Hybrids in *Juncus* section *Juncotypus*, with a description of *J.* x *lancastriensis* (Juncaceae)

Clive A. Stace

Appletree House, Larters Lane, Middlewood Green, Suffolk IP14 5HB

Corresponding author: cstace@btinternet.com

Abstract

The differences between the five native species of *Juncus* section *Juncotypus* that occur in the British Isles are summarised, and the occurrence of five hybrids surveyed. The diagnostic morphological and anatomical details of the hybrids are presented, with emphasis on the endemic *J. balticus* x *J. inflexus*, which is described as ***J.* x *lancastriensis*** Stace and of which two nothovars are distinguished.

Keywords: *Juncus inflexus*, *Juncus balticus*, *Juncus effusus*, *Juncus conglomeratus*, *Juncus filiformis*, stem anatomy, Lancashire coast.

Introduction

The five native species of *Juncus* section *Juncotypus* Dumort. (subgenus *Genuini* Buchenau) in the British Isles are well exemplified by the commonest species of the genus, *J .effusus* L. (Fig. 1), which by the year 2000 had been recorded from 97% of the approximately 3859 hectads (10 x 10 km squares) (Preston *et al.*, 2002). The other species are *J. conglomeratus* L. (Fig. 2), *J. inflexus* L., *J. balticus* Willd. and *J. filiformis* L. (all shown in Fig. 3). These five differ from all other British species (in nine sections) in that their leaves, apart from the lowest inflorescence bract, are represented by brown sheaths (cataphylls) at the base of the stems. Sometimes in *J. filiformis* a single cataphyll has a short green blade. Species in all other sections have green leaves borne on and/or at the base of the stems. Section *Juncotypus* is perennial and rhizomatous, the rhizomes having long internodes which give rise to scattered stems in *J. balticus* and *J. filiformis*, or shorter internodes with many branches producing a clumped growth-habit in the other three species (Fig. 4). The stems are erect and cylindrical, and carry a single, usually rather compact inflorescence that is technically apical, but which appears to be lateral because it is displaced laterally by the lowest bract, which is also cylindrical and is effectively a continuation of the stem beyond the inflorescence (and has the same anatomy).

The five species are easily distinguishable (Stace, 2019), and their characters will not be repeated here, except that *J. effusus* and *J. conglomeratus* are frequently confused, partly because some Floras and identification guides rely solely on the degree of stem ridging to separate them. These characters are usually but not totally reliable, and counting ridges on a cylindrical stem is not easy. A clear difference is that the main (lowest) bract is somewhat opened out at its base in *J. conglomeratus* (Fig. 2), forming a point of weakness so that in autumn the bract often characteristically hinges over backwards or frontwards at that point (Fig. 2), whereas in *J. effusus* the bract is subcylindrical and scarcely opened out at its base, so that it

usually remains stiffly erect into winter or is bent irregularly by the winds. Both species exist as variants with either compact or diffuse inflorescences (e.g. Fig. 1; Stace, 2019). In the fresh state they are distinguishable with experience by the dull green stems with usually <30 longitudinal ridges counted just below the inflorescence (see below) in *J. conglomeratus*, as opposed to the bright green smooth stems in *J. effusus*. In the latter species, as the stems dry out, ridges (usually >30 in number, see below, and less prominent/sharp) appear. Other estimates of this feature can be obtained by cutting stem-sections and counting the major vascular bundles, or counting the subepidermal girders (see below). These three measures give slightly different sets of figures. The main bract of *J. conglomeratus* is also shorter, and occupies a smaller proportion of the total stem/bract height, than in *J. effusus*. Where the two species co-exist *J. conglomeratus* dies down more quickly in autumn, the main bract quickly browning, then bending over and often breaking off.

Figure 1. Inflorescences of *Juncus effusus* var. *effusus* (left), *J. effusus* var. *subglomeratus* DC (var. *compactus* Lej & Coutois) lateral view (centre) and abaxial view (right). All photos by Richard Stace

Figure 2. Inflorescences of *Juncus congomeratus.* Lateral view (left), abaxial view (centre left), with bract bend backwards (centre right), and with bract bent forwards (right). All photos by Richard Stace

Figure 3. Inflorescences of *Juncus inflexus* (left, Richard Stace), *Juncus balticus* (centre, Phil Smith) and *Juncus filiformis* (right, Mike Wilcox)

Figure 4. Rhizomes of *Juncus balticus* (left), *J. inflexus* (right) and their hybrid (centre)

Stem anatomy provides important features separating all five species, best displayed by cutting thin transverse sections with a razor-blade (Stace, 1970b). Working inwards from the epidermis there are three main zones: an outer palisade zone of living chloroplast-containing cells (chlorenchyma); a zone of parenchyma cells in which many vascular bundles are embedded and are surrounded or capped by a sclerenchyma sheath; and a central pith. Abutting on to the epidermis in the chlorenchyma, in all the species apart from *J. balticus*, are longitudinal subepidermal sclerenchyma girders, which are very conspicuous in transverse section. The larger ones sometimes join up with the sclerenchyma bundle-sheaths of some of the vascular bundles. In *J. conglomeratus* and *J. inflexus* particularly, their presence

coincides with the position of the external ridges. The four main distinguishing anatomical features of the stems are summarized below and in Fig. 5.

J. effusus (Fig. 5, top left)
Epidermal cells all ± same size
Subepidermal sclerenchyma girders 36-62 (mostly 40-55) in number (Chater, pers. comm.; Wilcox, 2010), linear to narrowly triangular in section, often stretching across chlorenchyma zone and joining up with some sclerenchyma bundle-sheaths; not causing epidermis to bulge externally to form stem-ridges in fresh state
Pith longitudinally continuous, dense
Pith-cells strongly stellate

J. conglomeratus (Fig. 5, top right)
Epidermal cells all ± same size, or sometimes slightly enlarged over girders
Subepidermal sclerenchyma girders 12-29 (mostly 15-25) in number (Chater, pers. comm.; Wilcox, 2010), more or less triangular in section, sometimes stretching across chlorenchyma zone and joining up with sclerenchyma bundle-sheaths; causing epidermis to bulge externally to form stem-ridges
Pith longitudinally continuous, usually less dense than in *J. effusus*
Pith-cells strongly stellate

J. inflexus (Fig. 5, centre left and right)
Epidermal cells markedly enlarged over girders, accentuating stem ridging
Subepidermal sclerenchyma girders mostly 10-18 in number (Wilcox, 2010), triangular to broadly triangular in section, often stretching across chlorenchyma zone and joining up with some sclerenchyma bundle-sheaths; causing epidermis to bulge externally to form strong stem-ridges
Pith regularly interrupted longitudinally, forming numerous and close septa across pith cavity
Pith-cells strongly stellate

J. filiformis
Epidermal cells all ± same size
Subepidermal sclerenchyma girders mostly c. 15-22 in number, compact, markedly wider in tangential than radial plane, not stretching across chlorenchyma zone and joining up with sclerenchyma bundle-sheaths; not causing epidermis to bulge externally to form strong stem-ridges
Pith longitudinally ± continuous, not dense
Pith-cells angular or balloon-shaped, not stellate

J. balticus (Fig. 5, bottom left and right)
Epidermal cells all same size
Subepidermal sclerenchyma girders absent
Pith longitudinally ± continuous, not dense
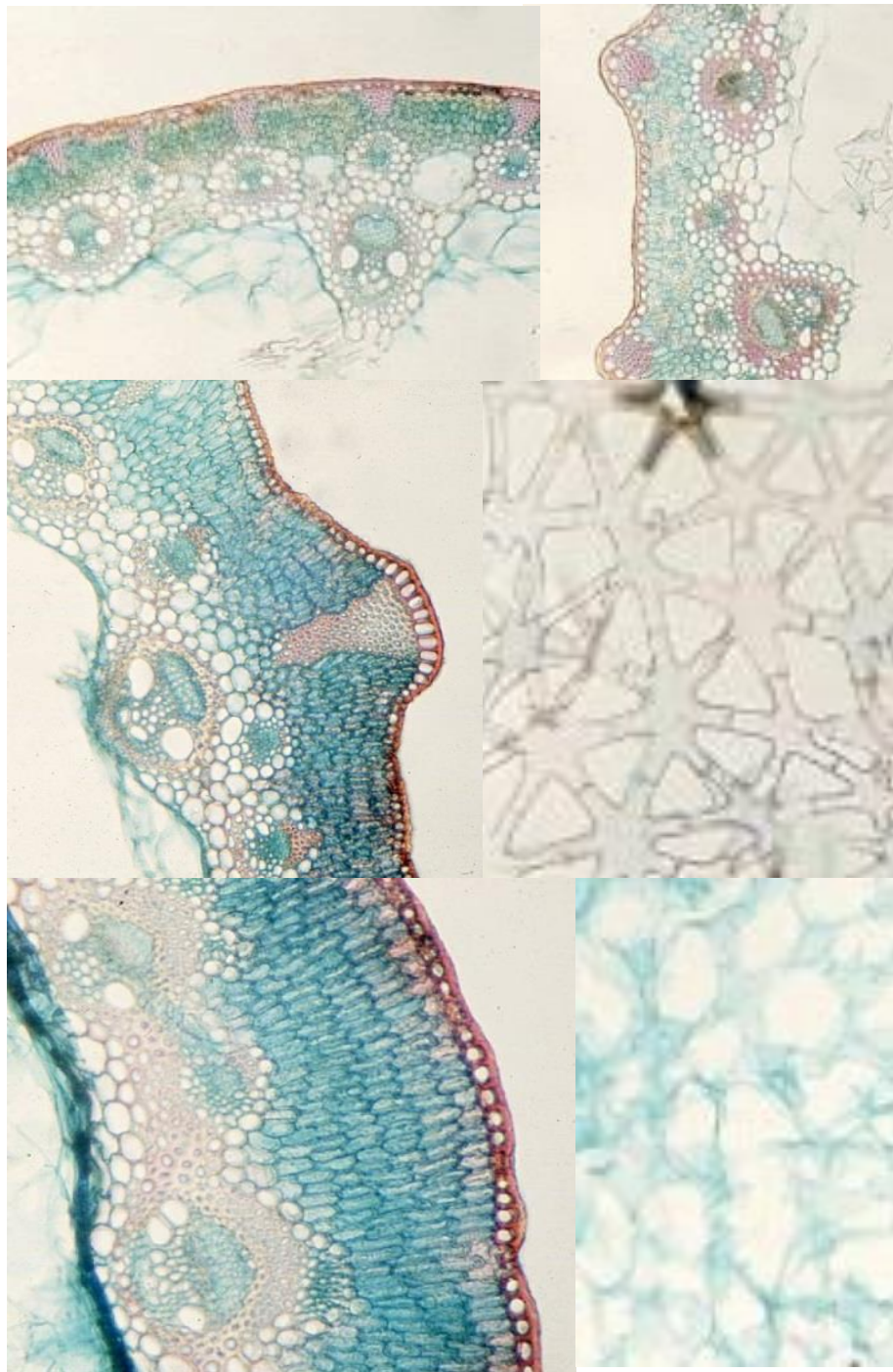Pith-cells angular or balloon-shaped, not stellate

Figure 5. Stem anatomy of *Juncus* taxa. Top left: *J. effusus*, showing slender subepidermal sclerenchyma girders and non-enlarged epidermal cells; Top right: *J. conglomeratus*, showing triangular subepidermal sclerenchyma girders and non-enlarged epidermal cells; Centre left: *J. inflexus*, showing large subepidermal sclerenchyma girders with overlying enlarged epidermal cells; Centre right: long-armed stellate pith-cells of *J. inflexus*; Bottom left: *J. balticus*, showing absence of subepidermal sclerenchyma girders and non-enlarged epidermal cells; Bottom right: balloon-shaped pith-cells of *J. balticus*

Occurrence of hybrids in section Juncotypus

Four hybrids involving four of the five species occur in Britain, a further one in Scandinavia, and there is a sixth dubious combination (Stace 1970a, 1970b, 1972, 1975a, 1975b; Stace et al., 2015).

Juncus effusus x *J. inflexus* (=*J.* x *diffusus* Hoppe) was described in 1819 and has been known in this country since at least 1843, originally being treated as a full species and not fully accepted as a hybrid until the 1880s. Although it is easily recognized (Figs. 6 & 7) after practice by intermediacy of inflorescence form and by shape and size of sclerenchyma girders, in the past it has often been misidentified, usually mistaken for sterile specimens of *J. inflexus* (which are not rare), and this still happens. Clifford (1959) discussed this problem in some detail. It is well scattered but not common throughout the British Isles as far north as the northern limit of *J. inflexus* in central Scotland. Early accounts noted the small capsules with few seeds, and several considered it to be a sterile hybrid. The seeds, however, although relatively few, are not sterile and are easily germinated. I have raised a vigorous F_2 generation which showed segregation of the parental characters, producing some plants much closer to the parental species. Moreover, in central France (Puy de Dôme) in 1969 I discovered many plants in an obviously segregating hybrid swarm; to my knowledge such a population has not been reported from Britain, where the hybrid usually occurs as isolated individuals in mixed populations. In Anglesey, however, in 1970 I found several plants of this hybrid that showed two distinct variants, one with bright green stems, the other with grey-green stems, but, in those situations where several plants have been found, studies sufficient to determine whether they are all F_1 individuals or a segregating population have apparently not been made.

Figure 6. Inflorescences of *Juncus* x *diffusus* (left), *J.* x *kern-reichgeltii* (centre, Richard Stace) and artificial *J. conglomeratus* x *J. inflexus* (right, Richard Stace)
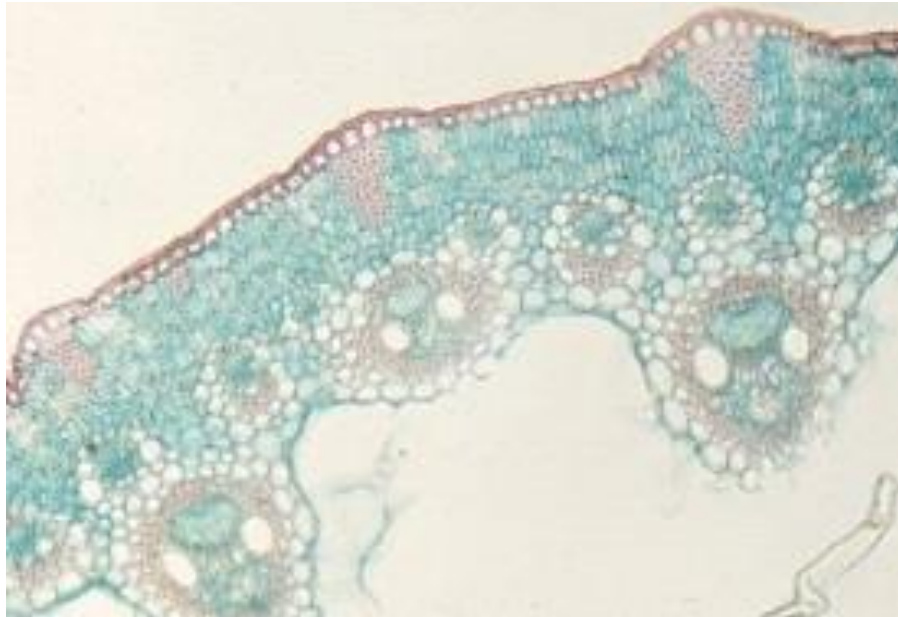
Figure 7. Stem section of *Juncus* x *diffusus*, showing intermediate subepidermal sclerenchyma girders

Juncus conglomeratus x *J. effusus* (=*J.* x *kern-reichgeltii* Jansen & Wacht. ex Reichg.) has a more chequered history (Fig. 6). It was not described validly until 1964, but there are scattered old British records going back over a century. However, determination was very uncertain and for long the existence of this hybrid in Britain was not accepted. I had seen no convincing examples up to 1971. Much of the evidence for the records was based on the supposed sterility of this hybrid, but sterility, of unknown cause, is common in plants of section *Juncotypus* (especially in *J. inflexus*), and the use of unreliable characters to separate the two parents which was prevalent in the mid-20th century (see above) did not help identification. However, Agnew (1968) reported this hybrid from the uplands of Snowdonia, and in 1971 I visited his locality in Cwm Idwal, where it occurs in a contiguous zone between stands of the two parents. Using the reliable bract character, as well as ridge number and prominence, and stem/bract ratio, there can be no doubt that Agnew was correct. The plants, however, are highly (perhaps fully) fertile, as noted by Agnew, and since then this observation has been confirmed in other localities scattered across most of the British Isles (Wilcox, 2010). Moreover, the hybrid also occurs in lowland areas and is probably under-recorded due to continuing uncertainty of determination, which is best carried out in the field where both parents coexist. Probably its greater frequency in upland areas is due to the larger number of suitable habitats there. In 2019, in the fenland of the Weerribben in the Netherlands, lying at less than 10 m either side of sea-level, I found the hybrid and both parents to be exceptionally abundant over several hectares. British records from before 1968 not supported by vouchers, and any claiming sterility, should not be accepted. I have grown a very extensive F_2 population from Cwm Idwal seed, which completely bridged the characters of the two parents (Stace, 1975a, pp. 82-83) and retained full fertility. A detailed analysis of wild populations was carried out by Wilcox (2010), who demonstrated extensive introgression in some mixed

populations. Due to back-crossing the whole range of intermediates between the two parents is often exhibited.

Juncus conglomeratus x *J. inflexus* (? =*J.* x *ruhmeri* Asch. & Graebn.) is accepted in several European countries but I know of no valid records for Britain. There are, however, unsubstantiated British records going back to the early part of the 20th century, many under the name *J.* x *leersii* T. Marsson, but in 1968 S. Snogerup examined the type of this name in Vienna (**W**) and found it to be *J. conglomeratus*. The application of the binomial *J.* x *ruhmeri* of course rests upon confirmation of its identity as this hybrid. The type, collected by G.F. Ruhmer from "Brandenburg, Friedeberg, zwischen Wildenow und dem Busch", was in Berlin (**B)** but was destroyed in the Second World War, so we shall probably never know its true identity. A specimen in **W** collected in 1965 as *J.* x *ruhmeri* by H. Melzer from Südkärnten, near Bleiburg Railway Station, Austria, was examined by S. Snogerup in 1978, and he confirmed its identity, saying on a label that the stem ridges are fewer and sharper than in *J.* x *diffusus*. But in 2017 M.P. Wilcox re-examined it (including stem sections) and concluded that it is *J.* x *diffusus* (Wilcox, 2017). Based on the number of stem ridges and sclerenchyma girders observed by me in these two hybrids and in the Melzer specimen, Wilcox's opinion prevails. In 2013/14 Wilcox obtained a few seeds from an artificial cross between the parents (*J. inflexus* as female parent); four plants were raised from this and are still in cultivation (Wilcox, 2015). The existence of this hybrid in the wild anywhere is still *sub judice*, and certain identification would be difficult.

Juncus balticus x *J. effusus* (=*J.* x *obotritorum* Rothm.) has been recorded from the Baltic coast twice. The first record was from what is now Kaliningrad, where it was described in 1893 as *J.* x *scalovicus* Asch. & Graebn. S. Snogerup, however, informed me (*in litt.*) that he examined the type and found it to be *J. balticus* x *J. filiformis,* hence a synonym of *J.* x *inundatus*. The hybrid was later described from near Rostock in north-eastern Germany in 1965 as *J.* x *obotritorum* Rothm. Snogerup and I have both examined the type and agree that it is *J. balticus* x *J. effusus*. The discovery of this hybrid by S. Taylor at Ainsdale, South Lancs, v.c. 59, England in 1933, and its subsequent history, naming and extinction, are detailed by Stace (1972) and updated by Smith (1984, 2006) and Smith & Lockwood (2016). By 1966 the original patch in a wet dune-slack measured about 40 x 20 m (Fig. 8), but in 1967/68 it was completely eradicated by the development of a holiday camp on the site. In 1966 and 1973 two other very small (no more than 1 x 1 m) patches were found by V. Gordon and E.F. Greenwood respectively about 9km south of the original at Hightown, but these too were soon eradicated, the first by new houses before 1974, the second by erosion around 1978. Fortunately living pieces were taken from the 1933 and 1973 wild sites and these are now established in wet dune-slacks in the Ainsdale National Nature Reserve. On the Continent the Rostock locality is still the only confirmed site.

Figure 8. Original site of *Juncus* x *obotritorum* at Ainsdale, 1967

Juncus balticus x *J. inflexus* has never been found outside Lancashire; its discovery by D.E. Allen at Birkdale, only about 2 km north of the original *J. balticus* x *J. effusus* colony (Figs. 9 & 10) in 1951 and subsequent history and naming are again detailed by Stace (1972) and updated by Smith (1984, 2006) and Smith & Lockwood (2016). A second colony was discovered independently by B. Blanchard about the same time about 4 km to the south of the first, in the Ainsdale N.N.R. near Freshfield (Fig. 11). This area of Lancashire (the Sefton coast, roughly between Crosby and Southport, South Lancs, v.c.59) is particularly rich in this section of *Juncus*, and supports the only English colonies of *J. balticus* itself (Stace, 1970a). A third colony of the hybrid was found by C.A. Stace in July 1966 outside this area, about 18km further north, on the Fylde coast (between Lytham St Annes and Blackpool, West Lancs, v.c. 60), in the Lytham St Annes Local Nature Reserve, in an area where *J. balticus* was once known but no longer occurs (Fig. 12). All three of these colonies measured at least 10 m across in 1970, and were still thriving into the next decade (Smith 1984). However, Smith (2006) reported that the Freshfield site had been lost in the late 1980s due to sand-blow which, together with colonising scrub (mainly *Salix repens*, *S. cinerea* and *Hippophae rhamnoides*), is a constant threat to the dune-slacks. The two remaining colonies were still thriving in 2015 (Smith & Lockwood, 2016), the Birkdale colony occupying 1260 m^2 and the Fylde colony 398 m^2. Material from the Freshfield and Fylde sites has been planted in other dune-slacks in the Ainsdale N.N.R., where they are now increasing. This paper provides a valid binomial for *J. balticus* x *J. inflexus*.

Juncus balticus x *J. filiformis* was named in 1839 as *J.* x *inundatus* Drejer. It is not known in Britain, where both species are quite rare and are not known to co-exist, but there are many sites for it in northern Europe.

Figure 9. Birkdale site of _Juncus_ x _lancastriensis_ nothovar. _lancastriensis_, 1969

Figure. 10. Birkdale site of _Juncus_ x _lancastriensis_ nothovar. _lancastriensis_, 1969, with Pauline Moorhouse indicating stem height

Characters of the hybrids

A rule of thumb in identifying hybrids is that they are generally intermediate between their parents and sterile. Both these presumptions are true and untrue to varying degrees in these rushes. Some generalisations may be made:

- The hybrids between _J. balticus_, which has elongated rhizomes, and the compact species _J. effusus_ and _J. inflexus_ have rhizomes at least as elongated as those of _J. balticus_.
- In hybrids between two species that both possess subepidermal sclerenchyma girders (_J. conglomeratus_ x _J. effusus_ and _J. effusus_ x _J. inflexus_), the size and number of girders is intermediate. But in crosses between a species without girders (_J. balticus_) and one with girders (_J. effusus_, _J. inflexus_ or _J. filiformis_) girders are completely absent.

275

Figure 11. Freshfield site of *Juncus* x *lancastriensis* nothovar. *lancastriensis*, 1968, now gone, with Eric Greenwood and John Tallis

Figure 12. Lytham St. Anne's site of *Juncus* x *lancastriensis* nothovar. *fyldensis*, 1969

- The enlarged epidermal cells over the girders evident in *J. inflexus* are sometimes apparent in its hybrid with *J. effusus* (Fig. 7), but are often conspicuous in its hybrid with *J. balticus* (Fig. 14), even though *J. balticus* and the hybrid have no subepidermal girders.
- *J. inflexus* alone has a septate (discontinuous) pith. In its hybrids with *J. effusus* and *J. conglomeratus* the pith is more or less continuous, but in the *J. effusus* hybrid it is less dense than in *J. effusus* itself and sometimes it shows irregular discontinuity. In its hybrid with *J. balticus* the pith is discontinuous in the Sefton hybrids (though much less regularly so than in *J. inflexus*) but continuous in the Fylde plants.
- In hybrids between *J. balticus*, which has angular or balloon-shaped pith-cells, and *J. effusus* or *J. inflexus*, which have stellate pith-cells with long arms, the

276

pith-cells are intermediate, being stellate but with much shorter arms (Fig. 14).

- Fertility covers a broad scale. *J. conglomeratus* x *J. effusus* is highly, perhaps fully, fertile; *J. effusus* x *J. inflexus* and *J. conglomeratus* x *J. inflexus* have a much reduced fertility; and the two hybrids of *J. balticus* are highly (though not completely) sterile. It is worth mentioning that in *Juncus* the pollen is dispersed in tetrads, and that in all the hybrids, even those highly sterile, the pollen appears perfectly normal and stainable. Moreover it germinates on and penetrates the stigma, but the pollen-tubes do not progress far (J.W. Grimes & C.A. Stace, unpubl.).

As may be deduced from the above list, the most important characters identifying the hybrids involve stem anatomy rather than external morphology. The main diagnostic characters of five of the hybrids are as follows; *J. balticus* x *J. inflexus* is covered in the next section.

J. effusus x *J. inflexus* = *J.* x *diffusus* (Figs. 6 & 7)
The inflorescence shape is slightly more like that of *J. inflexus*, with its mainly upswept branches, but the stem-pith is continuous, as in *J. effusus*, albeit usually less dense than in the latter. The other characters are more or less intermediate: the subepidermal sclerenchyma girders and therefore the external stem ridging are intermediate in number (mostly 30-42 according to Wilcox, 2010; c.18-45 according to Richards, 1962), size and shape; and the stems are neither bright green and glossy as in *J. effusus* nor glaucous as in *J. inflexus*. The characteristically enlarged epidermal cells overlying the girders of *J. inflexus* are sometimes apparent. Fertility is greatly reduced, but some seeds, which germinate readily, are usually produced.

J. conglomeratus x *J. effusus* = *J.* x *kern-reichgeltii* (Fig. 6)
The hybrid displays intermediate characteristics in the degree of opening of the base of the main bract, in the relative lengths of bract and stem, and in the duller green stems with an intermediate number of ridges which are usually visible even in the young fresh state (not completely smooth as in fresh *J. effusus*). The number of ridges was stated as (30)35-42(55) by Wilcox (2010) and 30-40 by Chater (pers. comm). The degree of compactness of the inflorescence depends upon that of its *J. effusus* parent. The hybrid is highly (perhaps fully) fertile and often gives rise to populations displaying the total range of morphology, so that a precise number of stem-ridges cannot be indicated.

J. conglomeratus x *J. inflexus* = ? *J.* x *ruhmeri* (Fig. 6)
Comments here are based solely on the artificial hybrid raised by M.P. Wilcox, in which the stems and inflorescences resemble those of *J.* x *diffusus*, but the base of the bract is slightly opened out indicating the influence of *J. conglomeratus*. The stems are dark green in colour and the pith is continuous and dense. Fertility is very low but some full seeds are formed (probably a similar percentage to those in *J.* x *diffusus*). The inflorescence branches are more erect than is usual in in *J.* x *diffusus*, without any spreading lower branches and, as might be expected, there are fewer (12-20) stem ridges.

J. balticus x *J. effusus* = *J.* x *obotritorum* (Fig. 13)

The hybrid resembles *J. balticus* more than its other parent. The inflorescence is very similar in shape to that of *J. balticus*, although often somewhat longer and more branched, the rhizomes are equal to it in degree of elongation, and subepidermal sclerenchyma girders and stem ridging are completely absent. The colonies formerly known were more vigorous than *J. balticus*, forming dense stands of up to about 600 m^2, and this vigour was retained in cultivation. The Ainsdale and Hightown colonies probably represented different origins, because the stems of the latter were taller and slenderer and the inflorescences less dense, again retained in cultivation. The most reliable ways of distinguishing this hybrid from *J. balticus* are the intermediate (short-armed stellate) shape of its pith-cells and its high sterility. Wilcox (2011) obtained "some seed" from the transplanted Hightown1973 clone. Chromosome counts of all three wild colonies were 2n = 80-82 (J.W. Grimes, J.P. Bailey & C.A. Stace, unpubl.) (see under *J. balticus* x *J. inflexus* for explanation).

J. balticus x *J. filiformis* = *J.* x *inundatus* (Fig. 13)

This non-British hybrid resembles *J.* x *obotritorum* and *J. balticus*, from which it can be distinguished by characters derived from *J. filiformis*: the thinner stems and the smaller, sparser inflorescences which are borne lower down on the stem-bract axis. It does produce a small amount of apparently good seed.

Juncus balticus x *J. inflexus* (Figs. 13 & 14)

Juncus balticus x *J. inflexus* has been discovered in three sites in Lancashire, where it is endemic. Probably all are single clones, one of them now extending over 1000 m^2.

Morphology and anatomy

This hybrid rush is very distinctive among all British *Juncus* in its extreme vigour, at least in the two Sefton colonies, making it easily our largest *Juncus* taxon. The stems regularly attain 1.5 m, and occasionally 2 m, in height (Fig. 10). Rhizome growth is also notable; one transplant of the Birkdale colony in the Ainsdale N.N.R. increased in area from 14 m^2 in 2003 to 804 m^2 in 2015, an increase of 5743% in 12 years (Smith & Lockwood, 2016). Measured on site, rhizomes were found to grow about 0.5 m per year, i.e. a patch would increase in diameter by about 1 m (Stace, unpubl.). The internode length in the rhizomes, however, seems no greater than in *J. balticus* (Fig. 4). These features render the two Sefton colonies instantly recognizable. They agree with *J.* x *obotritorum* in completely lacking subepidermal sclerenchyma girders, and in having intermediate (short-armed stellate) shaped pith-cells (Fig. 14). However, the enlarged epidermal cells overlying what would have been the position of subepidermal girders, marked in this hybrid by the position of the larger deeper-seated vascular bundles, are usually clearly developed, so much so that they often form very low albeit visible external stem-ridges. The pith is distinctly interrupted, but not as regularly septate as in *J. inflexus*. The inflorescence has longer branches (up to 14.5 cm) and is more diffuse than in any species or other hybrid of section *Juncotypus*; all the branches are upswept as in *J. inflexus*.

Figure 13. Inflorescences of *Juncus x obotritorum* (left, Phil Smith), *Juncus x inundatus* (centre), and *Juncus x lancastriensis* (right, Phil Smith)
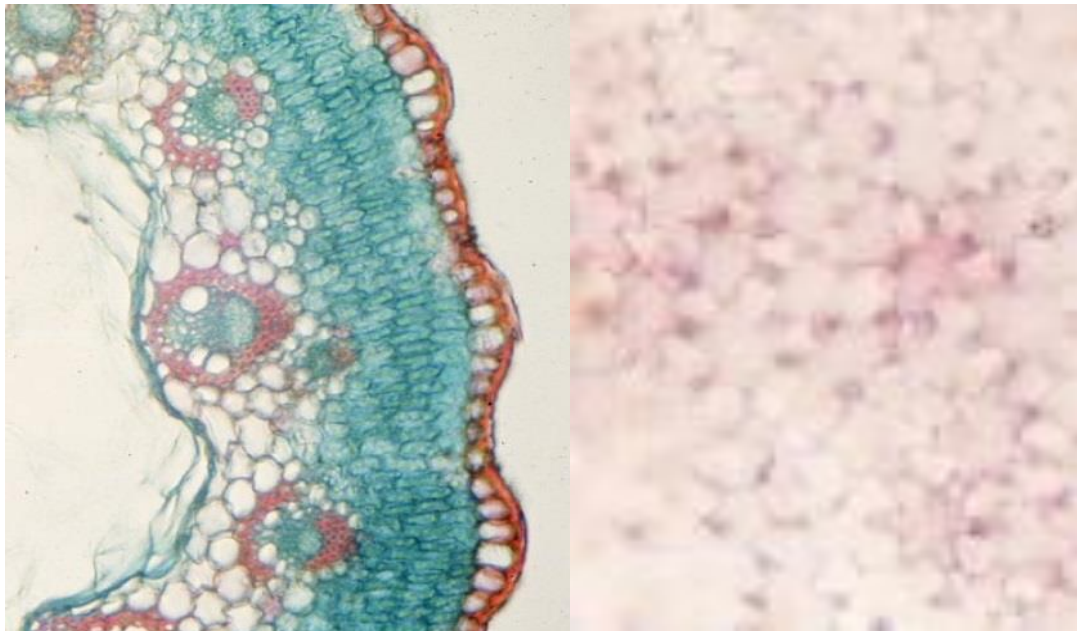

Figure 14. Stem anatomy of *Juncus x lancastriensis*. Left: stem section showing absence of subepidermal sclerenchyma girders but presence of areas of enlarged epidermal cells; Right: short-armed stellate pith-cells

There is some evidence that the two Sefton colonies are different clones representing different hybridisation events. My colleague J.W. Grimes noticed that it was easier to break off a stem by hand in one of the clones than in the other, a

feature of both wild and cultivated plants. Sure enough, stem sections showed that there is more sclerenchymatous tissue surrounding the vascular bundles in the tougher clone. The third colony (Fylde) differs considerably from the two Sefton colonies, which (having experience of the latter two) delayed my identification of it until anatomical characters were employed. The Fylde plant is less robust, with shorter, thinner stems closer to 1 m rather than 1.5 m tall, although it also has a good rate of rhizome extension. A transplant in the Ainsdale N.N.R. increased in area by 180% in 12 years (Smith & Lockwood, 2016). The inflorescence of the Fylde colony is also much shorter (usually <5 cm) than those of the Sefton colonies, and the stems are darker green. The most notable difference, however, is that in the Fylde clone the pith is more or less continuous. Detailed measurements of various characters of the Sefton and Fylde populations were tabulated by Wilcox (2011). It seems very likely that the Fylde colony arose from a different hybridisation event. Soon after the discovery of *J. balticus* on the Fylde coast by E.S. Marshall in 1914 (Marshall, 1915a), A Bennett (Marshall, 1915b) expressed the opinion that the plants belonged to var. *pseudoinundatus* Asch. & Graebn., which differs from the type (represented by the Sefton *J. balticus*) in its slenderer, greener stems and fewer-flowered shorter inflorescences. It seems likely that the difference between the Sefton and Fylde hybrids rests on this different parentage. The epithet *pseudoinundatus* refers to the fact that the plant resembles the hybrid *J. balticus* x *J. filiformis* (*J.* x *inundatus*) in general morphology.

Chromosomes
The chromosomes of *Juncus* are very small and difficult to study. They are holocentric, i.e. there is no visible constriction or centromere, centromeric activity being dispersed along the chromosome length. This means that chromosome fragments (which commonly arise by mishap in most plants, usually causing death) persist as viable chromosomal components, giving rise to a range of chromosome counts in different plants of one species Hence differences in chromosome number of one or few pairs are probably not very significant. (This phenomenon is even more prevalent in *Carex*).

The three common species (*J. conglomeratus*, *J. effusus* and *J. inflexus*) have chromosome counts of 2n = 40 or 42, while the two rarer species (*J. balticus* and *J. filiformis*) are usually reported as 2n = 80 or 84, although there are a few reports of 2n = 40 for both. Our own counts (J.W. Grimes, J.P. Bailey & C.A. Stace., unpubl.) agree with these, being 2n = 84 for *J. balticus*. Our counts for *J. balticus* x *J. inflexus* from all three wild colonies were unexpectedly 2n = 80-84, indicating either that the *J. inflexus* parent contributed unreduced chromosomes or, less likely, that two pollen grains from the tetrad effected fertilisation. The situation regarding *J. balticus* x *J. effusus* is similar (see above).

Fertility
This hybrid, like *J. balticus* x *J. effusus*, is highly sterile, much more so than *J.* x *diffusus*, and seed-bearing capsules are usually hard to find. Nevertheless Wilcox (2011) found capsules containing on average 1-6 seeds in 33 of 2013 flowers (0.75%) in the Fylde clone, 41 of 2805 (0.57%) in the transplanted Freshfield clone, and 104 of 2948 (3.53%) in the Birkdale clone. Wilcox found that the seed harvested could be germinated and he grew some derived from the Birkdale clone to

maturity. They closely resembled their F_1 parent and were similarly highly sterile. One plant is still in cultivation.

Hybrid synthesis
Artificial hybridization is difficult because the flowers are very small, many are borne close together, and the plants are self-fertile. Nevertheless Wilcox managed to synthesise *J. conglomeratus* x *J. inflexus* (see above), and my colleague J.W. Grimes achieved the same with *J. balticus* x *J. inflexus*, using Freshfield material of *J. inflexus* as the female parent and Birkdale material of *J. balticus* as male. Only one plant was obtained, but it was grown to maturity (**LTR**) and found to agree in all details with the wild Sefton hybrids. Interestingly, its chromosome number was 2n = c.62 (J.P. Bailey, unpubl.), indicating that, unlike the case with all the wild hybrids, both parents contributed unreduced gametes.

Hybrid binomial
All other hybrids in this section have valid binomials and, as the present hybrid still thrives in the wild, one is provided for that here.

Juncus x lancastriensis Stace, **nothosp. nov.** (*J. balticus* Willd. x *J. inflexus* L.)
Stems isolated, not clustered, borne on vigorous rhizomes with internodes mostly ≥1 cm long, commonly 1.5 m (up to 2 m) in height, mid green in colour, without subepidermal sclerenchyma girders, with irregularly longitudinally interrupted pith; pith-cells stellate with short arms; longitudinal rows of epidermal cells enlarged, mostly in clusters overlying the larger vascular bundles; inflorescences very diffuse, with upswept branches 2.5-14.5 cm; tepals pale brown to straw-coloured; highly sterile but some capsules (mostly <1%) have viable seeds.
    Inflorescence lengths are from Wilcox (2011). The elongated rhizomes and the tall stems with elongated diffuse inflorescences, lacking sclerenchyma girders and with short-armed stellate pith-cells and zones of enlarged epidermal cells are diagnostic.

Holotype: In extensive dune-slacks among dunes near sea, Ainsdale sand-dunes nature reserve (Freshfield site, Ainsdale N.N.R.), Sefton coast, South Lancashire, v.c.59, Grid reference SD308143, C.A. Stace *s.n.*, September 1970 (**LTR**). (Fig. 15). Isotypes or topotypes (other collections of the same clone) are in **BM**, **K**, **LTR** and **MANCH**. A wild-collected sheet is selected as holotype; more fully representative material cultivated in Manchester is present in **LTR** and **MANCH.**

Figure 15. Holotype of *Juncus x lancastriensis*. Image by Stuart Desjardins

The above material represents nothovar. *lancastriensis*, its *J. balticus* parent being referable to var. *balticus*. The clone on the Fylde coast differs substantially from this, and deserves naming as a distinct nothovar.

Juncus x lancastriensis Stace nothovar. **fyldensis** Stace, **nothovar. nov.** (*J. balticus* var. *pseudoinundatus* Asch. & Graebn. x *J. inflexus*)
Differs from nothovar. *lancastriensis* in: shorter stems (mostly c.1 m, up to 1.35 m) darker green in colour; less elongated inflorescences (1.3-5.5 cm); more darkly pigmented tepals; and stems with non-interrupted pith.

Holotype: Dune-slack, Fylde coast between Lytham and Blackpool (Lytham St Anne's Local Nature Reserve, Starr Hills), West Lancashire, v.c.60, Grid reference SD311303, C.A. Stace *s.n.*, July 1966 (**LTR**) (Fig. 16).

Figure 16. Holotype of *Juncus* x *lancastriensis* nothovar. *fyldensis*. Image by Stuart Desjardins

A specimen collected in 1968 is in **MANCH**.

References
Agnew, A.D.Q. 1968. The interspecific relationships of *Juncus effusus* and *J. conglomeratus* in Britain. *Watsonia* 6: 377-388.

Clifford, H.T. 1959. On putative hybrids between *Juncus inflexus* L. and *Juncus effusus* L. *Kew Bulletin* 13: 392-395.

Marshall, E.S. 1915a. *Juncus balticus* Willd. in W. Lancs. *The Journal of Botany, British and Foreign* 53: 91.

Marshall, E.S. 1915b. *Juncus balticus* Willd. *The Journal of Botany, British and Foreign* 53: 147-148.

Preston, C.D., Pearman, D.A. & Dines, T.D. 2002. *New Atlas of the British and Irish Flora*, p. 696. Oxford: Oxford University Press.

Richards, P.W. 1962. *Juncus* L., pp. 984-994. In: Clapham, A.R., Tutin, T.G. & Warburg, E.F. *Flora of the British Isles*, 2nd. ed. Cambridge: Cambridge University Press.

Smith, P.H. 1984. The distribution, status and conservation of *Juncus balticus* Willd. in England. *Watsonia*, 15: 15-26. http://archive.bsbi.org.uk/Wats15p15.pdf

Smith, P.H. 2006. Revisiting *Juncus balticus* Willd. in England. *Watsonia*, 26: 57-65. http://archive.bsbi.org.uk/Wats26p57.pdf

Smith, P.H. & Lockwood, P.A. 2016. Status of *Juncus balticus* (Baltic Rush) and its hybrids in England. *BSBI News* 131: 8-16.

Stace, C.A. 1970a. Anatomy and taxonomy in *Juncus* subgenus *Genuini*, pp. 75-81. In: Robson, N.K.B., Cutler, D.F. & Gregory, M., eds, *New Research in Plant Anatomy*. London: Academic Press.

Stace, C.A. 1970b. Unique *Juncus* hybrids in Lancashire. *Nature, London* 226: 180.

Stace, C.A. 1972. The history and occurrence in Britain of hybrids in *Juncus* subgenus *Genuini*. *Watsonia* 9: 1-11. http://archive.bsbi.org.uk/Wats9p1.pdf

Stace, C.A. 1975a. *Juncus* L., pp. 461-467. In: Stace, C.A., ed., *Hybridization and the Flora of the British Isles*. London: Academic Press.

Stace, C.A. 1975b. Wild hybrids in the British flora, pp. 111-125. In: Walters, S.M. & King, C.J., eds, *European Floristic and Taxonomic Studies.* Faringdon: E.W. Classey Ltd.

Stace, C.A., Preston, C.D. & Pearman, D.A. 2015. *Hybrid Flora of the British Isles*, pp. 372-376. Bristol: Botanical Society of Britain & Ireland.

Stace, C.A. 2019. *New Flora of the British Isles*, 4th ed., pp. 974-986. Middlewood Green, Suffolk: C & M Floristics.

Wilcox, M.P. 2010. A novel approach to the determination and identification of *Juncus* x *diffusus* Hoppe and *J.* x *kern-reichgeltii* Jansen & Wacht. ex Reichg. *Watsonia* 28: 43-56. http://archive.bsbi.org.uk/Wats28p43.pdf

Wilcox, M.P. 2011. Hybrid rushes in the U.K. – sterility and fertility. *BSBI News* 116: 21-27.

Wilcox, M.P. 2015. *Juncus inflexus* x *J. conglomeratus*. *BSBI News* 130: 31.

Wilcox, M.P. 2017. *Juncus inflexus* x *J. conglomeratus* – Postscript. *BSBI News* 135: 40.