A new British species, *Senecio eboracensis* (Asteraceae), another hybrid derivative of *S. vulgaris* L. and *S. squalidus* L.

A. J. LOWE

Centre for Ecology and Hydrology–Edinburgh, Bush Estate, Penicuik, Midlothian, EH26 0QB

and

R. J. ABBOTT

Division of Environmental & Evolutionary Biology, School of Biology, Mitchell Building, University of St. Andrews, St Andrews, Fife, KY16 9TH

ABSTRACT

A new species of *Senecio* from York, England, is described and named as *Senecio eboracensis*. Evidence is reviewed that this fully fertile, tetraploid species (2n = 40), which was first discovered in 1979, is a hybrid product of *S. vulgaris* (2n = 40) and *S. squalidus* (2n = 20), and is distinct from another tetraploid hybrid product, the stabilized introgressant, *S. vulgaris* var. *hibernicus*, and also from the hexaploid hybrid product, *S. cambrensis*. Other studies have shown that *S. eboracensis* is reproductively isolated from its parents due to a high level of selfing, phenological separation, sterility of products of back crosses to *S. squalidus* and reduced fertility of products of back-crosses to *S. vulgaris*. The morphological similarity of *S. eboracensis* to partially fertile, intermediate hybrid plants collected from other locations in the British Isles is discussed, and would indicate that it could arise polytopically following hybridisation between the two parent species. However, other such intermediate hybrid products do not appear to have persisted at their site of origin.

KEYWORDS: hybrid evolution, speciation, *Senecio,* Asteraceae, allopolyploidy, introgression.

INTRODUCTION

Since the introduction of *Senecio squalidus* L. (2n = 2x = 20) to Britain from Sicily in the early part of the 18th Century (Harris 2002), and its subsequent spread to many parts of the British Isles (Kent 1954–5; 1956; 1960; 1962–4; 1963; 1964a; 1964b; 1964c; 1964d and 1966; Crisp, 1972), there have been several notable instances of hybridisation with native *Senecio*, leading to the establishment of hybrid taxa and hybrid derivatives (Crisp 1972; Abbott & Lowe 1996). Some of the most prolific hybridisation events, and the only ones to generate fertile taxa in the wild, have been those with the common groundsel, *S. vulgaris* L. var. *vulgaris* (2n = 4x = 40). The triploid hybrid between the two species, *S.* × *baxteri* Druce (2n = 3x = 30) (Druce, 1893, 1907), has been recorded periodically when the parent species occur in large mixed populations (Crisp 1972; Benoit, Crisp & Jones 1975; Marshall & Abbott, 1980), and is almost completely sterile. The first fertile hybrid derivative to be reported was a radiate variant of common groundsel, *S. vulgaris* var. *hibernicus* Syme, which was initially found in Oxford in 1832 (Crisp 1972). However, Syme's (1875) description of this taxon was made on material from Cork, in Ireland, collected in 1866. This variant, of known introgressive origin (Ingram, Weir & Abbott 1980; Abbott, Ashton & Forbes, 1992), is now a common component of town and wasteland floras in many parts of the British Isles (Stace 1991).

A second fertile hybrid *Senecio* taxon that arose last century in the British Isles is the allohexaploid *S. cambrensis* Rosser. It was first discovered in 1948 by H. E. Green at Cefn-y-Bedd, North Wales (Rosser 1955), and is now commonly found in Wrexham and the surrounding area. *S. cambrensis* has also been reported from Leith, Edinburgh, Scotland, (Abbott, Ingram & Noltie 1983) and there is good molecular evidence for independent origins of this new hybrid species at these two locations (Ashton & Abbott 1992; Harris & Ingram 1992; Lowe & Abbott 1996). However, the Edinburgh lineage is now believed to be extinct (Abbott & Forbes, 2002).

A third fertile hybrid derivative was first recorded near York railway station (OS105 594 516) by R. J. Abbott and D. F. Marshall in 1979. The overall morphology of individuals in the population was intermediate between *S. squalidus* and *S. vulgaris* and plants were highly fertile (Fig. 1). Subsequent investigation of material raised in a glasshouse showed that this hybrid possessed 'showy capitula', had long achenes (3·0–3·5 mm), exhibited large leaves which were highly dissected with many lobes and had large, four-pored pollen (Irwin & Abbott 1992). Progeny of the hybrid bred true to type over several generations of cultivation under self and open-pollination conditions (Lowe 1996; Lowe & Abbott 2000). Cytological examination revealed that plants were tetraploid (2n = 4x = 40) and formed bivalents at meiosis (Irwin & Abbott 1992). Since 1979, this hybrid radiate groundsel has expanded its range in York to new sites located adjacent to Lendal Bridge (OS105 601 518) and at Dalton Terrace (OS105 593 512), and in 1991, York populations were estimated to contain some 250 individuals. Morphometric and isozyme analysis (Irwin & Abbott 1992) clearly demonstrated that the York plants were hybrid derivatives of *S. vulgaris* and *S. squalidus* and were distinct from the common inland radiate groundsel, *S. vulgaris* var. *hibernicus*. However, no formal description was made of the new taxon and it was referred to as 'York radiate groundsel'.

Recent work by Lowe and Abbott (2000) has indicated that 'York radiate groundsel' is not likely to be a first generation tetraploid hybrid of *S. vulgaris* and *S. squalidus*, but is probably the product of backcrossing an F1 hybrid to *S. vulgaris*. Analysis of random amplified polymorphic DNA (RAPD) variation (Lowe 1996; James 1999) has shown that it contains significantly more genetic material derived from *S. squalidus* than does *S. vulgaris* var. *hibernicus*. In regard to

FIGURE 1. Pressed specimen of *Senecio eboracensis* collected from the south embankment of the River Ouse, adjacent to Lendal Bridge, York, in May 1991 (K: holotype).

reproductive isolation, *S. vulgaris* var. *hibernicus* and 'York radiate groundsel' are both tetraploid and generate highly sterile triploid progeny when crossed with the diploid *S. squalidus* (mean pollen stainability of 36·6% and mean seed set of 0·63% for crosses involving 'York radiate groundsel' and mean pollen stainability of 33% and mean seed set of less than 0·01% for crosses involving var. *hibernicus*, Lowe and Abbott 2000). However, while *S. vulgaris* var. *hibernicus* is completely interfertile with var. *vulgaris* (Trow 1912), second generation offspring of crosses between 'York radiate groundsel' and var. *vulgaris* exhibit a significant reduction in seed set (F2 progeny set on average 58·8% seed compared to mean seed set for parental taxa which were over 80%, $P < 0{\cdot}01$, Lowe 1996; Lowe and Abbott, in review). The cause of this lowered fertility has not yet been fully established; however, the formation of univalents at meiosis in some F2 progeny suggests that mispairing between chromosomes may contribute to the observed reduction in fertility (Lowe 1996; Lowe & Abbott, in review). There are also some prezygotic breeding barriers between York radiate groundsel and *S. vulgaris* that reduce the frequency of inter-taxon crossing at field sites to well below 1·5% (percentage of seed arising from intertaxon crosses relative to total number of seed collected; Lowe 1996; Lowe and Abbott, in review). These prezygotic isolating mechanisms include predominant autogamy of both taxa and substantial differences in flowering time at field sites. All of these mechanisms have been shown to drastically reduce intertaxon crossing at sympatric sites and in common garden experiments (Lowe 1996, Lowe and Abbott, in review). This contrasts with the higher levels of inter-varietal crossing that have been recorded between *S. vulgaris* var. *vulgaris* and var. *hibernicus* (up to 35% of total open pollinated seed set at a field site, Marshall & Abbott 1984).

Taken overall, we consider that the tetraploid hybrid derivative found in York, which has been loosely termed 'York radiate groundsel', should be described as a new species. Therefore, we have taken the classical name of York, *Eboracum*, to derive the species name *eboracensis*; and a formal description of *Senecio eboracensis* Abbott & Lowe follows.

Senecio eboracensis R. J. Abbott & A. J. Lowe, **sp. nov**.

DIAGNOSIS

A *S. vulgari* L. var. *hibernico* Syme acheniis longioribus (2·5–3·5 mm longis, potius quam brevioribus quam 2·3 mm), foliis longioribus magisque lobatis et papillis stigmaticis 10–30 praesentibus (in var. *hibernico* absentibus vel brevissimis); a *S. squalido* L. et *S. vernali* Waldst. & Kit. acheniis longioribus rectis (2·5–3·5 mm, potius quam brevioribus quam 2·3 mm, neque curvatis), ligulis paulo brevioribus (5·0–6·0 mm longis potius quam longioribus quam 7·0 mm) et paulo angustioribus (1·2–1·7 mm latis, potius quam latioribus quam 1·8 mm); a *S. cambrensi* Rosser ligulis 8 (potius quam pluribus quam 10), capitulis angustioribus (3·5–4·2 mm, nec latioribus quam 5·0 mm) et ligulis angustioribus (in *S. cambrensi* c. 2·0 mm latis); a *S.* × *baxteri* Druce et *S.* × *helwingii* Berger ex Hegi acheniis longioribus ample formatis (potius quam sterillimis, seminibus fertilibus paene nullis evolutis) differt.

DESCRIPTION

An annual herb, up to 40 cm high (Fig. 2). Stem erect to ascending, occasionally with horizontal base section (up to 5 cm) and adventitious roots at base. Lower and upper leaves petiolate. Leaves up to 8 × 3 cm with oval outline, widest around the midpoint, irregularly pinnatifid with lobes reaching (0·125–)0·25–0·5(–0·75) of the way to the midrib (Fig. 3), with upper leaves generally the more deeply lobed, lobe pairs (3–)5–7(–8); on fertile soils and under glasshouse cultivation, leaves may be much more luxurious and highly dissected, up to 17 × 8·5 cm with lobes reaching (0·5–)0·75–0·875(–0·92) of the way to the midrib (Fig. 2); lobes making between a 90 degree and a 45 degree angle with the midrib, lanceolate to linear, (1–)3–5(–8) times as long as wide, with apex usually acute with a very small tooth; leaf margin throughout dentate or sometimes lobulate. Apical inflorescence comprises 3–7 florets in a grouped corymb, at first dense and leafy, but later laxer with peduncles 0·5–2·0 cm; peduncles elongating further when fruiting (up to 2·5 cm). Capitula broadly cylindrical (c. 10·0 × 4·0 mm), becoming slightly campanulate when ray florets

open. Involucral bracts sparse (4–8), elongated (c. 3·5–4·0 mm), usually without black tips. Ray florets (6) 8 (9), bright yellow, with ligules narrow and long (c. 5·0–6·0 mm long and 1·5 mm broad), occasionally becoming revolute. Stigmatic papillae 10–30. Pollen grains in polar view c. 30–35 μm when fully expanded, mostly four-pored. Achenes 2·5–3·5 mm long, straight, shallowly grooved, with ribs glabrous and grooves hirtellous; pappus white, silky, readily becoming detached from the fruit. Fl. 4–10. Occurs on disturbed ground, car park perimeters, pavement cracks and other urban/industrial sites. 2n = 40.

FIGURE 2. *Senecio eboracensis* raised under glass from seed collected at site adjacent to Lendal Bridge, York, in May 1991. Note the luxuriance of the leaves under high nutrient conditions.

FIRST RECORD

R. J. Abbott and D. F. Marshall 1979, waste ground near railway station, York (v.c. 64; OS105 594 516).

Type: England, York, v.c. 64, South embankment of River Ouse adjacent to Lendal Bridge (OS105 601 518) May, 1991, R. J. Abbott (*sine numero*; Fig. 1a) (holo. **K**, iso. **BM**, **E**, **LTR**, **OXF**, **RNG**).

DISTINCTNESS FROM CLOSELY RELATED *SENECIO* TAXA

Senecio eboracensis possesses a number of morphological features that distinguish it from several closely related *Senecio* taxa found in the British Isles. These are summarised in Table 1 and Fig. 3.

1. Common inland radiate groundsel, *S. vulgaris* L. var. *hibernicus* Syme. *S. eboracensis* may be distinguished in the field from inland forms of radiate groundsel by its longer achenes (<2·5 mm in *S. vulgaris*), and longer, more lobate and lanceolate shaped leaves (usually around 12 lobes in *S. vulgaris*). Primary peduncles are well developed and tend to be clustered at stem apex in *S. eboracensis* and are longer than those of *S. vulgaris*. Comparison of pollen grains (three-pored and 20–25 µm in diameter in *S. vulgaris*) and presence of stigmatic papillae (absent in *S. vulgaris*) may also be used in determination of herbarium material or fresh material in the laboratory. These characters, in addition to the presence of ray florets, may also be used to distinguish *S. eboracensis* from the eligulate *S. vulgaris* var. *vulgaris*.

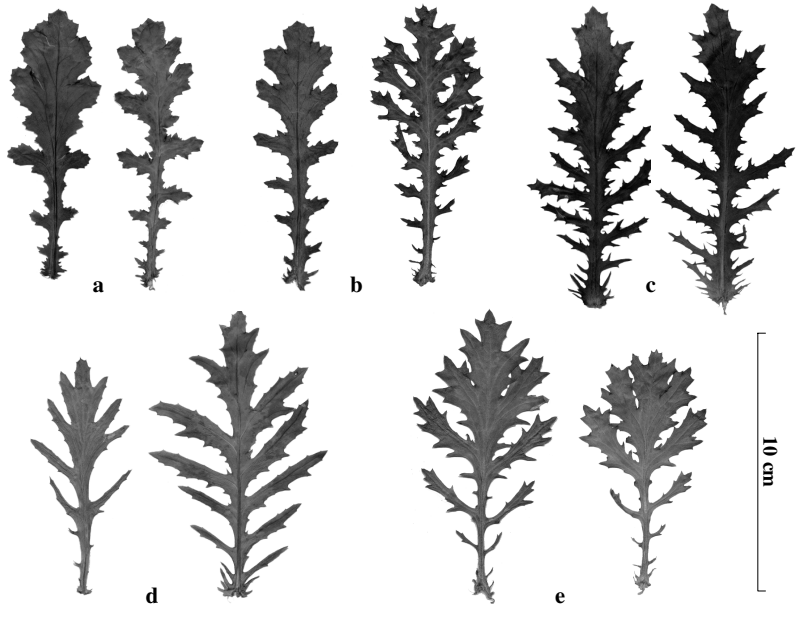

FIGURE 3. Leaf silhouettes of *S. vulgaris* and *S. squalidus* together with their hybrid derivatives: a. *S. vulgaris* var. *vulgaris*; b. *S. vulgaris* var. *hibernicus*; c. *S. eboracensis*; d. *S. squalidus*; e. *S. cambrensis*. Each taxon is represented by two leaves to give an indication of the range of variation expected in the field and a scale is shown in cm. Plants from which leaves were harvested were raised together under glass from seed collected from plants in the field in 1993. All field plants were sampled from York, except those of *S. vulgaris* var. *hibernicus*, which were from Edinburgh.

TABLE 1. LIST OF MAIN DIAGNOSTIC FEATURES THAT DIFFERENTIATE *S. EBORACENSIS* FROM ITS PARENTAL TAXA, *S. VULGARIS* AND *S. SQUALIDUS*, AND OTHER CLOSELY RELATED TAXA (DATA FROM ALLEN 1967; STACE 1991; LOWE 1996; LOWE & ABBOTT 1996; LOWE & ABBOTT 2000)

Character	*S. eboracensis*	*S. squalidus*	*S. vulgaris* var. *vulgaris*	*S. vulgaris* var. *hibernicus*	*S. vulgaris* ssp. *denticulatus*	*S. cambrensis*	*S.* × *baxteri*
Ray floret no. (length, mm)	8 (5–6)	12–15 (8–10)	0	7–13 (5)	7–13 (2–3)	8–15 (4–7)	8–13 (4–10)
Capitulum dimensions (mm)	10 × 4	10 × 5	10 × 3·5	10 × 3·5–4	11–13 × 3·5–4	11–13 × 4–5	10 × 2–3
Involucral bracts no. (length mm)	4–8 (3·5–4)	4–8 (3)	10–12 (3)	10–12 (3)	10–12 (3)	10–12 (4–5)	variable 4–12 (3–4)
Number of leaf lobes	13–19	9–13	9–13	9–13	9–13	9–13	9–13
Leaf length (cm)	8–13	5–9	7–11	7–11	5–10	10–15	5–11
Leaf shape	dissected	highly dissected to almost entire	spathulate	spathulate	spathulate, very hairy	dissected	highly dissected
Achene length (mm)	2·5–3·5	2·0–2·5	2·0–2·5	2·0–2·5	2·5–3·5	2·5–3·5	usually sterile (2·0–2·5)
Pollen grain diameter (μm)	30–35	20–25	20–25	20–25	20–25	30–35	very variable (10–40)
Number of pollen pores	4	3	3	3	3	4	2–6
Stigmatic papillae	10–30	40–60	0	0	0	30–50	0–30
Chromosomes (ploidy)	2n = 40 (4x)	2n = 20 (2x)	2n = 40 (4x)	2n = 40 (4x)	2n = 40 (4x)	2n = 60 (6x)	2n = 30 (3x)
Life history	ephemeral	annual, short-lived perennial	ephemeral	ephemeral	annual	ephemeral	ephemeral
Ecology/habitat	ruderal	ruderal	ruderal	ruderal	sand dunes and sea cliffs	ruderal	ruderal
Location	York	throughout British Isles	throughout British Isles	British Isles, with *S. vulgaris*	western coast	North Wales and Edinburgh	British Isles (infrequently)
Frequency	small populations	large populations	large populations	inter-mixed with *S. vulgaris*	small populations	small populations	isolated individuals

2. Coastal radiate groundsel, *S. vulgaris* L. ssp. *denticulatus* (O. F. Mueller) P. D. Sell. *S. eboracensis* may be distinguished in the field from coastal forms of radiate groundsel by its longer ray florets and longer, more lobate and lanceolate shaped leaves (usually around 12 lobes in *S. vulgaris*); the leaves are spathulate and covered in an arachnoid indumentum in ssp. *denticulatus*. Primary peduncles tend to be clustered at the stem apex in *S. eboracensis* and are longer and more numerous than those of *S. vulgaris* ssp. *denticulatus*. Comparison of pollen grains (three-pored and 20–25 μm in diameter in *S. vulgaris*) may also be used in determination of herbarium material or fresh material in the laboratory. In addition, *S. vulgaris* ssp. *denticulatus* is only found in Britain on dunes and sandy cliffs in the west and south-west and in the Channel Islands (Allen 1967).

3. Oxford ragwort, *S. squalidus* L.
Its longer, straight achenes (achenes, slightly curved and <2·5 mm in *S. squalidus*), more entire and lobate leaf and shorter ligules distinguish *S. eboracensis* from *S. squalidus*. As in *S. vulgaris*, pollen grains of *S. squalidus* are smaller and only three pored (20–25 μm).

4. Welsh groundsel, *S. cambrensis* Rosser
Both *S. cambrensis* and *S. eboracensis* are relatively robust, radiate plants, with large achenes (2·5–3·5 mm) and large (30–35 μm), mainly four-pored pollen grains. *S. eboracensis* possesses shorter involucral bracts (>11 mm in *S. cambrensis*), narrower capitula (4·0–5·0 mm diameter in *S. cambrensis*) and usually eight rather than the 13 ray florets typical for *S. cambrensis*. *S. eboracensis* also has fewer, shorter involucral bracts (less than 8 and less than 4 mm long) than *S. cambrensis* (more than 10 and greater than 4 mm long). Generally *S. eboracensis* exhibits narrower, less dissected and more lobate leaves than *S. cambrensis*, although there may be some variation in this character for both taxa under heterogeneous environmental conditions. Chromosome counts may be used for anomalous individuals, but the geographic location of a specimen is also a significant factor, as their ranges are not known to overlap.

5. *S. squalidus* × *S. vulgaris* = *S.* × *baxteri* Druce
Probably the best character to differentiate *S.* × *baxteri* from *S. eboracensis* is the high percentage of abortive fruit set by the former. However, at the end of the season, *S. eboracensis* may also set low numbers of seed, as is the case with other *Senecio* species (e.g. *S. sylvaticus*, *S. viscosus* and *S. cambrensis*, Rosser 1955). The low seed set of *S.* × *baxteri* is also manifest in the narrowness of its capitula (<3·0 mm), compared to *S. eboracensis* (typically 4·0 mm). Any full seed produced by *S.* × *baxteri* tends to be small (<2·5 mm) and is often deformed (straight achenes, 2·3–3·5 mm, in *S. eboracensis*). Also, the pollen of *S.* × *baxteri* has low acetocarmine stainability (less than 10%) and grains are highly irregular in size and pore number (10–45 μm and 2 to 6 pored), which is in contrast to the near 100% stainability and uniformly four-pored nature of *S. eboracensis* pollen. The leaf dimensions of *S.* × *baxteri* are generally smaller than those of *S. eboracensis* (typical length 8–3 cm), although some specimens of *S.* × *baxteri* may exhibit unusual leaf morphology. However, in a morphometric examination of *S. eboracensis* and *S.* × *baxteri* plants, the two taxa were easily distinguished using several leaf and capitulum characters (Lowe and Abbott 2000). Chromosome counts are also a good method for distinguishing the taxa. In addition, *S.* × *baxteri* usually occurs as a single ephemeral plant amongst its parent taxa (*S. vulgaris* and *S. squalidus*) and never as a population of morphologically similar individuals as does *S. eboracensis*.

6. Eastern groundsel, *S. vernalis* Waldst. & Kit. and *S. vulgaris* × *S. vernalis* = *S.* × *helwingii* Berger ex Hegi.
Another taxon which may be confused with *S. eboracensis* is *S. vernalis* Waldst. & Kit. This species is extending its range from the Continent into the British Isles (Kadereit, 1983). Diploid *S. vernalis* (2n = 2x = 20) can be distinguished from *S. eboracensis* by the possession of longer ray florets, smaller achenes and small, three-pored pollen. However, *S. vernalis* also hybridises with *S. vulgaris*, producing the sterile triploid *S.* × *helwingii* Berger ex Hegi (2n = 3x = 30). Although this hybrid has been recorded only rarely in the British Isles, it is likely to increase in abundance in the future if *S. vernalis* becomes more widespread. As with *S.* × *baxteri*, *S.* × *helwingii* sets practically no fertile fruit, its pollen is irregular and stainability is very low. The ray florets of *S.* × *helwingii* are also shorter (3·0 mm) than those of *S. eboracensis*.

A dichotomous key separating *S. vulgaris*, *S. squalidus*, and their hybrid derivatives (adapted from *Senecio* key presented in Stace, 1991) follows:

1 Ligules <8 mm or 0; capitula (excluding ligules) cylindical in flower, twice as long as wide..... 2
1 Ligules usually ≥8 mm, rarely shorter or 0; capitula (excl. ligules) campanulate in flower, <1·5 times as long as wide 5

2 Achenes ≤2·5 mm; pollen grains 20–25 microns across, 3 pored 3
2 Achenes >3 mm; pollen grains 30–36 microns across, mostly 4 pored 4

3 Ligules absent ..... *S. vulgaris* var. *vulgaris*
3 Ligules present (7–13) ..... *S. vulgaris* var. *hibernicus*

4 Involucral bracts > 9, usually >4 mm in length, ligules ≥8, leaf lobes <12 ..... *S. cambrensis*
4 Involucral bracts < 9, usually <4 mm in length, ligules 8, leaf lobes >12..... *S. eboracensis*

5 Leaves usually flat, with lateral lobes much longer than width of central undivided portion, usually glabrous or nearly so ..... *S. squalidus*
5 Leaves usually undulate, with lateral lobes approximately as long as width of central undivided portion, usually conspicuously pubescent ..... *S. vernalis*

RECORDS OF INTERMEDIATE HYBRIDS FROM AROUND YORK

It is not certain how long *S. eboracensis* has occurred in York. There are early reports of radiate groundsel from York, e.g. an individual was found under a beech hedge on the banks of the Ouse, South West of Lendal Bridge by T. Medd in 1958 (T. Medd, pers. comm., 1996) and a population of rayed groundsel was also seen by T. Medd on a building site at Acomb Road in 1960. However, detailed description of these specimens is lacking, and so it is not possible to determine whether these reports refer to var. *hibernicus* or *S. eboracensis*. The first record of *S. squalidus* near the city of York was made by E. J. Payne at Acomb on 2. 5. 1938 (T. Medd, pers. comm., 1996). It was not recorded again until 1948 when it was seen by K.G. Payne at Tadcaster Road (T. Medd, pers. comm., 1996), but by 1957 it had become widespread in York (Kent, 1964c). It is most probable that *S. eboracensis* did not arise much before 1979, when it was first noted, as no other individuals with its distinctive morphology were recorded previously by local botanists. It cannot be ruled out, however, that *S. eboracensis* may have originated soon after the arrival of *S. squalidus* in York (around 1948) or was introduced from another locality elsewhere.

York radiate groundsel *Senecio eboracensis* was first noted as different from var. *hibernicus* (which also occurs around York but seldom in sympatry), when it was collected in 1979 from the edge of a car park near York railway station (OS105 595 517) by R. J. Abbott and D. F. Marshall (Fig. 1). Since then, this hybrid derivative has been recorded at several sites in and around York. During the 1980s, populations of the plant were discovered along the River Ouse East, downstream of Lendal Bridge (OS105 606 513, J. Warren, University of York), on the river bank around Lendal Bridge (OS105 601 518, R. J. Abbott), around the Barbican centre (OS105 618 513, J. Warren), in the grounds of Lawrence St Church (OS105 613 513, T. Crawford, University of York) and at the site of the construction of the Bishopthorpe Road roundabout (OS105 602 509, T. Crawford). During the early 1990s, in addition to sites around Lendal Bridge, the species spread to the car park of the Dalton Terrace church (OS105 593 512, R. J. Abbott) and along Tanner Row (OS105 599 517, A. J. Lowe). At some of these sites population sizes were quite large (up to 100 individuals at Lendal Bridge and Dalton Terrace). However, city redevelopments and increased weeding appears to have lead to a more recent decline. The species' current distribution is limited (a census in 1999 found small populations of plants persisting around Lendal Bridge and along Tanner Row) and it needs to expand rapidly in number and size of populations to avoid the risk of extinction caused by stochastic environmental and demographic perturbations (see Levin 2000).

RECORDS OF INTERMEDIATE HYBRIDS FROM AROUND THE BRITISH ISLES

Over the past century, specimens of putative, semi-fertile hybrids between *S. vulgaris* and *S. squalidus* have been recorded from various locations throughout the British Isles (see Appendix 1, which lists reliable reports of such intermediate, semi-fertile hybrids that are probably tetraploid). According to Benoit *et al*. (1975), hybrid swarms that are distinct from *S. vulgaris* var. *hibernicus* have been recorded in at least 20 English and Welsh vice-counties and in three Irish vice-counties; these hybrid swarms were viewed as tetraploid and described as exhibiting "..lower seed- and pollen-fertility than the parent species, but fertile achenes are often larger, and stainable pollen-grains often have four rather than three pores." Crisp (1972) and Lowe (1996) have listed nearly 50 herbarium specimens/botanical reports from the British Isles of fertile intermediates between *S. vulgaris* and *S. squalidus*, and noted that such hybrid specimens have tended to be found in four main geographic areas: Cork, Cardiff/Bristol, North Wales/Cheshire/Merseyside and Oxford. Both workers used similar morphological criteria to identify hybrids, including: partial or full seed infertility, possession of ray florets, large capitula, long achenes (>2·5 mm) and a ragged or highly dissected leaf shape. Crisp also discovered a single fertile, tetraploid hybrid in London in November 1966 (Crisp & Jones 1970; referred to as S602 by Crisp, 1972). Progeny of this plant segregated for a wide range of morphological characters and fertility, but Crisp (1972) recommended that if a true breeding population of such intermediate hybrids were found in the future, these hybrids might warrant taxonomic recognition.

In more recent times, other workers, experienced in the taxonomy of the group, have also found what might be considered to be fertile hybrid individuals; for example, near Temple Meads railway station, Bristol, in 1986 (Warren 1987), at Avonmouth in 1991 (R. Milne, pers. comm., 1994), at Turnham Green, London in July 1992 (S. Harris, pers. comm., 1993) and at Passage West, Cork in 1991 (R. J. Abbott, unpub., 1993; Lowe, 1996). However, to our knowledge no other tetraploid hybrid individuals, apart from those at York, have become established as populations and bred true to type. From visits to sites where hybrid individuals have been recorded in the past, it would appear that many sites where large mixed populations had previously been abundant (Second World War bomb sites and industrial waste land) have since been redeveloped, and habitat loss may be one reason for the absence of these individuals at these and adjacent sites. Another possible explanation, favoured by Crisp (1972), is that, following the generation of fertile tetraploid hybrids, the genetic character of later generation progeny is diluted due to backcrossing to *S. vulgaris*, until only a few or single characters remain as evidence of past hybridisation, e.g. the ligule character of *S. vulgaris* var. *hibernicus*. Certainly the role of backcrossing in the origin of *S. eboracensis* is strongly suggested by resynthesis experiments (Lowe and Abbott 2000). Further evidence in favour of this hypothesis comes from the observation of herbarium specimens and botanical journal reports that show 'introgression sequences' at certain sites containing plants ranging from hybrid individuals intermediate in morphology between *S. vulgaris* and *S. squalidus* to those apparently differing from *S. vulgaris* only by the possession of ray florets (Crisp 1972; Lowe 1996). For example the following comments were made by Crisp on specimens from Bristol, Jamaica St/St James collected in July 1948 by I. W. Evans (506/4, **BRISTM**!): 'In view of their 'squalidus' type leaves, largish heads, large seeds (many of which are unset) and slight laxity of flowering habit, I would suggest that this plant is one of the intermediate stages referred to above. As such, it has no strict taxonomic name, being intermediate between *S. vulgaris* × *S. squalidus* (= *S.* × *baxteri* Druce) and *S. vulgaris* var. *hibernicus* Syme. Probably the best one could do is refer to them as segregating tetraploid *S.* × *baxteri* progeny. I am assuming them to be tetraploid from my experience of similar plants'.

Although no formal name has been used to describe any fertile, tetraploid intermediate hybrid specimens found previously, (i.e. of a type resembling 'York radiate groundsel'), G. C. Druce recognized that some of them were sufficiently distinct to warrant a new name, and loosely attached the name *Senecio advena* to them (Fig. 4; Crisp 1972). However, the name was never validly published and no type specimen exists (*Index Kewensis*). It is difficult to compare the various hybrid specimens that have arisen in the past directly to individuals of *S. eboracensis* from York. Many specimens share a number of morphological characters with *S. eboracensis* which differentiate them from other recognised hybrid derivatives. The route of origin of these other hybrid specimens is unknown; some may be tetraploid F1 hybrids between *S. vulgaris* and

FIGURE 4. Herbarium specimen collected by G. C. Druce from Burton-on-Trent in July 1930, and described by the *nomen nudum*, *Senecio advena* (**RNG**). This specimen is a fertile intermediate hybrid of *S. vulgaris* and *S. squalidus* and possesses a number of morphological features in common with *S. eboracensis*, including ray florets, long achenes and dissected leaves – but see text for discussion.

S. squalidus and others may be segregating elements in a hybrid swarm or introgression sequence (Lowe and Abbott 2000). Certainly, not all herbarium specimens and botanical journal reports of hybrid individuals (including those labelled as *S. advena* by Druce) should be classified as *S. eboracensis*. However, it should be acknowledged that hybrids similar in morphology to *S. eboracensis* arise periodically when the two parent species occur together, and thus a polytopic origin for *S. eboracensis* would be feasible.

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APPENDIX 1

The following specimens are fertile hybrids between *S. vulgaris* and *S. squalidus* and similar in morphology to *S. eboracensis*.

FROM AROUND OXFORD

Oxford (v.c. 23) 3.10.1867, W. J. Dyer '*Senecio squalidus* L.'; 'The dried specimens have very much the appearance of the rayed form of *S. vulgaris* L. M. J. Dyer proposes the name *parviflorus* for this variety. It grew sparingly amongst thousands of the normal form' *Rep. Bot. Exch. Club Brit. I*. 1867:9. **BM**! **K** (Crisp 1972). This plant appears to be sterile, it could also be *S.* × *baxteri*.

Oxford (v.c. 23) June 1886, G. C. Druce '*Senecio crassifolius* Willd'; 'resembles S602, but near to *S. vulgaris* var. *hibernicus*; pollen regular' Crisp, 1972. **BM**! **MANCH** (Crisp 1972).

Oxford (v.c. 23) 1887 'On waste ground (but rarely about Oxford)' G. C. Druce, *Rep. Bot. Exch. Club Brit. I*. 1887:184; Crisp 1972.

Oxford (v.c. 23) 1891 '*S. crassifolius* – J. G. Baker, *S.* × *baxteri* – G. C. Druce' *Rep. Bot. Exch. Club Brit. I*: 1891:337; Crisp 1972.

Burton-on-Trent (v.c. 39) July 1930, Herb. J. E. Lousley, Coll. G. C. Druce '*Senecio advena* Druce n.p.; Det. H. J. M. Bowen '*Senecio vulgaris* L.'; An S602 type' Crisp, 1972. **RNG**!

Didcot (v.c. 22) 1929 '*Senecio advena* Druce (a name used loosely by Druce to refer to plants of an intermediate nature); resembles S602' Crisp, 1972. **BM** (Crisp 1972).

FROM BRISTOL/CARDIFF

Bristol, University Rd. (v.c. 34) 2.3.1945, Herb. Gibbons & Bell 960 '*Senecio*, long spreading ray'; 'Rather strongly ribbed glabrescent achenes. I believe *S. squalidus* × *vulgaris*' N.J.S., 1946. **LTR**!

Bristol, Jamaica St. (v.c. 34) 19.3.1945, Herb. Gibbons & Bell 960 '*Senecio*, short tubular ray'; 'Too young for examination of achenes, but may be *S. squalidus* × *vulgaris* L.'N.J.S., 1946. **LTR**!

Bristol, University Rd. (v.c. 34) 23.4.1945, Herb. Gibbons & Bell 960 '*Senecio*, long strap ray'; 'Thick-ribbed glabrous or glabescent achenes. *S. squalidus L.* × *vulgaris* L.'N.J.S., 1946. **LTR**!

Bristol, Jamaica St. (v.c. 34) 20.4.1946, Herb. Gibbons & Bell 956 '*Senecio*, short tubular ray'; '*S. vulgaris* var. *radiatus*, I believe. The achenes seem to be those of *vulgaris*' N.H.S., 1946. **LTR**!

Bristol, Jamaica St/St James (v.c. 34) July 1948, Herb. I. W.Evans 506/4 '*Senecio squalidus* × *vulgaris'* P. Crisp, March, 1968. **BRISTM**!

Cardiff, Docks (v.c. 41) June, 1905, Ex Herb. H. J. Riddelsdell '*Senecio* Sp. B.' see *Rep. Bot Exch. Club Brit. I.* 1906: 228; 'Pollen large, some 4 pored, low stainability; ligules short and broad; leaves resemble *squalidus* type. Definitely S602 type' Crisp, 1972. **MANCH**, **CGE** (Crisp 1972).

Cardiff, Docks (v.c. 41) 15.5.1906, Ex Herb. H. J. Riddelsdell '*Senecio* sp. A.'; 'I believe this to be very near *S. vernalis*, Waldst. And Kit.' H. J. Riddelsdell 1906. *Rep. Bot Exch. Club Brit. I*.:227–228. 'Heads large, with small ligules; leaves resemble *S. squalidus*; heads clustered, and the general growth form resembles that of *S. vulgaris*' Crisp, 1972. **BM**! **LIVU**! **CGE** (Crisp 1972).

Llanduff (v.c. 41) 1.7.1910, Herb. H. J. Riddelsdell '*Senecio vulgaris*, L. Rayed-very short rays'. **BM**!

Llanduff (v.c. 41) 9.8.1912, Herb. H. J. Riddelsdell '*Senecio vulgaris* Linn. Rays ½ length'. **BM**!

Brigend, Glamorgan (v.c. 410 10.8.1946, Coll. R. P. Libbey 1391/2 '*Senecio vulgaris* L. var. radiatus Koch'; 'This is a hybrid; *S.vulgaris* × *squalidus*'. **LTR**!

FROM AROUND CORK

Cork, Boreenmana Rd. (v.c. H4) June 1895, Ex Herb. & Leg. R. A. Phillips 413 '*Senecio hibernica* Syme = *S.vulgaris* × *S. squalidus*'. **DBN**!

Cork, near Blackrock (v.c. H4) Dec. 1896, Herb. N. Colgan, Leg. R. A. Philips 413 '*S. vulgaris* × *squalidus*'; 'a small, hirsute, erect S602 type with large heads' Crisp 1972. **DBN**!

Cork (v.c. H4) 1903, Coll. N. Colgan 413 '*Senecio vulgaris* var. *radiatus*, grown in garden from seed gathered in Cork'. **DBN**!

Passage West (v.c. H6) 1907, M. Persse 6 '*Senecio vulgaris* rayed f.'; 'An intermediate in the *S. vulgaris* × *squalidus* to *S. vulgaris* var. *hibernicus* Syme introgression sequence' P. Crisp, April, 1969; 'Large plant with large broad ligules, large heads, leaves resembling *vulgaris* type, seed set and of medium length' Crisp 1972. **DBN**!

OTHER LOCATIONS

Denbigh (v.c. 50) 12.6.1948, Leg. E. P. A. Jones, Conf. S. E. Chandler & J. E. Lousley '*Senecio squalidus*'. **BM**! Could also be *S. cambrensis*.

Ewloe Green/Alltami, Flintshire (v.c. 50) 1.5.1977, L. D. Wallace, *sin numero* 'very robust plant'. **LIV** (S. Harris!)

Ffrith, Cefn-y-Bedd Rd. (v.c. 50) 12.6.1948, Leg. E. M. J ones, Det. J. E. Lousley 2660 '*Senecio vulgaris* × *squalidus* tetraploid'; 'yes a form with longer ray florets than previously seen' J.E.G. 30.9.1948. **BM**! Could also be *S. cambrensis*.

Glasgow, Strathclyde Univeristy (v.c. 77) 6.7.1974, R. P. Libbey 3243 '*Senecio vulgaris/squalidus* introgressant (long ligulate), garden grown from seed supplied by P. Hull. See P. Hull. 1974. *Watsonia*. 10(1): 69–75.'**LTR**!

Kings Lynn, Coddeshell Walk (v.c. 28) 16.6.1972, Coll. R. P. Libbey 2269, Det. G. Jones '*Senecio squalidus* × *vulgaris*'. **LTR**!

Kings Lynn, Hospital (v.c. 28) 30.4.1973, Coll. R. P. Libbey 2640 '*Senecio squalidus* × *vulgaris* (fertile hybrid), see sheet 2641 of putative parents'; 'The papillae on the stigmas are intermediate between those of *vulgaris* and *squalidus*, a few long, a few short on a partly swollen stigmatic head'. **LTR**!

Liverpool (v.c. 59) Aug. 1976, Coll. A. J. Coombes '*Senecio squalidus* × *vulgaris*?' **LIVU**! Small specimen, could also be *S. cambrensis*.

Oldham, Failworth (v.c. 59) 9.10.1962, Coll. C. E. Shaw '*Senecio vulgaris* L. × *Senecio squalidus* L. (= *S.*× *baxteri* Druce)'; 'N.B. this specimen is fertile'; 'ach[enes] 2·7 mm'. **K**!

Parkstone, Dorset (v.c. 9) 6.9.1945, Ex. Herb. J. E. Lousley '*Senecio vulgaris* L. × *S. squalidus* L.'; '*S.* × *baxteri*' Crisp, 1972. **BM**!

Plymouth, Devon (v.c. 3) 17.5.1945, Herb. J. E. Lousley, Leg. E. M. Phillips '*Senecio squalidus* L. × *vulgaris* L?' **RNG**!

Unstone, Derbys. (v.c. 57) 1956, '*Senecio vulgaris* × *S. squalidus*'. **LIVU**!