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Identification and taxonomy of *Betula* (Betulaceae) in Great Britain and Ireland

Andy Amphlett
Grantown on Spey, Scotland

Corresponding author: amphlett1958@gmail.com

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Abstract
Floras and identification guides typically do not list the full range of identification features that discriminate between *Betula pendula* Roth and *B. pubescens* Ehrh., and some accounts contain errors. Discriminatory identification features are described and illustrated. Introgression from the diploid, *B. pendula* into *B. pubescens* is widespread. It also occurs from *B. nana* L. into *B. pubescens*, but obviously introgressed examples of the latter are probably rare. *Betula pubescens* presents the greatest unresolved identification difficulties. Trees identified as *B. pubescens* subsp. *celtiberica* (Rothm. & Vasc.) Rivas Mart., particularly in Wales, may be part of the variation within British *B. pubescens*, due to introgression from *B. pendula*. The most widespread of the small-leaved forms of *B. pubescens* is correctly named var. *fragrans* Ashburner & McAll. Several misapplied names have been given to this taxon, most recently subsp. *tortuosa* (Ledeb.) Nyman, which does not occur in Europe. Not all small-leaved *B. pubescens* are var. *fragrans*; some examples show clear signs of introgression from *B. nana*, and may be referable to the northern *var. pumila* (L.) Govaerts.

Keywords: introgression; ploidy level; hybridisation

Introduction

The taxonomy and naming of Birch (*Betula*) has been the source of confusion and dispute ever since Linnaeus published his Species Plantarum in 1753. Linnaeus's *Betula alba* L. is now accepted as comprising two species, *B. pendula* Roth (Silver Birch) and *B. pubescens* Ehrh. (Downy Birch). A third species *Betula nana* L. (Dwarf Birch) is distinctive, and taxonomically uncontroversial.

In combination, *B. pendula* and *B. pubescens* are almost ubiquitous at hectad scale in Great Britain and Ireland. However their frequency relative to each other varies markedly (Fig. 1). *B. pubescens* is the more frequent species across almost all of Ireland, Scotland (except the east), Wales, north-west and parts of south-west England. *B. pendula* is the more frequent species in north-east, central and southern England, and in east and north-east Scotland. It is likely that distribution maps for these two species contain some errors (e.g. Worrell & Malcolm, 1998).

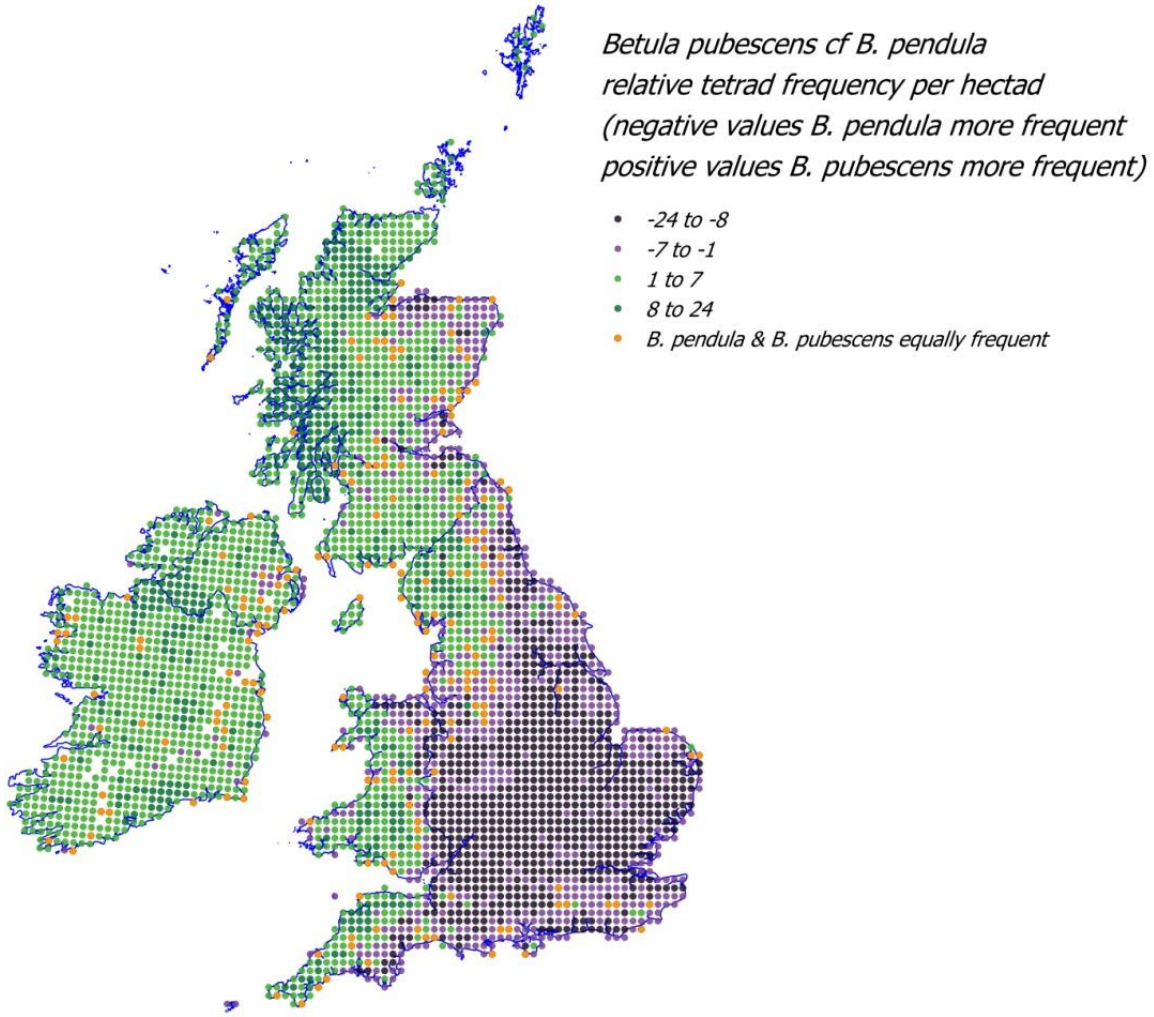

Figure 1. Relative tetrad frequency per hectad of *Betula pubescens* and *B. pendula* in Great Britain and Ireland (From BSBI Distribution Database, https://database.bsbi.org/, accessed February 2021)

Problems relating to the identification of British and Irish *Betula* are due to:

1) Identification features of *B. pendula* and *B. pubescens* being poorly and incompletely described in some popular Floras and Field Guides.
2) The occurrence of the F1 hybrid between *B. pendula* and *B. pubescens*, *Betula x aurata* (Borkh.).
3) Introgression from the diploid (2n=28) *B. pendula* and *B. nana*, into the tetraploid (2n=56) *B. pubescens*.
4) The occurrence of distinctive local forms, especially of *B. pubescens*.
5) Planting of alien (to the local area) genotypes and species, and effects of habitat disturbance.
6) Misapplication of names to taxa within *B. pubescens*.
7) Misleading interpretations of the relationship between the small-leaved *B. pubescens* in the Highlands of Scotland and Scandinavian and Icelandic 'mountain birch'.

These issues are discussed in turn below.

1) Identification features of *B. pendula* vs. *B. pubescens* and of *B. nana*.
Commonly used Floras and identification guides typically do not list the full range of identification features that discriminate between *B. pendula* and *B. pubescens*, and some accounts contain errors. Examining a classic example of the small-leaved *B. pubescens* subsp. *tortuosa* (sensu Stace, 2019) in the Highlands of Scotland, a botanist using one of the two popular Field Guides (Rose, 2006; Streeter, 2009) might well be stumped as to what they were looking at. Given that such trees may have whitish bark, pendulous and glabrous fine twigs, that may have frequent glands (or warts), and leaves that may be almost glabrous later in the summer, they may well decide they are looking at a form of *B. pendula*. The latest edition of the *New Flora of the British Isles* (Stace, 2019), has some significant errors in the keys, text and illustrations. The key to species in Stace (2019) does satisfactorily distinguish between *B. pendula* and *B. pubescens*. However, the drawing of the fruiting bract of *B. pendula* does not show the diagnostic shape and the drawing of the fruiting bract of *B. pubescens* is wrong; the fruiting bracts are said to have lateral lobes "*directed laterally or slightly backwards*" whereas they point forwards (unless introgressed), which is a key difference from *B. pendula*. The leaves of subsp. *tortuosa* (sensu Stace, 2019) are not conspicuously hairy as stated in the key to subspecies, and the shoots frequently have many (not few) sessile glands. It is described as usually shrubby, but is almost always a tree. Of easily accessed identification guides, the account in *Plant Crib* (Rich & Jermy, 1998, and available online) is reliable. For discussion of *B. pubescens* subsp. *celtiberica* see Section 4, below.

The Atkinson discriminant function (ADF) (Atkinson & Codling, 1986) is a recommended tool to distinguish between *B. pendula* and *B. pubescens* using three leaf characters; details are given in Stace (2019). The function was based on a sample of 104 trees in 14 self-sown populations in England and Scotland. The discriminatory power of the function has recently been tested on a much larger dataset (Wang *et al*., 2014b). They calculated the ADF for 944 *Betula* trees (780 *B. pubescens* and 164 *B. pendula*) from 105 populations. The species identifications had previously been determined using 12 microsatellite loci (Wang et al, 2014a). Using an ADF value of zero as the boundary between the two species, as originally proposed, the ADF value correctly identified 96.4% of samples. Using a boundary value of -2 raised the success rate to 97.5%. However, between ADF values of -11 to +3, error rates exceeded 10%. (Fig. 2).

The practical usefulness of the ADF seems to be limited. It reliably distinguishes between the two species in cases where leaf shape is fairly obviously one or other species. When it would be most useful is when their leaf shapes are most similar. Here the error rate increases to over 10%. Some of the trees sampled by Wang *et al*. (2014b) showed evidence of introgression, but they concluded that the morphological continuum between the leaf shapes of the two species "is inherent to the species, and hybridisation is not its major cause".

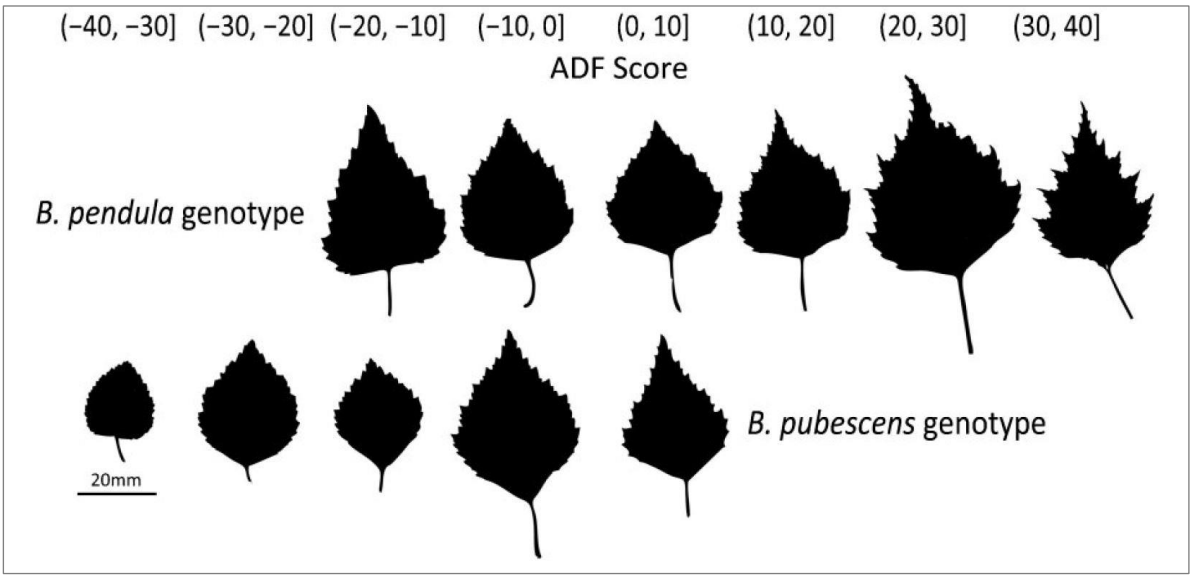

Figure 2. Representative leaf shapes of *Betula pendula* and *B. pubescens* (determined by microsatellite data) for different Atkinson discriminant function scores (from Wang et al, 2014b)

Betula nana (Fig. 3) is a highly distinctive shrub, prostrate or erect (maximum height *c.*1 metre), with small, shining, dark green, subcoriaceous, rounded leaves with crenate teeth (teeth not acute and triangular as in the other species and hybrids), and densely 'furry' hairy shoots. It has a totally different arrangement of catkins with overwintering male catkins never terminal, but lateral, usually below females, and over winter looking like elongated buds, and erect fruiting catkins. Its hybrid with *B. pubescens*, *B. x intermedia* (Fig. 27) is little known to British botanists, having only been recorded by *c.*12 recorders since 1987. *B. nana*, recorded from 101 hectads post 1999, is almost restricted to the Scottish Highlands; it is rare in northern England. The hybrid is recorded from 10 hectads post 1999, and was reported from Northumberland in 2020, new to England. (Hectad counts from BSBI Distribution Database, March 2021).

Figure 3. *Betula nana*

Identification features of *B. pendula* and *B. pubescens* are given in Table 1. Identifications should always be based on consideration of as many features as possible. I have drawn on a wide range of literature and personal experience in the field (mainly in north Scotland) when compiling this. Note that the name *B. pubescens* var. *fragrans* (Ashburner & McAllister) is used in place of *B. pubescens* subsp*. tortuosa* (sensu Stace, 2019); see Section 6 for discussion.

Table 1. Identification features of *Betula pendula* and *B. pubescens*

	B. pendula	***B. pubescens subsp. pubescens***	***B. pubescens var. fragrans****
Tree form / Habit	Tall trees, usually with a single trunk, extending into the canopy.		Except in very exposed or high altitude locations, forms a low (5m) to medium height tree, exceptionally to 12-15m. Trunk short, not usually extending into the canopy. Often multi-stemmed from, or near to, the base.
Branches	Ascending, with fine twigs and branchlets often (but not always) pendulous. Classic trees have all branches showing this pendulous character. Planted trees are sometimes exaggeratedly and atypically pendulous, eg *cv. tristis*. Some wild trees are hardly pendulous, and young trees do not display this trait. Beware markedly pendulous forms of *B. pubescens var. fragrans*	Ascending. Fine twigs and branchlets never pendulous.	Trees of great individual character. Branches variably twisting or contorted, creating intricate branching patterns. On most trees, fine twigs of lower branches somewhat to markedly pendulous. Fine twigs of upper branches typically spreading in all directions, and not pendulous. Some trees hardly display this pendulous character, while occasional trees

	which can look similar at a distance.		have pendulous fine twigs on all branches.
Bark of trunk	Upper trunk white, mid and lower parts with vertical splits or gashes, sometimes diamond-shaped. Bark thinly peeling. Black inverted V marks above branch / trunk junctions. Base of trunk often with no white bark, broken up into very rough dark, cubic or rectangular hard corky bosses.	Trunk typically white or grey-white, sometimes brown. Never with vertical splits or gashes. Base of trunk same colour as upper, never broken up into very rough dark bosses, often fluted. Bark may partially break up into curls. Horizontal lenticels creating obvious parallel lines. (Bark of var. *fragrans* in the Highlands, often largely obscured by lichens, bryophytes and algae, masking the actual colour).	
Young twigs (preceding year, and current year late in summer)	Thin. Glabrous, (never puberulent**), with round, pale, glands / warts in addition to oval lenticels. Glands are most abundant on vigorous shoots eg. of young trees. Twigs on old trees may ± lack glands. Twigs are sometimes covered by a greyish, peeling epidermis.	Usually pubescent (hairs visible to naked eye) and / or puberulent (use lens). Glands often described as absent, but may be sparse or frequent, with oval lenticels.	Thin; may be as thin as *B. pendula*. Glabrous or puberulent (use lens), with or without longer hairs, with resinous smelling, brown glands and oval lenticels.
Buds	Often more pointed than *B. pubescens*.	Usually not viscid, without resinous smell in spring.	Viscid. Resinous smell in spring.
Leaves (on short shoots, and pre-formed leaves at base of long shoots).	Acute to acuminate at apex, truncate to cuneate at base. Teeth double,	Leaves >(3) 3.5 cm length, without obvious primary teeth. Rounded to	Leaves ≤ 3 (3.5) cm length, frequently less than 3cm, without obvious primary

Ignore other leaves on long shoots (they differ in shape). Epicormic, basal or coppice shoots, and seedlings are usually hairy in both species (ignore).	primary teeth prominent, attenuate, often curving towards leaf apex. Glabrous.	cuneate at base. Usually hairy, at least below.	teeth. Rounded to cuneate at base. Apex usually >80°. Sparsely hairy to glabrous. Covered in frequent small brown glands. Resinous smell in spring. (If <(20) 15mm length, may be hybrids with *B. nana* or heavily introgressed from *B. nana*).
Fruiting catkin	Pendent	Pendent. (If variably erect, may suggest introgression from *B. nana*).	
Fruiting scales / bracts. Examine from middle of several mature catkins.	Lateral lobes spreading, ± falcate and sometimes strongly so. Look like a bird in flight, eg a Peregrine falcon, or 'fleur de lys' shaped.	Lateral lobes pointing forward at angle of *c.*45°. If spreading, with slight tendency for rear edge to curve backwards towards base of bract, may indicate introgression from *B. pendula*. If lateral lobes erect, or nearly so, suggests introgression from *B. nana*.	
Nutlets. Examine from middle of several mature catkins.	Glabrous. Narrow cf. length.	Tuft of very short hairs at base of styles (use lens x20). Relatively broad cf. length.	
Nutlet wing. Examine from middle of several mature catkins.	Each wing 2-3 times width of nutlet, typically extending beyond styles.	Each wing 1 (-2) times width of nutlet, typically not extending beyond styles. If wing << width of nutlet, may suggest introgression from *B. nana*.	

* *B. pubescens subsp. tortuosa* (sensu Stace)

**Puberulent refers to very short hairs, 0.03 - 0.3 mm in length, growing at right-angles to surfaces, e.g. of twigs. Hold specimen to the light and check with a hand lens for presence of hairs in silhouette. Such hairs are usually to be found on *B. pubescens*, and never on *B. pendula*. The shortest examples of these hairs can be easily missed with a cursory examination. Magnification of >x10 is advised.

It should be noted that:

- *B. pendula* may have occasional long (*c.*1 mm) hairs on leaf margins, bud scales and young leaf veins. Seedling stems and leaves are hairy.

- The characteristic 'fleur de lys' fruiting catkin scales of *B. pendula* with reflexed lateral lobes also occur in *B. pubescens* highly introgressed from *B. pendula*, in *B. celtiberica* and in some *B. papyrifera* Marshall.

In summary (and see Section 3 re. introgression), once the pure *B. pendula* and pure *B. nana* (both diploids) are known these can almost always be fairly easily distinguished from tetraploid *B. pubescens*. The latter may display evidence of variable amounts of introgression from one or other of these two species. In mixed stands of *B. pendula* and *B. pubescens* the important thing is to certainly identify *B. pendula* (if present); all the remaining birches are likely to be tetraploid and freely inter-fertile, and hence effectively comprising a breeding unit distinct from a 'pure' *B. pendula* breeding population. These tetraploids can be recorded as *B. pubescens*.

Many of the features listed in Table 1 are illustrated below: *Betula pendula* (Figs. 4 - 9; *Betula pubescens* subsp. *pubescens* (Figs. 10,11,21); *Betula pubescens* var. *fragrans* (Figs. 12-19,22); *Betula pubescens* s.l. (Fig. 20).

Figure 4. 'Classic' pendulous form of *Betula pendula*

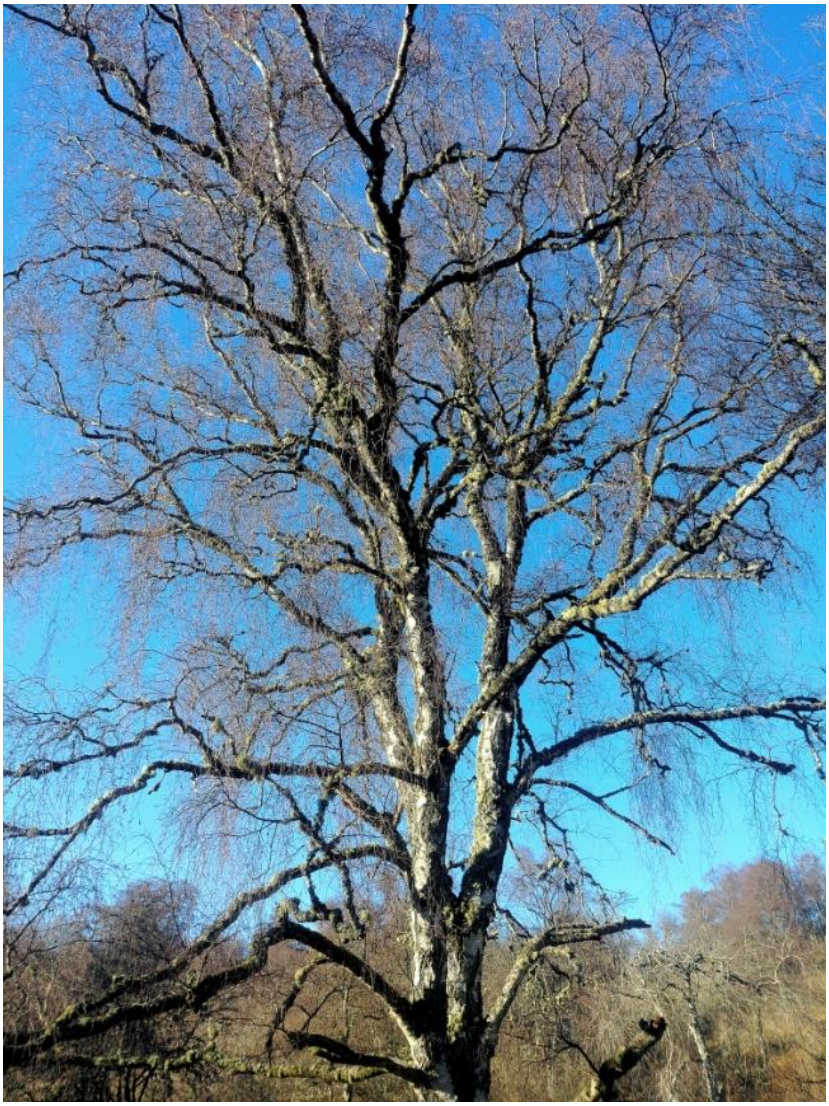

Figure 5. Old trees of *Betula pendula* can develop intricate, spreading branches

Figure 6. *Betula pendula* showing vertical splits in bark

Figure 7. *Betula pendula* lower trunk. Left: transition from white bark (above) with vertical splits to increasingly rugged lower trunk. Right: exceptionally rugged trunk on an old tree.

Figure 8. *Betula pendula* inverted dark V marks above branches (left), female catkin scales and fruits (right)

Figure 9. *Betula pendula*, twigs from vigorous saplings (top)
***Betula pendula* leaves (below)**

Figure 10. *Betula pubescens* subsp. *pubescens*

Figure 11. *Betula pubescens* subsp. *pubescens* lower trunks, showing prominent horizontal lenticels

Figure 12. *Betula pubescens* var. *fragrans*
A large tree showing complex branching and pendulous twigs on lower branches

Figure 13. *Betula pubescens* var. *fragrans*

Figure 14. *Betula pubescens* var. *fragrans*

Figure 15. Grazed *Betula pubescens* var*. fragrans* woodland

Figure 16. *Betula pubescens* var. *fragrans* - multi-trunked old tree

Figure 17. *Betula pubescens* var. *fragrans* (unusually pendulous form that, from a distance, might be mistaken for *B. pendula*)

Figure 18. *Betula pubescens* var. *fragrans*
Old tree, with fluting of trunk (an extreme example)

Figure 19. *Betula pubescens* var. *fragrans*
(glabrous young twig with glutinous bud, lenticels and glands

Figure 20. *Betula pubescens* female catkin scales and fruits (lower image © John Crossley)

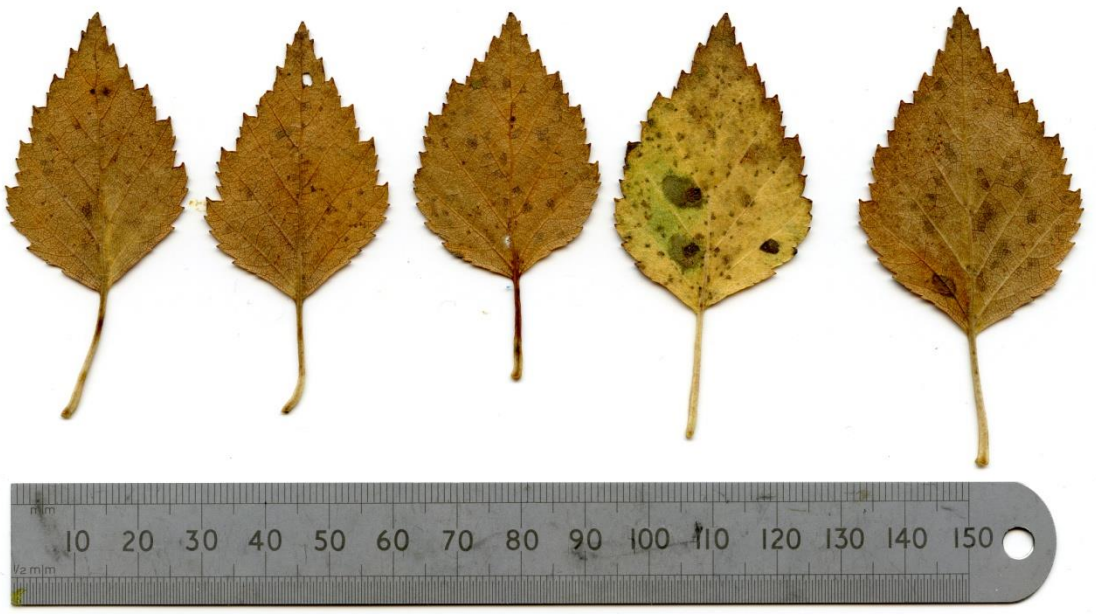

Figure 21. *Betula pubescens* subsp. *pubescens*
Leaves from tree in Fig. 10 (right). Leaf shape (teeth ± double, apex acute) suggests introgression from *B. pendula*, but all other ID features indicate that the tree is *B. pubescens*: (Fig. 11 (left) (lower trunk) and Fig. 20 (female catkin scales, third row from top).

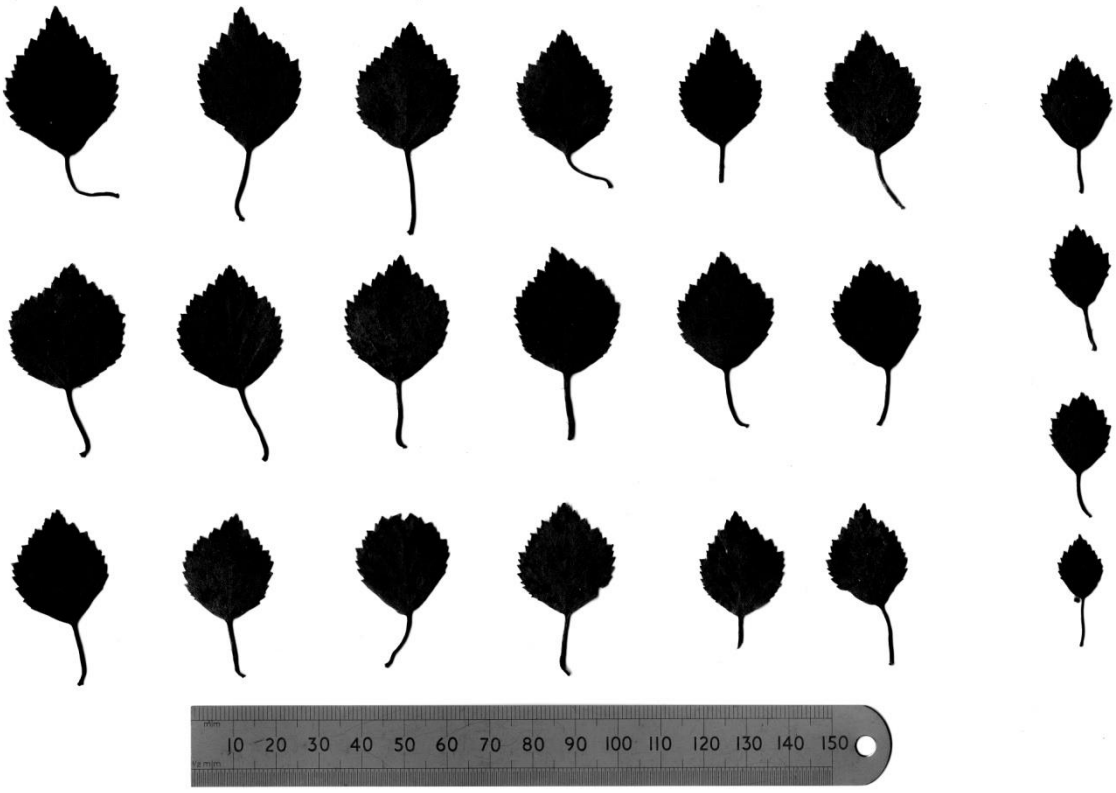

Figure 22. *Betula pubescens* var. *fragrans* leaves from single tree (Fig. 14, top left). Small leaves in right hand column are from apex of long shoots. Other leaves are typical short shoot leaves

2). The occurrence of the F1 hybrid between *B. pendula* and *B. pubescens*, *Betula* x *aurata* (Borkh.).

Trees intermediate in morphology between the parents have been considered to be hybrids and reported as common and widespread (Marshall, 1914; Walters, 1975). It is suggested by Walters (1975) that their common occurrence here is correlated with the secondary status of much birch woodland in which the original ecological isolation of the two species has broken down. Further discussion of naturally occurring and artificially created hybrids is contained in Atkinson (1992) and in the Hybrid Flora (Stace *et al.*, 2015), which reviews the pre-2000 literature.

However, while the F1 triploid hybrid (2n = 42) does occur, it appears to be rare. For example, studies in secondary mixed species birch woodland in East Anglia (Gill & Davy, 1983; Howland *et al.*, 1995) detected no F1 hybrids or aneuploids, within samples of 50 and 20 Birch trees. Zohren *et al.* (2016) used restriction site-associated (RAD) markers to analyse introgression within 37 *B. pendula* and 131 *B. pubescens* samples, from sites across the whole of Great Britain. They only detected a single F1 hybrid.

Chromosome counts do not resolve the issue, as trees with 2n=42, may be *B. x aurata*, or *B. pendula* (via unreduced gametes of one parent) or even *B. pubescens* (via double reduction meiosis of one parent), though the latter is doubtful (H. McAllister pers. comm.). To complicate matters further, tetraploid hybrids (2n=56) can be formed by unreduced gametes from *B. pendula* (Nokes, 1979).

F1 tetraploid hybrids would be expected to be exactly intermediate in morphology, while F1 triploid hybrids would be more like *B. pubescens*. Given widespread introgression from *B. pendula* into *B. pubescens* (Section 3), it is most unlikely that triploid hybrids can be identified with confidence in the field.

As stated earlier, trees of intermediate appearance are not unusual and can lead to difficulties in identification. In studies in secondary birch woodland in East Anglia (Gill & Davy, 1983; Howland *et al.*, 1995), diploids showed less morphological and molecular variation than tetraploids. Morphologically the diploids were a good match for *B. pendula*, while the tetraploids were much more variable. The range of variation in the tetraploids included some trees which corresponded well with *B. pubescens* and others which corresponded well with *B. pendula*; most of the tetraploids were intermediate in their expression of at least one, and usually more than one, of the characters measured (Gill & Davy, 1983).

Forbes & Kenworthy (1973), mapped the distribution of *B. pendula* and *B. pubescens* in the whole of the upper River Dee catchment in Aberdeenshire. They commented "We have obviated the problem of separating all individuals into *B. pendula* and *B. pubescens* by taking as a unit not individual trees but stands of trees. Although every tree in a stand cannot be assigned to one species or the other, it is possible, on the basis of trees which have been positively identified, to estimate the proportion of the two species which are present in the stand. This involves the assumption that the proportion of *B. pendula* in the unidentified trees is the same as that in the trees which can be identified. Errors arising from this assumption are insignificant, since in practice it is seldom that more than 10 percent of the trees in a stand cannot be placed in one species or the other." This approach provides a practical solution.

However, such an approach may inflate the actual abundance of *B. pendula*. H. McAllister's suggestion (pers. comm.) is to certainly identify *B. pendula* (if present), all the remaining trees are likely to be tetraploid and freely inter-fertile,

hence forming a breeding unit distinct from a 'pure' *B. pendula* breeding population. The tetraploids, though variable in appearance, can all be referred to *B. pubescens*. The above is as would be expected as diploids (2n=28) can produce unreduced gametes (n=28) which can fertilise the tetraploid (2n=56) *B. pubescens,* producing tetraploid hybrids inter-fertile with 'true' pure *B. pubescens.* There is no obvious way that tetraploid *B. pubescens* is likely to produce a gamete with n=14 to transfer genes from *B. pubescens* to the diploid *B. pendula*. Double reduction at meiosis is possible but likely to be extremely rare or nonexistent.

From my own observations in Strathspey, in north Scotland, it is straightforward to identify typical examples of both species, even where they occur in mixed stands, as long as determinations are based on as many identification features as possible (Table 1).

3). Introgression from the diploid (2n=28) *B. pendula* and *B. nana*, into the tetraploid (2n=56) *B. pubescens*.

While F1 hybrids may be rare, it has now been elegantly demonstrated (using two different molecular techniques) that introgression is widespread (Wang *et al*., 2014a and Zohren *et al*., 2016). Both studies clearly separated *B. pendula* from *B. pubescens*, and both from *B. nana*. Using genotyping at 12 microsatellite loci, and restriction site-associated (RAD) markers, they detected introgression from the two diploid species, *B. pendula* and *B. nana*, into the tetraploid *B. pubescens*, with negligible indication of introgression from *B. pubescens* into the other two species (Zohren *et al*., 2016). They also found there was an introgression gradient from the north of Scotland and Orkney to the south of England. Introgression from *B. pendula* into *B. pubescens* was very low in the north, increasing to the south. Introgression from *B. nana* into *B. pubescens* was the opposite; very low in the south, higher to the north. Both clines were highly statistically significant. The evidence of introgression from *B. nana* is remarkable, as evidence of its admixture in *B. pubescens* genotypes was detected far to the south of the species' current range in Great Britain. The authors concluded that "a zone of hybridization between *B. nana* and *B. pubescens* moved northwards through the UK since the last glacial maximum, leaving behind a footprint of introgressed genes in the genome of *B. pubescens*".

From the supporting evidence file, Table S1, (Zohren *et al*., 2016), I have calculated the percentage admixture within samples of *B. pubescens* (Table 2).

Table 2. Introgression of *Betula nana* and *B. pendula* into *B. pubescens* (Zohren *et al*., 2016).

		Percentage introgression from:		Percentage frequency of samples introgressed from:	
Latitude	(n)	*B. nana*	*B. pendula*	*B. nana*	*B. pendula*
North of 56°N, (ie. north of Edinburgh)	81	2.0	1.1	93.8	85.2
South of 53°N, (ie south of Stoke on Trent & Nottingham)	31	0.1	7.9	22.6	93.6

That introgression from *B. pendula* into *B. pubescens* is widespread across Great Britain, and that the degree of introgression is seven times higher in the south than in the north, is an important consideration when identifying *B. pubescens*. While none of these samples would be referred to *B. x aurata* (if that name is restricted to the F1 hybrid), it can be hypothesised that *B. pubescens* in the south of Britain will be more likely to show morphological features associated with *B. pendula*, than trees in the north of Britain. That suggestion is supported by studies in secondary birch woodland in East Anglia (Gill & Davy, 1983; Howland *et al*., 1995).

Introgression from *B. nana* into *B. pubescens* is only occasional in the south of Britain, and the degree of introgression is merely vestigial; it is truly a 'ghost' of *B. nana*'s former range earlier in the current post glacial period. In the north of Britain, introgression from *B. nana* is widespread, and while the degree of introgression is low, it is still higher than that from *B. pendula*. See Section 7.

4). The occurrence of distinctive local forms, especially of *B. pubescens*.
In their *Betula* monograph, Ashburner & McAllister (2013) give great emphasis to chromosome number (ploidy level) when making taxonomic decisions. Given that closely related species with the same ploidy level usually interbreed freely, within a single geographic area there is likely to be only one species with each chromosome number, unless flowering times have little or no overlap. Birches are wind pollinated, and mostly self-incompatible. Pollen can be dispersed over long distances, hence within an area there should be few differences between individuals or populations. This is a good taxonomic and evolutionary argument for lumping rather than splitting taxa, at least at species level.

Nevertheless, morphologically more or less distinctive forms of *B. pubescens* do exist within relatively restricted geographic areas. If we were to consider the whole of Britain as a unit, we might expect all *B. pubescens* to be broadly similar in appearance. Even allowing for the observed gradients in introgression from *B. pendula* and *B. nana* (discussed above), *B. pubescens* is not homogenous.

Warburg (1952) stated that *B. pubescens* was (in Britain and Ireland) "A very variable species perhaps divisible into several subspecies", probably reflecting Marshall's account of *Betula* in The Cambridge British Flora (Marshall, 1914) in which he divided *B. pubescens* into five varieties.

Two of Marshall's taxa (*B. pubescens* var. *vestita* Grenier et Gordon and *B. pubescens* var. *glabrata* Wahlenberg) refer to tall, erect growing trees. The former, and perhaps the latter, fall within Warburg's subsp. *pubescens*, and both fall within Ashburner & McAllister's var. *pubescens*. Marshall describes his var. *vestita* as common in lowland England. From his description and illustrations, this variety appears to exhibit signs of introgression from *B. pendula*. His var. *glabrata*, he describes as "commoner among the hills of the west and north of Great Britain than in the lowlands of the south and east; on lowland peat-moors in the north of England; common on the Pennines".

Two of Marshall's taxa (*B. pubescens* var. *microphylla* E.S. Marshall and *B. pubescens* var. *sudetica* E.S. Marshall) he described as taken "*together are almost sufficiently distinct from the other forms of B. pubescens to justify their being regarded as a separate species*". His *var. microphylla* is clearly the same taxon as Ashburner & McAllister's var. *fragrans*, though there are discrepancies in some of the details, i.e. Marshall states the bark is brown and shining (cf. white or grey-white, sometimes brown) and the female catkins are suberect (cf. pendulous). He

described it as rare in England and Wales, locally abundant in Scotland. Marshall's var. *sudetica*, is perhaps just a variant with narrower rhomboidal leaves, with acute apices, cuneate base and coarser teeth. He thought it rare.

Marshall described his final variety, *B. pubescens* var. *alpigena* Blytt, as a low tree or shrub, branches tortuous, leaves deeply, singly or doubly dentate, occurring between 500-700 m AOD in Scotland. It is not clear how to interpret this taxon. It is not illustrated in the Cambridge British Flora. There is material in the herbarium at Cambridge, but images are not available on line. Sell & Murrell (2018), who were based at Cambridge when writing their Flora do not refer to it, but would have been familiar with Marshall's collections.

At least two other additional forms within *B. pubescens sensu lato* have been described in Britain. Ashburner & McAllister (2013, pp. 313-314) mention a very distinctive form of *B. pubescens* (which they chose not to name) on the fringes of Dartmoor (in SW England) and in Brittany (NW France), sometimes referred to as the 'brown birch'. This is a tall tree, with whitish-brown or brown bark, velvety-hairy shoots, twigs and leaves, and twigs ± rough with brown resinous warts. It is part of the variation within their *var. pubescens*.

Trees closer to *B. pendula* in general appearance, but with persistent abaxial axillary hair tufts on leaves are tetraploids, the result of introgression from *B. pendula* into *B. pubescens*. Such trees in the Cantabrian Mountains in northern Spain are *Betula celtiberica* Rothm. & Vasc.. Ashburner & McAllister (2013) accept *B. celtiberica* as occurring in the Cantabrian Mountains, but consider other populations in mountain ranges in Spain and Portugal, formerly identified as *B. celtiberica*, as more likely to be *B. pendula* or *B. pubescens*. They consider *B. celtiberica* to be a stabilised tetraploid population derived from *B. pubescens* heavily introgressed with *B. pendula*, maintaining itself in geographic (and hence reproductive) isolation from populations of *B. pubescens*. Hence it is acting as a species. Correctly identified trees from the Cantabrian mountains are at Ness Botanic Gardens, 10 miles north-west of Chester; and Stone Lane Gardens, Devon, 15 miles west of Exeter (both open to the public).

Betula celtiberica has been reported, mainly from Wales, as well as Arran (Chater, 2010a, Chater, 2010b, Sell & Murrell, 2018) and is included as *B. pubescens* subsp. *celtiberica* (Rothm. & Vasc.) Rivas Mart. in the 4th edition of Stace's Flora (Stace, 2019). Sell & Murrell (2018) report it as planted in Cambridgeshire and probably planted widely elsewhere. Chater (2010b) records it as a native and occasionally planted tree in Cardiganshire (v.c.46). However, the RHS website lists no suppliers for this species, so nurseries may be listing this tree under a different name.

Tetraploid populations of *Betula* in an area will be expected to form an inter-fertile breeding unit, and so, for trees with '*celtiberica*' morphology to persist, there would have to be some mechanism that created reproductive isolation, eg. period of flowering, which could be correlated with altitude. Alternatively, trees with '*celtiberica*' morphology might repeatedly arise *de novo* through hybridisation and introgression.

These trees, very distinctive in Cardiganshire (A. Chater pers. comm.) require further study. The application of molecular techniques will be required to establish their links to other *Betula* populations. Currently the more parsimonious explanation is that trees with the appearance of '*celtiberica*' are part of the variation within British *B. pubescens*, due to introgression from *B. pendula*, a view with which H. McAllister agrees (pers. comm. March 2020).

A selection of images of material from Puerto de Pajares, Oviedo, Spain can be viewed at the Arboretum Wespelaar website. Fig. 23 shows typical leaves from this location. Fig. 24 shows a Cardiganshire (west Wales) example of what is identified as *B. celtiberica* by A. Chater and P. Sell.

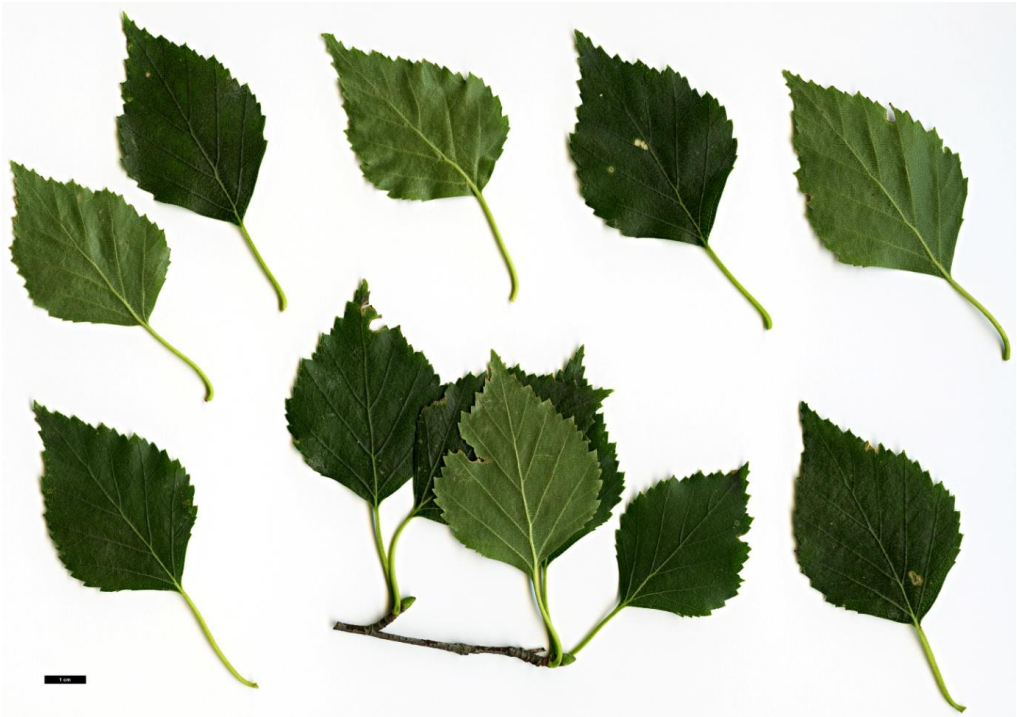

Figure 23. *Betula celtiberica* - Puerto de Pajares, Oviedo, Spain. © Jan De Langhe - Arboretum Wespelaar / Ghent University Botanical Garden

Figure 24. *Betula celtiberica*. Pontrhyd-y-groes area v.c.46 © A.O. Chater

5). Planting of alien (to the local area) genotypes and species, and effects of habitat disturbance.

In relatively undisturbed habitats, *B. pendula* and *B. pubescens* occupy rather different habitats, their distributions differ somewhat, and *B. pubescens* occurs at higher altitude. With disturbance to habitats, road and track construction, tree felling and planting, these differences have partially broken down. For example, Abernethy Forest in the Highlands is the largest of the remnant native pinewoods in Scotland. Within the core native pinewood only *B. pubescens* occurs. However, *B. pendula* is now colonising the verges of manmade tracks through the forest. On an area of bog, previously drained and planted with *Pinus contorta* (Lodgepole Pine), the non-native pines have been removed and the site re-wetted. The area now has dense regeneration of *B. pendula*, where none would have been expected before.

Provenance of planting stock is often not local. In Strathspey, in the Cairngorms, occasional *B. pubescens* is found as a planted tree. Such examples are clearly subsp. *pubescens*, whereas the usual type found in semi-natural woods locally is var. *fragrans*.

It is especially concerning that *B. pendula* is sometimes being planted beyond its native distribution in the far north and west of Scotland, potentially compromising the small-leaved *B. pubescens* in this area which has, to date, extremely low introgression from *B. pendula*. *Betula nana* and *B. pendula* have, at tetrad scale, allopatric distributions, with virtually no overlap. Hence, despite both being diploids, hybridization and introgression is rare. Wang et al (2014a), found diploid hybrids amongst seedlings grown from seeds collected from *B. nana* in Scotland, in an area recently planted with *B. pendula*, suggesting that *B. nana x B. pendula* hybrids do form in Scotland. Maintenance of the geographical separation between *B. nana* and *B. pendula* may be key to preventing future hybridization between them.

Many *Betula* species are grown in gardens and as street trees, and some are appearing in new woodland plantings. The most commonly seen are probably very white barked forms of *B. utilis* subsp. *jacquemontii* (with 'knobbly' male catkins) and its probable hybrid with *B. ermanii, B.* 'Doorenbos' (male catkins not 'knobbly' but with some fruiting catkins more or less upright/erect suggesting *B. ermanii* in its parentage). Of the other most widespread non native *Betula*, *B. papyrifera* (Paper Birch) should be particularly kept in mind. Some forms of this species closely mimic *B. pubescens* (Figs. 25 and 26). It has large ovate leaves, hairy in the leaf axils below. The fruiting scales are variable in shape; the lateral lobes may point forward as in *B. pubescens* or (as in Fig. 26) have lateral lobes with a shape similar to *B. pendula*. Seedlings have very hairy stems.


10 20 30 40 50 60 70 80 90 100 110 120 130 140 150

Figure 25. *Betula papyrifera*. Top left, centre & bottom - planted street tree, Ashbourne, v.c.57; top right - probably planted tree in wild location, Strath Mashie, v.c.96

Figure 26. *Betula papyrifera*. Top - female catkin scales and fruits; bottom - leaf underside detail (hair tufts in vein axils - veins have sparse silky hairs not visible on scan). Planted street tree, Ashbourne, v.c.57

6). Misapplication of names to taxa within *B. pubescens*.

The name *B. pubescens* subsp. *pubescens* has been used in all British Floras since Warburg's account (Clapham *et al*., 1952). Ashburner & McAllister (2013) apply the name at variety level. Other than that the name presents no problems.

However, the small-leaved form of *B. pubescens* in Great Britain has gone by five different names over the last 70 years: *Betula pubescens* subsp. *odorata* (Bechst.) E.F.Warb., *B. pubescens* subsp. *carpatica* (Willd.) Ascherson & Graebner, *B. pubescens* subsp. *tortuosa* (Ledeb.) Nyman and *B. odorata* Bechst. All these names were incorrectly applied to this taxon.

Gardiner (1984) noted that the small-leaved *B. pubescens* in the north west Highlands of Scotland, were distinctive cf. other populations in lowland Britain and Europe. Ashburner & McAllister (2013) agreed that these trees were distinctive. In their monograph it is named *B. pubescens var. fragrans*.

The incorrect or misapplied names are discussed below.

Betula pubescens subsp. *odorata* (Bechst.) E.F.Warb and *B. odorata* Bechst.

Gardiner (1984) provides a summary of Bechstein's original description of *B. odorata*. Bechstein described it as a single-stemmed tree, taller than *B. pendula* and with coarser branching, bark strikingly white, twigs pubescent without warts, leaves larger and broader, buds viscid, aromatic. Apart from the viscid buds and being aromatic, the description is almost the complete opposite of the taxon that Warburg described as *B. pubescens* subsp. *odorata*. Gardiner therefore concluded that *B. odorata* falls within *B. pubescens* subsp. *pubescens*. Marshall (1914) had synonymised *B. odorata* with his *B. pubescens* var. *vestita*, which falls within Warburg's subsp. *pubescens*, so it is surprising that Warburg used this name for the small-leaved taxon. Sell & Murrell (2018) elevate this taxon to a full species, *B. odorata* Bechst. Putting aside that it is debateable to recognise the taxon at species level, the name is incorrect. Ashburner & McAllister (2013) synonymised *B. odorata* with *B. pubescens* var. *pubescens*.

Betula pubescens subsp. *carpatica* (Willd.) Ascherson & Graebner

In *Flora Europaea*, *B. pubescens* subsp. *odorata* and *B. odorata* are synonymised with B. *pubescens* subsp. *carpatica* (Walters, 1964). This name was subsequently adopted in several British accounts, including Clapham *et al*. (1968) and Clapham *et al*. (1987).

Marshall (1914) had already synonymised *B. carpatica* with his *B. pubescens* var. *glabrata* Wahlenberg, which falls within Warburg's subsp. *pubescens*. Ashburner & McAllister (2013) comment that *B. carpatica* / var. *glabrata* do not differ significantly from their *var. pubescens*.

Betula carpatica Wild. was described from the Carpathian Mountains, and is one of several names that have been applied to disjunct populations of *B. pubescens s.l.* confined to mountains and hills in central and south-eastern Europe (Ashburner & McAllister, 2013). The *Flora Europaea* account also states that subsp. *carpatica* occurs in Arctic Europe, however this has been subsequently rejected (Jonsell, 2000; Väre, 2001).

Betula pubescens subsp. *tortuosa* (Ledeb.) Nyman

Based on a principal component analysis of leaf measurements, Gardiner (1984) synonymised B. *pubescens* subsp. *carpatica* with *B. pubescens* subsp. *tortuosa*. He noted that the name *tortuosa*, when used as a subspecies name, took precedence

over *carpatica*, and hence he argued that "both the Arctic populations of Scandinavia, Finland and Russia and the montane populations of southern Europe of *B. pubescens s.l.* may be referred to *B. pubescens* subsp*. tortuosa*". As mentioned earlier, Gardiner also noted that the small-leaved birch in the north west Highlands of Scotland, were distinctive from other populations in Europe, and he recommended that they should be recognised at variety level (following Marshall, 1914) as *B. pubescens* subsp*. tortuosa* var. *microphylla* Hartman, though he did not formally publish this combination.

Stace (1991) accepted Gardiner's conclusion, and adopted the name *B. pubescens* subsp. *tortuosa* for the small-leaved trees of upland areas of northern Britain. This name has been repeated in subsequent editions of this Flora with subsp. *carpatica* and subsp. *odorata* (*sensu* Warburg) as synonyms.

Betula tortuousa Ledeb. was described by Ledebour from the Altai Mountains, on the Russia / Mongolia / China / Kazakhstan border, and so was likely to have little (or no) evolutionary relationship with northern *B. pubescens* affected by introgression from *B. nana*. The type specimen is at St. Petersburg and was not examined by Ashburner & McAllister in the preparation of their monograph. However, Orlova (1978) in a paper written in Russian, summarised by Hämet-Ahti (1987), showed that there were distinct morphological differences between *B. tortuosa* from the Altai and the 'mountain birch' of NW Europe. Orlova (1978) considered *B. tortuosa* to possibly be a hybrid between *B. microphylla* Bunge and *B. rotundifolia* Spach (= *B. glandulosa* Michx.). Orlova named the 'mountain birch' of NW Europe *B. czerepanovii*, which Hämet-Ahti (1987) published at subspecies level as *B. pubescens* subsp. *czerepanovii* (Orlova) Hämet-Ahti.

The *Betula* account in Flora Nordica (Jonsell, 2000) also rejects the name *B. tortuosa*, agreeing with the conclusions of Orlova and Hämet-Ahti. Jonsell suggests that the 'mountain birch' is the result of introgression from *B. nana*, and that the correct name would be *B. pubescens* subsp. *czerepanovii*. However, because the transition to *B. pubescens s.s.* is completely clinal, and because the 'mountain birch' is not a homogenous taxon he does not recognise it. Väre (2001) for practical reasons adopts the name *B. pubescens* subsp. *czerepanovii*. Ashburner & McAllister (2013) also come to very similar conclusions to Jonsell (2000), but favour taxonomic recognition as *B. pubescens* var. *pumila* (L.) Govaerts. (Linnaeus had used the name pumila at variety level in his Flora Suecica, 1745). Unfortunately the name var. *pumila* invites confusion with the North American *Betula pumila* (L.).

7). Misleading interpretations of the relationship between the small-leaved *B. pubescens* in the Highlands of Scotland *cf.* Scandinavian 'mountain birch'.

In Scandinavia and Iceland a more or less distinctive form of *B. pubescens* is dominant in the subalpine zone, often referred to as 'mountain birch (Jonsell, 2000). In recent literature (see Section 6), this is referred to *B. pubescens* subsp*. czerepanovii, B. pubescens* var. *pumila*, or is not given taxonomic recognition. It was formerly often incorrectly named *tortuosa* at species or subspecies rank. The adoption of the subspecies name *tortuosa* in the New Flora (Stace, 1991), wrongly indicates a close similarity of the small-leaved *B. pubescens* in the Highlands of Scotland, and the Scandinavian 'mountain birch'.

The northern form of *B. pubescens*, *i.e.* var. *pumila*, is thought to be derived from subsp./var*. pubescens* through adaptive selection and introgression from *B. nana* (Ashburner and McAllister, 2013). In Scandinavia and Iceland, both

introgressed *B. pubescens* and its triploid hybrid with *B. nana* occur, the latter much more frequently than in Scotland (Jonsell, 2000, Thórsson *et al*., 2007).

In Scotland introgression from *B. nana* into *B. pubescens* is frequent, but at a very low level (see Section 3). It is disputed to what extent such introgression is the cause of the small leaf size observed in (at least some) *B. pubescens*. In the first edition of the *New Flora* (Stace, 1991) it is suggested that "small-leaved variants of (subsp. *tortuosa*, *sensu* Stace) may have arisen by introgression from *B. nana*". However, the fourth edition (Stace, 2019) says "Suggestions that the small leaves (of subsp. *tortuosa*) are derived from past hybridisation with *B. nana* are purely conjectural". The earlier suggestion was that only the small-leaved variants of the subspecies were introgressed from *B. nana*. H. McAllister (pers. comm. 2016) commented that var*. fragrans* (the widespread small-leaved type in Scotland) shows no signs of morphological influence from *B. nana*. He also added that he would "probably refer some Scottish *Betula* specimens to var. *pumila*, though I have not mentioned it in the monograph as occurring in the UK".

Marshall's account of *Betula* (Marshall, 1914) is instructive. He describes two forms of the *B. nana x B. pubescens* hybrid: *x B. alpestris* Gurke, which he described as very rare (only certainly from Ben Loyal (Fig. 27, left) and Rannoch Moor), and *x B. intermedia* Gurke (Fig. 27, right), which he described as rare, but recorded from several sites in Scotland. (I have retained the hybrid names used by Marshall (1914), to maintain compatibility with his account. However this naming convention is now used for intergeneric hybrids which these are not.)

Marshall also commented that some forms of his var. *microphylla* (i.e. var *fragrans*) show a strong resemblance to his *x B. intermedia*. From Marshall's descriptions, his *x B. alpestris* is closer to *B. nana*, probably the F1 hybrid, and his *x B. intermedia* closer to *B. pubescens*. The latter appear to be backcrosses to *B. pubescens* (or even *var. pumila*, see below), being taller bushes (to 4 m) with morphology of leaves, fruits and fruiting catkin scales closer to *B. pubescens* (Table 3).

The Glen Callater plant (Fig. 27, right) was described as a "good sized tree" (Marshall, 1901). Another example collected by Marshall (as x *B. intermedia*) was from a stream side (1,400 ft.), near Bachnagairn, Clova District, v.c.90, 29/6/1904. "It was about 12 feet (3.7 m) high, conspicuously differing from the surrounding *B. pubescens* at a good distance by its much darker foliage, thickly interlacing branches, and peculiar rounded outline, which resembled that of a giant bush, rather than of an ordinary tree." (Druce, 1905).

Figure 27. Left - Ben Loyal (v.c.108). Marshall 7/8/1900 (as x *B. alpestris*). http://herbariaunited.org/specimen/264309/?image
Right - Glen Callater (v.c.92). Marshall 7/1886 (as x *B. intermedia*). http://herbariaunited.org/specimen/367655/?image

Betula pubescens var*. pumila* displays evidence of introgression from *B. nana* by its low growing habit, stems growing from the base, with often erect fruiting catkins on densely puberulent twigs. Marshall's x *B. intermedia* is probably best treated as *B. pubescens* var*. pumila* (H. McAllister, pers. comm., March 2021). See Table 3 for a comparison of these taxa. *B. pubescens* var. *pumila* is hitherto unreported from Great Britain. Bushes or trees answering to var. *pumila* need to be re-found to confirm its presence here.

It is therefore clear that not all examples of small-leaved *B. pubescens* (in Scotland) are var. *fragrans*. For example, trees on Hoy, Orkney, including those in the northernmost native woodland in Great Britain, at Berriedale, are not var. *fragrans* (det. H. McAllister, J. Crossley, pers. comm., March, 2021). Leaves from a tree at Quoys (Hoy, Orkney) are illustrated in Fig. 28. This tree, from the shape of the fruits and female catkin scales, is introgressed from *B. nana*. The leaves are very similar to the Glen Callater plant in Fig. 27, but larger, and the fruiting catkins pendulous. *B. nana* does not occur on Orkney, and so this tree must reflect its former presence here, or colonisation of Hoy by heavily introgressed *B. pubescens* at some point in the past. This example, while approaching var. *pumila*, is probably best recorded as *B. pubescens*, but a form displaying morphological signs of introgression from *B. nana*.

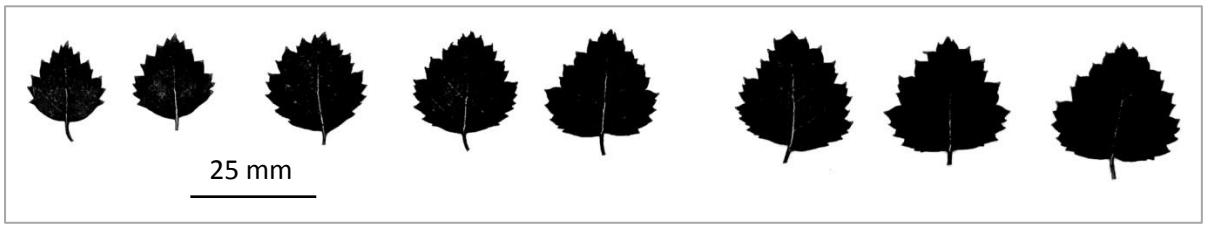

Figure 28. *Betula pubescens*, small-leaved tree introgressed from *B. nana*
Quoys, Hoy, Orkney (v.c.111) © John Crossley
Silhouettes of representative sample of leaves (top)

Table 3. Identification features of *Betula x intermedia* (two forms recognised by E.S. Marshall) and *B. pubescens* var. *pumila*

	***x Betula alpestris* (*sensu* Marshall, 1914)**	***x Betula intermedia* (*sensu* Marshall, 1914)**	***Betula pubescens* var. *pumila***
Habit / form	Shrub or undershrub, max, height 2 m, usually much lower	Small tree or large shrub, height 2.5 — 4 m, densely branched	Small tree (to 6 m) to dwarf shrub (0.5 m), with stiff branchlets.
Young twigs / branches	Glabrous, rugose, slightly glandular at tips. Shorter than in *x B. intermedia*.	Usually glabrous except at tips, where pubescent & glandular.	Thicker than subsp. *pubescens*, to as thin as *B. nana*. Young shoots densely hairy.
Lamina	Rather smaller than x *B. intermedia*, serrations more regular, shallower, blunter.	Suborbicular, or suborbicular - rhomboidal, sometimes broader than long, truncate or broadly cuneate at base, ultimately glabrous, subcoriaceous, dark green above, grey-green & strongly reticulate below. 1.5 - 1.8 cm long x 1.0 - 1.5 cm wide.	Usually smaller than subsp. *pubescens*, vein pairs 6 or fewer.
Fruiting catkins	Smaller than *x B. intermedia*.	Erect or ascending	Often erect.
Fruiting scales / bracts	Scarcely different to *B. nana*.	Lateral lobes ascending.	Lateral lobes ascending / erect.
Nutlet wing	Narrower than nutlet, sometimes rudimentary or absent.	Variable, sometimes as *B. pubescens* & sometimes much narrower.	
Frequency	Very rare. Ben Loyal (v.c.108) & Rannoch Moor (v.c.98).	Rare, more frequent than *x B. alpestris*.	Not confirmed.

Conclusions and further work

Regarding identification of *Betula*, the following should be kept in mind:

1. Always make use of as many identification features as possible when making a determination (Table 1). Published studies that report difficulties in distinguishing *B. pendula* and *B. pubescens* restrict consideration to a limited range of parameters, particularly quantitative measures of leaf shape. Additional discriminatory identification features should always be used.
2. Not every example of *B. pendula / pubescens* can be reliably identified, but most can as long as a suite of identification features can be assessed.
3. The F1 hybrid between *B. pendula* and *B. pubescens*, *B. x aurata* cannot be reliably identified in the field. Almost all trees with a mix of characters are *B. pubescens* with variable evidence of introgression from *B. pendula*.
4. Variation within *B. pubescens* should be accepted at subspecies and / or variety level. Raising these forms to species level (Sell & Murrell, 2018) is not supported as they are all inter-fertile tetraploids.

Unresolved issues and further fieldwork:

1. Not all small-leaved *B. pubescens* in Britain and Ireland are referable to var. *fragrans*. Trees recorded under one or other of the names associated with small-leaved *B. pubescens*, have been recorded from 46 vice-counties in Great Britain and Ireland. Away from the Highlands of Scotland, correspondence with BSBI vice-county recorders indicates that very few records can, with any confidence, be assigned to var. *fragrans*. It is confirmed from Wales (Lake Bala) and England (Northumberland) (Ashburner & McAllister, 2013). Irish records are unconfirmed. If some records of small-leaved *B. pubescens* are not of var. *fragrans*, what are they?
2. What is the distribution of var. *fragrans*? It is certainly the most frequent form of *B. pubescens* in many upland parts of the Scottish Highlands. It is the typical type in the Cairngorms glens, and it occurs at least as far north as Strath Naver in Sutherland. The type specimen is from the Isle of Bute (v.c.100), so it may also occur throughout the western Highlands. However not all *B. pubescens* in northern Scotland is var. *fragrans*. Trees close to the coast near Lochinver (v.c.108) are much larger leaved, and fall within subsp*. pubescens*.
3. *Betula pubescens var. fragrans* is not reported from mainland Europe. Does it occur there, or is it endemic to Great Britain (and possibly Ireland)?
4. Do examples of *B. pubescens* occur in Scotland that could be referred to var. *pumila*? As discussed above, almost certainly yes, but thought to be rare. The frequency of B. *pubescens* with clear signs of introgression from *B. nana* is unknown.
5. Do discrete, identifiable forms of *B. pubescens* occur in geographically limited areas? If so, how do they maintain their separate identity?
6. What are the trees referred to as '*celtiberica*' in Wales? Do trees with similar appearance occur elsewhere?
7. Regarding the recording of birches. The BSBI distribution database, popular recording software, eg. MapMate and web-based recording, eg. iRecord, only give the option of using the taxon name *B. pubescens* subsp*. tortuosa* when recording small-leaved trees. Trees positively recorded as var. *fragrans*, should as a temporary, stop-gap measure be recorded using the name *tortuosa*, but the correct identification should be added to the Comments field. These records can then be transferred to the correct taxon as and when database dictionaries are updated.

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This paper could not have been written without Ashburner and McAllister's *Betula* monograph. Hugh McAllister also provided detailed comments on earlier drafts of this paper, and discussed *Betula* identifications over recent years. John Crossley commented on earlier drafts of this paper, shares an enthusiasm for *Betula* in northern Scotland and provided images for Figs. 20 and 28. Arthur Chater discussed his records of *B. celtiberica* in Wales and provided the image for Fig. 24.

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