

Potamogeton pectinatus L. × *P. vaginatus* Turcz. (*P.* × *bottnicus* Hagstr.), a newly identified hybrid in the British Isles

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ABSTRACT

A hybrid *Potamogeton* (Potamogetonaceae) which grows in shallow, rapidly flowing water in the River Till (Cheviot) and River Tweed (Berwickshire (v.c. 81) and Cheviot (v.c. 68)) is apparently referable to *P.* × *bottnicus* Hagstr. (*P. pectinatus* L. × *P. vaginatus* Turcz.). Both morphological and isozyme characters are consistent with this hybrid combination rather than with the previous identification of these plants as *P.* × *suecicus* K. Richt. (*P. pectinatus* × *P. filiformis* Pers.). British plants of *P.* × *bottnicus* and European plants of *P. vaginatus* are described and the differences between them, *P. pectinatus* and *P.* × *suecicus* outlined. Possible explanations for the presence of *P.* × *bottnicus* in Britain in the absence of *P. vaginatus* are discussed. The name *P.* × *bottnicus* is lectotypified by a syntype referable to *P. pectinatus* × *P. vaginatus*. Examination of type material of *P.* × *meinshausenii* Juz., described from the vicinity of St Petersburg, indicates that it is not a hybrid between *P. pectinatus* and *P. vaginatus* as hitherto supposed.

KEYWORDS: Potamogetonaceae, *Potamogeton filiformis*, *P.* × *suecicus*, *P.* × *meinshausenii*.

INTRODUCTION

Two species in *Potamogeton* subgenus *Coleogeton* Rchb. are found in the British Isles, *P. filiformis* Pers. (Slender-leaved Pondweed) and *P. pectinatus* L. (Fennel Pondweed). The hybrid between them, *P.* × *suecicus* K. Richt., is one of the more difficult *Potamogeton* hybrids to identify, partly because of the extreme variability of the commoner parent, *P. pectinatus*, and partly because the crucial character which separates this parent from the hybrid, the structure of the leaf sheaths, can only be ascertained by dissection under the microscope. The first correct records of *P.* × *suecicus* in the British Isles were published by Dandy & Taylor (1940). The hybrid has subsequently been discovered in scattered localities in Scotland and Ireland, where both the widespread *P. pectinatus* and the more northerly *P. filiformis* occur (Preston & Croft 1997). More significantly, *P.* × *suecicus* was reported by Dandy & Taylor (1946) from the River Tweed in Berwickshire (v.c. 81) and Cheviot (v.c. 68), and the River Wharfe and River Ure in Yorkshire (v.c. 64 and v.c. 65); a similar plant has subsequently been found in a tributary of the Tweed, the River Till (Dandy 1975; Holmes & Whitton 1975a, b; Swan 1993). At the time of Dandy & Taylor's paper these localities all lay south of the extant sites for *P. filiformis* in Britain. *P. filiformis* has since been found in Rayburn Lake, S. Northumberland (v.c. 67), south of the Tweed and the Till, but the Yorkshire sites are still some 150 km south of the nearest known *P. filiformis* population.

We have recently re-investigated *P.* × *suecicus* in Britain, examining the morphology of populations and using isozyme electrophoresis to investigate the variation in both the hybrid and its putative parents (Hollingsworth *et al.* 1996a, b). Most populations hitherto identified as *P.* ×

suecicus, and a number of new populations discovered during the course of this study, have proved to be intermediate morphologically between *P. filiformis* and *P. pectinatus*, and the results of the isozyme analysis offered strong support to the hypothesis that they represent the hybrid between these two species. This applies both to plants in sites in Scotland, where the hybrid often grows in proximity to both parents, and to the outlying populations in the River Wharfe and River Ure. Hollingsworth *et al.* (1996a) concluded that the evidence that the populations studied are the hybrid between *P. filiformis* and *P. pectinatus* is "virtually conclusive". An updated account of the distribution of *P. × suecicus* in the British Isles is in preparation.

Although the identity of most populations of *P. × suecicus* was confirmed by our recent study, the plants in the River Till and River Tweed were a conspicuous exception. We were unable to identify them as *P. × suecicus* either on morphological grounds or from the isozyme evidence. Both morphology and isozyme evidence is, however, consistent with the hypothesis that these plants are *P. × bottnicus* Hagstr., the hybrid between *P. pectinatus* and the third European member of subgenus *Coleogeton*, *P. vaginatus* Turcz. This is a surprising conclusion, as in Europe *P. vaginatus* is confined to Norway, Sweden and Finland (Elven & Johansen 1984); the nearest population lies some 1500 km from the sites in the River Tweed and River Till. The species is also found in central Asia and is widespread in North America (Hultén & Fries 1986). The hybrid is described below, and the evidence for its identity outlined.

POTAMOGETON × BOTTNICUS IN BRITAIN

DESCRIPTION

The following description of *P. × bottnicus* is based on fresh material and herbarium specimens collected from the British sites.

Plants forming large and vigorous clumps. Rhizomes to at least 0.45 m long, 1.5–6.5 mm in diameter. Stems up to 1.5 m long, 1.7–4.3 mm in diameter, terete, with frequent branches lying more or less parallel to the main stem; nodal glands absent. Scales 10–64 mm long, present on lowest (0–)1–3 nodes of the stem, clasping the stem throughout their length or with the distal part free, incurved and leaf-like, or bearing rudimentary leaves. Submerged leaves linear, mid to dark green, sometimes tinged with brown when growing near the surface of the water, leaves at the first 4 nodes above the basal scales 25–206 × (1.2–)2.0–3.5 mm, 11–90 times as long as wide, 0.8–3.7 times as long as the sheath, stiff, markedly canaliculate, acute; leaves towards the apex of mature stems (72–)110–200(–250) × 0.8–3.1 mm, (45–)60–110(–140) times as long as wide, (2.6–)3.0–5.7 times as long as the sheath, canaliculate, more or less truncate, rounded or obtuse at the apex, sometimes slightly mucronate and often slightly asymmetrical, sometimes more or less acute on flowering stems, entire and plane at the margin, the midrib bordered on each side by 1–2 inconspicuous lateral veins and several air channels. Floating leaves absent. Leaf sheaths green with hyaline margins, the margins sometimes with a brownish tinge, open and usually convolute unless forced apart by branches arising at the node, 25–78 × 2.1–5.5 mm at the first 4 nodes above the basal scales, 23–70 mm long towards the apex of mature vegetative stems, only 17–28 mm long towards the apex of flowering stems; ligules 6–17 mm, hyaline, rounded or truncate at the apex. Turions absent. Inflorescences 10–26 × 4–5.5 mm; peduncles 36–90 × 0.6–0.7 mm, pale pink, terete, flexuous. Flowers 5–10, in 3–5 groups of 1–2; anthers small, hidden by the tepals, not filled and not dehiscent readily, the pollen misshapen; carpels 4, the stigmas sessile. Fruits not seen, and almost certainly do not develop. Vegetative reproduction by small plantlets which develop on short axillary stolons; perhaps also by tubers which are formed on the rhizomes of both parents but these not yet seen on the hybrid.

COMPARISON OF *P. × BOTTNICUS* WITH *P. PECTINATUS* AND *P. × SUECICUS*

The salient characters distinguishing the three European species in subgenus *Coleogeton* and the hybrids *P. × bottnicus* and *P. × suecicus* are set out in Table 1. British and Irish botanists are most likely to overlook *P. × bottnicus* as a form of the variable *P. pectinatus*. Fortunately, both *P. pectinatus* and *P. × bottnicus* grow together in the River Tweed on the S. side of St Thomas's Island, Norham Mains, and in July 1995 the differences between the taxa were clearly apparent in this mixed stand. The clumps of *P. × bottnicus* reached the surface, where the leaves were brownish green, and scarcely moved in the current. The leaves had blunt apices and long, broad sheaths. The

clumps were flowering rather sparingly, with approximately 160 inflorescences per square metre, and the anthers were hidden by the tepals and did not appear to be releasing pollen on to the water surface. *P. pectinatus* formed bright green clumps which at that time did not reach the surface of the water but were waving in the current. The plants were richly branched, and it was difficult to distinguish a single main stem. The leaves were narrower and more finely tapered towards the apex than those of *P. × bottnicus*, and their sheaths were shorter and more slender. Flowers were more frequent than on the clumps of *P. × bottnicus*, with approximately 600 inflorescences per square metre of water surface; the anthers exceeded the tepals, were clearly full, and dehisced on the surface of the water to release pollen which drifted downstream. Pollen from both taxa in this stand was subsequently examined microscopically, and the well-formed pollen of *P. pectinatus* contrasted with the misshapen pollen of *P. × bottnicus* (Table 2).

Measurements based on stems of *P. × bottnicus* and *P. pectinatus* collected at random from the mixed stand in the R. Tweed and the population of *P. × bottnicus* in the River Till are presented in Table 3 and Fig. 1. These clearly illustrate the vegetative differences between the two taxa at these sites. One complicating factor in comparing the two taxa is the ontogenetic variation which is shown by most members of subgenus *Coleogeton*: lower leaves (especially on short pioneer shoots) tend to be broader and more obtuse than upper leaves, and leaves on vegetative stems tend to be broader than those on flowering stems. The leaves at the apex of long flowering shoots of *P. × bottnicus* are, therefore, more like those of *P. pectinatus* than other leaves. *P. pectinatus* is a very variable species and some populations, such as those which were formerly segregated as *P. flabellatus* Bab., may be indistinguishable vegetatively from *P. × bottnicus*. However, the sessile stigmas of the hybrid are crucial in distinguishing it from all forms of *P. pectinatus* which may resemble it vegetatively.

In vegetative characters *P. × bottnicus* is usually closer to *P. × suecicus* than *P. pectinatus*, and in particular it resembles the robust forms of that hybrid in the R. Wharfe and R. Ure. Characteristic specimens of *P. × suecicus* from these rivers are illustrated by Dandy & Taylor (1946) and Preston (1995). *P. × bottnicus* and *P. × suecicus* are both sterile hybrids with obtuse leaves and sessile stigmas. The large lower leaf sheaths of *P. × bottnicus* might be thought to be derived from the similar sheaths of *P. vaginatus* (which they closely resemble) and thus provide a character to distinguish it from *P. × suecicus*, but some pioneer shoots of the latter have surprisingly large sheaths, as do some plants of *P. pectinatus*. The crucial distinction between *P. × bottnicus* and *P. × suecicus* lies in the fact that the leaf sheaths of the former are open whereas at least some of the sheaths of *P. × suecicus* are closed and tubular at the base. Data for selected populations are provided in Table 4. In interpreting this table it should be remembered that a closed sheath is an unambiguous character, whereas a sheath may be recorded as open because it actually is open, or because it is closed for an undetectably short distance above the base, or because it is a closed sheath which has split. Nevertheless, the data in Table 4 (which are based on the dissection of young and apparently intact sheaths) demonstrate that in some *P. × suecicus* populations all the sheaths are tubular, whereas others consist of plants with a mixture of open and tubular sheaths.

The following key to the British and Irish taxa in subgenus *Coleogeton* can be used in place of that presented by Preston (1995, p. 133).

- 1a. All sheaths open to the base 2
- 1b. Some or all sheaths tubular at the base 3
- 2a. Mature leaves on the vegetative stems usually acute to finely acuminate at the apex; stigmas borne on a distinct style c. 0.2 mm long; pollen well-formed; fruits 3.3–4.7 mm *P. pectinatus*
- 2b. Mature leaves on the vegetative stems more or less truncate, rounded or obtuse at the apex; stigmas sessile; pollen misshapen; fruits not developing *P. × bottnicus*
- 3a. Stems branched at base, otherwise unbranched or very sparingly branched; all sheaths tubular at the base; stigmas sessile; pollen well-formed; fruits 2.2–2.8(–3.2) mm *P. filiformis*
- 3b. Stems usually sparingly or richly branched above the base; all sheaths tubular at the base or some tubular and others open and convolute; stigmas sessile or borne on a distinct style; pollen misshapen; fruits not developing *P. × suecicus*

TABLE 1. COMPARISON OF SOME CHARACTERS OF *POTAMOGETON FILIFORMIS*, *P. PECTINATUS*, *P. × SUECICUS* (*P. FILIFORMIS* × *P. PECTINATUS*) AND *P. × BOTTNICUS* (*P. PECTINATUS* × *VAGINATUS*) FROM THE BRITISH ISLES, AND *P. VAGINATUS* FROM SCANDINAVIA

	<i>P. filiformis</i>	<i>P. × suecicus</i>	<i>P. pectinatus</i>	<i>P. × bottnicus</i>	<i>P. vaginatus</i>
Leaf sheaths	Tubular	Tubular or some tubular, some open	Open	Open	Open
Short, broad stem leaves differing from branch leaves	Absent	Sometimes present	Sometimes present	Present	Present
Apex of branch leaves	Obtuse to acute	Subacute to acuminate	Acute to acuminate	Truncate to acute	Obtuse to acute
Ligules (mm)	5–15	7–24	5–15	6–17	0.5–4
Stigmas	Sessile	Sessile or stalked	Stalked	Sessile	Sessile
Pollen	Fertile	Sterile	Fertile	Sterile	Fertile
Fruit (mm)	2.2–2.8(–3.2)	–	3.3–4.7	–	2.6–3.8

TABLE 2. POLLEN STAINABILITY OF *POTAMOGETON PECTINATUS* AND *P. × BOTTNICUS* FROM A MIXED STAND IN THE RIVER TWEED, AND *P. VAGINATUS* FROM FINLAND

Taxon	Locality	Date	Pollen stainability (%)
<i>P. pectinatus</i>	St Thomas's Island, Norham Mains	1995	86.6
<i>P. × bottnicus</i>	St Thomas's Island, Norham Mains	1995	0.8
<i>P. vaginatus</i>	Kuljunniemi, Saloinen, Raahe	1987	93.9
<i>P. vaginatus</i>	Martinlahti, Piehinki, Raahe	1992	95.9

Stainability based on at least 300 grains from at least three anthers stained with safranin in glycerol. Based on material of *P. pectinatus* and *P. × bottnicus* collected by the authors and herbarium specimens of *P. vaginatus* collected by J. Särkkä (OULU and herb. J.Särkkä).

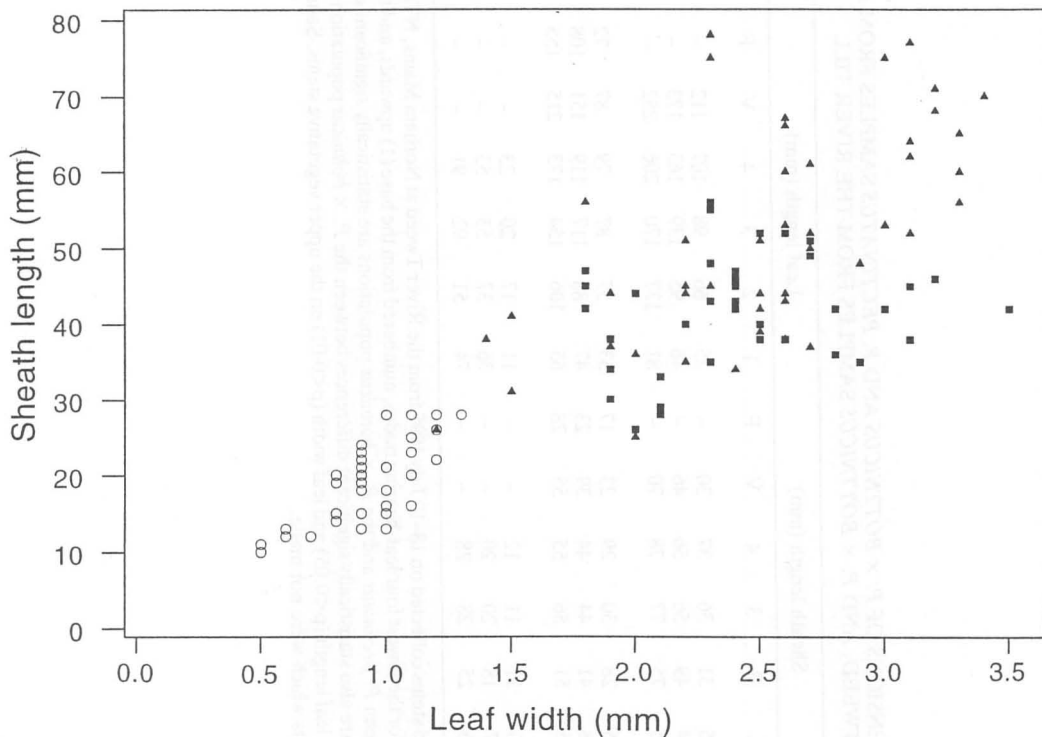


FIGURE 1. Sheath length (mm) plotted against leaf width (mm) for *Potamogeton × bottnicus* and *P. pectinatus*, based on measurements at the lowest four leaf-bearing nodes of randomly sampled fresh vegetative stems collected on 18–19 July 1995. Samples of *P. × bottnicus* collected from the River Tweed at Norham Mains (solid squares; $n = 40$) and the River Till below Twizel Bridge, NT/883.433 (solid triangles; $n = 46$). Samples of *P. pectinatus* (open circles; $n = 43$) collected from the same site as the River Tweed *P. × bottnicus*.

COMPARISON OF *P. × BOTTNICUS* WITH *P. VAGINATUS*

In Europe *Potamogeton vaginatus* is restricted to Norway, Sweden and Finland. We are not aware of a detailed description of the European plant in English, and therefore include one here. The following description has been drawn up primarily from Finnish material in OULU and in the private herbarium of J. Särkkä, supplemented by specimens from Finland and Sweden in BM, CGE and LTR. As it is based entirely on dried specimens, it is likely to under-estimate the range of variation of the species, especially in features such as stem length, and it lacks characters which cannot be deduced from pressed plants. The illustration of *P. vaginatus* in Fryer & Bennett (1915) is based on

TABLE 3. SHEATH AND LEAF DIMENSIONS OF *P. × BOTTNICUS* AND *P. PECTINATUS* SAMPLES FROM A MIXED STAND IN THE RIVER TWEED, AND *P. × BOTTNICUS* SAMPLES FROM THE RIVER TILL

	Sheath length (mm)						Leaf length (mm)						Leaf width (mm)					
	1	2	3	4	V	F	1	2	3	4	V	F	1	2	3	4	V	F
<i>P. × bottnicus</i> (R. Till)																		
Minimum	25	31	36	37	30	—	25	66	98	107	112	—	1.2	1.5	1.4	1.5	1.1	—
Mean	44	49	56	56	46	—	46	95	139	163	173	—	2.5	2.5	2.6	2.5	2.2	—
Maximum	65	75	77	78	70	—	81	137	170	206	252	—	3.3	3.3	3.4	3.2	3.1	—
<i>P. × bottnicus</i> (R. Tweed)																		
Minimum	26	28	30	29	23	17	33	57	87	79	87	72	2.0	1.8	1.8	1.8	0.8	0.8
Mean	38	41	44	44	39	23	47	88	117	119	151	108	2.5	2.5	2.4	2.4	1.8	1.1
Maximum	46	51	56	55	55	28	65	106	154	173	215	155	3.2	3.5	3.0	2.8	2.5	1.3
<i>P. pectinatus</i> (R. Tweed)																		
Minimum	10	11	11	12	—	—	11	17	20	23	—	—	0.5	0.5	0.5	0.6	—	—
Mean	17	18	20	20	—	—	36	37	53	53	—	—	0.9	0.9	0.9	0.9	—	—
Maximum	26	25	28	28	—	—	74	51	92	91	—	—	1.2	1.2	1.2	1.3	—	—

Measurements based on randomly sampled stems collected on 18–19 July 1995 from the River Tweed at Norham Mains, NT/923.493, and River Till below Twizel Bridge, NT/883.433. Values are provided for the lowest four leaf-bearing nodes, numbered from the base (1) upwards, and the upper nodes of vegetative (V) and flowering (F) stems. The differences between *P. pectinatus* and the *P. × bottnicus* populations are statistically significant except those for leaf length at node 1 (Mann-Whitney U test, $p < 0.001$). There are also statistically significant differences between the *P. × bottnicus* populations themselves for leaf length at node 4 ($p < 0.05$), and for sheath length ($p < 0.05$), leaf length ($p < 0.05$) and leaf width ($p < 0.01$) on the upper vegetative stems. Sample size: 7–12 (nodes 1–4), 20–33 (V) and 12 (F). A dash indicates measurements which were not made.

TABLE 4. SHEATH MORPHOLOGY OF POPULATIONS OF *POTAMOGETON* × *BOTTNICUS* AND *P.* × *SUECICUS* FROM THE BRITISH ISLES

Taxon	Locality	Grid ref.	No. of sheaths examined		
			Open	Tubular	Total
<i>Potamogeton</i> × <i>bottnicus</i>	R. Till, Twizel Bridge, v.c. 68	NT/88.43	60	0	60
	R. Tweed, Norham Mains, v.c. 68	NT/92.49	68	0	68
<i>Potamogeton</i> × <i>suecicus</i>	R. Wharfe, Harewood Bridge, v.c. 64	SE/26.78	37	21	58
	Loch Fitty, v.c. 85	NT/12.91	0	21	21
	R. Lossie, v.c. 95	NT/2.6	0	20	20
	Loch of Strathbeg, v.c. 95	NK/08.58	17	25	42
	Little Loch Borve, v.c. 110	NF/91.81	2	13	15
	Loch a'Chaolais, v.c. 110	NF/89.78	22	14	36
	Loch an Duin Bhig, v.c. 110	NF/75.46	1	21	22
	Loch Bhruist, v.c. 110	NF/91.82	5	34	39
	Loch of Langamay, v.c. 111	HY/74.44	4	12	16
	Loch of Clickimin, v.c. 112	HU/46.41	15	15	30
	Lough Gill, v.c. H1	Q/61.13	5	58	63
Rosapenna, v.c. H35	C/11.38	17	23	40	

correctly identified Swedish material, although the British records of this species cited in the same work are erroneous.

Rhizomes to at least 0.45 m long, 1.0–6.0 mm in diameter. Stems up to at least 1.6 m long, 1.2–5.5 mm in diameter near the base, with 1–5 branches emerging from most of the leaf sheaths on the main stem, some or all of these branches long and richly branched; nodal glands absent. Scales 18–70 mm long present on the lowest 0–3 nodes of the stem, clasping the stem throughout their length or with the distal part free, incurved and leaf-like or with rudimentary leaves at the apex. Submerged leaves linear; leaves on the main stem 17–82 × 0.7–2.5(–3.3) mm, 13–67 times as long as wide, 0.5–2.2 times as long as the sheath, more or less canaliculate, truncate, rounded or obtuse at the apex, the midrib bordered on each side by 2–4 inconspicuous lateral veins; mature leaves on the branches 39–125 × 0.3–0.8(–1.25) mm, (30–)100–420 times as long as wide, (1.4–)2.0–6.2 times as long as the sheath, obtuse or more or less acute at the apex, the midrib bordered on each side by an inconspicuous lateral vein. Floating leaves absent. Leaf sheaths green with hyaline margins and ligules, open, sometimes convolute, the sheaths on the main stem 16–80 × (1.5–)2.0–7.0 mm, more or less inflated, with ligules 0.5–3.0 mm, the sheaths on the branches 15–30 mm, slightly inflated at the base of the larger branches, otherwise tightly enclosing the stem, with ligules 2.5–4.0 mm. Turions absent. Inflorescences (25–)35–55(–80) × 3–5 mm; peduncles (33–)45–140(–165) mm, very slender, flexuous. Flowers 9–20, in 5–9(–11) groups of (1–)2, the group more or less evenly spaced approximately 5–10 mm apart at maturity; carpels 4, the stigmas sessile. Fruits 2.6–3.8 × 1.8–3.0 mm, olive green or brown; beak 0.1–0.3 mm, ventral, subventral or subapical, verruciform. Vegetative reproduction by tubers 40–50 mm long formed on the rhizome is described and illustrated by Hagström (1916) and Elven & Johansen (1984).

P. vaginatus is more likely to be mistaken for *P. pectinatus* than for *P. filiformis*, as it is a robust, richly branched plant with open leaf sheaths. It differs from *P. pectinatus* in its distinctive habit, with short, broad, blunt leaves borne on large inflated sheaths on the main stem. The branches emerge from these sheaths, and are often leafless close to the sheaths but richly branched above, giving rise to a mass of leafy shoots. The branch leaves are much more like those of *P. pectinatus* than those on the main stems, with narrower sheaths and longer, narrower leaves but with apices which are more obtuse than those of that species. A further difference lies in the short ligules, which are often less than 1.5 mm long on the stem leaves and together with the more or less hyaline upper edge of the sheath form a “dog collar” at the top of the sheath. The mature inflorescences of *P. vaginatus* have a distinctive appearance, as the pairs of flowers on the axis of the inflorescence are more or less evenly spaced, although the proximal two pairs tend to be further apart and the distal two pairs nearer together than the others. A more critical difference from *P. pectinatus* lies in the sessile rather than stalked stigmas. The fruits of *P. vaginatus* are intermediate in size between those of *P. filiformis* and *P. pectinatus*, and the stigmas persist as a very small boss at the distal end.

TABLE 5. SPECIES ASSOCIATED WITH *POTAMOGETON* × *BOTTNICUS* IN TEN QUADRATS RECORDED IN THE RIVER TWEED AND RIVER TILL

	Quadrat no.									
	16	26	23	22	20	21	25	19	17	18
<i>Potamogeton</i> × <i>bottnicus</i>	10	10	10	10	6	6	5	9	7	8
<i>Ranunculus</i> × <i>kelchoensis</i>			2	1	7	7	9		5	
<i>Potamogeton perfoliatus</i>				2	5					
<i>Ranunculus penicillatus</i> subsp. <i>pseudofluitans</i>						5				4
<i>Potamogeton pectinatus</i>								5		
Bare substrate (%)	0	0	0	5	20	5	0	8	35	20
Substrate	s	s	s	s	s	s	s	s	m	s
Water depth (cm)	55	35	20	30	25	25	20	45	20	25

Based on 1 × 1 m quadrats recorded on 18–19 July 1995 at R. Till below Twizel Bridge, NT/883.433 (quadrats 16–18) and R. Tweed S. of St Thomas's Island, Norham Mains, NT/923.493 (quadrats 19–23, 25–26). Cover-abundance of plants estimated on the Domin scale. Substrates recorded as s (stones) or m (mixture of fine sediment, stones and rocks). The identity of the *Ranunculus* taxa is discussed in the text.

As *P. pectinatus* and *P. vaginatus* are similar, the hybrid *P.* × *bottnicus* is not easy to identify on morphological grounds. However, the plants from the Rivers Tweed and Till differ from *P. vaginatus* in the absence of the characteristic habit of that species (although they grow in a very different habitat from that of *P. vaginatus* in the Gulf of Bothnia), in the longer ligules, especially on the lower stem leaves, the shorter inflorescences and the sterile pollen.

ISOZYME EVIDENCE

The isozyme evidence for the identity of *P.* × *bottnicus* is derived from work which we have reported in detail elsewhere (Hollingsworth *et al.* 1996a, b). In this study, 26 populations (447 plants) of *P. pectinatus*, 13 populations (270 plants) of *P. filiformis* and eleven populations (275 plants) of *P.* × *suecicus* were analysed. Although most of these samples were collected in Britain, material of *P. filiformis* from Sweden and *P. pectinatus* from Sweden and Crete was also included. In addition, we collected material from two populations (32 plants) of *P.* × *bottnicus* from the Rivers Till and Tweed and from a single population of *P. vaginatus* (24 plants) from Sweden.

Two of the nine enzyme systems which we studied (G6PDH, LDH) proved to be invariant across all the taxa and therefore offer no evidence about their inter-relationships. For the remaining seven systems, *P.* × *suecicus* showed additive banding patterns consistent with the hypothesis that it is a hybrid between *P. filiformis* and *P. pectinatus*. These systems included four which differed consistently between the putative parents in banding pattern (AAT, FBA and IDH) or in staining intensity (PGD).

The plants from the Till and Tweed differed in banding pattern from all the *P.* × *suecicus* populations studied in three enzyme systems (AAT, PGM and SKD). They also differed in staining intensity in a fourth system (PGD). The isozyme results are consistent with the hypothesis that these populations are of hybrid origin and that *P. pectinatus* is one of the parents, but do not support the suggestion that the other parent is *P. filiformis*. They are, however, explicable as the result of additive inheritance between *P. pectinatus* and *P. vaginatus*. The 32 plants sampled from the Till and Tweed showed no variation, suggesting that they may represent only a single clone (although the isozyme loci studied represent only a minute proportion of the total genome, and there may be variation which we have not detected).

DISTRIBUTION AND HABITAT

The plants referred here to *P.* × *bottnicus* are known from two rivers. Quadrats illustrating the vegetation in which they grow are presented in Table 5. In the River Till downstream of Twizel Bridge *P.* × *bottnicus* grows in rapidly flowing water 20–55 cm deep, where the plants are rooted in a stony substrate or in a mixture of fine sediment, stones and rocks. Beds of *P. perfoliatus* also grow in this stretch of river, and there are also stands of *Ranunculus* spp. A few fronds of *Lemna minor* are

found in places where rooted macrophytes reach the water surface and impede the flow of the river. *P. pectinatus* does not occur in this stretch of the river, but it does grow elsewhere in the River Till. At Ford Bridge, 13–14 km upstream of the *P. × bottnicus* colony, *P. pectinatus* is found with *Myriophyllum spicatum*, rooted in fine silt. *P. pectinatus* is also found in the River Tweed at its junction with the River Till, some 1.5 km downstream of Twizel Bridge, where it grows in a sandy substrate. *P. filiformis* is not recorded from the River Tweed or any of its tributaries.

The lower stretches of the River Tweed are difficult to survey, and we have not been able to examine the entire length of the river. We know of only one colony of *P. × bottnicus*, in a swiftly flowing stretch of river on the south side of St Thomas's Island. Here it grows in some quantity in water 15–45 cm deep, rooted in a substrate of stones. *P. pectinatus* is occasionally mixed with *P. × bottnicus* but usually grows nearby as separate clumps. *P. × bottnicus* also grows with clumps of *Ranunculus* spp. and is occasionally associated with small quantities of *P. crispus* and *P. × salicifolius*. *P. × bottnicus* is absent from deeper stretches of the river immediately upstream and downstream of this colony; these areas are characterised by large beds of the broad-leaved species *P. lucens* and *P. perfoliatus* and their hybrid *P. × salicifolius*. There are earlier records of "*P. × suecicus*" from stretches of the Tweed between the River Till and St Thomas's Island (including some herbarium specimens now re-identified as *P. × bottnicus* and cited below). The hybrid is often washed up by the edge of the river downstream of St Thomas's Island, and we have regularly found it in flotsam at Union Bridge. Existing records and our own fieldwork suggest that *P. × bottnicus* has a restricted distribution in the lower stretches of the river.

The *Ranunculus* plants in the River Tweed and its tributaries are difficult to identify as they include at least three sterile hybrids of uncertain parentage (Holmes & Whitton 1975b). The most frequent associate of *P. × bottnicus* at St Thomas's Island is a very robust sterile *Ranunculus* hybrid with capillary leaves which have rather few segments, and intermediate and laminar leaves on some (but not all) stems. This is the plant which Holmes & Whitton (1975a, b) refer to as "*R. fluitans* × ?" and which appears to us to be the hybrid subsequently described by Webster (1990) as *R. × kelchoensis* (*R. fluitans* × *R. peltatus*). Robust *Ranunculus* plants which grow with *P. × bottnicus* in the R. Till resemble this hybrid in most characters, but we have not seen any intermediate or laminar leaves on this population. Nevertheless, we have also (albeit rather tentatively) referred these to *R. × kelchoensis*. At both sites there is also a less robust *Ranunculus* with bushier capillary leaves and no laminar leaves. This closely resembles *R. penicillatus* subsp. *pseudofluitans* and is named as such in Table 5. However, it is less vigorous than typical material of that taxon and we did not collect any fruiting plants, so we cannot rule out the possibility that it is a sterile hybrid which has *R. penicillatus* subsp. *pseudofluitans* as one parent.

The herbarium specimens of *Potamogeton × bottnicus* from Britain that we have seen, or collected, are listed below:

ENGLAND: Cheviot, v.c. 68: River Tweed, Bankhead, Loanend, 30 August 1942, G. Taylor (BM, E). Right bank of River Tweed, Norham, NT/901.477, 3 August 1972, N. T. H. Holmes (BM). South bank of River Tweed, Norham Mains, NT/920.496, 20 September 1971, N. T. H. Holmes (BM). River Tweed near Tweed Villa, Norham, NT/893.467, 25 May 1974, G. A. Swan (BM). River Tweed opposite St Thomas's Island, Norham Mains, NT/919.494, 25 May 1974, G. A. Swan (BM). River Tweed S. of St Thomas's Island, Norham Mains, NT/923.493, 19 July 1995, R. J. Gornall, P. M. Hollingsworth & C. D. Preston (Preston 95/43) (BM, CGE, E, LD, LTR). River Till below Twizel Bridge, Tillmouth Park, Twizel, NT/885.434, 15 May 1972, N. T. H. Holmes (BM). River Till below Twizel Bridge, NT/883.433, 25 June 1992, P. M. Hollingsworth & C. D. Preston (Preston 92/88, 92/89) (BM, CGE, LTR); —, 26 August 1994, P. M. Hollingsworth & C. D. Preston (Preston 94/210, 94/217) (CGE, E, LTR); —, 18 July 1995, R. J. Gornall, P. M. Hollingsworth & C. D. Preston (Preston 95/45) (BM, CGE, LTR).

SCOTLAND: Berwicks., v.c. 81: River Tweed above Union Bridge, Hutton, 30 August 1942, G. Taylor (BM).

P. × BOTTNICUS IN EUROPE

The centre of diversity of *Potamogeton* subgenus *Coleogeton* in Europe is the Gulf of Bothnia, where all three European species occur, and where the three possible hybrids have all been

reported, *P. filiformis* × *P. pectinatus* (*P.* × *suecicus*), *P. filiformis* × *P. vaginatus* (*P.* × *fennicus* Hagstr.) and *P. pectinatus* × *P. vaginatus* (*P.* × *bottnicus*). A thorough understanding of *P.* × *bottnicus* in Europe would require a detailed study of the subgenus in this area. We have not had the opportunity to make such a study, so we have restricted our remarks to two topics. These are the lectotypification of *P.* × *bottnicus*, which is necessary in order to justify the use of this binomial, and the identity of *P.* × *meinshausenii*, a robust plant described as the hybrid between *P. pectinatus* and *P. vaginatus* from rivers in Europe south of the range of *P. vaginatus*, and therefore a potential parallel to the British *P.* × *bottnicus*.

LECTOTYPIFICATION OF *P.* × *BOTTNICUS* HAGSTR.

In his description of *P.* × *bottnicus*, Hagström (1916) mentioned material from three localities. C. W. Fontell first discovered the plant near Jakobstad, Finland, but although he published a description of the plant (Fontell 1902, 1903, 1909) he did not give it a binomial. In addition to this locality, Hagström reported the hybrid from two Swedish localities, Tynderö near Sundsvall in Medelpad and Hernösand to Angermania. Hagström also mentioned a specimen from a Russian site, but as he only identified this as either *P.* × *bottnicus* or *P.* × *fennicus*, this plant need not be considered further.

We requested type material of *P.* × *bottnicus* from a number of herbaria (BM, C, H, LD, OULU, RIG, S, TURA) and located possible syntypes from all the localities cited by Hagström. These collections are listed below, preceded by the name given originally to the material by the collector if this is apparent from the label.

A. *P. pectinatus* × *vaginatus*. Östrobottnia media. Pedersöre. Sandön prope Jacobstad in mare, 15 July 1898, C. W. Fontell (C). Apparent duplicates with less detailed labels at LD (ex herb. J. O. Hagström), S.

B. *P. pectinatus* × *vaginatus*. Ostrobottnia media: på sandbotten invid Sandön i Bottniska viken, 18 July 1899, C. W. Fontell (TURA).

C. *P. pectinatus* × *vaginatus*. Ostrobottnia media. Pedersöre. På sandbotten invid Sandön, 19 September 1900, C. W. Fontell (TURA).

D. Medelpad. Tynderö, undated, K. A. Holm (LD). Determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. bottnicus* m. in mscr.) by J. O. Hagström, 1 May 1909.

E. *P. vaginatus*. Suecia: in prov. Ångermanland, in mari ad oppidum Hernösand, freto australi, 62°, 37' lat. bor, 29 July 1899, G. Tiselius, Pot. scand. no. 207 (S). Determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. bottnicus* Hagstr.) by J. O. Hagström, 1910.

Two other collections may be mentioned. A specimen at LD collected as *P. pectinatus* by J. A. Sandman on 20 July 1884 at Karlö, Ostrobottnia borealis, was determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. bottnicus* m.) by Hagström on 8 October 1906 but is not cited in the protologue. Secondly, specimens collected by E. af Hällström from Kuolajärvi, Finland, on 29 August 1910 and distributed from H were initially determined as *P. filiformis* × *vaginatus* by Hagström but redetermined by him as *P. pectinatus* × *vaginatus* in 1920, after the publication of the binomial *P.* × *bottnicus*. Some of these specimens bear modern labels on which the date of the redetermination is not apparent.

The lectotype of *P.* × *bottnicus* should be selected from collections A-E above. We have chosen collection D. Although this is undated and has a modern label, it also bears a note signed by Hagström and dated 1 May 1909. P. Lassen has kindly provided an approximate translation:

This plant ought to be among the most fine and precious in your herbarium. Because it is the hybrid *P. pectinatus* L. × *vaginatus* Turcz. (*P. bottnicus* m. in mscr.). It is not known before from Sweden, but from the Finnish coast of the Gulf of Bothnia. I have eagerly looked for it in herbaria and am happy to have found it now from the Swedish side. Please make a trip to Tynderö this summer and try to find its growing-place. There is a locality for *P. vaginatus* there and there it should be sought. I believe the Reverend Holm would like to accompany you, because he is evidently a keen botanist. Possibly you could also find there the hybrid *P. filiformis* × *vaginatus* as well as *P. filiformis* × *pectinatus*!

The lectotype conforms to Hagström's description of the hybrid, and the citation "m. in mscr." clearly links it to the protologue. Curiously, Hagström did not describe the morphology of the

sheaths despite the fact that he usually stressed the taxonomic importance of closed as opposed to open stipules and sheaths. However, we dissected twelve young sheaths of specimen D, all of which were open, and the carpels have sessile stigmas. We therefore conclude that it is indeed *P. pectinatus* × *P. vaginatus*.

Of the other collections, A also has open sheaths (26 dissected, 23 open, three inconclusive) and is also referable to *P. pectinatus* × *P. vaginatus*, although all the specimens lack flowers. There is no direct evidence that Hagström saw collections B and C. Specimen B is probably erroneously identified as *P. pectinatus* × *P. vaginatus*. We dissected 31 sheaths of which 27 were open but two appeared to be distinctly tubular (two were inconclusive), but it must be admitted that the interpretation of the sheath morphology of old herbarium specimens is not easy, even after the material has been rehydrated. We found no evidence to doubt the identity of C. Collection E bears Hagström's determinavit slip as *P. × bottnicus*, but of the 15 sheaths we dissected six were tubular and five open (with four inconclusive), and this plant is therefore a hybrid of *P. filiformis* (possibly *P. filiformis* × *P. vaginatus*).

The nomenclature and typification of *P. × bottnicus* can be summarised as follows:

Potamogeton × bottnicus Hagstr., *Kungl. Svenska Vet.-Akad. Handl.* 55(5): 52 (1916). Lectotype: Medelpad. Tynderö, undated, K. A. Holm (LD), designated here. Hybrid formula: *P. pectinatus* L. × *P. vaginatus* Turcz.

THE IDENTITY OF *P. × MEINSHAUSENII* JUZ.

Juzepczuk (1955) reported *P. pectinatus* × *P. vaginatus* from the River Pudostj near Gatchina, S.W. of St Petersburg, Russia. This grew "in aqua frigida e pura fluminis (celeriter fluentis)". It was originally discovered by K. F. Meinshausen, who had collected it on several occasions between 1887 and 1896, but named it *P. pectinatus* var., *P. flabellatus* and, subsequently, *P. vaginatus*. Juzepczuk gave his plant the binomial *P. × meinshausenii*, distinguishing it from *P. × bottnicus* by a number of characters including its much more robust habit, wider sheaths, longer leaves and longer inflorescences. Although he accepted that both *P. × bottnicus* and *P. × meinshausenii* were hybrids between *P. pectinatus* and *P. vaginatus*, he had a number of reasons for giving the Russian plant a new binomial including the fact that *P. × bottnicus* is a product of recent hybridisation and grows with its parents, whereas the Russian plant is probably a very ancient and relict clone growing in the absence of closely related species. *P. × meinshausenii* has subsequently been reported by Galinis (1977) from lakes and a number of strongly flowing rivers near Trakai and Vilnius in Lithuania. Both the Russian and the Lithuanian sites for the hybrid are well south of the current distribution of *P. vaginatus*.

Isotypes of *P. meinshausenii* were widely distributed, and we have seen them in **BM**, **E** and **H**. The appearance of this hybrid is extremely similar to that of the British *P. × bottnicus*. At first we thought that these populations represented a parallel situation to the one we have described in the Rivers Tweed and Till, citing them as such in Hollingsworth *et al.* (1996a). However, we have subsequently examined the material more closely and find that the sheaths of *P. × meinshausenii* are consistently and manifestly tubular (17 examined). The stigmas are sessile and the pollen appears to be sterile. These characters suggest that *P. × meinshausenii* is referable to *P. × suecicus*, but the very robust sheaths which are clearly tubular differ from those of the British populations of *P. × suecicus*, which have sheaths with a very thin, hyaline adaxial side which has to be dissected very carefully in order to establish its tubular nature. An isozyme study of *P. × meinshausenii* would be rewarding. Whatever its identity, the morphology of the sheaths rules out *P. × bottnicus*, unless the type population is displaying a character found in neither of the parental species.

DISCUSSION

Dandy & Taylor (1946) first identified plants from the Rivers Ure, Wharfe and Tweed as *P. × suecicus*. Their paper was based on a very detailed study of material from the Wharfe and Ure in Yorkshire, which Taylor collected repeatedly from different sites along these rivers over a period of

six years. By contrast, they only knew the plant from the Tweed from Taylor's collections made at two sites on a single day (the population in the Till was not discovered until later). Bance's (1946) detailed anatomical studies of *P. × suecicus*, which provided powerful support for Dandy & Taylor's hypothesis, was based exclusively on material from the Wharfe and the Ure.

The identification of *P. × suecicus* from the Yorkshire rivers has been supported by recent studies (Hollingsworth *et al.* 1996a). However, the morphological and isozyme evidence reviewed in this paper have thrown great doubt on the previous identification of *P. × suecicus* in the Till and Tweed. Plants of *P. × suecicus* either have all the leaf sheaths tubular or a mixture of tubular and open sheaths, whereas the sheaths of the plants in the Till and Tweed are consistently open. If only morphological evidence were available, one might argue that this merely represents one extreme in the range of variation of *P. × suecicus*. However, the isozyme evidence has virtually ruled out this possibility. We must admit, however, that one cannot use isozyme evidence to categorically disprove a suggested parentage of a hybrid growing in the absence of one or both parents, as it is impossible to rule out the possibility that the hybrid may have been the product of parental genotypes which have not been detected. Despite these caveats, the suggestion that the Till and Tweed plants are *P. × suecicus* is scarcely tenable in the light of recent evidence.

We have published the identification of the Till and Tweed plants as *P. × bottnicus* as all the evidence we have is consistent with this hypothesis, and we cannot come up with any other explanation of the data. However, we regard the identification as a hypothesis to be tested by future work rather than an established fact. Further isozyme studies involving *P. vaginatus* and *P. × bottnicus* from the Gulf of Bothnia, and other molecular studies, would be likely to provide valuable additional evidence.

If we assume that our identification of the Till and Tweed plants as *P. × bottnicus* is correct, how can we account for its presence in these rivers? The Quaternary history of many *Potamogeton* species is relatively well known, as their fruits are often preserved in lake sediments (Godwin 1975). The same evidence is not available for sterile hybrids, and we can only speculate about their history. One possible explanation for the presence of *P. × bottnicus* in the Rivers Tweed and Till is that it is a relict hybrid. Although *P. vaginatus* is now restricted in Europe to Scandinavia, there is fossil evidence that it formerly grew as far south as Britain and the Netherlands. Fruits of *P. cf. vaginatus* have been found in deposits near Mundesley, Norfolk, which date from the first British glacial period, the early Anglian (West 1980). *P. vaginatus* fruits have been found in deposits from the last (Weichselian) glacial period at Sourlie, S.W. of Glasgow, dating from 30,000 BP (H. Bos & J. H. Dickson, pers. comm.), and from the Netherlands where they have been dated at 45,000 BP (Cappers 1993; Cappers *et al.* 1993). It seems unlikely that a sterile hybrid could have persisted in our area for 30,000 years, and the hypothesis that *P. × bottnicus* is a relict hybrid would be more plausible if there were evidence that *P. vaginatus* had survived in Britain after the last glacial period. An alternative explanation for the presence of *P. × bottnicus* in the Rivers Tweed and Till is long-distance dispersal of vegetative fragments, or seed resulting from a cross between *P. pectinatus* and *P. vaginatus*, from northern Europe.

It is not unusual for *Potamogeton* hybrids to occur in lakes or rivers from which one or both parents are absent, although these sites usually lie within the total range of both parents. There are, however, some *Potamogeton* and other hybrids in Britain which occur naturally outside the current distributional limit of the rarer parent. A striking parallel to *P. × bottnicus* is provided by *Carex recta*. This is usually treated as a species, but it is derived from hybridisation between *C. aquatilis*, which is widespread in northern Britain, and *C. paleacea*, which is confined in Europe to the coasts of Scandinavia and N.W. Russia (Faulkner 1972, 1973). Other hybrids which extend outside the limit of the rarer parent include *Circaea × intermedia* (Raven 1963), *Nuphar × spenneriana* (Heslop-Harrison 1953), *Potamogeton × suecicus* (Dandy & Taylor 1946) and *Ranunculus × levenensis* (Padmore 1957; Gibbs & Gornall 1976; Gornall 1987), although both parents of these hybrids are found in Britain. It has been suggested that all these hybrids may be relicts persisting by vegetative reproduction in an area where the rarer parent formerly grew or, in the case of *R. × levenensis*, in areas to which the seeds of *R. reptans* are thought to be repeatedly introduced by waterfowl. *Circaea × intermedia* is also capable of vegetative spread from these relict populations into disturbed habitats. In Ireland the fertile hybrid *Saxifraga × polita* is present north of the current range of *S. hirsuta*, and its presence is thought to indicate that *S. hirsuta* was once more widespread (Webb 1948, 1975). All these hybrids were known for many years before their origin was

appreciated, and their hybrid nature was often revealed by detailed morphological or genetical studies. This suggests that there may be further rather cryptic hybrids awaiting discovery in the British Isles.

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