

A re-assessment of montane willow (*Salix* L., Salicaceae) hybrids in Scotland

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ABSTRACT

A review of the hybrids of willows (*Salix* L.) occurring on Scottish mountains has been undertaken. Field surveys were carried out in selected areas and the hybrids which were found were brought into cultivation for further study and ultimately for their conservation. The distribution of these hybrids in the chosen areas and their status are discussed. Seven hybrid combinations new to Britain have been proposed and described based on morphological characters, whereas seven other hybrid combinations that had recently been published for Britain have now been rejected. The British list of willow hybrids has been tentatively revised as an interim step, although preparation has also been made for DNA studies to be carried out in a programme planned to test the hypotheses of their hybridity and parentage.

KEYWORDS: Hybridization, plant surveys, conservation, chromosomes.

INTRODUCTION

A survey of the willow (*Salix* L.) hybrids occurring on Scottish mountains has been carried out, mainly during the last decade. This is a very difficult but important group in the Scottish mountain flora, especially as extensive hybridization has taken place leading to great variation, which, combined with the inaccessibility and extreme rarity of many individual hybrids in their natural habitat, has led to their neglect for many years. A major revision was published by F. Buchanan White (White 1890) in which several new hybrids were described. White's findings were later incorporated into an extensive monograph on British *Salix* by the Rev. E. F. Linton (Linton 1913), with considerable addition and further revision. Linton described 39 willow hybrid combinations which were likely to have occurred in montane habitats in Scotland. Since that time hardly any further progress was made until a full re-assessment was completed by R. D. Meikle (Meikle 1975) and a handbook published (Meikle 1984) in which several of the willow hybrids accepted by Linton were rejected, either due to lack of satisfactory evidence or due to earlier re-determination by non-British salicologists, notably S. J. Enander and B. Floderus. Two new hybrid combinations found in the Scottish mountains were included in the list prepared by Meikle. However, in many cases *Salix* hybrids are extremely difficult to determine, particularly from herbarium material, and, as fresh specimens of some of the rarer hybrids from montane habitats were unavailable at the time, the 1975 re-assessment left many questions unanswered. Fortunately, R. D. Meikle is still the leading British salicologist and through his considerable help with the determinations a new re-assessment has been possible.

In this paper willows have been divided into two groups according to their usual natural habitat. First are those species which are more or less confined to mountain habitats in Scotland, and usually with an alpine or sub-arctic distribution elsewhere ('montane willows'). Second are those species which generally occur at low altitudes but which sometimes extend their upper altitudinal range to overlap in habitat with the first group ('lowland willows'); these are listed and more precisely defined under Materials and Methods. This re-assessment has concentrated primarily on those hybrids which have at least one montane species as a parent, and hybrids which involved only lowland species are generally included only where they were found to occur with or near hybrids or species of montane willows.

The overall distribution of the willow species, montane or lowland, is not given in this paper, but can be seen in Preston *et al.* (2002); however, an indication is provided under Materials and Methods of their frequency in the selected areas surveyed.

In addition to the establishment of a living collection of willow hybrids from Scottish montane habitats, the wider objectives of this re-assessment can be summarised here as follows:

1. To establish the status of previous records and to match them with newly collected material, providing updated records for local county recorders and for databases.
2. To revise the British list of *Salix* hybrids (Stace 1997; Kent & Stace 2000) and to provide information for the *Vice-county census catalogue* (Stace *et al.* 2003).
3. To produce selected hybrids by design in cultivation for comparison with herbarium and newly collected specimens and with published descriptions, and to provide these as control examples for further studies.
4. To provide recently confirmed material to herbarium collections, thus reducing the need for further collection from their native sites.
5. To prepare hybrid descriptions based on recently confirmed material and to build up photographic records for future identification purposes.
6. To provide living material to botanic gardens and other institutions for future research.
7. To consider their conservation. The majority of the hybrids are extremely rare and very vulnerable in their native habitats. Their establishment in botanic gardens will form one type of conservation. However, a carefully controlled programme for the introduction of the rarest hybrids into their original place of collection should also be given consideration.
8. It became apparent during the survey that there was a need to advance identification techniques for willow hybrids. Consequently, an additional objective has been to seek a source where molecular studies could be carried out and then to select and prepare DNA samples from the cultivated plants.

MATERIALS AND METHODS

HERBARIUM RECORDS

The initial step in this survey was the examination of herbarium collections in order to establish the distribution of hybrids and to select the areas for the field studies (Table 1), and also to become familiar with the characters of the willow species and their hybrids and to match these with published data. The following herbarium collections were studied in detail: **BM**, **CGE**, **E**, **K**, **LIV**, **NMW** and **OXF**. The information abstracted from these sources formed the main basis for the field-work. The free exchange of specimens between the early salicologists, and the issue of a set of British willows to major herbaria by E. F. & W. R. Linton in the late 19th century, enabled virtually all of the important hybrid specimens to be traced.

FIELD-SURVEY LOCATIONS

The field-work was commenced in 1991, although a few of the important willow hybrids had been discovered earlier. In the latter part of the 1990s the field surveys were extended after the necessary permits and permissions from land-owners were obtained. The areas surveyed (Table 1) were those which the early salicologists had found to be rich in montane willow hybrids, in order to relocate all of the described hybrids and to bring them into cultivation for further studies. The areas have been given code letters for the sake of brevity.

DEFINITION OF MONTANE AND LOWLAND WILLOWS

Montane willows occurring on British mountains are defined here as those species with a lower altitudinal limit of usually more than 610 m and an upper limit of over 850 m (and usually to 1000 m). All but two of the six species meeting these criteria are now confined to Scotland.

S. lapponum L. Widespread and frequent in locations 2, 3 and 4, more local and usually in smaller numbers (in the pure state) in location 1, not found in the areas surveyed in locations 5, 6 or 7. Descends to 210 m in West Perth, v.c. 87.

S. lanata L. Locally frequent at MNS (location 1), GCS (location 3) and CK (location 4), local and very scarce elsewhere in location 1 and in location 2, absent or very rare elsewhere. Descends to 620 m in Westernness, v.c. 97.

TABLE 1. FIELD SURVEY LOCATIONS

Location	V.C.	Main sites	Grid square	Site code
1. Central Highlands: Mid Perthshire	88	a. Creag Roro	NN 64	CR
		b. Meall na Samhna	NN 43	MNS
		c. Meall Ghaordie	NN54	MG
2. Eastern Central Highlands: East Perthshire	89	a. North and north-west of Spittal of Glenshee	NO 07	GS
3. Eastern Highlands: Angus	90	a. Glen Doll	NO 27	GCD
		b. Glen Fee	NO 27	GCF
		c. Corrie Sharroch	NO 27	GCS
		d. Glen South Esk	NO 28	GCE
		e. Loch Brandy	NO 37	GCB
4. Eastern Highlands: South Aberdeen	92	a. Glen Callater & Coire Kander	NO 18 & 28	CK
		b. Lochnagar	NO 28	LGR
5. Western Highlands: Main Argyll	98	a. Allt nan Giubhas	NN 25	ANG
6. Northern Highlands: West Ross	105	a. An Teallach	NH 08	AT
7. Northern Highlands: West Sutherland	108	a. Inchnadamph	NC 22	IDH

S. arbuscula L. Abundant on MG, much of CR and local and in smaller numbers on MNS (all location 1), not recently reported from locations 3 or 4 and absent from locations 2, 6 and 7 and ANG (location 5). Descends to 460 m in Mid Perth, v.c. 88.

S. myrsinites L. Locally frequent in CK in location 4, local and often rather scarce (in the pure state) in locations 1, 3 and 7 and absent in the areas surveyed in locations 2, 5 and 6. Descends as low as 180 m in West Sutherland, v.c. 108.

S. herbacea L. Very frequent and widespread in all of the locations surveyed, especially at higher altitudes where it is reported to exceed 1300 m, yet it descends almost to sea level in Shetland, v.c. 112.

S. reticulata L. Frequent and locally abundant at CR, MG and MNS (all location 1). Local and rather scarce throughout location 3 and in CK (location 4). Absent from the other areas surveyed. Descends to 650 m in Mid Perth, v.c. 88.

The lowland willows included in this survey are defined as those species with an upper altitudinal limit of at least 610 m in Scotland, but the majority have a maximum limit below 800 m; all have their lower limit more or less at sea-level throughout Scotland. Six Scottish willow species meet these criteria and occur throughout the areas surveyed, although seldom in large numbers at higher altitudes.

S. caprea L. Most frequently represented at high altitudes in the areas surveyed by its subspecies *sphacelata* (Sm.) Macreight, or by intermediates between the latter and subsp. *caprea*.

S. cinerea L. Usually represented in the Scottish mountains by its subspecies *oleifolia* Macreight, but it seldom reaches the altitudes or habitats where the montane species occur in Scotland.

S. aurita L. Frequent even at moderately high altitudes, but absent on the basic rocks favoured by most of the montane willows.

S. myrsinifolia Salisb. Throughout most of the areas surveyed and not uncommon at higher altitudes with the montane species where it often occurs in a much dwarfed form.

S. phyllicifolia L. Surprisingly scarce or apparently absent in nearly all of the areas surveyed, although usually frequent in the form of its hybrid with *S. myrsinifolia*. Some of the existing records undoubtedly refer to this hybrid.

S. repens L. Occurs in nearly all of the areas surveyed, although often locally and in small numbers and usually absent at the altitudes and habitats favoured by the montane species, but abundant in location 2.

All of the montane species are known to hybridize with at least one of the others in Scotland, and the lowland species often cross freely with each other. Four of the six lowland willows hybridize directly with montane species in Scotland; the fifth, *S. cinerea*, does not, although such

crosses are known in Scandinavia. The sixth, *S. phylicifolia*, may have crossed with montane species only as a secondary hybrid, after it had first crossed with *S. myrsinifolia*, although direct crosses between *S. phylicifolia* and montane species are reported from Scandinavia.

Cuttings of nearly all of the hybrids given in the list of records below were collected in the field for their propagation and the success rate in rooting these exceeded 95%, which eventually resulted in the establishment of a collection of over 500 pots of living willow hybrids. Most of these are now at the Royal Botanic Garden, Edinburgh, adding to ones earlier donated. A few living willow hybrids were also given to Ness Botanic Gardens, Merseyside, and the remainder (c. 200 plants) is at present in cultivation in my garden in North Yorkshire.

At the time this manuscript was prepared some of the hybrid binomials used below had not been used in recent British publications. These unfamiliar names are taken from *Flora Nordica* (Elven & Karlsson 2000), with the more familiar name placed in parentheses.

RESULTS

FIELD RECORDS OF *SALIX* HYBRIDS

The field records made during this survey and a few earlier records from the areas surveyed are listed below. The sites concerned are indicated by the letter-codes given in Table 1. Except where stated otherwise, especially references to old herbarium specimens, the records are field-records made by me and the identities of specimens were confirmed or initially determined by R. D. Meikle, although in some cases after re-assessment following new evidence. The probable status of individual records is given where known, but this is sometimes uncertain due to lack of published information. More precise details of individual records have been sent to the Biological Records Centre, CEH Monks Wood, and herbarium material has been placed in **E** with the remaining specimens now in **herb. DJT** (later to be placed in **BM**). Unconfirmed or doubtful identifications have been placed in square brackets. The seven combinations asterisked are new to or restored to the British list, and are described in the next section.

Salix caprea × *S. cinerea* = *S.* × *reichardtii* A. Kern. GCF, 1995.

S. caprea × *S. aurita* = *S.* × *capreola* Jos. Kern. ex Andersson. CR, 1997.

S. caprea × *S. myrsinifolia* = *S.* × *latifolia* J. Forbes. GCF, 1996. Not listed in *Flora Nordica* but a recent gathering in Norway is probably this (H. Väre, pers. comm.).

**S. caprea* × *S. myrsinifolia* × *S. phylicifolia*. CR, 1997, 1st. confirmed British record, 2000; GCF, 1996 (probable). Endemic.

[*S. caprea* × *S. myrsinifolia* × *S. myrsinites*. GCF, 1996 (possibly, but more likely the previous cross and this hybrid combination is therefore rejected)].

S. caprea × *S. phylicifolia*. IDH, 2000 (probable).

S. caprea × *S. repens* = *S.* × *laschiana* Zahn. GS, 1997; CK, 1995; IDH, 2000.

S. caprea × *S. lapponum* = *S.* × *canescens* Willd. (*S.* × *laestadiana* Hartm.). GS, 1994, 1997, previous v.c. 89 record 1906 (**E**); GCE, 1981, GCF, 1996, previous v.c. 90 record 1904 (**E**); CK, 1995 (probable).

S. cinerea × *S. aurita* = *S.* × *multinervis* Döll. IDH, 2000.

S. aurita × *S. myrsinifolia* = *S.* × *coriacea* J. Forbes. GS, 1997; GCF, 1996, 1998.

S. aurita × *S. myrsinifolia* × *S. phylicifolia* = *S.* × *saxetana* F. B. White. GS, 1997; GCF, 1996, 1998; CK, 1996. Not reported from Scandinavia.

[*S. aurita* × *S. myrsinifolia* × *S. myrsinites*. GCF, 1996, initially thought to be this cross, but following cultivation later determined as *S.* × *saxetana*].

S. aurita × *S. phylicifolia* = *S.* × *ludificans* F. B. White. ANG, 1994.

S. aurita × *S. repens* = *S.* × *ambigua* Ehrh. CR, 1997; MG, 2000; GS, 1994; GCF, 1996; CK, 1996.

[*S. aurita* × *S. repens* × *S. lapponum*. A few plants collected locally in GS, 1994 and in CK, 1995 and 1996 appeared to be this cross. They were initially determined as *S. repens* × *S. lapponum* but also resembled *S. aurita* × *S. lapponum*, which occurred nearby in both localities. E. F. Linton also considered a specimen collected in CK by E. S. Marshall (No. 2958, **CGE**) was this cross, but did not include it in his *Monograph* (1913). However, these plants could not be determined with complete certainty and, although this cross is reported from Norway, the records must remain tentative].

S. aurita × *S. repens* × *S. herbacea* = *S. × grahamii* Borrer ex Baker. Originally found in v.c.c. 108 and H35, but not found in the areas surveyed.

S. aurita × *S. lapponum* = *S. × obtusifolia* Willd. CR, 1997; MG, 2000, probable 1st. recent v.c. 88 records; GS, 1994, 1997, previous v.c. 89 record 1906 (CGE); GCB, GCD, GCF, GCS, 1995–2002, 2nd v.c. 90 record, 1st post 1930 record (E); CK, 1995, 1996.

**S. aurita* × *S. lapponum* × *S. herbacea*. GCS, 1998 (3 plants); CK, 1996 (2 plants). These were found to match artificially-produced hybrids of the same cross between *S. × obtusifolia* and *S. herbacea*. 1st British record. Endemic.

S. aurita × *S. herbacea* = *S. × margarita* F. B. White. GS, 1997 in two widely separated localities, previous v.c. 89 record 1892 (CGE); CK, 1996, single plant, 1st v.c. 92 record.

S. myrsinifolia × *S. phylicifolia* = *S. × tetrapla* Walker. CR, MG, MNS, 1991–2002; GS, 1994; GCD, GCF, GCS, 1995–2002; CK, 1995–1996.

**S. myrsinifolia* × *S. phylicifolia* × *S. repens*. GS, 1997, two plants, 1st. British record. (However, *S. phylicifolia* × *S. repens* (below) reported from v.c. 90 in 1959 (Meikle 1975) might refer to this cross). Endemic.

[*S. myrsinifolia* × *S. phylicifolia* × *S. lapponum*. A specimen was obtained from CK, 1996, but the determination is not certain. Very similar plants were collected from CGD and MG in 2002].

[*S. myrsinifolia* × *S. phylicifolia* × *S. arbuscula*. Some specimens determined as *S. myrsinifolia* × *S. arbuscula* from CR and MG, 2000, 2002, might represent this cross as these two hybrids are extremely difficult to separate, but none of these specimens has been definitely confirmed as this hybrid].

S. myrsinifolia × *S. phylicifolia* × *S. myrsinites* = *S. × blyttiana* Andersson. MG, 1994, 2000, previous v.c. 88 record 1918 (E); GCF, 1996; GCS, 1995, previous v.c. 90 records 1918 (E) and 1955 (K).

S. myrsinifolia × *S. repens* = *S. × felina* Buser ex E.G. & A. Camus. GS, 1997. Two separate gatherings were determined as this cross and on this basis it is included in the records; however, it is very difficult to distinguish from *S. myrsinifolia* × *S. phylicifolia* × *S. repens* above. A specimen collected in 1898 (E) is labelled as the former but has not been recently confirmed, so the recent determinations probably represent the 1st confirmed v.c. records.

**S. myrsinifolia* × *S. lapponum* (= *S. × dalecarlica* auct., non Rouy). No. LGR 1/59, D. J. Tennant, 1959 (E), determined recently by R. D. Meikle. Single gathering, 1st. confirmed British record. Endemic?

**S. myrsinifolia* × *S. arbuscula* (= *S. × breadalbensis* Druce, nom. nud.). CR, 2000 (possibly); MG, 1998, 2002, previous v.c. 88 record 1896 (Linton 1913), but all old records were doubted by Meikle (1975), so this possibly represents the 1st confirmed British record. Endemic?

S. myrsinifolia × *S. myrsinites* = *S. × punctata* Wahlenb. MG, 1992, 2000; GCF, GCS, 1995–2002 (frequent); CK, 1995, 1996 (locally frequent).

[*S. myrsinifolia* × *S. myrsinites* × *S. herbacea*. Specimens collected in GCS, 1998, were initially thought to represent this cross. However, following cultivation they have been found to match *S. aurita* × *S. lapponum* × *S. herbacea* (above), and although this hybrid is likely to exist in Scotland it has now been removed from the list].

[*S. myrsinifolia* × *S. herbacea* = *S. × semireticulata* F. B. White. Recorded in v.c. 90 in the late 19th century but in my opinion none of the specimens is convincing and none of the specimens collected during this survey was determined as this cross, so there is now no strong evidence for its existence in Britain].

S. phylicifolia × *S. repens* (= *S. × schraderiana* auct., non Willd). Occurs in Orkney, v.c. 111, but was not found in the areas surveyed. A record from v.c. 90 (K) in 1959 (Meikle 1975) might alternatively refer to *S. myrsinifolia* × *S. phylicifolia* × *S. repens* (above).

S. repens × *S. lapponum* (= *S. × pithoensis* Rouy, nom. nud.). GS, 1996, 1997. Previous British confirmed record GS, 1906 (E, CGE).

**S. repens* × *S. arbuscula*. MG, 1994. 2 plants, 1st confirmed British record. Endemic. A report of this hybrid by Meikle (1978) in v.c. 88 can be discounted as the specimen was doubtful (R. D. Meikle pers. comm.).

[*S. repens* × *S. lapponum* × *S. arbuscula*. A single specimen gathered with *S. repens* × *S. arbuscula*, MG, 1994, D. J. Tennant, appears to be this cross, but has still not been confirmed].

S. repens × *S. herbacea* = *S. × cernua* E. F. Linton. GS, 1994, 1997, in two widely separated localities, previous v.c. 89 record 1906 (E); AT, 1986.

**S. lapponum* × *S. lanata* (= *S. × stuartii* hort.). GCS, 1995, 1998, previous v.c. 90 record 1918 (E), [GCF, 1977 (Ingram & Noltie 1981), specimen not traced]; CK, 1996, previous correctly named v.c. 92 record 1897 (BM, CGE), but an earlier specimen collected in CK by K.R. Wallis in 1884 (BM) is possibly also this cross. Not reported from Scandinavia.

S. lapponum × *S. arbuscula* = *S. × pseudoglauca* Andersson (*S. × pseudospuria* Rouy, nom. nud.). CR, MG, MNS, 1992–2002, locally frequent, previous v.c. 88 record 1933 (E); GCS, 2000, 1st recent v.c. 90 record. There are old records for Angus, v.c. 90 (Ingram & Noltie 1981).

[*S. lapponum* × *S. myrsinites* × *S. herbacea*. Two specimens collected in GCS, 1998 and two in CK, 1996, were initially determined as this cross, but following cultivation are now thought to be *S. aurita* × *S. lapponum* × *S. herbacea*. A further specimen collected in GCS, 1998, could represent this cross but might alternatively be a form of *S. lapponum* × *S. herbacea*, which is also the identity of all specimens that were named *S. × eugenes* E. F. & W. R. Linton (Linton 1913). This hybrid therefore remains unconfirmed].

S. lapponum × *S. herbacea* = *S. × sobrina* F. B. White. CR, 2000, MG, 2002, MNS, 1998, previous v.c. 88 record 1900 (BM); GS, 1994, single plant, previous v.c. 89 record 1906 (E, CGE); GCS, 1995, 1998, previous v.c. 90 record 1918 (E); CK, 1996, 2 plants, previous v.c. 92 record 1906 (E).

S. × boydii E. F. Linton. This hybrid has not been rediscovered since its original collection in GCF over 100 years ago, and is presumed extinct there; it is not known elsewhere. Its parentage, which is discussed later in this paper, is not known with certainty, but it is included here as *S. lapponum* and *S. herbacea* both appear to be involved. Endemic.

S. lanata hybrid. MNS, 1994, single plant. This appears to be a hybrid between *S. lanata* and a lowland species, which was initially thought to be *S. myrsinifolia*. However, a chromosome count on the hybrid suggested that *S. myrsinifolia* could not be involved. See below under chromosome numbers, where it is suggested that either *S. repens* or *S. aurita* might be the other parent. There are no confirmed records of such a cross in Britain, although Linton (1913) produced a hybrid between *S. repens* and *S. lanata* in cultivation.

S. lanata × *S. herbacea* = *S. × sadleri* Syme. MNS, 1994, previous v.c. 88 record ?1894 (BM) but a 1961 BM specimen from v.c. 88 could be correctly named; GCS, 1995–2002, previous definite v.c. 90 record 1918 (E), although reported from GCS in 1975 (Ingram & Noltie 1981); CK, 1996 (topotype), previous definite v.c. 92 record 1892 (BM, LIV). CK specimens collected in 1934 (E) could be correctly named but might alternatively be small or juvenile *S. lanata*.

[*S. lanata* × *S. myrsinites* × *S. herbacea*. A single plant collected in GCS, 1998, was determined as this cross. E. F. Linton also suggested that a specimen collected by W. R. Linton in the same locality in 1894 (LIV, no. 329) involved both *S. lanata* and *S. myrsinites*, but did not publish the record in his *Monograph* (Linton 1913). Linton's specimen is very similar to my 1998 plant and there is good evidence that *S. herbacea* is also one parent of the LIV specimen. However, both of these hybrids might alternatively be unusual forms of *S. × sadleri* and therefore this cross should remain as unconfirmed until further evidence becomes available].

S. arbuscula × *S. herbacea* = *S. × simulatrix* F.B. White. MNS, 1991, 1998, previous v.c. 88 records 1932 (BM) and 1959 (*Proc. B.S.B.I.* 5: 34 (1963)).

S. arbuscula × *S. reticulata* = *S. × ganderi* Huter ex Zahn. MG, 2001, single plants from two widely separated localities, previous v.c. 88 record 1938 (E). A single plant collected at CR in 2002 is probably the same cross. A report of this hybrid in v.c. 88 by Meikle (1978) can be discounted (R.D. Meikle pers. comm.). The 1938 specimen represents the only confirmed British herbarium specimen that has been traced; the 2001 gatherings therefore represent the 2nd confirmed British record.

S. myrsinites × *S. herbacea*. MNS, 1998, previous v.c. 88 record 1922 (BM); GCS, 1998–2002, previous correctly named v.c. 90 record 1888 (CGE); CK, 1995, 1996, previous v.c. 92 record 1878 (E).

DESCRIPTIONS OF NEW *SALIX* HYBRIDS

Four of the *Salix* hybrids included in the list of field records given above, i.e. excluding the incompletely determined hybrid of *S. lanata*, are combinations new to Britain which have been

proposed during the course of this study. These are *S. caprea* × *S. myrsinifolia* × *S. phyllicifolia*, *S. aurita* × *S. lapponum* × *S. herbacea*, *S. myrsinifolia* × *S. phyllicifolia* × *S. repens*, and *S. repens* × *S. arbuscula*. A further hybrid reported previously in Britain, but apparently then in error, is included in the present list and is therefore also new to Britain: this is *S. myrsinifolia* × *S. lapponum*. In addition, two hybrids previously recorded in Britain but later rejected, due to either lack of satisfactory evidence or subsequent erroneous re-determination, have been restored to the present list; these are *S. myrsinifolia* × *S. arbuscula*, and *S. lapponum* × *S. lanata*. One other hybrid, *S. arbuscula* × *S. reticulata*, found during my field studies, had not previously been described from British material, and another, *S. myrsinites* × *S. herbacea*, had been inaccurately described. The above nine 'new' hybrids are described below. Descriptions of most British *Salix* hybrids can be found in Linton (1913) and Meikle (1975, 1984).

SALIX CAPREA L. × *S. MYRSINIFOLIA* SALISB. × *S. PHYLICIFOLIA* L.

An earlier description of this hybrid was recently published (Tennant 2001), following its discovery, but an extended description is given here.

Vouchers: Near Creag Roro, Glen Lyon, Mid Perth, v.c. 88, GR NN64, D.J. Tennant Nos. CR9/00 (male), 7 July 2000 (E); CR 8/01 (female), 25 July 2001 (E).

Ascending bush up to c. 3 m high; twigs at first pubescent, becoming dark reddish-brown, glossy and glabrous; buds large, 5–6 × 2–3 mm, narrowly ovoid, blunt, at first pubescent, yellowish; leaves obovate to broadly obovate or subrotund, the larger when mature typically 50 mm long and 35 mm wide, the smaller acute, acuminate, the larger obtuse, mucronate to broadly rounded-obtuse and cuspidate at apex, with narrowly recurved margins, shallowly serrate to remotely serrulate, the smaller narrowly rounded, the larger broadly rounded at base, all coriaceous, dark bright green and glossy on upper surface and rather thinly pubescent with the hairs usually confined to the midrib and near to the apex, or subglabrous, pale green, glaucous and glabrous on lower surface with prominent venation; petioles rather short, 5–15 mm long, mainly moderately pubescent, eventually becoming thinly pubescent; stipules absent or up to 3.5 × 1.5 mm, narrowly ear-shaped, acute, denticulate at margin. Catkins appearing with leaves, broadly cylindrical to cylindrical, usually terminal on lateral shoots; peduncles 4–5 × 1.5 mm, with scattered to dense, medium to rather long, somewhat appressed hairs; catkin-scales 2.5–3 × 0.75–0.9 mm, oblanceolate to narrowly obovate, narrowly obtuse at apex, pale green with upper part usually brown, with numerous hairs on surface projecting by 1.0–2 mm beyond apex. Male catkins c. 18 × 15 mm, with two free stamens; filaments 5.5–7.5 mm, glabrous, pale greenish-white; anthers 0.9 × 0.8 mm, yellow; nectary single, oblong, green. Female catkins c. 35 × 10 mm; ovary flask-shaped, c. 3 × 1 mm, green, moderately pubescent; pedicel c. 2 mm long, shortly pubescent; style c. 5 mm long, pale olive-green; stigmas 0.5–0.7 mm long, fused but deeply notched; nectary single, 0.8 × 0.3 mm, linear-oblong, truncate at apex, greenish. Capsule c. 5 × 1.5 mm, with scattered pubescent hairs. Endemic.

SALIX AURITA L. × *S. LAPPONUM* L. × *S. HERBACEA* L.

Vouchers: Coire Kander in Glen Callater, South Aberdeen, v.c. 92, GR NO18, 28 July 1996, D.J. Tennant No. CK 18B/96 (E); Corrie Sharroch in Glen Clova, Angus, v.c. 90, GR N027, 14 July 1998, DJT Nos. GCS 13/98, GCS 18/98 (E).

Ascending or semi-procumbent dwarf shrub, usually less than 30 cm high; twigs at first glossy olive-green or brownish-yellow, thinly lanuginose or with scattered, fine, short pubescent hairs, becoming glossy, reddish-brown and glabrous; buds 2–3.5 × 0.9–1.2 mm, narrowly ovoid, more or less acute at apex, olive-green or yellowish and pubescent at first, becoming glossy, reddish-brown and glabrous; leaves typically 15–23(–33) × 10–13(–18) mm at maturity, broadly elliptic, ovate, oblong-ovate or obovate, often shallowly channelled, broadly acute, subacute or rounded and often twisted at apex, sometimes broadly twisted at margins, slightly recurved, crenulate-denticulate to markedly crenate-serrate with red-tipped teeth, mainly more or less rounded, rounded-subtruncate or subcordate and often irregular at base, at first moderately to densely clothed with short, fine, more or less appressed pubescent hairs, especially towards margins on upper surface, becoming subglabrous, bright or olive-grey-green, glossy and often rugose with impressed veins, slightly paler green, matt and at first shortly villose below with more or less appressed hairs projecting beyond margins and apex, or with shorter fine pubescent hairs, later becoming rather glossy and

subglabrous, but with appressed, fine hairs persisting on the conspicuous, markedly raised reticulate veins; petioles short, 0.5–5(–9) mm long, moderately pubescent; stipules absent or occasional and of two types, linear-lanceolate, truncate at apex, entire, 1.5–4 × 0.5–0.8 mm, or minute and sometimes with three rounded lobes. Catkins appearing with leaves, mainly terminal on lateral shoots; peduncles 2.5–10 × 0.7–1 mm, moderately to densely pubescent or with rather long, appressed, silky hairs; catkin-scales 2–3 × 0.7–1 mm, ovate to rather narrowly spatulate, rounded-obtuse or occasionally acute at apex, pale yellow-green, pale reddish-brown or crimson at apex, with numerous to dense hairs usually confined to upper half or only at apex and projecting by 0.4–1.0 mm or more beyond apex. Male catkins c. 10 × 5–7 mm, with two free stamens; filaments 4–5 mm, glabrous, very pale greenish-white; anthers 0.5–0.65 mm long, deep yellow, often suffused with red; nectary single, linear-oblong, occasionally linear-spathulate, 0.8–1.5 × 0.2–0.4 mm, olive-green. Female catkins 7.5–10 × 4–5 mm, slightly lax with few (c. 8–14) forwardly-directed fruits; ovary flask-shaped, 1.5–2 × 0.6–0.7 mm, olive-green or purplish towards apex, glabrous or with few to numerous short, sometimes very fine, appressed hairs or extremely short hair-like projections towards apex; pedicel 0.25–0.35 mm long, glabrous; style 0.7–1 mm long, pale olive-green; stigmas 0.4–0.8 mm long, largely fused or notched, pale olive-green; nectary single, linear-oblong, apex truncate, 0.7–1 mm long, bright olive-green. Capsules not adequately observed, but pedicel finally extending up to 1.0 mm.

The above description is based on the specimens that were collected in Glen Clova and Glen Callater and hybrids of this cross produced in cultivation by design. The collected specimens had previously defied identification, but the artificially produced crosses were found to match these very closely indeed. This cross was produced readily in cultivation using *S. × obtusifolia* and *S. herbacea* as parents and, as both of these were frequent in the two places where the collected specimens were found, it is likely that this is how they arose there. This hybrid has not been recorded previously in Europe. All of these hybrids approach *S. × sobrina* (*S. lapponum* × *S. herbacea*) in general appearance, but the presence of some largish stipules and eventually an extended pedicel in some of the collected specimens provides additional evidence that a further parent species, i.e. *S. aurita*, was involved. Endemic.

SALIX MYRSINIFOLIA SALISB. × *S. PHYLICIFOLIA* L. × *S. REPENS* L.

Vouchers: Near the Spittal of Glenshee, East Perth, v.c. 89, GR NO07, 5 August 1997, D. J. Tennant Nos. GSB 2H/97 & GSB 12/97 (E).

Decumbent or semi-decumbent shrub, usually less than 20 cm high, with long spreading branches; twigs slender, at first olive-green or olive-brown and thinly to moderately pubescent, often becoming red and finally purplish-brown and glabrous; buds c. 2 × 1 mm, ellipsoid, blunt or subacute, usually yellow at first and thinly pubescent, soon becoming dark reddish-brown and glabrous; leaves typically 20–30 × 5–15 mm at maturity, elliptic to narrowly obovate, more or less obtuse and often shortly acuminate at apex, revolute at margins, undulate, denticulate or with regular or irregular, often curved, sharply acute, serrate or serrate-dentate teeth, at least towards the base, the teeth and margins reddish-stained, narrowly rounded to cuneate at base, at first with long, appressed, sericeous hairs on both surfaces, projecting beyond the margins and the apex, soon becoming more or less glabrous, glossy and medium to deepish green above, or occasionally purplish towards the apex, paler, almost subglaucous-green below with rather prominent, raised veins and scattered to dense, straight, fine, appressed, sericeous hairs, eventually becoming subglabrous, but hairs usually persisting at least on midrib; petioles very short and slender, 1–5 mm long, sometimes reddish-coloured, thinly pubescent; stipules not found. Catkins appearing slightly before leaves, numerous, in the majority of leaf-axils; peduncles short 3–5(–10) × 1 mm, with rather appressed hairs; catkin-scales 2.5–3.5 × 0.7–0.8 mm, narrowly spatulate to spatulate or obovate, rounded or subacute at apex, largely enclosing ovaries initially, wholly pale green or largely pale brown with moderate to numerous, longish, slightly coarse hairs projecting by 0.4–0.8 mm beyond apex. Male catkins not found. Female catkins 9–18 × 4–8.5 mm, with forwardly-directed fruits; ovary flask-shaped, 2.0–2.5 × 0.7–0.85 mm, green and moderately pubescent, with pubescent pedicel, 0.4–0.85 mm long; style 0.2–0.6 mm long, very shortly bifid, olive-green; stigmas 0.35–0.55 mm long, deeply divided, olive-yellow; nectary single, more or less linear to obspathulate, 0.5–0.9 × 0.2–0.5 mm, dark olive-green. Capsules up to 3.5 × 1.5 mm, eventually becoming subglabrous.

Other material collected in the same area, GSB 9/96 and GSB 10/96, with less densely sericeous, sometimes subentire, slightly larger leaves with more prominent raised veins beneath are possibly also this hybrid but have been excluded from the description given above as their identity is less certain. This appears to be the first confirmed European record of this cross and simple hybrids between either *S. myrsinifolia* or *S. phylicifolia* and *S. repens* also appear to be rare in Britain. The hybrid most probably arose as a cross between *S. × tetrapla* and *S. repens*, which are both abundant in the locality. Endemic.

SALIX MYRSINIFOLIA SALISB. × *S. LAPPONUM* L.

Voucher: Lochnagar, near Ballater, South Aberdeen, v.c. 92, GR NO28, mid August 1959, D. J. Tennant No. LGR 1/59 (E).

Ascending bush, less than 1 m high; twigs at first with dense, white hairs, later becoming thinly pubescent; buds narrowly ovoid, c. 3×1.5 mm, blunt at apex, at first densely white-pubescent; leaves up to 55×20 mm, rather narrowly elliptic, acuminate at apex, the margins slightly undulate, the younger leaves with very numerous, regular, obtuse, serrate teeth, the larger becoming denticulate, narrowed or very narrowly rounded at base, at first tomentose above, later becoming moderately clothed with longish hairs, greyish-white in appearance, persistently greyish-white tomentose below with numerous, longer, sericeous hairs on the prominent, raised veins; petioles rather short, up to 10 mm long, densely pubescent; stipules $2.5\text{--}4.0 \times 1.0\text{--}2.5$ mm, broadly ear-shaped, acute, serrate-dentate, broadly rounded at base, pubescent. Catkins not collected.

The above description is incomplete as it is based solely on the Lochnagar specimen collected in 1959, which is now the only certainly confirmed British example, and other recently collected material queried as this cross remains doubtful. Linton (1913) did not include this hybrid in his list and none of the herbarium specimens collected earlier in Britain tentatively suggested to be this cross is now accepted to be correctly named; there are no confirmed reports of it from elsewhere in Europe. The plant described strongly resembles *S. lapponum*, but is distinguished from it by the presence of numerous, regular, very distinct teeth on the margins of the leaves, which also have prominent, raised veins beneath and darken somewhat when dried, and by the presence of large, ear-shaped, dentate stipules which blacken on drying. It is distinguished from *S. myrsinifolia* mainly by the shape, colour and indumentum of the leaves. Endemic.

SALIX MYRSINIFOLIA SALISB. × *S. ARBUSCULA* L.

Although two recent gatherings made during the field-work were determined positively as this cross by R. D. Meikle, no description has been prepared as several other gatherings thought to represent this hybrid were not determined with certainty. Consequently, the range of variation of this hybrid is at present not fully known and further evidence of identity of the remaining material is required before a meaningful description can be prepared. Endemic.

SALIX REPENS L. × *S. ARBUSCULA* L.

Vouchers: Meall Ghaordie in Glen Lyon, Mid Perth, v.c. 88, GR NN54, 1 September 1994, D. J. Tennant Nos. MG 2C/94 & MG 8/94 (E).

Ascending dwarf bush, less than 30 cm high; twigs at first pinkish-purple and pubescent, soon becoming yellowish-green, glossy and more or less glabrous; buds c. 2×1 mm, ovoid, subacute at apex, initially pubescent, later becoming glabrous, glossy and reddish-brown; leaves $6\text{--}17(\text{--}25) \times 3\text{--}7(\text{--}10)$ mm, rather narrowly elliptic, broadly acute and often mucronate, or obtuse at apex, serrate-dentate with numerous, small, regular, gland-tipped teeth on margins, cuneate or narrowly rounded at base, medium to deepish green and rather glossy above, at first with scattered to numerous, very short, fine, appressed hairs, finally becoming more or less glabrous, with dense, appressed, shortish, straight, silvery, sericeous hairs and rather obscure venation below; petioles slender and very short, usually 1–5 mm long, moderately and shortly lanuginose to subglabrous; stipules minute or absent. Catkins lateral, appearing with or slightly before leaves; peduncles $3\text{--}10 \times 1.5$ mm, moderately to densely pubescent; catkin-scales $1.7\text{--}2.5 \times 0.75\text{--}0.9$ mm, spatulate to narrowly obovate, rounded-obtuse or occasionally emarginate at apex, very pale yellowish-green with brown apex, densely villose with the hairs projecting by up to 1 mm beyond apex. Male catkins not found. Female catkins $12\text{--}18 \times 5\text{--}6.5$ mm; ovaries patent, $1.5\text{--}2 \times 0.75\text{--}0.8$ mm, ovoid, acute, whitish-green, rather densely clothed with semi-patent hairs; pedicel very short, 0.1–0.5 mm

long; style 0.4–0.8 mm long, olive-yellow; stigmas 0.4(–0.6) mm long, narrow, mainly fused, olive-yellow; nectary single, 0.7–1 mm long, narrowly oblong or furcate, olive-yellow. Capsule c. 2.5 mm long, pubescent.

The described specimens are similar to *S. repens* in the size and shape of the leaves and in their indumentum, but form a generally more upright bush and the teeth on the leaf-margins and the ovaries are more characteristic of *S. arbuscula*. This hybrid does not appear to have been reported previously. Endemic.

SALIX LAPPONUM L. × *S. LANATA* L.

Voucher: Corrie Sharroch in Glen Clova, Angus, v.c. 90, GR NO27, 14 July 1998, D.J. Tennant No. GCS 16/98 (E).

Ascending bush, usually less than 60 cm high; twigs thick, olive-green, finally becoming purplish-brown, glossy and glabrous; buds 4–6 × 1.5–2.5 mm, narrowly ovoid, subacute, pubescent, soon becoming glabrous, yellow to reddish-brown; leaves 30–60 × 14–38 mm (or wider in cultivation), rather narrowly elliptic to obovate, acute or acuminate at apex, entire at margins but sometimes undulate with a crenate appearance, narrowly cuneate to rounded at base, at first densely, long, semi-appressed villose above with hairs projecting well beyond margins and apex, later becoming tomentose and sometimes finally glossy, greyish-green and pubescent with scattered to numerous, fine, rather appressed hairs, tomentose below or often villose on veins, finally becoming pale, dull, subglaucous-green with prominent, raised, reticulate veins and thinly to moderately, appressed-pubescent; petioles 3–10 mm long, with dense, longish, wavy hairs; stipules very small, or foliaceous, broadly lanceolate, 10–15 × 5–6 mm, sharply acute, entire, with dense, long, villose hairs. Catkins appearing just before leaves, usually terminal on lateral shoots, initially sub-sessile, later with densely villose or lanuginose peduncles up to 12 mm long; catkin-scales 2.5–4.0 × 1.5 mm, more or less obovate, subacute at apex, dark brown, clothed with dense, long villose hairs projecting well beyond apex. Male catkins not found. Female catkins usually very large, 40–90 × 17–21 mm, cylindrical, dense; ovary narrowly flask-shaped, c. 3.5 × 1.0 mm, green, with many short, wavy hairs sometimes confined to near base and apex; pedicel short, glabrous; style long, up to 2.0(–2.5) mm, simple or only shortly furcate, pale green; stigmas 0.4–0.65 mm long, mostly fused, pale green; nectary single, narrowly oblong, c. 0.8 × 0.4 mm, truncate at apex, yellowish-green. Capsules 5–7 × 1.4–1.6 mm, with scattered hairs or subglabrous; pedicel extending up to c. 1 mm.

The plants described have foliage which is similar in shape to that of either parent. They differ from *S. lanata* mainly in their usually olive-green twigs with rather narrower, less obtuse buds and sometimes narrowly elliptical leaves, their sometimes lacking stipules, and their often exceptionally long catkins with hairy ovaries and capsules. They are distinguished from *S. lapponum*, when the leaves are similar in shape, by the longer villose hairs on the younger leaves, by the mature leaves often eventually becoming much less hairy, with prominent, reticulate veins below, by the frequent presence of obvious stipules, and by the wider and often longer female catkins with much less hairy ovaries and capsules. Linton (1913) described this hybrid from foliage specimens only, which he had collected in South Aberdeen, v.c. 92, but these specimens were later rejected as this cross and the hybrid was excluded from British lists (Meikle 1975). However, both Linton's specimens and his description match the confirmed specimen described above very well and therefore it is probable that Linton's v.c. 92 specimens were correctly named, as had been suggested by B. Floderus in 1932 on the herbarium sheet in **BM**. Endemic?

SALIX ARBUSCULA L. × *S. RETICULATA* L. = *S. × GANDERI HUTER EX ZAHN*

Vouchers: Meall Ghaordie in Glen Lyon, Mid Perth, v.c. 88, 1938, W.A. Sledge (E); GR NN54, 26 July 2001, D.J. Tennant No. MG 5/01 (E); Creag Roro in Glen Lyon, Mid Perth, v.c. 88, GR NN64, July 2002, DJT No. CR 3/02 (E).

Dwarf, decumbent shrub forming a loose mat, less than 10 cm high; twigs rather slender and trailing, at first deep olive-green, later becoming very dark reddish-purple-brown, glossy and glabrous; buds 3.5–4.5 × 1.5 mm, more or less shortly cylindrical with a blunt apex, initially deep olive-green, glabrous or with scattered pubescent hairs, later becoming reddish-brown, glossy and glabrous; leaves 5–20 × 2.5–17 mm, mainly ovate and elliptic with the remainder obovate, or sometimes subrotund, usually subacute and sometimes broadly twisted, or broadly rounded and

sometimes slightly retuse at apex, occasionally undulate, slightly revolute, with several to numerous, distinct, very small, often red-tipped, serrate, serrate-dentate or denticulate teeth at margins, broadly cuneate or rounded at base, bright medium to deepish, glossy green and rugose, with markedly sunken veins on the upper surface, at first with many, long, rather appressed hairs but soon becoming glabrous, underside pale, glaucous-green with very conspicuous, raised, dark green or greenish-brown, strongly reticulate veins, with midrib sometimes reddish towards base, at first with numerous, often long, rather appressed hairs, but soon becoming glabrous; petioles short, 10–13 mm long, slender, green or reddish-brown, villose at first, soon becoming glabrous; stipules absent. Catkins not found.

The known British examples are all similar and closer to *S. reticulata*, but differ mainly in their usually smaller, often more ovate, occasionally much narrower, more acute and some distinctly dentate leaves, which generally have shorter petioles.

SALIX MYRSINITES L. × *S. HERBACEA* L.

Vouchers: Coire Kander, Glen Callater, South Aberdeen, v.c. 92, GR NO18, 28 July 1996, D.J. Tennant Nos. CK7C/96 & CK7D/96 (E); Corrie Sharroch, Glen Clova, Angus, v.c. 90, GR NO27, 14 July 1998, DJT Nos. GCS 8/98 & GCS 10/98 (E); Meall na Samhna, Glen Lochay, Mid Perth, v.c. 88, GR NN43, 16 July 1998, DJT No. MNS 5/98 (E).

Dwarf, semi-decumbent shrub, usually less than 10 cm high; twigs rather slender, at first olive-green, pubescent, soon becoming glabrous, very glossy and purplish-brown; buds 2–2.5 × 1 mm, rounded or narrowly obtuse at apex, at first thinly pubescent, soon becoming glabrous and glossy, reddish-brown; leaves 6–25(–37 cult.) × 4–16(–25) mm, ovate, obovate, broadly elliptic or seldom subrotund, subacute to broadly rounded, occasionally retuse or emarginate, sometimes twisted downwards at apex, often undulate with crenate-serrate, often red-tipped teeth, or occasionally with aquiline teeth at margins, narrowed, narrowly subtruncate, more or less rounded, or seldom cordate, and often channelled and irregular at base, very glossy, bright medium green above and below, glabrous above, at first with several, long, semi-appressed hairs below, especially on midvein, margins and apex, but soon becoming glabrous with very conspicuous raised reticulate veins; petioles short and slender, up to 10 mm long, at first pubescent, soon becoming glabrous; stipules absent, or oblanceolate, denticulate and up to 3 mm long. Catkins terminal, appearing with leaves; peduncles moderately to densely lanuginose-pubescent, 2.5–6 mm long; catkin-scales 1.5–3(–4.5) × 0.7–1 mm, linear-oblanceolate to narrowly obovate, convex and fully enclosing the ovary at anthesis, obtuse or notched at apex, silvery-white to pale olive-yellow, concolorous, or suffused with red, or red at apex, usually glabrous on both surfaces with numerous wavy hairs 0.4–1.2 mm long on the apex. Male catkins not found. Female catkins 6.5–10 × 2–4 mm, with few, forwardly-directed fruits; ovary 1–2 × 0.6–0.9 mm, narrowly ovoid or flask-shaped, pale green to amber-brown, often suffused with red or purple towards apex, faintly glossy, glabrous or with scattered, very short hairs; pedicel usually very short, 0.1–0.25(–0.6) mm long; style 0.2–0.8 mm long, pale olive-green or purplish; stigmas 0.35–0.7 mm long, deeply divided, filiform, curled when long, olive-yellow to deep yellow; nectary 0.3–1.5 × 0.2–0.5 mm, linear-oblong, single or double, occasionally obcordate, deep yellow, sometimes tinged with reddish-brown. Capsule up to 5 × 2 mm, glabrous or with extremely short, hair-like projections, the pedicel extending up to 0.8 mm.

This is a variable hybrid, vegetatively usually either more or less intermediate between the parents or closer to *S. herbacea*. The catkins found are very small and in most respects much closer to those of *S. herbacea*. However, this hybrid is sometimes not readily distinguished from *S. × simulatrix* (*S. arbuscula* × *S. herbacea*) and specimens which are in doubt in this respect, having longer catkins and more hairy ovaries with longer pedicels, have been excluded from the description given above. This description is given here because the description published by Linton (1913) for this hybrid incorporated that of *S. × grahamii*, which Linton incorrectly referred to this cross.

A few other British montane willow hybrids described by Linton (1913) or claimed by other early salicologists were not located during the present survey, either because their location fell outside the areas surveyed, or because they appear to have been originally recorded in error, or are extinct, and some of these deserve mention as follows.

SALIX × *BOYDII* E. F. LINTON

This willow was found in Scotland over 100 years ago and never collected again, but fortunately plants propagated from the type material are widely available in horticulture. Following a re-examination of cultivated plants and much discussion with R. D. Meikle, we now agree that *S.* × *boydii* probably arose as a cross between more than two parents, two of which were *S. lapponum* and *S. herbacea*, the third or further parentage remaining uncertain. We also agree that *S. reticulata* played no part in this hybrid, as originally suggested, but rather the apparent *S. reticulata* characters arose in part from *S. herbacea*. Although the ovaries superficially resemble those of *S. reticulata*, this character could equally have been derived from *S. herbacea*, and the catkins themselves bear no resemblance whatsoever to those of *S. reticulata* but rather to those of *S. lapponum* and *S. lanata*. We thought earlier that *S. aurita* was involved, but more recently that *S. lanata* could have been one parent, yet neither alone as the third parent entirely seems to explain the unique vegetative appearance of *S.* × *boydii*. A further character which *S.* × *boydii* shares with the hybrid *S. lapponum* × *S. lanata* is the distinctive stout, erect, bright olive-green appearance of the twigs arising from the base, which supports the view that *S. lanata* may be involved.

The origin of *S.* × *boydii* also poses some problems because of comments made shortly after its discovery. *Salix* × *boydii* was discovered by William Brack Boyd, and in a letter written by Boyd to E. F. Linton in 1913 (BM), he stated that the plant was discovered as a seedling plant in a part of Glen Fee in Clova, v.c. 90 (localised in an annotation by Linton), where *S. lapponum* and *S. reticulata* grew plentifully, which were the parents which Boyd had proposed. However, *S. lapponum* is scarce and *S. reticulata* is now absent at the location described by Linton and, even if the latter had occurred there in Boyd's time, it is doubtful that it was ever plentiful, although it still occurs within 1 km of the supposed site. No fewer than seven of the willow species included in this survey and ten different hybrids are present now at this site where *S.* × *boydii* was discovered. Linton and other salicologists at that time certainly visited the location yet no-one ever refound *S.* × *boydii*, and Boyd stated in his 1913 letter to Linton that he never visited the place again, which, coupled to Boyd's reference to a seedling plant, suggests that he might have dug up the only plant. There is a further discrepancy in the same letter where Boyd implied that the plant was originally collected in 1905 or 1906, whereas a specimen in BM is marked by Linton "hort. Faldonside [Boyd's house] 1902, W.B.B." This specimen bears catkins and must therefore have been grown for well over a year by that date to have developed from the seedling, suggesting that it must in fact have been collected by 1900 or earlier. Furthermore, there is another case where Boyd's account of a unique plant which he discovered in Scotland in 1878 is unsatisfactory, namely *Sagina boydii*, which he found in his garden but which he claimed to have had no recollection of collecting (Raven & Walters 1956), and which Raven described as probably the greatest mystery in the annals of British botany. In addition, Boyd produced numerous hybrids in his garden, many of which still exist in horticulture today, and he also received living plants from Switzerland (Raven & Walters 1956). He probably grew other Scottish willows, and perhaps also *S. helvetica* Vill., a then popular European species in cultivation. It is difficult to prevent willow seedlings from straying into adjacent areas, after which growth can be rapid, as Linton (1913) had discovered, and I have had the same experience. Other than the inaccurate statements by Boyd above, there is no evidence to suggest that he did not collect the hybrid where he stated, but the possibility that it arose accidentally in his garden should not be entirely discounted, as the accounts of its discovery are not completely satisfactory.

The absence of *S. reticulata* at Boyd's site tends to support our belief that this species was not involved and, whereas *S. lapponum* still occurs there in small quantity, it is mainly in the form of *S.* × *obtusifolia* Willd., its hybrid with *S. aurita*. A combination of the latter with *S.* × *sadleri* Syme (*S. lanata* × *S. herbacea*), which also occurs in Glen Fee, perhaps might explain the unique characters of *S.* × *boydii*, however remote the chance that this combination arose there. Attempts

have been made by me to recreate *S. × boydii* from deliberate crosses of such potential parents, but the resultant seedlings are extremely slow in growth and are still too immature to draw any conclusions. Endemic.

S. × GRAHAMII BORRER EX BAKER

R. D. Meikle (1975, 1984) proposed that this hybrid was the triple cross, *S. aurita × S. repens × S. herbacea*, which in my opinion is almost certainly correct. There is no doubt that two of the parents are *S. repens* and *S. herbacea* but, as Meikle suggests, a third species appears to be involved. I have produced this triple cross by design in cultivation, as described later under 'Hybrid synthesis in cultivation', and the resultant hybrids closely resembled *S. × grahamii*, the only obvious differences being the leaves, which were slightly paler beneath.

S. × grahamii was first discovered in Scotland, probably in 1827 or 1833 on Foinaven in West Sutherland, v.c. 108. An almost identical hybrid which had been found on Muckish Mountain in West Donegal, v.c. H35, in 1866, was considered to be the same cross by Meikle (1984), but given separate status as variety *moorei* (F. B. White) Meikle; neither has been collected anywhere in Britain or Ireland again. Both varieties were cultivated in botanic gardens and elsewhere in horticulture, but there has been much confusion between the two varieties which has led to doubts concerning their origin and the accuracy of labelling, and this in turn has hindered a comparison of the characters of the two varieties. Variety *moorei* is the most frequently encountered one in horticulture. At the time of writing, although plants that are claimed to represent the Scottish type material have been traced, they have not yet been examined to confirm their identity. The same hybrid possibly occurs in Norway (Elven & Karlsson 2000).

S. HERBACEA × S. RETICULATA

There are no recent records from Scotland for this hybrid and none of the old records has been confirmed. The majority of old records undoubtedly referred to *S. lapponum × S. herbacea*, and have been redetermined as this cross, especially records from Clova, v.c. 90, and a specimen collected by W. R. Linton on Ben Lawers, v.c. 88, in 1891 (E) which was queried as *S. herbacea × S. reticulata* on the herbarium sheet by Meikle in 1996 and which is probably the same. On the other hand, E.F. Linton's specimens from MNS, v.c. 88, collected in 1891 (BM) and originally thought to be this cross, appear to be *S. lanata × S. herbacea*. Linton (1913) cited a specimen collected on MG, v.c. 88, which was determined by S. J. Enander, but this was unsatisfactory as the determination was based solely on a small piece of catkin; Linton claimed the parentage involved *S. myrsinifolia* and not *S. reticulata*. Another specimen determined by Enander, collected in 1896 on Aonach Beg, v.c. 97, by W. A. Shoobred (BM), was later redetermined by B. Floderus as *S. lanata × S. herbacea*. Meikle (1975) referred to a specimen collected by D. Patton on Ben Laoigh (Lui), v.c. ?88, a record of which was published in 1924, suggesting this might be correctly named, but I have not traced this specimen. Linton (1913) claimed to have produced this cross in his garden and he distributed specimens; these might have been correctly named, but I know of no surviving living material so cannot confirm them. However, attempts which I have made to produce this cross have so far failed, as the resultant seedlings, assuming that these were the intended cross, died at an early stage after germination. The hybrid could, however, occur in Scotland, as it is reported from Austria and Scandinavia. Linton (1913, p. 85) reported that Enander had stated that the binomial *S. × onychiophylla* Andersson, which had been used for this cross, was incorrectly applied, as it had been originally applied to a sheet of specimens containing two different hybrids, neither of which was *S. herbacea × S. reticulata*.

Similarly, other old reports of hybrids of *S. reticulata* with *S. lapponum* or with *S. lanata*, other than *S. × boydii* as discussed above, also usually refer to either *S. lapponum × S. herbacea* or to *S. lanata × S. herbacea*.

TREATMENT IN *FLORA NORDICA*

Outside Britain, the montane willow flora which most closely matches that of Scotland occurs in Scandinavia and, fortunately, a recent publication, *Flora Nordica* (Elven & Karlsson 2000), lists the willow hybrids which are at present accepted there. Ten hybrids involving British species and which could occur in Scottish montane habitats but which are so far not recorded or are not

confirmed in Britain are included in the Scandinavian list; nine of these involve montane species, the tenth involves lowland species. Several other hybrids listed involve species which do not occur in Britain. On the other hand, six montane and four lowland hybrids now included in the Scottish list are not given in *Flora Nordica*, and these have been marked above accordingly, or tentatively suggested to be endemic to Scotland.

Flora Nordica also gives several binomials for willow hybrids that are so far unfamiliar in British publications, and those which appear to be valid have been adopted here. However, no attempts have been made to locate the relevant type material, and therefore it has not been established that the new name has in all cases been applied correctly. These unfamiliar binomials which have been used here are *S. × canescens* Willd. (*S. caprea* × *S. lapponum*), *S. × blyttiana* Andersson (*S. myrsinifolia* × *S. phyllicifolia* × *S. myrsinites*) and *S. × pseudoglauca* Andersson (*S. lapponum* × *S. arbuscula*). Other binomials used in *Flora Nordica* which appear to be predated by those in current use in British publications have not been adopted here.

HYBRID SYNTHESIS IN CULTIVATION

Attempts to produce hybrids in cultivation have been carried out by me annually for five years, and this has provided useful information about hybrid characters and compatibility between species. However, the period of anthesis was found to be brief and different willow species or hybrids often did not coincide seasonally in this respect, so many of the desired crosses could not be attempted. The majority of species were found to be compatible with each other and the resultant hybrids were usually fertile, but some combinations did appear to be incompatible. As expected, in cultivation the montane willow species were found to produce the earliest catkins, usually in April, *S. lapponum* and its hybrids usually being the first, followed by *S. myrsinites* and *S. herbacea*, then *S. arbuscula* and finally *S. lanata* and *S. reticulata*. Among the lowland species, *S. repens* and its hybrids and pure *S. phyllicifolia* were the earliest to flower, although *S. caprea* might have been included here if the cultivated examples had produced catkins.

In these five years 80 separate hybrid crosses were attempted in combinations involving all the montane species. The full results are too extensive to include in this paper, but some of the most interesting results are as follows. Hybrid combinations which were produced without difficulty included *S. × obtusifolia* (*S. aurita* × *S. lapponum*) × *S. herbacea*, which was found to match specimens that had been collected earlier in two places in Scotland (see records above) and led to the identification of the latter and the recognition of this cross as a new British hybrid. *Salix × grahamii*, which is discussed above, was thought to be *S. aurita* × *S. repens* × *S. herbacea* by Meikle (1984), and successful attempts were made to produce this cross from all three possible combinations, using *S. × ambigua* (*S. aurita* × *S. repens*), *S. × margarita* (*S. aurita* × *S. herbacea*) and *S. × cernua* (*S. repens* × *S. herbacea*); in two cases male and female examples were also used. The resultant hybrids of the cross between *S. × ambigua* and *S. herbacea* were close enough to *S. × grahamii* to suggest that Meikle's proposed parentage was correct, and this is probably how both it and its variety *moorei* arose, as the other possible parents, *S. × margarita* and *S. × cernua*, are both rare. *Salix × ambigua* also crossed readily with *S. × tetrapla* (*S. myrsinifolia* × *S. phyllicifolia*), and as both these hybrids are common in Scotland this cross might occur there. Attempts have been made recently to reproduce *S. × boydii*, as discussed above, but it is too early to draw any conclusions, although *S. × boydii* itself crossed with *S. × obtusifolia* with incredible vigour. Another successful and vigorous cross was *S. × laschiana* (*S. caprea* × *S. repens*) × *S. lapponum*, suggesting that this combination could occur in Scotland. *Salix × obtusifolia* appears to have crossed with *S. myrsinites*, but only very few seedlings have resulted.

A number of other attempted crosses were not successful. These include *S. × tetrapla* with *S. lapponum* and with *S. × obtusifolia*; *S. × tetrapla*, *S. myrsinifolia* and *S. × punctata* (*S. myrsinifolia* × *S. myrsinites*) with *S. herbacea*; *S. repens* with *S. lanata*; and all attempted crosses between *S. reticulata* and other montane species. Clearly such experiments should be repeated under controlled conditions.

CHROMOSOME NUMBERS

Published data on chromosome counts of British material (Stace 1997) suggest that all the Scottish montane species and two of the lowland species, *S. caprea* and *S. repens*, are diploid ($2n = 38$), *S. cinerea* and *S. aurita* are tetraploid ($2n = 76$), and the remaining lowland species, *S. myrsinifolia* and *S. phylicifolia*, have $2n = 114$ and $2n = 88$ respectively.

Only a single chromosome count was undertaken on a willow collected during this work, carried out by Dr. H. A. McAllister on a plant which appeared to be a hybrid between *S. lanata* and a lowland species. Assuming that this plant was a hybrid, the resulting figure of $2n = 38$ suggested that both parents were diploid, which, if the second parent was a lowland species, should be either *S. caprea* or *S. repens* according to the figures above. However, no evidence of *S. caprea* was found and the presence of *S. repens* was by no means obvious in this plant. Stace (1997) quotes a chromosome count for the hybrid *S. aurita* \times *S. phylicifolia* of $2n = 42$ – 64 , a range much lower than the theoretical figure (82). The low count of $2n = 64$ suggests that one parent was diploid, and the even lower figure of $2n = 42$, if correct, might suggest that back-crossing with a further diploid parent has occurred in this case. Earlier reports on chromosome counts (Warburg 1952) state that *S. aurita* is both diploid and tetraploid, which, if correct, might suggest that the above count of $2n = 64$ represents either an error for $2n = 63$ or an aneuploid of this, derived from a diploid form of *S. aurita* ($2n = 38$) and *S. phylicifolia* ($2n = 88$). If diploid *S. aurita* does occur then this might also be an additional possibility as a parent of the hybrid of *S. lanata* mentioned above. The variation in chromosome number of these willows suggests that chromosome counts might be useful in the confirmation of their hybrids, especially those involving *S. myrsinifolia* and *S. phylicifolia*. However, it is not known whether willows behave according to theory in this respect, and chromosome counts on willows are known to be difficult. It is also clear that some of the published data require verification to establish whether more than one ploidy level might occur in some species. In the case of *S. myrsinifolia* and *S. phylicifolia*, special care in the selection of material is essential, as these species are often difficult to distinguish from hybrids between them. Selected plants collected during this survey in areas where these species do not overlap geographically would be ideal material for such studies, and hybrids deliberately synthesized from such cultivated material could also be used as controls to examine the behaviour of chromosomes in crosses of known parentage.

DISTRIBUTION OF HYBRIDS

The distribution of the willow species can be consulted in Preston *et al.* (2002). The extreme rarity of many montane willow hybrids seems to suggest that, where no apparent genetic barriers exist, they originated as the result of rare events, coupled with the probability that few survive to maturity. Many of the rarest hybrids are curiously local, yet may occur in reasonable numbers in their known localities. As the majority appear to be fertile, many extant hybrids may be the progeny of a single original cross, which might also partially explain why given hybrids from one locality can have distinctive characters which are not seen in the same cross from other localities. Triple hybrids, such as *S. \times grahamii*, discussed earlier, could have arisen theoretically from three different binary hybrids, and male or female examples of any of these, which would be likely to give rise to considerable local variation, and the same would apply to other multiple hybrids and back-crosses.

The earliest British determinations of willow hybrids, and their descriptions, notably those by White (1890), were based on the few initial gatherings available, and the descriptions, although no doubt accurate in content, if not always in conclusion, do not take into account sufficiently the range of variation which was found in subsequently discovered examples.

The local distribution of some willow hybrids is unexpected, and in a few cases seems to bear little relationship to the abundance of the parent species concerned, or at least one of them. However, it is possible that some of these hybrids have been overlooked in Scotland, and one such example could be the apparently rare *S. \times margarita*, whose parents, *S. aurita* and *S. herbacea*, are both widely distributed and common there. Some unusually hairy examples determined as *S. herbacea*, collected in more than one locality in north-western Scotland, might represent back-

crosses of the latter with *S. × margarita*, which itself may have died out. In location 3 (Angus), nearly all examples of apparent *S. myrsinites* which are now present seem to be hybrids, mainly with *S. myrsinifolia*. Pure material does exist locally there in small numbers, but most of these hybrids closely resemble *S. myrsinites*, which suggests that many are probably back-crosses. There is a strong impression that present environmental conditions account for the spread of the hybrids, and this in turn may be one reason for the decline of *S. myrsinites* there. A similar situation appears to occur in parts of location 1 (Mid Perthshire), where the hybrid *S. lapponum × S. arbuscula* dominates over one of the parents, *S. lapponum*, but not over the other, and, in a few of the areas surveyed there, seems to have more or less replaced it. Furthermore, in the pure state, *S. phyllicifolia* appears to be absent or scarce in all of the areas surveyed within locations 1–4, whereas *S. × tetrapla*, its hybrid with *S. myrsinifolia*, is very frequent, although there is otherwise no evidence that *S. phyllicifolia* was ever common there. Another very local and scarce hybrid with widespread and common parents in location 1 and further west is *S. arbuscula × S. herbacea*, which was found during the fieldwork in many places, but only within a single site (MNS), whereas *S. arbuscula* was not noticed there; yet on a nearby hill (MG), where both parents are locally dominant, the hybrid has not been found. *Salix repens × S. herbacea* is a further example of a hybrid with widespread and common parents which is itself widely distributed but apparently rather rare.

DISCUSSION AND CONCLUSIONS

The present list of willow hybrids found on Scottish mountains now includes 36 combinations, 21 of which involve at least one montane species. Five of these proposed combinations are new to Britain and apparently endemic to Scotland. Two further hybrids were earlier included in the list prepared by Linton (1913), but were later rejected and are here reinstated. Three of the hybrids listed in Stace (1997) and a further four added by Kent & Stace (2000) have now been removed on the basis of insufficient evidence. Two of the former three deletions, *S. caprea × S. myrsinites* and *S. myrsinifolia × S. herbacea*, are already published (Kent & Stace 2000) and the third, *S. myrsinifolia × S. phyllicifolia × S. lapponum*, is rejected here. The four combinations added by Kent & Stace (2000) but now removed from the list are *S. aurita × S. myrsinifolia × S. myrsinites*, *S. myrsinifolia × S. phyllicifolia × S. arbuscula*, *S. myrsinifolia × S. myrsinites × S. herbacea*, and *S. lapponum × S. myrsinites × S. herbacea*.

All but two of the Scottish willow hybrids recorded in montane habitats and now considered to be correctly named have been relocated in the field, and the majority of these have been brought into cultivation. The two remaining hybrids are *S. × boydii*, which is considered extinct in the wild state, and *S. × grahamii*, which has not been collected recently and was originally found outside the locations included in this survey. Fortunately, both of these hybrids are available from horticulture and therefore have been included in this study.

Even with the availability of freshly collected material and plants in cultivation, determinations which had been positive sometimes required later change, especially when transient characters were exhibited, or when catkins were produced for the first time in cultivation, and suggested the involvement of a previously unsuspected parent species. In addition, it became clear that useful foliage characters such as gloss, texture and raised veins, as well as colour, largely disappeared when some hybrids were pressed, but apparently did not do so in others, which, together with the transient variation mentioned above, emphasizes the hazards of herbarium determinations of willow hybrids. It has also been confirmed from deliberate crossing experiments between known species or hybrids that the characters of at least one of the parents may be more or less fully suppressed in the resultant hybrid, and such plants recognised in the field or herbarium as simple crosses may in fact be triple hybrids. Few of the latter can be determined with absolute certainty. Hybrids with one parent in common often overlap in their characters and at the extremes can be difficult to distinguish, for example hybrids of *S. herbacea* with *S. arbuscula* and *S. myrsinites*. Additionally, as hybrids vary between the parental characters, those at either extreme are likely to have been overlooked, which is also a potential problem in the selection of control material for scientific studies and deliberate hybrid synthesis. Some present determinations are still based largely on matching recently collected material with original herbarium specimens on the

assumption that the latter were correctly named, which has not always later proved to have been the case. The confidence with which the early salicologists named willow hybrids has often been shown to have been misplaced and even today the full range of variation in some species is still not known. This was additionally confirmed where some of the hybrids produced by design in cultivation were found to have few distinctive or diagnostic characters; had they been found in the wild state they would have defied identification.

In view of these difficulties it was decided to admit hybrids to the British list which had been determined as having probable status, as more positive opinion was often not possible, and as a consequence some of the records given in this paper, including some of the seven new combinations proposed, especially the triple combinations, should perhaps be considered as tentative until new evidence is available to confirm their identity beyond doubt. Most of the objectives of this work as listed in the introduction to this paper have been completed. *The List of Vascular Plants of the British Isles* has been revised and information for the *Vice-county census catalogue* has been updated. Some of the descriptions and others in preparation will be made available for the *Flora of Great Britain and Ireland* (Sell & Murrell, in prep.). Herbarium material continues to be gathered, both in the field and from the cultivated plants and will be later distributed to various herbaria. Other than the establishment of living hybrids at botanic gardens, aspects of conservation of montane willow hybrids are still to be discussed. Finally, the difficulties of identification of willow hybrids, as discussed here, emphasize the necessity of a more scientific approach to their determination. Accordingly, a programme which will include molecular studies of the willows and their hybrids that occur in Scottish montane habitats is now underway at the Royal Botanic Garden, Edinburgh and other collaborating institutions. Some 200 DNA samples have been prepared from the cultivated collection and donated to the RBGE for inclusion in this programme in an attempt to confirm identities.

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