

Notes on a hybrid spearwort, *Ranunculus flammula* L. × *R. reptans* L.

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ABSTRACT

Hybrid Creeping Spearworts (*Ranunculus flammula* L. × *R. reptans* L.) are given the binomial **Ranunculus × levenensis** Druce ex Gornall, **hybr. nov.** The character most useful in distinguishing the hybrid from its parents is the relative length of the achene beak. In the British Isles, hybrids occur sporadically on a few northern lake shores; they also occur in southern Scandinavia, northern-central Germany and the Alps. Their presence in the British Isles is due to hybridization between native *R. flammula* and plants of *R. reptans* that have probably been dispersed to these islands by waterfowl migrating from Iceland, Scandinavia and the northern part of the U.S.S.R.

INTRODUCTION

Padmore (1957) and Candlish [née Padmore] (1975) concluded that the Creeping Spearworts in the British Isles are hybrid derivatives of *Ranunculus flammula* L. and *R. reptans* L. (Ranunculaceae). This hybrid hypothesis, which can be traced to Druce (1913), has received substantial experimental support (Gibbs & Gornall 1976). Since most British collections are of the hybrid, rather than of *R. reptans*, it seems desirable to validate the binomial bestowed on them as a nomen nudum by Druce (1929a,b), so as to provide them with a convenient name.

DESCRIPTION

Ranunculus × levenensis Druce ex Gornall, **hybr. nov.**

TYPUS: Damp, sandy, and gravelly margin of Loch Leven, Kinross, Aug. 1912, *G. C. Druce* (Holotypus: **OXF!** Isotypi: **BM! E! OXF! STA!** and probably elsewhere). Specimens of artificially synthesized hybrids have been placed in **LTR** and **STA**.

Hybrida inter *Ranunculus flammula* L. et *R. reptans* L. Caulis procumbens, 0.50–2.75 mm diam., ad nodos radicans, internodiis saepe arcuatis. Folia basalia plerumque manifesta petiolata, lamina 5–20(–30) mm longa × 1–4(–10) mm lata, lineares vel spathulata usque anguste ovata. Flores 1–2(–6) in inflorescentia, 6–12(–15) mm diam., petalis obovatis, 1.2–3.0(–4.5) mm latis ad latissimam partem. Achenia ellipsoidea vel ovata, (1.0–)1.2–1.5(–1.7) mm longa (rostrum excluso), in rostrum plus minusve abrupte angustata, (0.15–)0.2–0.4 mm longum, longitudine achenii rostro c.5-plo longiore. Chromosomatum numerus 2n=32.

Hybrid between *Ranunculus flammula* L. and *R. reptans* L. Stems procumbent, 0.50–2.75 mm in diameter, rooting at the nodes, the internodes often arcuate. Basal leaves usually with a distinct petiole, the blades 5–20(–30) mm long × 1–4(–10) mm wide, linear or spathulate to narrowly ovate. Flowers 1–2(–6) per inflorescence, 6–12(–15) mm in diameter, the petals obovate, 1.2–3.0(–4.5) mm wide at the widest point. Achenes ellipsoid to ovate, (1.0–)1.2–1.5(–1.7) mm long (excluding beak), narrowed more or less abruptly to a beak, (0.15–)0.2–0.4 mm long, the ratio of beak length/achene length being about 1/5. Chromosome number 2n=32.

TABLE 1. CHARACTERS USED TO SEPARATE *RANUNCULUS*×*LEVENENSIS* FROM ITS PARENTS

Values quoted are means, standard errors (in brackets) and sample sizes. All measurements have been made on wild-collected, herbarium material. Equivalent data on cultivated plants can be found in Gibbs & Gornall (1976).

Character	<i>R. flammula</i>			
	erect	procumbent	<i>R. ×levenensis</i>	<i>R. reptans</i>
Stem diameter, mm	3.3 (0.14)	1.9 (0.08)	1.2 (0.06)	0.9 (0.03)
	109	58	81	87
Width of largest basal leaf, mm	10.2 (0.59)	4.8 (0.47)	1.7 (0.10)	0.9 (0.04)
	100	56	79	87
Diameter of largest flower, mm	13.5 (0.27)	10.4 (0.38)	9.2 (0.22)	8.8 (0.16)
	103	36	64	73
Width of largest petal, mm	4.6 (0.14)	3.3 (0.17)	2.5 (0.09)	2.1 (0.06)
	103	36	64	73
Achene beak length/achene length, %	11.1 (0.67)	11.1 (0.55)	18.7 (0.52)	26.8 (0.84)
	28	45	48	16
Habit in cultivation	erect	erect	procumbent	procumbent

The hybrid can usually be distinguished from its parents by a combination of the characters shown in Table 1. Unfortunately, most of these characters are highly plastic, and sometimes it can be particularly difficult to tell the hybrid from either the procumbent plastodeme of *R. flammula* (var. *tenuifolius* Wallr.) without a cultivation experiment, or from pure *R. reptans*, although Table 1 shows that the achene beak length/achene length ratio is reasonably diagnostic in both cases. Extreme difficulties arise in situations where the hybrid is a product of backcrossing to one parent or where it is a parental-type segregate. In such cases there is no easy answer except arbitrarily to treat all variants that fall within the established morphological ranges of the parents as pure

TABLE 2. LOCALITIES FOR *RANUNCULUS*×*LEVENENSIS* IN THE BRITISH ISLES

Asterisked (*) localities are major arrival centres for migrating waterfowl. Subsidiary centres are indented and are within c.25 km of the 'parent' centre.

LOCH AWE, Main Argyll, v.c. 98: GR 27/1.2 (LTR).

*LOCH OF STRATHBEG, N. Aberdeen, v.c. 93: GR 48/0.5 (E).

*LOCH LEVEN, Fife, v.c. 85: GR 36/1.9, 37/1.0 (BM, E, STA).

Lindores Loch, Fife, v.c. 85: GR 37/2.1 (STA)^a.

Luthrie Water Works, Fife, v.c. 85: GR 37/3.1 (STA)^a.

*SOLWAY FIRTH

Loch Ken, Kirkcudbrights., v.c. 73: GR 25/7.6 (E)

Loch Whinyeon, Kirkcudbrights., v.c. 73: GR 25/6.6 (E) (Stewart 1975).

Lochmaben, Dumfriess., v.c. 72: GR 35/0.8 (Scott-Elliot 1896)^a.

ULLSWATER, Cumberland, v.c. 70: near Pooley Bridge, GR 35/4.2 (BM); Aira Beck, GR 35/3.1 (BM)^a.

Westmorland, v.c. 69: Glencoyne Bridge, GR 35/3.1 (RNG); near Patterdale, GR 35/3.1 (LTR); Pooley Bridge to Sandwick, GR 35/4.2, (BM)^a.

CONISTON WATER, Westmorland, v.c. 69: south shore, GR 34/3.9 (LIV).

WINDERMERE, Westmorland, v.c. 69: Thompson's Holm Island, GR 34/3.9 (LIV)^a.

*LOUGH NEAGH area

Lough Fea, Co. Londonderry, v.c. H40, GR 23/7.8 (herb. Wareham River Lab.).

Intermediate specimens of uncertain identity (usually without fruits) have been collected from the following localities:

Cumberland, v.c. 70: Bassenthwaite Lake (BM)^a, Derwentwater (TCD)^a.

Westmorland, v.c. 69: Windermere, western shore, near ferry, GR 34/3.9 (BM, E)^a, River Leven, GR 34/3.8 (KDL)^a (Martindale 1886).

^a 19th century collections only; no 20th century material seen.

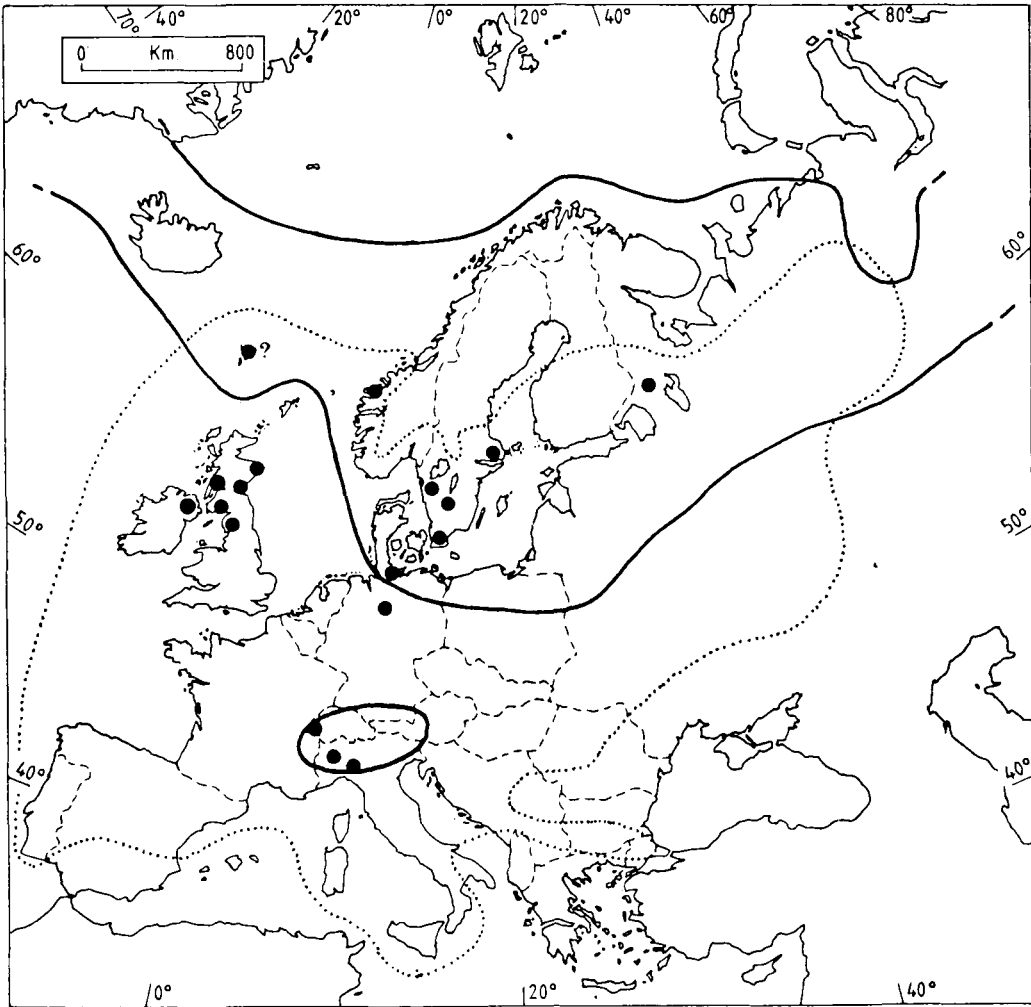


FIGURE 1. The distributions of *Ranunculus flammula* (.....), *R. reptans* (—) and *R. × levenensis* (●) in Europe. Ranges of the parents are taken from Meusel *et al.* (1965). Localities for hybrids are based on specimens housed at **BM**, **E** and **LTR**.

species, even if hybrids occur in the same population. The high levels of pollen sterility in natural hybrids that were reported by Padmore (1957) and Candlish (1975) were possibly due to chance environmental effects; Gibbs & Gornall (1976) found that hybrids, both synthetic and natural, form 16 bivalents at meiosis, show at least 88% pollen stainability, and set a full complement of fruit on cross-pollination.

DISTRIBUTION

The distributions of *R. × levenensis* and its parents in Europe are shown in Fig. 1. Except in the British Isles and northern-central Germany, it can be seen that *R. × levenensis* occurs where the ranges of its parents overlap, viz. in southern Scandinavia and the Alps.

Intermediate specimens from Iceland (**BM, STA**) need further investigation, as *R. flammula* is not known to be present in the Icelandic flora (Löve 1983). With this in mind, the possible occurrence of the North American *R. reptans* var. *ovalis* Torrey & A. Gray in northern Europe should be considered. Such plants are very similar to *R. × levenensis* in gross morphology.

The distribution of the hybrid in the British Isles is documented in Table 2. The earliest reference to *R. reptans* in the British Isles was by J. Hope (Balfour 1901) who noted its occurrence at Loch Leven in 1764, and there is a fine illustration of the plant from that locality on the frontispiece of *Flora Scotica* (Lightfoot 1777) – labelled *R. reptans* but clearly referable to *R. × levenensis*. Padmore (1957) believed there to be no pure *R. reptans* left in Britain, but as I shall suggest later, I think it is likely to occur, at least intermittently. If, however, *R. reptans* is not at present a regular member of our native flora, this raises the question of how the hybrid arose.

ORIGIN OF HYBRIDS IN THE BRITISH ISLES

There are three possible modes of origin for *R. × levenensis* in the British Isles: a) hybridization between native populations of *R. reptans* and *R. flammula*; b) introduction of foreign *R. reptans* and subsequent hybridization with native *R. flammula*; or c) dispersal of hybrid plants into these islands.

Padmore (1957) favoured hypothesis (a), believing that it was “probable that *R. reptans* was present in these islands in the Late Glacial and that relict populations survived at Loch Leven and Ullswater and became modified at a later date by hybridization”, leaving no genetically pure *R. reptans* in the British Isles. However, two pieces of evidence argue against this interpretation. Firstly, there is no unequivocal fossil evidence for the existence of *R. reptans* in the British Isles during the Late Glacial, unlike *R. flammula* which has a good fossil record dating from as far back as the Anglian stage (Godwin 1975). Secondly, both Loch Leven and Ullswater were fully covered by ice sheets during the last glaciation (Godwin 1975) and therefore these stations cannot be considered as refugia, although the species may have advanced there from the south, following the retreating ice.

The alternative hypotheses, (b) and (c), involve long-distance dispersal (Gibbs & Gornall 1976). Creeping Spearworts occur in a few, scattered localities, mainly in the north-east and points due south; they are strikingly absent from the shores of lochs in the northern and western Highlands, and from most of Ireland. In the case of the Irish and Scottish localities at least, the sites of *R. × levenensis*/*R. reptans* correspond to, or are very close to, major arrival centres for waterfowl migrating from Iceland, Scandinavia and the northern part of the U.S.S.R. (Table 2, Fig. 1). The birds arrive in north-eastern, rather than north-western, Scotland, and progress southwards through the central lowlands to the Solway Firth and suitable points beyond (Thom 1969; Boyd & Ogilvie 1969; M. Owen, pers. comm. 1985). This provides good, albeit circumstantial, evidence in support of the case for long-distance dispersal. The presence of *R. × levenensis* at the Cumbrian stations is a little harder to explain since, at least at present, the English Lakes are not important haunts of migratory waterfowl. However, they are likely to receive visits from stray birds roosting in the Solway Firth area; and in the past, they may have played host in the autumn to migrant Whooper Swans from Iceland (M. Owen, pers. comm. 1985).

Because Loch Leven has a well-studied waterfowl population, it is appropriate to use it as an example to elaborate on some additional points relating to long-distance dispersal. The loch is a major arrival point in Scotland for waterfowl and, at the peak of the autumn migration, it holds nearly 20,000 birds (Thom 1969; Allison & Newton 1974). *R. reptans* could be imported from different countries, corresponding to the departure points of the birds (Table 3). *R. reptans* is in fruit in September–October, and this fact, together with the data on numbers, arrival times and food preferences of the birds, suggests that the principal carriers of the species in recent years are likely to be Pink-footed Geese, Mallard and Wigeon (Table 3). The bulk of the Greylag Geese arrive during December, too late to have fed recently on achenes of *R. reptans*, which by then would have fallen from the plants.

According to Jones & Gillmor (1955), Pink-footed Geese leave central Iceland, where they feed on graminoids and seed-heads (Gardarsson 1972), in huge skeins as soon as the first snows fall.

TABLE 3. RECENT AUTUMN POPULATIONS OF THE MAIN, MIGRANT VEGETARIAN WATERFOWL AT LOCH LEVEN, FIFE
Compiled from Allison & Newton (1974) and Thom (1969).

Species	Origin ^a	Peak nos.	Date of first or main influx	Date of peak nos.
Pink-footed Goose	Is Gd	10,000–12,500	Sept.–Oct.	Sept.–Oct.
Greylag Goose	Is	4,000–5,000	?	Dec.–Feb.
Mallard	Is No Su Ge Be Ho	2,200–3,500	Aug.	Late Sept.
Wigeon	Is mainly No Su Fe Rs	1,000–2,000	Late Sept.	Jan.
Pochard	Da Europe Rs (B)	500–2,500	Aug.	Oct.
Tufted Duck	Is No Su Da Ge Ga Hb	up to 4,000	Mar.–Apr.	Late Sept.
Teal	Is No Su Po Ho Be Ga Rs	300–1,200	Aug.	Sept.–Oct.
Goldeneye Shoveler	No Su (north) Hs Ho Be Ge No Su Da	up to 1,000 up to 650	Sept.–Nov. Aug.	Mar.–Apr. Late Sept.
Whooper Swan	?	up to 430	Oct.	Nov.
Goosander	No Su Da	up to 150	Oct.	Feb.–Mar.
Pintail	Mainly Is	50	Late Aug.	Sept.–Oct.

^aTerritory abbreviations as in Tutin *et al.* (1964–1980); Gd=Greenland.

Some birds arrive in Britain the same day, others the day after departure; if ingested, spearwort achenes are therefore likely to be still inside the alimentary tracts of the birds on arrival at Loch Leven (M. Owen, pers. comm.). Vlaming & Proctor (1968) have provided evidence that some seeds can remain in a Mallard's gut for up to three days and be viable on excretion. At Loch Leven, Newton & Campbell (1970) observed that several thousand Pink-footed Geese arrive within two days of the first influx, and assemble on a mud bank in a few centimetres of water off the northern shore of St Serf's Island. Initially they drink and sleep on this mud bank, sometimes wading into deeper water, splashing and preening for long periods. It is during this initial period that any achenes present are likely to be excreted from the gut and/or washed from the body into the Loch. Within a day or so, many of the geese proceed southwards to the Solway Firth and beyond.

The distribution of Creeping Spearworts in the British Isles is therefore likely to depend on the arrival of a bird, carrying ripe fruits, at a place with a suitable habitat. To some extent then, occurrences will be a matter of serendipity. However, where major migration centres have suitable habitats, then *R. reptans* and/or its hybrid with *R. flammula* can be expected to occur in greater numbers. This is the case in Scotland, where Loch Leven and the Loch of Strathbeg are strongholds. Neighbouring freshwater bodies can also be expected to support the plants, although in smaller numbers and possibly on a less permanent basis. Similar long-distance dispersal may be involved in the origin of the hybrids in northern-central Germany.

Since the potential for long-distance dispersal has existed for about 10,000 years, i.e. the length of time that the waterfowl migration routes have been in existence (M. Owen, pers. comm. 1985), the introduction of spearworts is likely to be a repeated event. Given the northern origins of most of the migrating waterfowl, I suspect that pure *R. reptans* is imported, rather than the hybrid, which is both rarer and more southerly in its distribution. Indeed, a few collections referable to *R. reptans* have been made from Loch Leven (e.g. *Salmon*, 8th September 1896) and Ullswater (e.g. *Bickham*, 6th August 1917) (both **BM, E**). It is therefore my opinion that *R. reptans* is an intermittent member of the British flora and that, on arrival, it quickly interbreeds with *R. flammula*, or existing hybrids, to produce progeny which, on the loch shore, frequently closely resemble *R. reptans*.

However, since *R. reptans* is perennial, stoloniferous and partially self-fertile (Gibbs & Gornall 1976), there ought to be a population build-up of the species as well as of the hybrid, but this does

not seem to happen. Possibly one explanation is that the pure species is at a selective disadvantage compared with the hybrid when growing on the shores of lochs with fluctuating water levels. There is experimental evidence that the leaves of the hybrids are phenotypically more plastic than those of *R. reptans* (Gibbs & Gornall 1976), and that this plasticity in leaf shape is an advantage in a seasonally variable habitat (Cook & Johnson 1968).

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