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The history and occurrence in Britain of hybrids in *Juncus* subgenus Genuini

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ABSTRACT

The discovery and distribution of hybrids in *Juncus* subgenus Genuini are outlined. Special attention is paid to *J. effusus* × *J. inflexus* and to the Lancashire hybrids involving *J. balticus*. The latter are discussed in relation to the distribution of *J. balticus* itself.

INTRODUCTION

Early on in a programme of research into the taxonomy and biosystematics of the subgenus Genuini Buchenau of the genus *Juncus* it became clear that a great deal of confusion existed regarding the identification and occurrence of hybrids. Much of this confusion in identity results from a lack of knowledge of the literature, for, although there are several poor or misleading accounts to be found, there is no lack of sound and informative references. However, the occurrence of the two British hybrids of *J. balticus* (with which this research is mostly concerned) has received little attention in the literature. No precise statements concerning their identification, abundance or fate have appeared in print. Thus it seems advisable to place the available facts on record. Data on the identification and limits of variation of the species and hybrids will be published in a later paper.

In Britain there are five species of the subgenus Genuini: *J. effusus* L., *J. conglomeratus* L. (*J. subuliflorus* Drej.), *J. inflexus* L. (*J. glaucus* Sibth.), *J. filiformis* L. and *J. balticus* Willd. The first three are widespread over most of the British Isles. *J. filiformis* is confined to the Lake District apart from a very few scattered localities elsewhere in England and in Scotland. *J. balticus* occurs in Scotland as far south as Fifeshire, and in a very restricted area of Lancashire. It appears never to occur in close proximity to *J. filiformis*. Perring & Walters (1962) provide further details. All the species except *J. balticus* have been treated in the Biological Flora of the British Isles (Richards & Clapham 1941, Richards 1943), but much of the information is now of course out of date and was in any case published at a time when contributions to the series were much less detailed than is customary today. Tweed & Woodhead (1946) published much additional (and contradictory) information concerning *J. effusus* and *J. conglomeratus*.

The hybrids may be conveniently discussed in three groups.

JUNCUS EFFUSUS × *J. INFLEXUS*

This combination is the only well-known hybrid, and is known as *J.* × *diffusus* Hoppe.

The first British record appears to be a report by Babington (1843) that M. W. Sanden of Hamburg had received a specimen from Kincardine, Scotland. The collector and year were not given, but the latter must have been 1842 or earlier because Babington's note was dated January 1843. No original specimens have been traced, but there is a gathering at **MANCH** collected by J. W. Rimmington in 1849 from 'near Kincardine'. Nevertheless Boswell-Syme (1870) doubted the presence of the hybrid in Scotland. He distributed specimens of a sterile variant of *J. inflexus* (which he described as *J. glaucus* var. *pseudo-diffusus* Boswell-Syme) collected from the shores of the Firth of Forth (**BM**,**K**, **MANCH, OXF**) in 1869. He stated: 'It is probably to this form that all the Scotch specimens supposed to be *Juncus diffusus* belong.' He was, however, mistaken.

The first English record seems to have been made by W. H. Coleman in 1844, from Cole Green, 3 miles west of Hertford. The record was not published at the time, but specimens labelled Hertingfordbury, 1844, are at **BM** and **CGE**, and the discovery was mentioned by Ansell (1846) when describing a further discovery by Coleman and himself at Darman's Green, 3 miles south of Hertford in 1846. Specimens bearing these data are at **BM, CGE, E, MANCH** and **UCNW**. *J.* × *diffusus* was reported from east of Hunstanton, Norfolk, by Backhouse (1844), but a subsequent note by Notcutt (1846) states that Backhouse's specimens, as well as some collected from the same locality by Notcutt himself in 1846, were determined by Babington as a variant of *J. inflexus* with a solid pith.

After this period notices of the plant in the literature were mainly passing comments, because by about 1850 the existence of *J.* × *diffusus* as a British plant was well established. Specimens dating from then onwards are frequent in the major national herbaria.

Gibson (1862) is credited with the suggestion that *J.* × *diffusus* is a hybrid of *J. effusus* and *J. inflexus*. He based his idea on the occurrence of *J.* × *diffusus* usually 'in very small quantity only, and amongst abundance of *J. glaucus* and *J. effusus*, . . .' He gave four Essex records. This hybrid origin was not accepted, however, by all authorities. H. C. Watson, for example, considered that *J.* × *diffusus* was a distinct species (Druce 1884), but by the end of the century this view was no longer current. The *London Catalogue of British Plants* retained *J.* × *diffusus* as a species up to and including the eighth edition (Hanbury 1886), but the ninth (Hanbury 1895) and subsequent editions treated it as the hybrid.

The precise present-day distribution of *J.* × *diffusus* is not clear, largely due to mistaken identity. It is very frequently confused with sterile or partly sterile plants of *J. inflexus*, which are common, and in my view *J.* × *diffusus* is much less common than is often admitted. It is, however, undoubtedly widespread. Perring & Sell (1968) provide a map of the hybrid, described as 'readily recognised', which indicates that it is distributed from Cornwall and Kent to Northumberland in England, but that in Wales, Scotland and Ireland it is rare and very scattered. The data were obtained from four herbaria and from 'Floras'. The inclusion of the latter is unfortunate because a considerable number of erroneous records will have been included. This is indicated by a consideration of the herbaria consulted in the present study. Some largely contained correctly identified specimens (e.g. **MANCH**, by R. D. Tweed and N. Woodhead; **K**, by P. W. Richards and by L. A. S. Johnson) but others were not recently revised and contained numerous errors (e.g. **BM, CGE, OXF**). Perring & Sell's data

included records from **BM** and **CGE**, but whether the specimens were first determined correctly is not stated. Very few annotations were made on the sheets.

In the herbaria examined there are about 70 specimens at **BM**, 45 at **K**, 44 at **CGE**, 36 at **OXF**, 24 at **MANCH**, 17 at **NMW**, 14 at **E** and 4 at **UCNW**. Many of these are duplicates, but they include specimens from 37 British and 3 Irish vice-counties: 6, 9, 11, 13–15, 17, 19–21, 23, 24, 26–28, 30, 31, 33–38, 41, 52, 55, 57, 58, 62–67, 69, 85, 90, H20, 30, 38. This compares with 36 vice-counties given by Hanbury (1925) and 23 by Druce (1932). Druce included 8 not covered by my observations, and several more are given by Perring & Sell (1968); they should all be carefully checked before acceptance.

Nevertheless the contention that the hybrid is rare is supported by many sources. Clifford (1959), after two years searching in Durham, found only one locality, and found hybrids 'very rare' in Surrey even though he investigated localities from which they had been reported. J. G. Dony, a B.S.B.I. referee for *Juncus*, has made careful searches for *J.* × *diffusus* for many years, but never with success. P. W. Richards has found it only four times in over thirty years. I have searched scores of localities in the past six years but in Britain have encountered it only in one of Richards' known sites. There is no evidence that the hybrid is now less or more common than it was last century. It is very widespread on the continent of Europe.

HYBRIDS INVOLVING *JUNCUS CONGLOMERATUS*

Hybrids between this species and both *J. effusus* and *J. inflexus* have been reported.

Of *J. inflexus* × *J. conglomeratus* Richards & Clapham (1941) wrote: 'reported in Britain, but must be very rare', and Richards (1952, 1962) states 'doubtfully reported as British'. It was included in the plant lists of Hanbury (1908, 1925) and Druce (1908, 1928), but not in the immediately previous edition of Hanbury (1895) nor in the plant list of Dandy (1958). Druce (1919) implied that he discovered this hybrid in Berkshire. Bowen (1968), however, referred the record to a specimen in **OXF** collected by W. Holliday in 1861, and added that it is probably a variant of *J. inflexus*. I have seen the specimen and consider it undoubtedly *J. inflexus*. A specimen in **BM** labelled '*J. conglomeratus* × *glaucus*?', collected by E. S. Marshall from Kent in 1893, seems to be *J.* × *diffusus*.

Present evidence is thus not sufficient to maintain this hybrid as a British plant.

J. effusus × *J. conglomeratus* has been reported more frequently than the last hybrid in recent years, although it was not included in any of the British plant lists before that of Dandy (1958). Specimens thought to be this were collected in 1919 by Adamson (1920) in Cheshire from a single clump growing among *J. conglomeratus*, but the specimen in **NMW** is in my opinion *J.* × *diffusus*, which was also suggested by J. W. White at the time. The supposed duplicate at **BM** appears to me to be *J. effusus*. Tweed & Woodhead (1949) implied that they never encountered hybrids between these species. Richards & Clapham (1941) stated that the hybrid 'with intermediate characters and high sterility' was 'reported from Britain but needs confirmation', and Richards (1952, 1962) later made similar comments.

Agnew (1968) took a different view, for he considered that 'hybrids exist both as populations of hybrids and as populations introgressing with *J. effusus*',

and that 'hybrids observed in the field moreover appeared fully fertile'. Agnew recorded these hybrids only above 152m altitude, and mostly above 300m, in Scotland and north Wales. Davis (1970) reported this hybrid in Pembrokeshire at 120m in 1969, but the specimen deposited in **NMW** has well developed capsules and appears to me to be simply *J. conglomeratus*. There are specimens labelled *J. effusus* × *J. conglomeratus* in the herbaria at **BM**, **K**, **NMW** and **UCNW** from a range of localities in England, Wales and Scotland. In my view, however, all of these specimens can be at least equally well placed with one or other of the putative parents. Some of the specimens are too young, others are too old, yet others are abnormal in some way or have deteriorated on drying; as a result various workers have doubted that such specimens can be conveniently accommodated in either species. The relatively close similarity of the species and their considerable variability has added to the problem. I am not attempting to deny that hybrids exist, but I have seen none despite many searches in mixed populations, and I have not heard any convincing evidence of their existence.

Much the same situation exists on the continent of Europe as in Britain. Both the above hybrids involving *J. conglomeratus* were recorded by Ascherson & Graebner (1904) from several European countries, and there are many subsequent records in Floras and many specimens so labelled in herbaria. Krisa (1962), from a study in Czechoslovakia, considered that *J. effusus* and *J. conglomeratus* represented only end-points in a continuous series, whereas most other authors (except Agnew) have identified hybrids by their sterility. But to me the evidence concerning the existence of either hybrid in Europe is as unconvincing as it is in Britain.

Both the hybrids have received binomials: the hybrid with *J. inflexus* has been described as *J.* × *ruhmeri* Aschers. & Graebn.; that with *J. effusus* as *J.* × *kern-reichgeltii* Janch. & Wacht. ex van Ooststr. The earlier names for the latter (*J.* × *brueggeri* Domin and *J.* × *haussknechtii* P. Fourn., non Ruhm.) are both invalid, and the validly published names are, of course, only applicable if the type specimens are genuine hybrids.

HYBRIDS INVOLVING *JUNCUS BALTICUS* AGG.

In Europe there are two taxa which are sometimes considered specifically distinct from *J. balticus*: *J. pyrenaeus* Jeanb. & Timb. and *J. arcticus* Willd. The first is confined to the Pyrenees and is not known to form hybrids. It is nowadays usually reduced to a synonym of *J. balticus*. *J. arcticus* is variously considered a distinct species or a subspecies of *J. balticus*. It occurs in more northern latitudes than *J. balticus*, but like that taxon it is also found on mountain ranges further south in Europe, where, however, the two taxa are never sympatric.

Both *J. arcticus* and *J. balticus* form hybrids with *J. filiformis*. The combination *J. balticus* × *J. filiformis* is known as *J.* × *inundatus* Drej., and appears to be frequent in suitable areas (usually duneslacks) all around the Baltic Sea where the two parents occur together, and similarly in Norway (Flatberg 1970) and Iceland. *J. arcticus* × *J. filiformis* (= *J.* × *montellii* Vierh.) is recorded in northern parts of Scandinavia (including Iceland) and in south Greenland, where *J. arcticus* replaces *J. balticus*, and also in a few areas of the Alps of Switzerland (Welten 1967) and France.

Neither of these two hybrids occurs in Britain; *J. arcticus* is not British, and *J. balticus* never occurs in close proximity to *J. filiformis* in this country. Hybrids between *J. balticus* and *J. arcticus* are sometimes recognised in Scandinavia (including Iceland). By those botanists who consider these two taxa subspecies of one species such presumed hybrids are known as *J. arcticus* subsp. *intermedius* Hyl. Hylander (1953) also recognises hybrids between this taxon and *J. filiformis*.

The only other hybrid reported for the continent of Europe is *J. balticus* × *J. effusus*, of which I have traced three records. It was described as *J. scalovicus* by Ascherson & Graebner (1893), from wet sand-dunes near the Baltic Sea coast of East Prussia (now Kaliningrad, U.S.S.R.), but S. Snogerup of Lund has informed me that the type specimen is probably *J. balticus* ×*J. filiformis*. Rothmaler (1965) described the hybrid *J. balticus* × *J. effusus* var. *compactus* Hoppe under the binomial *J.* × *obotritorum* Rothm. from the Baltic Sea coast of northern East Germany. This locality is about 600 km west of the locality of *J.* × *scalovicus*, but both lie in the geographical range of *J. balticus* × *J. filiformis*. Further comment on these two plants must await a close examination of the type specimens. Flatberg (1970, *in litt.*) has informed me that he discovered what he considers to be *J. balticus* × *J. effusus* in Norway in 1970.

In Britain there exist colonies of *J. balticus* × *J. effusus* and *J. balticus* × *J. inflexus* (Stace 1970, 1970a); at least the latter is believed to be endemic. The former hybrid has been found in two sites and the latter in three; all five localities are in the Lancashire coastal dune systems between Liverpool and Blackpool (Fig. 1). None of the discoveries was published at the time, and it seems that the only printed records apart from the two mentioned above are in *Travis's Flora of South Lancashire* (Savidge *et al.* 1963), and in the report of a B.S.B.I. field trip to the area in 1954 (Allen 1955).

J. balticus × *J. effusus* was first noticed by S. Taylor in July 1933, and was sent by F. W. Holder to Kew, where it was wrongly determined as *J.* × *diffusus*. This specimen at **K** has since been determined as *J. balticus* by two independent authorities. The colony was apparently first correctly named in 1954, on the above B.S.B.I. field meeting, the name representing a concensus of obviously expert opinion. Confirmation of its identity rests on anatomical evidence (Stace 1970, 1970a). The locality remained known to a few local botanists, who now and then pointed it out to interested visitors, and it was independently discovered by several others. The colony lay in a fairly wet duneslack just to the south of the tip of the road from Ainsdale Station to the shore, at Locality 1 in Fig. 1. Unfortunately there is no note of the extent of the colony at the time of its discovery, but in 1966 it completely covered an area approximately 40 by 20 metres in the wettest part of the duneslack. The colony then also had a few disjunct offshoots up to 20m from the main patch, presumably originating from the extensive human disturbance in the area. In 1968 the entire colony was eradicated by the construction of a holiday camp as part of a large-scale development of the Ainsdale Beach area. Fortunately samples of the colony had previously been removed to the Ainsdale Sand Dunes National Nature Reserve, 2km south-west of the development, where they are thriving (Fig. 1, Locality 9). Herbarium specimens collected after the last war are present at **BM**, **CGE**, **K** and **LIV**.

In 1966 Miss V. Gordon noticed a single tuft of '6-inches' diameter of an unusual *Juncus* in the small dune system close to Hightown (Fig. 1, Locality 2), some 9km south of the Ainsdale hybrid. In 1970 she refound the tuft, then

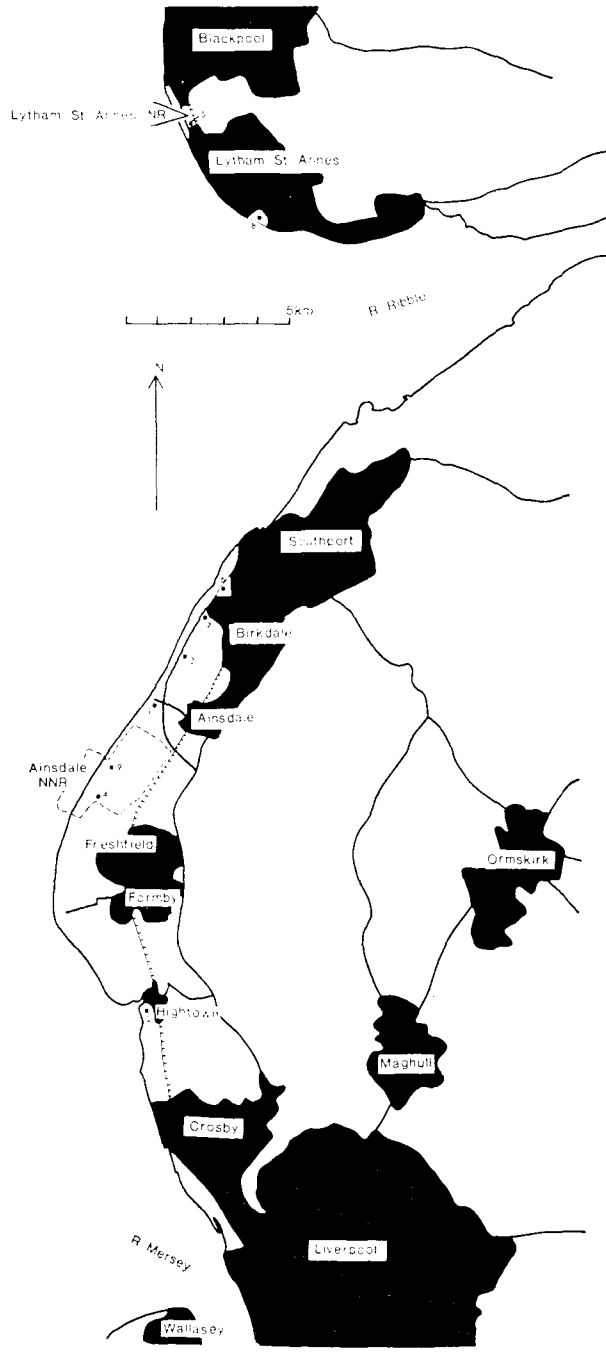

FIGURE 1. Distribution of *Juncus balticus* and its hybrids in Lancashire.

about 0·5 square m, and kindly brought it to my attention. Anatomical study showed that it represents the same taxon as the Ainsdale hybrid, of which it is therefore the only remaining wild representative. The colony is close to new housing development.

J. balticus × *J. inflexus* exists in three localities. It was first discovered by D. E. Allen in 1951 (not 1952 as given by Savidge *et al.* (1963) and repeated by Stace (1970)) in a duneslack between Birkdale and Ainsdale (Fig. 1, Locality 3), about 2km north-east of the Ainsdale hybrid locality. It also was apparently first named accurately by the combined efforts of the members of the 1954 B.S.B.I. field meeting, and their identification has since been checked anatomically (Stace 1970, 1970a). In 1970 the colony measured approximately 20m square, and was obviously spreading vigorously. A further colony of the same hybrid was discovered in the period 1950–52 about 4km to the south-west, in what is now the Ainsdale Sand Dunes National Nature Reserve (Fig. 1, Locality 4), by Miss B. Blanchard, who surveyed that area in the years 1949–52 (Blanchard 1952). She referred to the plant as '*Juncus* sp.', but mentioned that P. W. Richards, to whom she sent a sample, had commented that it was 'possibly' *J. inflexus* × *J. balticus*. Her discovery was not publicised at the time, and the colony has been independently rediscovered since by several other workers. In 1970 the plant covered an area about 15m to 20m square. Specimens from both these colonies of *J. balticus* × *J. inflexus* are in **BM** and **K**.

In 1966 I came across a clone of an obviously hybrid *Juncus*, approximately 10m by 5m in extent, on the area of coast known as Starr Hills, about 18km north of Ainsdale (Fig. 1, Locality 5). The site is in the dunes on the Fylde coast, viz. that stretch of coastline lying between the Ribble and Lune estuaries, and therefore in v.c. 60 (West Lancaster) rather than v.c. 59 (South Lancaster). The area forms a small but significant buffer between the heavily developed urban areas of Blackpool and Lytham St Annes, and in 1968 the latter Borough declared it the 'Lytham St Annes Nature Reserve'. It is the last remaining undeveloped area of dunes in the Fylde. Anatomical study shows that the plant is undoubtedly *J. balticus* × *J. inflexus*, although in morphological features (particularly height and vigour) it differs somewhat from the other two colonies of that hybrid.

J. balticus × *J. inflexus* has not so far received a binomial.

DISCUSSION

Using any yardstick the occurrence of five colonies of two extremely rare or endemic hybrids on less than 30km of coast is certainly remarkable. Conceivably the two *J. effusus* × *J. balticus* colonies, and the two south Lancashire *J. inflexus* × *J. balticus* colonies, are single clones, but even in that case three separate hybridizations must have taken place. The situation is all the more remarkable since the putative parents are frequently found in close association in many other areas of Europe, particularly in parts of Scotland and the Baltic Sea coasts. Many possible explanations of this anomaly present themselves, but clearly the correct one can be obtained only by experimental work.

There remains the possibility, of course, that these hybrids may occur elsewhere than in Lancashire. *J. inflexus* × *J. balticus* is a distinctive plant, and one unlikely to be overlooked in a well-explored region. But *J. effusus* × *J. balticus* is superficially very similar to *J. filiformis* × *J. balticus*, which is widespread in

the Baltic region and may have caused the former to be overlooked. Moreover, both these hybrids superficially resemble certain slender specimens of *J. balticus* itself, particularly the variant known as var. *pseudo-inundatus* Aschers. & Graebn.

There are other aspects of these plants which can only be explained by experimental work. The variation of the hybrids, particularly *J. inflexus* × *J. balticus* and to a lesser extent *J. inflexus* × *J. effusus*, is a notable feature and one which demands an investigation of the fertility of the hybrids. A high level of sterility is often considered characteristic of *Juncus* hybrids. The hybrids of *J. balticus* seem completely seed-sterile, except some variants of *J. balticus* × *J. filiformis*, but *J. inflexus* × *J. effusus* produces a varying amount (albeit often nil) of fertile (i.e. germinable) seed, a fact which contributed to the relatively late recognition of this plant as a hybrid. Plants which have been named as hybrids involving *J. conglomeratus* are sometimes sterile, but sometimes highly fertile. The question of the very existence or otherwise of *J. conglomeratus* hybrids is one which will not be settled until comprehensive breeding programmes have been completed.

A further feature of significance with regard to the Lancashire hybrids of *J. balticus* is the distribution of *J. balticus* in Britain. According to Druce (1932) it was first recorded in Scotland in 1821. Elsewhere in Britain it is confined to Lancashire, where it was first discovered on 29th May, 1913 by R. S. Adamson (Adamson 1913, 1914, Wheldon 1914). Several comments make it clear that it was there 'very local' as it is now. Adamson (1913) concluded that it occurred in only 'one series of dune hollows', and Wheldon (1914), after much unsuccessful searching in July 1914, concluded that 'it seems to be limited on our dunes to the very restricted area in which it was first discovered.' Specimens exist in several national and local herbaria (e.g. **BM**, **CGE**, **K**, **LIV**, **MANCH**, **NMW** and **OXF**) dating from the first record and from a return visit to the colony made by Adamson, Wheldon and W. G. Travis on 4th October, 1913. Nevertheless the precise location and distribution of the plant at that time is still uncertain.

At present three separate colonies are known to me within about 1km of one another at the southern end of Birkdale, close to the limit of housing development (Fig. 1, Localities 6 & 7). The main colony at Locality 6 was largely destroyed in 1968 by the construction of the new coastal road from Ainsdale to Birkdale, but a very small part remains on the seaward side. Moreover in 1969 N. A. Robinson discovered a further colony approximately 50m to the southwest, a few yards seaward from the new road, thinly distributed over an area about 20m by 15m. The third colony (Locality 7) is in a slack about 1km southwards, just beyond the present limit of housing, a few yards landward of the new road. It is scattered over an area approximately 20m by 10m.

Clearly all these colonies are in danger of eradication; and so one or two portions have been transferred to the Ainsdale Sand Dunes National Nature Reserve further south (Fig. 1, Locality 9), where they are just holding their own. These are not the first attempts at transplantation. In a letter to A. Bennett, dated 28.X.1913 and attached to an herbarium sheet in **BM**, Travis wrote: 'We thought it advisable to put down some rhizomes and scatter seeds of the plant in a large slack nearer to Ainsdale where it is less likely to be disturbed'. Whether or not these survived is unknown.

Localities 6 and 7 are referred to by Savidge *et al.* (1963) as 'Birkdale' and

'Hillside' respectively. Judging from notes from various sources (especially Travis's manuscript Flora at **LIV**) it seems likely that the original locality was at Birkdale, and that the Hillside site was discovered by Travis in 1929, but whether the present sites are exactly the same as the original one(s) or not is uncertain. The above three localities lie between approximately 1·5 and 13·5km from the five Lancashire localities of *J. balticus* hybrids.

The second Lancashire record of *J. balticus* was made by E. S. Marshall on 10th August, 1914 (Marshall 1915, 1916, Wheldon & Wilson 1925) at Ansdell, near Lytham St Annes (Fig. 1, Locality 8), in West Lancaster. This was interestingly enough only about 4km from the third site for *J. inflexus* × *J. balticus*. Only two specimens collected at the time have been traced (**E** and **NMW**), but a specimen collected by the late H. E. Bunker in 1947 at 'St. Annes, by Queen Mary School' is present in Bunker's herbarium, which is now in the possession of Mrs Bunker (*fide* E. F. Greenwood). Marshall originally described the plant as 'rare' at Ansdell, but Whellan (1948) found it 'abundant in one damp spot in the dunes' in 1946. The colony was eradicated by development in 1965. Literature comments and the herbarium material make it clear that the plants belonged to the var. *pseudo-inundatus* referred to previously, and not (like the Birkdale examples) to the type variety.

J. balticus has also been recorded on the coast of Furness in north Lancashire (Druce 1932, Wilson 1938, Perring & Walters 1962), but no herbarium specimens have been traced and the circumstances of the alleged discovery have not been uncovered. Unless confirmation is obtained the record is best treated as dubious.

The origin of the *J. balticus* hybrids is presumably from recent crosses in Lancashire. But the origin of the Lancashire *J. balticus* is less obvious. The lack of any records prior to 1913, and the very restricted extent of the colonies, tend to suggest a recent arrival, perhaps by sea-borne rhizomes. If the var. *pseudo-inundatus* is a genetically-determined variant, it would seem that at least two separate immigrations have occurred.

Because of the great rarity and precarious existence of these colonies of *J. balticus* and its hybrids small portions of all of them (except from the extinct Locality 8) are kept in the Manchester University Botanic Garden. With occasional weeding but no other attention they thrive in ordinary garden soil and show a rate of spread not found in the wild populations. Voucher herbarium specimens from all these colonies are preserved at **MANCH**.

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