE/3.6, Nunwick, SE/3.7, and Ripon, SE/3.7, 1940–1942, *G. Taylor* (Dandy & Taylor 1946); near Ripon, SE/3.7, 1950, *U. K. Duncan & C. M. Rob* (Dandy index).

Tributary of River Ure, Westwick, SE/3.6, 1943, *G. Taylor* (Dandy & Taylor 1946).

N.W. YORKS. (V.C. 65)

River Ure: West Tanfield, SE/2.7, Masham, SE/2.8, Langthorpe, SE/3.6 and Norton Conyers, SE/3.7, 1940–1945, *G. Taylor* (Dandy & Taylor 1946); West Tanfield, SE/26.78 and Masham, SE/22.81, 1988–1996, *P.M.H. & C.D.P.* (CGE**, **LTR**, **NMW**, **RNG**).

[CHEVIOT (V.C. 68) AND BERWICKS. (V.C. 81)

Records from these vice-counties are based on material which we have identified as *P.* × *bottnicus* (Preston *et al.* 1998). Both *P. filiformis* and *P. pectinatus* are found in Coldingham Loch, v.c. 81, but we have been unable to find the hybrid there although the locality appears suitable.]

[MIDLOTHIAN (V.C. 83)

The record from Duddingston Loch published in *Watsonia* **15**: 138 (1984) was retracted in *Watsonia* **17**: 481 (1989) as it was based on a specimen which is indistinguishable from *P. pectinatus*.]

FIFE (V.C. 85)

Loch Fitty, NT/12.91, 1992–1994, *P.M.H. & C.D.P.* (BM**, **CGE**, **E**, **LTR**).

*Cameron Reservoir, NO/477.113, 1998, *J. M. Croft, R.J.G. & C.D.P.* (**BM**, **CGE**, **E**, **LTR**).

N. ABERDEEN (V.C. 93)

Canal, St Fergus, NK/0.5, 1876, *J. H. Walker* (Dandy & Taylor 1940); the canal is now disused and dry for most of its length and P.M.H., C.D.P. & D. Welch were unable to find any *Potamogeton* species except *P. natans* in the very shallow pools remaining near Inverugie, NK/09.48, in August 1994.

*Loch of Strathbeg, Starnakeppie, NK/083.585, 1994, *P.M.H., C.D.P. & D. Welch* (**CGE**, **E**).

MORAY (V.C. 95)

Innes Canal, Urquhart, NJ/2.6, 1946, *G. Taylor* (Dandy & Taylor 1946); not refound by C.D.P. & P.M.H., 1994.

River Lossie: Calcots, NJ/2.6, 1967 & 1972, *M. McCallum Webster* (Dandy index, cf McCallum Webster 1978); Bridge of Calcots, NJ/254.638, and Arthur's Bridge, NJ/253.672, 1994, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**, **NMW**).

Loch Spynie, NJ/2.6, 1972, *M. McCallum Webster* (Dandy index, cf McCallum Webster 1978); NJ/237.663, 1994, *P.M.H. & C.D.P.* (**CGE**, **E**).

S. EBUDES (V.C. 102)

Loch Fada, Colonsay, NR/3.9, 1908, *M. McNeill* (Dandy & Taylor 1940).

MID EBUDES (V.C. 103)

** Abhainn a'Bheidhe (the stream from Loch a'Phuill to Balephuil Bay), Tiree, NL/9.4, 1940, *W. A. Clark* (Dandy index; cf Heslop Harrison *et al.* 1941; Heslop Harrison 1949); 1968, *U. K. Duncan* (Dandy index; cf Duncan 1969); 1989–1997, *P.M.H., C.D.P. & N. F. Stewart* (**CGE**, **E**, **LTR**). Ditch N.W. of Loch a'Phuill, Tiree, NL/953.422, 1990, *D. A. Pearman*, det. C.D.P. (**CGE**, **E**). **Loch a'Phuill, Tiree, NL/9.4, 1993, *R. N. Evans & P.M.H.* (**LTR**).

An Fhaodhail, Tiree, NM/0.4, 1897, *S. M. Macvicar* (Dandy & Taylor 1940); in main stream, a large backwater (Poll Orisgal) and nearby pools, 1989–1997, *P.M.H., C.D.P. & N. F. Stewart* (CGE**, **E**, **LTR**).

OUTER HEBRIDES (V.C. 110)

Loch nam Budh, Monach Island, NF/63.61, 1949, *F. H. Perring*, det. C.D.P. (**CGE**, cf Preston in press).

*Loch Stilligarry, S. Uist, NF/766.379, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **LTR**). *Inflow stream to Loch Stilligarry, S. Uist, NF/767.380, 1995, *P.M.H. & C.D.P.* (**CGE**).

West Loch Ollay, S. Uist, NF/738.324, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

*Loch an Duin Bhig, S. Uist, NF/759.468 & 760.470, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**, **LTR**).

Loch na Liana Moire, Benbecula, NF/76.53, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941, 1949; Heslop Harrison & Clark 1941); 1987, *C.D.P., N. F. Stewart et al.* (CGE**, cf Preston 1991); 1994–1995, *P.M.H. & C.D.P.* (**CGE**, **LTR**). *Ditch between Loch na Liana Moire and Loch Torcusay, Benbecula, NF/763530, 1995, *P.M.H. & C.D.P.* (**CGE**).

*Loch Torcusay, Benbecula, NF/761.532, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**).

Loch Fada, Benbecula, NF/773.518, 1994–1995, *P.M.H. & C.D.P.* (BM**, **CGE**, **LTR**).

Loch near Borve Castle [this may be Loch a'Chinn Uacraich], Benbecula, NF/7.5, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941, 1949; Heslop Harrison & Clark 1941).

Loch a'Chinn Uacraich, Benbecula, NF/767.510, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

Lochan near Uachdar, Benbecula, NF/7.5 or 8.5, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941; Heslop Harrison & Clark 1941). The record from a lochan near Gramisdale, NF/8.5, cited by Heslop Harrison (1949) may refer to the same site.

*Loch na Paisg, Baleshare, NF/786.618, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**).

*Loch Mor, Baleshare, NF/789.621, 1995, *P.M.H. & C.D.P.* (**CGE**).

*Loch Sandary, N. Uist, NF/734.684, 1995, *P.M.H. & C.D.P.* (**CGE**, **E**, **LTR**).

Loch Grogary, N. Uist, NF/71.70 & 71.71, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

*Loch Scarie, N. Uist, NF/716.704, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**, **LTR**).

*Loch a'Chaolais, N. Uist, NF/897.780, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**).

*Loch Bhruist, Berneray, NF/9.8, 1938, *J. W. Campbell* & 1939, *A. J. Wilmott* (Dandy & Taylor 1940); NF/915.822 & 920.829, 1995, *P.M.H. & C.D.P.* (**CGE**, **E**, **LTR**). *Outflow stream at S. end of Loch Bhruist, Berneray, NF/914.820, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**).

Little Loch Borve, Berneray, NF/91.81, 1939, *W. A. Clark* (Dandy & Taylor 1940; cf Clark & Heslop Harrison 1940; Heslop Harrison 1941, 1949); 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**). *Outflow stream S. of Little Loch Borve, Berneray, NF/911.814, 1995, *P.M.H. & C.D.P.* (**CGE**).

Specimens at **BM** and **CGE** collected by A. J. Wilmott from Loch na Doirlinn, Barra, in 1938 (380718La) may be *P.* × *suecicus* but are inadequate for certain identification (Preston in press). We have not traced voucher specimens to support the records of *P.* × *suecicus* from Loch Bornish, Loch Hallan and lochs near Stoneybridge, all on S. Uist (Heslop Harrison 1949; Heslop Harrison & Clark 1942; Heslop Harrison *et al.* 1942) and Loch Cistavat, S. Harris (Heslop Harrison & Heslop Harrison 1950).

ORKNEY (V.C. 111)

Loch of the Riv, Sanday, HY/68.46, 1994, *N. F. Stewart*, det. C.D.P. (**CGE**, **E**, cf Preston & Stewart 1995).

Loch of Langamay, Sanday, HY/74.44, 1963, *E. R. Bullard*, det. C.D.P. (**BM**, cf Preston in press); 1986, *E. Charter*, det. C.D.P. (**CGE**, **NCCE**, cf Preston & Stewart 1995); 1994, *N. F. Stewart*, det. C.D.P. (**CGE**, **E**, **LTR**, cf Preston & Stewart 1995).

Loch of Rummie, Sanday, HY/75.44, 1920, *H. H. Johnston*, det. C.D.P. (**E**, cf. Preston in press); 1994, *N. F. Stewart*, det. C.D.P. (**BM**, **CGE**, **E**, cf Preston & Stewart 1995).

Loch Gretchen, North Ronaldsay, HY/74.52, 1920, *H. H. Johnston*, det. C.D.P. (**E**, cf. Preston in press).

SHETLAND (V.C. 112)

*Loch of Clickimin, HU/4.4, 1980, *R. C. Palmer*, det. C.D.P. (**SLBI**, **herb. R.C.P.**, cf Preston in press); HU/46.41, 1996, P.M.H. & C.D.P. (**BM**, **CGE**, **E**).

S. KERRY (V.C. H1)

*Lough Gill, V/61.14, 1993, *N. F. & R. J. Stewart*; V/61.13 & 61.14, 1994, *R. FitzGerald & C.D.P.* (**BM**, **CGE**, **DBN**, **LTR**).

ROSCOMMON (V.C. H25)

*Callow Lough, 1·5 km S. of Cuil Bridge, M/70.96, 1998, *A. B. Carter, D. C. F. Cotton, A. Hill, N. Raftery & C.D.P.* (**CGE**, **DBN**).

E. MAYO (V.C. H26)

Glore River, Kiltamagh, M/38.90, 1994, *C.D.P.* (**CGE**, **DBN**). Similar plants grew upstream at grid reference M/38.89 and M/40.89 but were not collected as in the field the plant was thought to be *P. pectinatus*.

W. DONEGAL (V.C. H35)

Rosapenna, C/11.38, 1989–1990, *C.D.P. & N. F. Stewart* (**BEL**, **BM**, **CGE**, **DBN**, **LTR**, cf Preston & Stewart 1994).

TABLE 1. SPECIES ASSOCIATED WITH *POTAMOGETON* × *SUECICUS* IN RIVERS, STREAMS AND LAKES

	Rivers	Streams	Lakes (1)	Lakes (2)
Potamogeton × *suecicus*	V (5–10)	V (5–10)	V (3–9)	V (4–10)
Myriophyllum spicatum	I (4)	III (1–7)	I (1–4)	III (1–7)
Potamogeton crispus	II (2–5)	I (6)	I (7)	I (1)
Potamogeton perfoliatus	I (4)		I (1)	II (1–2)
Potamogeton natans	II (3–6)	II (2–5)	III (1–5)	
Lemna minor	II (1–2)			I (2–3)
Elodea canadensis	I (6)			I (1–5)
Fontinalis antipyretica	I (4)			I (1)
Eleocharis palustris		III (1–3)	III (1–6)	II (1–4)
Potamogeton filiformis		II (2–3)	I (1–6)	II (6–8)
Potamogeton friesii		I (4)	II (1–2)	I (1–4)
Hippuris vulgaris		I (3)	I (2)	I (3–5)
Potamogeton × *nitens*		I (2)	I (1)	I (5–6)
Ranunculus baudotii		I (2)	I (6)	I (5)
Equisetum fluviatile		I (2)		II (1–3)
Chara aspera		II (5)	III (1–8)	
Chara vulgaris		III (1–3)	II (1–5)	
Chara contraria		II (6)	I (1–5)	
Potamogeton pusillus			I (3)	II (1–7)
Littorella uniflora			II (!–8)	I (2)
Callitriche hermaphroditica			I (1)	I (2–4)
Potamogeton pectinatus			I (3)	I (6)
Agrostis stolonifera		III (1)		
Sparganium erectum		II (1–5)		
Persicaria amphibia			II (4–7)	
Chara hispida			I (3–7)	
Chara virgata			I (1–3)	
Phragmites australis			I (2–3)	
Baldellia ranunculoides				I (2–5)
Carex rostrata				I (1–2)
Lemna trisulca				II (1–2)
Potamogeton gramineus				I (1–5)
Zannichellia palustris				I (2–4)

TABLE 1. CONTINUED

	Rivers	Streams	Lakes (1)	Lakes (2)
No. quadrats	9	7	10	14
No. vascular plants & bryophytes				
mean	2·3	5·0	4·7	4·9
(range)	(1–4)	(2–8)	(1–8)	(2–8)
No. charophytes				
mean	0	0·9	1·2	0
(range)		(1–2)	(1–4)	
% bare ground				
mean	16	9	5	15
(range)	(0–45)	(0–15)	(0–15)	(0–50)
Water depth (cm)				
mean	41	18	20	38
(range)	(15–80)	(15–25)	(10–45)	(12–70)
Substrate type (% quadrats)				
rocks	40	0	0	0
stones/gravel	30	0	0	5
sand	20	50	70	30
silt/mud	10	50	30	65

The roman numerals indicate the percentage of quadrats in which the taxon was recorded in each habitat: I, 1–20%; II, 21–40%; III, 41–60%; IV, 61–80% and V, 81–100%. The figures in brackets indicate the range of Domin cover-abundance values recorded. The lake quadrats are subdivided into two groups based primarily on the presence or absence of charophytes. The following taxa were recorded in a single quadrat: *Callitriche hamulata*, *Sparganium emersum* (rivers); *Caltha palustris*, *Mentha aquatica*, *Ranunculus trichophyllus*, *Rorippa* × *sterilis*, *Veronica anagallis-aquatica* (streams); *Myriophyllum alterniflorum*, *Potamogeton* × *billupsii* (lakes 1); *Potamogeton rutilus*, *P.* × *zizii* (lakes 2).

HABITAT OF *P.* × *SUECICUS* IN BRITAIN

Between 1994 and 1997 we visited 21 of the 28 localities in which *P.* × *suecicus* has been recorded in Britain recently, and recorded its habitat in forty 4m^2 quadrats. At each site one or more quadrat was recorded in stand(s) of vegetation where the cover of the hybrid was greatest. We assessed the cover-abundance of vascular plants, bryophytes and charophytes in each quadrat and noted details of substrate and water depth. The quadrats covered the range of water bodies from which the hybrid has been reported, including the River Lossie (v.c. 95), River Wharfe (v.c. 64) and River Ure (v.c. 65), the streams Abhainn a'Bheidhe and An Fhaodhail on Tiree (v.c. 103) and the outflow of Little Loch Borve, Berneray (v.c. 110), the ditch between Loch Torcusay and Loch Liana Moire, Benbecula (v.c. 110), and 15 lakes in Fife (Loch Fitty), Moray (Loch Spynie) and the Outer Hebrides (on Benbecula, Berneray, N. Uist and S. Uist). The number of sites covered should ensure that the quadrat data characterise the range of vegetation in which the hybrid occurs, although stands in deep water may have been overlooked.

The vegetation in the quadrats is summarised in Table 1. The quadrats from rivers, streams and ditches, and lakes are separated. The quadrats from lakes are presented in two groups, split primarily on the presence or absence of charophytes in the quadrat.

In rivers *P.* × *suecicus* is often present as robust plants growing in large, dominant stands. Very large, dense stands of *P.* × *suecicus* include those in the River Wharfe near Harewood Bridge (SE/31.46), East Keswick (SE/36.45) and Linton Bridge (SE/38.46) and the River Lossie near Bridge of Calcots (NJ/25.63) and Arthur's Bridge (NJ/25.67). Large stands of *P.* × *suecicus* are less frequent in the River Ure but the hybrid may often be found in abundance by the bridge at West Tanfield (SE/26.78), where it was photographed on 6 August 1945 (Dandy & Taylor 1946) and has therefore survived for over 50 years. In rivers *P.* × *suecicus* is rooted in a substrate of rocks, stones,

gravel or (on stretches of the River Lossie) pure sand. Where the substrate is rocky, plants of *P.* × *suecicus* are often rooted under boulders, stones or the masonry of bridge supports. Although the water flow in the *P.* × *suecicus* rivers is relatively rapid, patches of *P.* × *suecicus* may be so large that they impede the flow of water when they reach the surface, allowing a few fronds of *Lemna minor* to settle amongst them. Large stands may flower freely: flowering *P.* × *suecicus* in the River Lossie in August 1994 bore 9–42 inflorescences in sample areas of 400 cm^2, equivalent to 225–1050 m^{-2}. These totals include inflorescences at anthesis and others which were decaying; some were on the surface of the water and others buried amongst the submerged foliage. The river quadrats in Table 1 are species-poor. The vegetation in these quadrats is similar to that in which the related hybrid *P.* × *bottnicus* grows in the River Till and River Tweed (Hollingsworth *et al.* 1998). Although no *Ranunculus* species were recorded in the quadrats with *P.* × *suecicus*, *R. penicillatus* subsp. *pseudofluitans* and *R.* × *bachii* grow in the same stretches of the Wharfe as *P.* × *suecicus*.

The streams and ditches in which *P.* × *suecicus* was recorded in quadrats are shallow and flow slowly and gently over substrates of sand or silt. *P.* × *suecicus* may span the entire width of the narrow channel of both Abhainn a'Bheidhe and An Fhaodhail in Tiree. Heslop Harrison (1949) reported that *P.* × *suecicus* grew at Abhainn a'Bheidhe in "dense masses for considerable stretches of the stream", still an apt description of its abundance in 1997. The stream quadrats are more species-rich than those recorded in rivers, and in addition to submerged species they include emergents such as *Eleocharis palustris*, *Sparganium erectum* and a few shoots of the normally terrestrial *Agrostis stolonifera* which extend into the shallow water of An Fhaodhail. The vegetation is usually more or less closed and there is little bare ground.

In some lakes *P.* × *suecicus* may occur in large, dominant stands. The largest stands we have seen in lakes have been in the very shallow bay at the northern end of Loch Torcusay (NF/76.53) where the water is only 10 cm deep and is completely dominated over an area of many square metres by *P.* × *suecicus* and associated charophytes (*Chara contraria*, *C. hispida*, *C. virgata* and *C. vulgaris*), and in the north-west arm of Loch an Duin Bhig (NF/76.47) which is covered in *P.* × *suecicus*. Equally dense but smaller stands may be found in other lakes, such as Loch Fitty (NT/12.91) and Loch Sandary (NF/73.68). In other sites *P.* × *suecicus* may occur only as scattered plants in more open communities over stones and boulders, or amongst other macrophytes such as *Hippuris vulgaris*, *Littorella uniflora*, *Persicaria amphibia*, *Potamogeton filiformis*, *P.* × *nitens*, *P. pectinatus* or *Zannichellia palustris*.

The quadrats where *P.* × *suecicus* was recorded with charophytes (Table 1) tend to be in shallower water than those which lack charophytes, and are more often found with sand as a substrate than silt. *Eleocharis palustris*, *Potamogeton natans* and *Chara aspera* are the most frequent associates in these quadrats and *Persicaria amphibia* is confined to this group. Charophyte cover is often high and there is little bare ground. *Eleocharis palustris* is less frequent in the quadrats without charophytes and neither *Persicaria amphibia* nor *Potamogeton natans* are recorded. However, *Equisetum fluviatile* is present and *Myriophyllum spicatum* and *Potamogeton pusillus* are more frequent in these quadrats. *P. filiformis* and *P. pectinatus* occur with *P.* × *suecicus* in both groups of quadrats.

HABITAT OF *P.* × *SUECICUS* IN IRELAND

P. × *suecicus* grows in lakes at three of its four known Irish sites. Two of these lakes are similar to sites in Scotland where the hybrid occurs in charophyte-rich communities. In Donegal (v.c. H35) it is found in a shallow lake in the calcareous sand dunes at Rosapenna. This site, which is described by Preston & Stewart (1994), is fringed by *Eleocharis palustris*, *Littorella uniflora* and scattered *Persicaria amphibia*. In the open water charophytes are abundant and in addition to *P.* × *suecicus* the macrophytes include *Apium inundatum*, *Potamogeton natans* and *Ranunculus trichophyllus*. The second Irish site is a large coastal lake, Lough Gill (v.c. H1). Here *P.* × *suecicus* is locally frequent at the south-east edge of the lake, growing in shallow water 12–15 cm deep over a substrate of silt mixed with stones and sand. Associated species include *Potamogeton filiformis*, *P. pusillus*, *Chara contraria* and *C. curta*. By contrast, in Roscommon (v.c. H25) *P.* × *suecicus* has been found in water 30–50 cm deep over a stony substrate at the edge of Callow Lough, the southernmost lough in the Lough Gara complex. Here it grows as scattered plants or, in more sheltered bays, as somewhat larger patches, with few associated species.

TABLE 2. SITES WHERE *POTAMOGETON* × *SUECICUS* MAY GROW IN THE ABSENCE OF ONE OR BOTH PARENTS, *P. FILIFORMIS* (F) AND *P. PECTINATUS* (P)

Site	Parents present	Notes
River Wharfe, v.c. 64	P	South of current distribution of F
River Ure, v.c. 64, 65	P	South of current distribution of F
Canal, St Fergus, v.c. 93	F	Both taxa known only from specimens dated 1876
Loch of Strathbeg, v.c. 93	P	F recorded by Trail (1901a,b) but never confirmed
Innes Canal, Urquhart, v.c. 95	Neither	Hybrid known only from specimen dated 1946
River Lossie, v.c. 95	Neither	
Loch Spynie, v.c. 95	P	P collected regularly since 1831; F never found
Loch Fada, v.c. 102	P	F recorded by McNeill (1910, p. 78); no specimen seen and species has not been reported from the island again (Clarke & Clarke 1991)
Loch nam Budh, v.c. 110	Neither	Specimen determined as F by Dandy and reported as such by Perring & Randall (1972) is the hybrid
Loch an Duin Bhig, v.c. 110	P	F recorded by Royal Botanic Garden, Edinburgh (1983); no specimen seen
Loch Fada, v.c. 110	P	
Loch a'Chinn Uacraich, v.c. 110	P	F recorded by Royal Botanic Garden, Edinburgh (1983); no specimen seen
Loch Mor, v.c. 110	P	
Loch a'Chaolais, v.c. 110	Neither	Small site thoroughly surveyed in 1995
Little Loch Borve, v.c. 110	F	
Loch of the Riv, v.c. 111	F	
Loch of Langamay, v.c. 111	F	Specimen collected in 1963 and determined by Dandy as P is the hybrid (Preston in press)
Loch of Rummie, v.c. 111	F	Specimen reported by Johnston (1922) as F but determined by Dandy & Taylor as P is the hybrid (Preston in press)
Glore River, v.c. H26	Neither	
Rosapenna, v.c. H35	F	F collected in 1939 by Praeger but absent when this small site was thoroughly surveyed in 1989 & 1990

The remaining Irish site, the Glore River (v.c. H26), is a relatively shallow stream flowing over a substrate of silt and stones. *P.* × *suecicus* is recorded in patches up to 3 metres long, growing in water 40–50 cm deep with *Apium nodiflorum*, *Elodea canadensis*, *Myriophyllum alterniflorum* and the rare hybrid *Potamogeton* × *lanceolatus*. This stream has no close parallel to any of the other known sites for *P.* × *suecicus* in Britain, and perhaps provides a habitat which is intermediate between the large rivers of northern England and Scotland and the slowly flowing streams of the Hebrides.

OCCURRENCE OF *P.* × *SUECICUS* IN RELATION TO ITS PARENTS

In discussing the relationship between the distribution of *P.* × *suecicus* and its parents, three questions arise. What is the probability of finding *P.* × *suecicus* at sites where both *Potamogeton filiformis* and *P. pectinatus* occur? Does the hybrid occur at sites where one or both parents are absent? And is there any differentiation between the habitat of the three taxa when two or three grow together?

It is not easy to assess the frequency of the hybrid at sites where both parents occur as there are few areas in which the hybrid has been searched for systematically. In the Outer Hebrides in 1995 we visited 17 lochs which appeared to be likely sites for the hybrid, comprising 3 where *P.* ×

suecicus had already been recorded before we began our studies and 14 from which one or both parents had been recorded or seemed likely to occur. *P.* × *suecicus* grew in 15 of these 17 sites, the exceptions being one loch where we were only able to detect the parents in the limited area we were able to search and one small loch near the sea where *P. pectinatus* was the only one of the three taxa present. This is clear evidence to support Heslop Harrison & Clark's (1941) view that on Benbecula the hybrid "seems to occur wherever the parent species clash". However, *P.* × *suecicus* may be exceptionally frequent in the Outer Hebrides. In Shetland, where *P. filiformis* is much more frequent than *P. pectinatus*, we have visited all seven sites from which Scott & Palmer (1987) cite confirmed records of *P. pectinatus*. Despite the fact that *P. filiformis* grows in six of these seven sites, we detected *P.* × *suecicus* in only one locality.

The sites where *P.* × *suecicus* appears to grow in the absence of one or both parents are summarised in Table 2. The identification of such sites is not always straightforward. At some sites there are field or literature records of one of the parents made by recorders who did not report the hybrid; if these records are not supported by herbarium material it is not possible to say whether they are correct. At other sites the absence of the parents may be due to inadequate survey. Nevertheless, there are several localities where the presence of *P.* × *suecicus* in the absence of one or both parents is well-established. Three of the sites are rivers: the River Lossie, where neither parent is found, and the Rivers Wharfe and Ure, where only *P. pectinatus* occurs. The recently discovered population in the Glore River may also fall into this category. *P. filformis* does not usually occur in large rivers, and its absence from these sites may be explicable on ecological grounds. The Yorkshire rivers are also south of the current range of *P. filiformis*.

Another habitat where *P.* × *suecicus* occurs in the absence of one or both parents is in shallow coastal lakes over sand. At Loch a'Chaolais and Rosapenna the hybrid is currently present and locally abundant in the absence of both parents. Ecologically these sites have much in common; both sites are fringed by *Eleocharis palustris* swamp and *Persicaria amphibia*, *Potamogeton natans* and *Chara aspera* or the closely related *C. curta* grow in the water. There is reliable evidence for the former presence of one of the parents at Rosapenna, as R. L. Praeger collected fruiting material of *P. filiformis* there in 1939 (**DBN**). The Orkney sites for *P.* × *suecicus* are also shallow lakes over calcareous sand where the hybrid grows with *Chara aspera* and *C. curta*; it is accompanied here by *P. filiformis* but there is no reliable record of *P. pectinatus* from these sites.

The presence of "orphaned" *P.* × *suecicus* in larger lakes has still to be established with certainty but it is interesting that the hybrid grows in Loch Spynie, where many collectors from 1831 onwards have gathered *P. pectinatus* but where *P. filiformis* has not been recorded. The Loch of Strathbeg is also a possibility: *P. pectinatus* has been recorded since 1883 but the only record of *P. filiformis* (Trail 1901a, b) lacks a supporting specimen.

At large and complex sites where the hybrid and both parents are present, the taxa are often concentrated in different areas. At Loch a'Phuill *P. filiformis* grows on the shallow sandy flats around the edge and *P. pectinatus* in deeper water. *P.* × *suecicus* occurs in the loch but it is particularly abundant in the shallow and slowly flowing outflow stream (Abhainn a'Bheidhe) which runs from this loch through sand dunes to the sea. *P. filiformis* grows in this stream (though it is less abundant than the hybrid) but *P. pectinatus* does not. At An Fhaodhail, Tiree, the shallow river is dominated by *P.* × *suecicus*; *P. pectinatus* is represented by a few individuals scattered sporadically amongst the hybrid and *P. filiformis* grows in nearby pools (Hollingsworth *et al.* 1996a). At less complex sites the distinctions between the taxa are less obvious. *P. filiformis* tends to be a plant of shallow water and although it may grow with *P. pectinatus*, the latter attains maximum luxuriance in deeper, less turbulent water (van Wijk 1988). Unlike *P. filiformis*, which may be found in water only a few centimetres deep and in sites which dry out completely when water levels are low, *P.* × *suecicus* is not found in very shallow water. It does, however, grow in slightly deeper water well within the habitat range of *P. filiformis* and it is more frequently found with that species than with *P. pectinatus* (Table 1). It would, however, be even more easily overlooked in deeper water than it is when it grows in the shallows. At Loch Fitty *P. filiformis* tends to grow on coarse sand or gravel, *P. pectinatus* on fine silt and *P.* × *suecicus* gravel mixed with silt, although this may simply reflect differences in the water depth and exposure of the sites favoured by the three taxa.

In summary, the habitat of *P.* × *suecicus* in lakes is intermediate between that of its parents. It tends to be most abundant in water at the deeper end of the range characteristic of *P. filiformis*, but

it rarely extends into the still deeper water where *P. pectinatus* reaches maximum luxuriance. It may grow in the absence of both parents in shallow coastal lakes over sand. In rivers it grows in shallow, fairly rapidly flowing water over stones, gravel or sand, a habitat where neither parent is found. A more detailed insight into the habitat of the hybrid in relation to its parents might be obtained by more intensive studies at sites like Loch Fitty where all three taxa occur.

DISCUSSION

RECOGNITION AND RECORDING HISTORY

Plants of *P.* × *suecicus* can easily be confused with *P. pectinatus* as the resemblance to that species is obvious in the field whereas the influence of *P. filiformis* is often apparent only when plants are carefully examined under the binocular microscope. Many specimens of *P.* × *suecicus* have initially been identified (at least in the field) as *P. pectinatus*: these include those collected by G. Taylor from the River Wharfe in 1940, the first specimens collected from Shetland in 1980, plants gathered by C.D.P. & N. F. Stewart in Co. Donegal in 1989 and material collected by P.M.H. at Loch Fada and Loch a'Chinn Uacraich, Outer Hebrides, in 1994. *P.* × *suecicus* has also been overlooked (rather than mistaken for its parents) in Scotland and Ireland, perhaps because fruiting plants of *P. filiformis* and *P. pectinatus* may often be found without difficulty, so that botanists can record both species with certainty and therefore do not feel obliged to examine vegetative material. The ease with which *P.* × *suecicus* can escape detection is well illustrated in the Outer Hebrides. The hybrid is now known to be widespread in species-rich machair lochs which have attracted the attention of many individual botanists and ecologists and some survey teams in recent years (Preston 1991). Rare and critical taxa such as *Potamogeton* × *billupsii*, *P.* × *nitens*, *P. rutilus* and *P.* × *sparganifolius* were collected between 1960 and 1985 from lochs in which *P.* × *suecicus* is now known to occur, but *P.* × *suecicus* itself was never recorded during this period.

The fact that *Potamogeton* × *suecicus* tends to be recorded only by botanists who are familiar with its appearance, and is overlooked even by others who are specifically recording in aquatic habitats, explains the numerous records in the 1940s, when both Heslop Harrison's team from Newcastle and George Taylor were actively engaged in fieldwork, followed by the subsequent falling-off of new records. The hybrid is almost certainly still under-recorded. One would expect to find it elsewhere in eastern Scotland (e.g. in Angus) and at other sites in the west. There are many potential sites for the hybrid in the Outer Hebrides, for example, which we have not had an opportunity to visit. Four sites have been discovered in Ireland in the last decade and there are many more places in the north and west where it might occur.

We have improved our ability to recognise *P.* × *suecicus* only by collecting material in the field, examining it from a morphological or isozyme perspective and then returning to the field to reassess the populations in the light of these detailed studies. On our return from visits to N.E. Scotland, the Hebrides and Shetland C.D.P. has examined the morphology of our collections and P.M.H. has looked at the isozymes. We have then compared identifications which were reached without knowledge of the other person's view. We have always been in agreement, though sometimes the isozyme results have provided welcome confirmation of a tentative identification of fragmentary or aged material based on morphology, or *vice versa*. However, an identification based on morphology often requires flowering material, or a supply of vegetative material which is large enough to allow the dissection of numerous young leaf sheaths.

The hybrid is more likely to be detected by a thorough examination of populations in the field than by the collection of a few herbarium specimens for later examination or determination by others. Recognition of the hybrid using morphological criteria relies on proving the presence of characters derived from both parents, and it is helpful to demonstrate that the plant is sterile. Herbarium material often provides an inadequate representation of the habit of the plant and a very small number of leaf sheaths for dissection. Flowers may not be available, and even if a flowering plant lacks fruit there is usually no evidence to indicate whether this was typical of the population from which it was collected. Even J. E. Dandy and G. Taylor, the foremost authorities on the genus, identified material which we now believe to be *P.* × *suecicus* as one or other parent (Preston in press).

DOES *P.* × *SUECICUS* BACKCROSS WITH EITHER PARENT?

Heslop Harrison & Clark (1942), in commenting on the application of the name *P.* × *suecicus* to the hybrid plant from South Uist which "grows in the Stoneybridge lochs, as elsewhere, in forms displaying a great variation range" said that "in our opinion, it is wrong to include these in one ragbag under the name *P. suecicus* because they differ phenotypically and genotypically. Clearly, F_1 hybrids, backcrosses and segregates of F_2 and later generations are concerned; a common name cannot be forced to cover plants ranging from "almost" *P. filiformis* to "almost" *P. pectinatus*. It would, at present, be better to label them *P. filiformis* × *P. pectinatus*, and to leave them until further study and experiment have clarified the position." This description suggests that a complex hybrid swarm is present in the Hebrides. We know of no evidence to support this suggestion. The plants of *P.* × *suecicus* in those localities where we have studied them in detail show little variation. The hybrid does vary in morphology from population to population, and some of these variants are closer to *P. pectinatus* than others, but this pattern of variation is much more easily explained by phenotypic response to different habitat factors or by the presence in different sites of a first generation (F_1) hybrid of different genetic origin than it is by invoking the possibility of backcrossing with the parents. The isozyme studies of eleven populations reported by Hollingsworth *et al.* (1996a) confirm this pattern of variation: no variation was detected at six sites and only two isozyme phenotypes were detected at a further four. This suggests that there may have been only one or two clones present at ten of the localities (although isozyme data are based on a small proportion of the genome and provide an estimate of the *minimum* number of clones present). An Fhaodhail on Tiree, where six isozyme phenotypes were detected, was the only exception. All isozyme phenotypes, including those from An Fhaodhail, were consistent with the assumption that the plants were F_1 hybrids, and there was no evidence for the disruption of additive inheritance of species-specific markers which would be expected if backcrossing had taken place.

SIGNIFICANCE OF STERILE *POTAMOGETON* HYBRIDS

P. × *suecicus* is one of eight widespread *Potamogeton* hybrids in Britain and Ireland identified by Preston (1995) and mapped by Preston & Croft (1997). Like most of these hybrids, its distribution is neither completely independent of the parents nor completely determined by the sites where they currently occur. Despite the fact that *P.* × *suecicus* was not recognised in Britain until 1940, it is known to have been present in three sites for at least 100 years (River Wharfe, River Ure, An Fhaodhail) and in a further five for at least 50 years (Abhainn a'Bheidhe, Loch na Liana Moire, Loch Bhruist, Little Loch Borve and Loch of Rummie). In sites where at least one parent is absent the presence over this period is almost certainly caused by the persistence of particular clones; if both parents are present one cannot conclude that individual clones are long-lived as the hybrid may have arisen by repeated hybridisation. Another notable feature that *P.* × *suecicus* shares with many of the widespread hybrids is that at some sites it is a significant feature of the aquatic vegetation, and may even be present in dominant stands. The further study of the ecology of these sterile hybrids in relation to their fertile parents might throw considerable light on the reproductive biology, dispersal and ecology of aquatic plants.

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