

***Hedera helix* L. and *H. hibernica* (Kirchner) Bean (Araliaceae) in the British Isles**

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ABSTRACT

Hedera helix L. sensu lato consists of diploids, *H. helix* L. sensu stricto, and tetraploids, *H. hibernica* (Kirchner) Bean, which have distinct geographical distributions and can be differentiated morphologically especially by their trichomes.

INTRODUCTION

The plant known as Irish Ivy, *Hedera hibernica* hort. or *H. helix* subsp. *hibernica* (Kirchner) McClintock, is widely used as a ground cover plant which frequently escapes from cultivation and may be found far from habitation. Its rapid growth, large and uniform leaves, hardiness, shade tolerance and lack of inclination to climb make it a landscape architect's ideal subject for planting beneath trees and shrubs and for stabilising steep slopes.

The origin of the material in cultivation has long been a matter for dispute (Lawrence & Schulze 1942) though many writers have stated that it is native in Ireland, and Mackay (1836) mentions receiving specimens from Ballybunion in Kerry. However, this ivy is rare in cultivation in Ireland and Andrews, who was the originator of the myth of 'Irish' ivy in Ireland (Mackay 1836), is known to have been unreliable over the labelling of his plants (M. J. P. Scannell, pers. comm.). By the second half of the last century, it was not regarded as native there (Hooker 1870; Colgan & Scully 1898). Whatever its origin, it is now very common throughout Britain (Rutherford 1979), America (Lawrence & Schulze 1942) and probably many other countries.

In an attempt to discover more about the plant, A. R. originated the B.S.B.I. Network Research Project on Irish Ivy (1975–1979); see Rutherford (1979). Apart from the gross morphological characters of large, uniform, broadly lobed leaves, Irish Ivy can usually be distinguished from the common ivy by its smell. The odour of *H. helix* L. is very disagreeable to many people, but the scent of cut twigs or petioles of Irish Ivy is much more powerful, distinctly sweeter and more resinous. Only *H. colchica* K. Koch and *H. algeriensis* Hibb. are equally odoriferous. Jacobsen (1954) reported *H. hibernica* hort. to be tetraploid ($2n=96$) and *H. helix* to be diploid ($2n=48$). He used cultivated material of *H. hibernica* but believed it to represent a wild species.

CYTOLOGICAL METHODS

The method used was a modification of Dyer's lacto-propionic orcein technique (Dyer 1963) in which the root tips were squashed in the undiluted saturated solution of orcein in 1:1 lactic acid:propionic acid. Rapidly growing root tips were placed in vials of a saturated solution of α -monobromonaphthalene in tap water for about 4 h at room temperature. The root tips were then

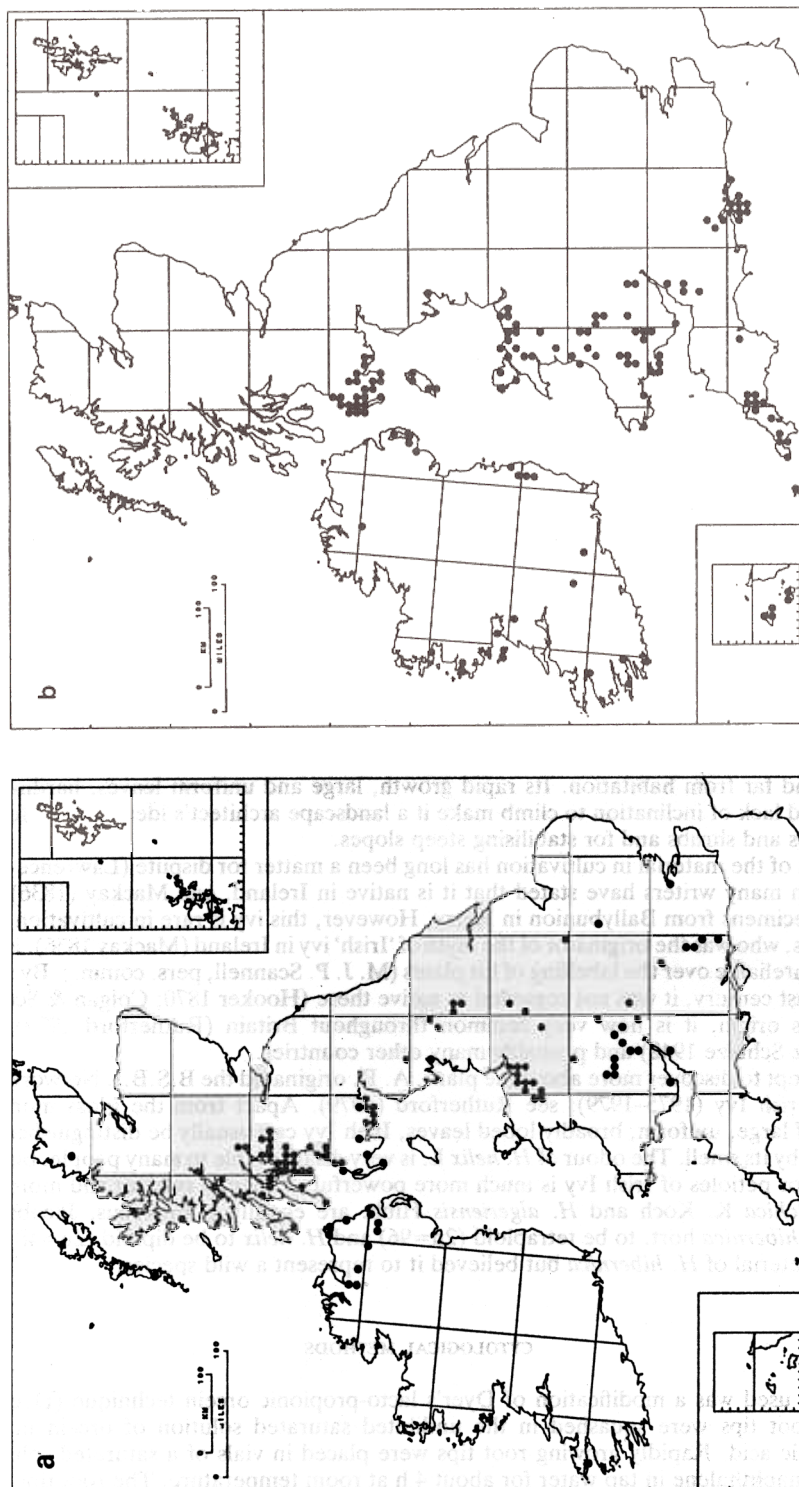


FIGURE 1. Distribution of counts of (a) diploid (2n=48) *Hedera helix* L. and (b) tetraploid (2n=96) *H. (Kirchner) Bean* in the British Isles.

fixed in 1:3 methanoic (acetic) acid:ethanol (98%) for at least 24 h, before being hydrolysed in 1M hydrochloric acid at 60°C for about 5 minutes in a water bath, and then transferred to 70% ethanol for storage. A root tip was then examined under a dissecting microscope, placed in a drop of stain, macerated with needles, tapped and squashed.

The squash preparations were examined for cells containing well separated chromosomes and, when such were found, the chromosomes were counted. With clear preparations, counts of precisely $2n=48$ or $2n=96$ were obtained, but on poorer preparations, where only approximate counts (45–48 or 90–96) could be made, the results were recorded as $2n=c.48$ or $2n=c.96$.

CYTOLOGICAL RESULTS

It was soon confirmed that the cultivated Irish Ivy, *H. hibernica* hort., and some other cultivars were tetraploid, as well as much of the wild material from all along the western seaboard of Britain and Ireland, western France and Spain. In the wild, tetraploids seem to occur to the exclusion of diploids in southern Ireland, the Isle of Man, western Wales, the West Country eastwards to the Isle of Wight and the New Forest, the Channel Isles, western France, northern Spain and probably most of that country except the Sierra Nevada region where diploids occur, and in the Algeciras–Gibraltar area and in Portugal, near Lisbon, where hexaploids ($2n=144$) have been found. Diploids and tetraploids were found together along the eastern boundary of the area of distribution of the tetraploids, but further east only diploids were found, apart from the occasional naturalised tetraploid *H. hibernica* hort. (Fig. 1).

The diploid thus appears to be the native ivy north and east of the tetraploid's area in Britain. Diploids have been counted from eastern France, Denmark, Switzerland, Italy, Yugoslavia, Turkey, the Crimea and the Caucasus. Thus the tetraploid seems to occur to the exclusion of the diploid on the Atlantic seaboard of Europe, from Gibraltar to southern Scotland, and the diploid to the exclusion of the tetraploid north and east of these areas, extending eastwards to the Crimea and the Caucasus. It would appear that the diploid only reaches the Atlantic in central and northern Scotland. The one notable exception to this is the isolated occurrence in Sicily of tetraploids which are morphologically like diploid *H. helix*.

As the diploids and tetraploids have distinct, barely overlapping, geographical distributions, it may be said that they are behaving as distinct 'biological' species, with different climatic preferences, so the two cytotypes are probably in competition with one another where they meet. No hybrids (triploids, $2n=72$) have yet been found despite many cytological determinations on material from areas where the two species meet.

MORPHOLOGY

As both the wild diploids and tetraploids have clearly all been previously referred to *H. helix*, it was considered that any character which might distinguish the two cytotypes was likely to be fairly cryptic. *H. hibernica* hort. was thought to be perhaps an extreme variant of the tetraploid, so it was carefully compared with a typical diploid *H. helix*. As the trichomes on the young leaves give useful diagnostic characters for distinguishing other species of *Hedera*, those on *H. helix* and *H. hibernica* hort. were examined in detail. These trichomes always consist of a short stalk bearing a central boss from which radiate a variable number of unicellular rays. In the diploid some of the rays of most of the trichomes stand up at an angle to the leaf surface giving a bristling appearance (Fig. 2a). By contrast, in *H. hibernica* hort. these rays almost always lie flat along the surface of the leaf, all in one plane (Fig. 2b). It was soon evident that all the tetraploids, excepting those from Sicily, had trichomes of the *H. hibernica* hort. type, while all the diploids had trichomes of the type found in the typical diploid examined. It therefore seemed clear that *H. hibernica* hort. was a distinctive clone or variety of a widespread tetraploid taxon, most specimens of which would previously have been classified as *H. helix*.

Although very obvious in young leaves on rapidly growing shoots, the trichome character is by no

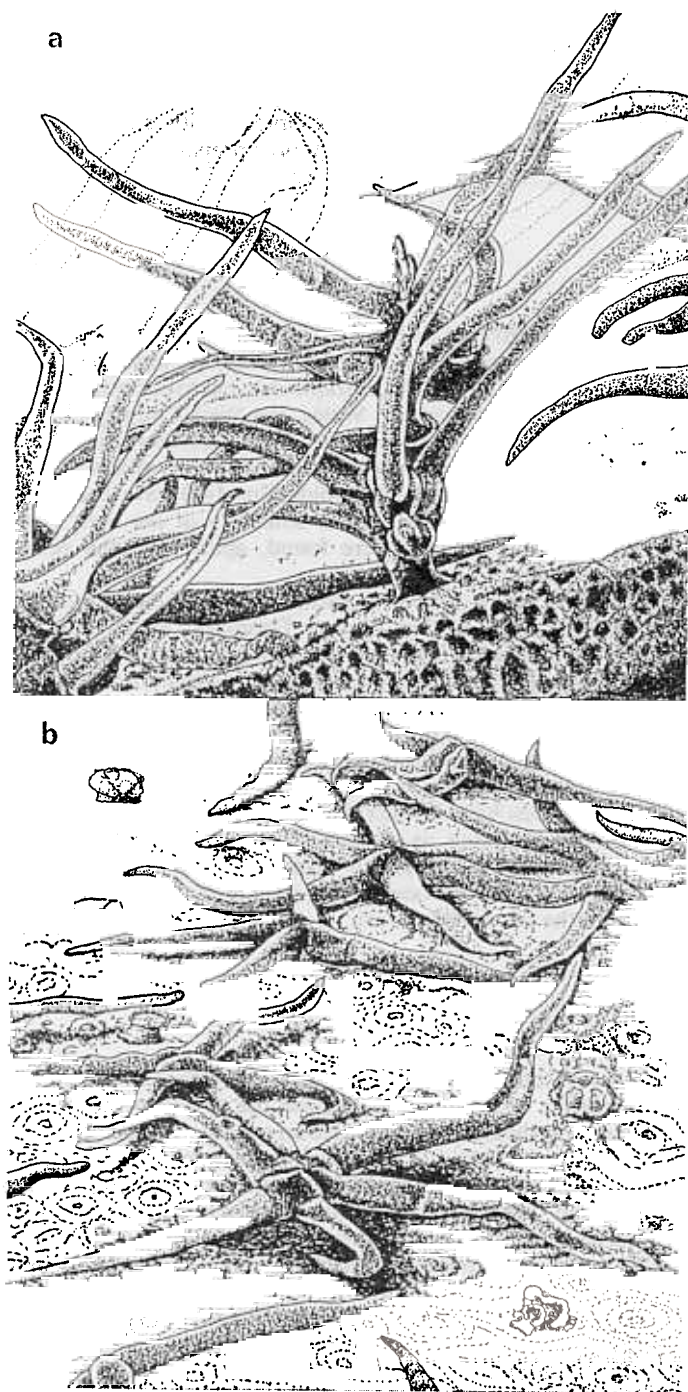


FIGURE 2. Drawings from stereoscan electron micrographs of the trichomes of (a) *Hedera helix* L., (b) *H. hibernica* (Kirchner) Bean.

means easy to use. Very young leaves of the diploid seem to be covered in fine grey-white velvet, the effect being created by the densely packed trichomes. On the tetraploid comparable young leaves seem much less hairy, since few of the trichomes stand out at an angle from the surface of the leaf. However, the best leaves to examine for determination of this character are slightly further back on the shoot, where the lamina expansion has separated the trichomes so that individual trichomes can be clearly distinguished. Observations in a good light with a $\times 20$ hand lens are usually adequate, and with good, young, vigorous material held up to the light the cytotypes can often be distinguished with the naked eye – but such observations should always be checked with a lens. It is best to examine trichomes on the underside of the leaves, but those on the upper surface and on young leaves may also be examined. Trichomes on the upper surface and trichomes with rays standing out from the surface tend to be lost first as these are most likely to be abraded, so surfaces presenting few trichomes may give unreliable determinations. The last sites to lose their trichomes are the interveinal areas between the main veins, where they adjoin the petiole, on the underside of the leaf. Trichomes on slightly older stems of both cytotypes tend to have all their rays appressed to the stem, and some trichomes on the veins of the tetraploid have rays standing out from the leaf surface, so trichomes on stems and veins are best disregarded.

Furthermore, in winter, in exposed positions, on slow-growing or flowering shoots, the trichomes of the diploids with their projecting rays may become dislodged or be flattened on to the leaf surface, and such material may be unidentifiable unless taken into cultivation and fresh young leaves examined. It can be seen, therefore, that on the trichome character, the diploid is much more likely to be misidentified as the tetraploid than vice versa.

Used with care, examination of the trichomes is a reliable means of distinguishing between the Common (diploid) and the Atlantic (tetraploid) Ivies, but other characteristics are also more or less correlated with the chromosome number (Table 1). The leaf shape is very variable in both. Many 'races' of each pass through many changes between the creeping, sterile phase and the flowering, mature phase. Some tetraploids scarcely alter, having almost flowering-type foliage at all stages, and a variant of this has long been known from the Channel Isles (Druce 1912). Both cytotypes usually produce the familiar ivy-shaped leaves at an early stage in the plant's development. Later, before the mature phase is reached, both have, usually, a pedate-leaved phase in which the lobes are attenuate and the central much longer than the side lobes, and towards the flowering branches these lateral lobes diminish and entire leaves are produced.

ECOLOGY

In moist, sheltered sites the tetraploid is capable of dominating the woodland floor, roadside banks and cliffs in a manner of which the diploid seems incapable, even in the most favourable conditions. As early as 1872, Hibberd remarked on ivies with giant leaves in the Vale of Conwy and we have noted populations on Porkellis Moor, Cornwall, near Blackgang on the Isle of Wight, West Symonds Yat in Avon and even in woods by the mouth of the River Stinchar in Ayrshire, near the northern limit of the natural distribution of the tetraploid. The ability of the tetraploid to produce larger leaves on longer petioles, and to have longer internodes, apparently allows it to invade habitats unavailable to the other cytotype. Shingle banks just above high water level of spring tides are often colonised by the tetraploid, but the diploid has never been found in such habitats.

The vigour of the tetraploid is clearly seen among the sea-cliffs at Kennedy's Pass and at Pinbain Burn-foot, Ayrshire, where it is the dominant plant. Ivy grows to a considerable height up the cliffs, covers the seaside boulders and creeps through dry sunny roadside verges where it is not discouraged by being mown. Where not cut, this ivy competes successfully with *Pteridium aquilinum*, *Dryopteris filix-mas*, *Mercurialis perennis*, *Filipendula ulmaria*, *Poa pratensis*, *Rumex crispus* and *Rubus latifolius*, among other tall-growing species. It flourishes in two habitats at the former site which would probably have proved too extreme for the diploid, these being a dry, sunny exposure in very well-drained soil and a marshy ditch. In areas where both cytotypes occur, especially in Galloway in south-western Scotland (A. J. Silverside, pers. comm.), the tetraploid is mostly found in the milder, coastal regions while the diploid tends to be the ivy of the inland woods.

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TABLE 1. A COMPARISON OF THE CHARACTERISTICS OF *HEDERA HIBERNICA* AND *H. HELIX*

Character	<i>H. hibernica</i> (Kirchner) Bean	<i>H. helix</i> L.
Growth	Fast and vigorous, often has long internodes, up to 18 cm or more. New shoots may be thick and succulent.	Markedly less vigorous and usually slower; internodes often quite short. New growth often wiry.
Leaf size	Leaves variable both at different phases and among different plants but overall considerably larger, up to 10 cm wide by 10 cm long in moist sheltered localities.	Leaves variable at different phases and among different plants, but generally markedly smaller at all phases.
Pedate leaves	The leaves at the pedate phase frequently the largest and almost equal in surface area to those at sub-fertile and fertile phases. The tip of the longer central lobe usually rounded.	The leaves at the pedate phase mostly produced near the ground and on the whole plant almost always the smallest; the tips of the longest lobes acute.
Leaf texture	Leaves usually coriaceous, frequently fleshy-waxy.	Leaves leathery, often of papery texture, but thin in coastal areas.
Leaf colour	In cold the interveinal areas of leaves may turn pinkish or light bronze. The veins develop apple-green borders. Some forms with low anthocyanin content only have red margins or do not darken at all, rarely the leaf becomes red-maroon.	In cold, particularly in frosty places, the leaves may turn purple-black all over; the ground colour darkens considerably.
Hyaline layer	The hyaline layer is more readily apparent and may appear thicker due to the up-turned margins.	The hyaline layer is not readily visible, due to the down-turned margins.
Leaf sinuses	The sinuses are mostly deep and often strongly arched; leaves may be funnel-shaped.	The sinuses may be deep but the blade usually flat, apart from the margins.
Leaf veins	The veins at the sterile phases rarely raised on the leaf surface and seldom differ in colour from the ground, usually bordered in a paler shade or yellow-green.	The veins at the sterile phases almost always raised on the leaf surface like fine wires, often silver-white, rarely edged with paler colour.
Trichomes	Trichomes appear sparse due to the rays lying parallel to the leaf surface; they are often tinted fawn or more rarely orange-brown.	Trichomes appear as grey-white pubescence on new tips, due to the rays projecting at various angles and becoming enmeshed.
Sap	Sap odour strong, often pine-like and sweet.	Sap odour much weaker and usually rather acid.

TAXONOMY

The original aim of the investigation was to elucidate the status of *H. hibernica* hort. When tetraploids were found to be widespread in the wild, the question arose as to what was the relationship between the morphologically very distinct tetraploid, *H. hibernica* hort., and the wild tetraploids which previously would have been included within *H. helix*. The agreement in trichome characters between *H. hibernica* hort. and the wild tetraploids led us to believe that the cultivated plant might be a clone or group of clones of the wild tetraploid. However, the so-called Irish Ivy was unusual in its uniformly large leaf size and non-climbing habit, contrasting with the variable leaf size and normal climbing of most of the wild tetraploids. On the Isle of Wight wild tetraploids were discovered producing some leaves identical to those of the cultivated plant, and in Herefordshire at

Symonds Yat, colonies of wild ivies were found almost a match to *H. hibernica* hort. The Isle of Wight plants bear the Irish Ivy leaves on shoots in transition from the vegetative to the flowering (mature) state. Most of the wild tetraploids produce leaves of this type, but the Isle of Wight samples were most pronounced.

It therefore seems that the cultivated Irish Ivy is a clone, or group of similar clones, stabilised in the semi-arboreal condition. It resembles the creeping/juvenile phase in having pliant stems bearing some of the specialised attaching roots, but these are less numerous than normal in juvenile ivies. The stems run along the ground, sometimes climbing walls and more rarely trees, and cuttings root very readily. The chief similarities to the arboreal phase are in the reduction of the ability to cling and thus to climb, due to fewer adhesive roots, and the broader leaves with shorter, wider lobes. When it does climb it can mature into the flowering condition with radially symmetrical shoots of brittle wood, totally lacking rootlets and having entire leaves. Seedlings are very like the parent, but do seem more ready to climb, and, like it, have rather larger and broader leaves than is typical for the younger stages of wild tetraploids. Similar observations have been made in Germany (G. Grüber, pers. comm.). *H. hibernica* hort. therefore probably consists of a clone or clones from the south of England. Horticulturalists have long been aware of slight variation in *H. hibernica* hort. Some clones are darker in the foliage or are not glossy, and another clone has more sharply lobed leaves than normal. In the main, however, it is uniform. Variegated sports occur, including 'Variegata', 'Sulphurea', 'Marmorata' and 'Rona'. Also, seedlings may arise by self-fertilisation.

The present situation is that there are diploids and tetraploids normally referred to *H. helix*, with a tetraploid cultivar being called *H. hibernica* hort. or *H. helix* subsp. *hibernica*, a name that has become current in horticulture, and that has recently been validated nomenclaturally (McClintock 1987). At what taxonomic level should they be recognised? As they differ in ploidy level, geographic distribution, distinctly in one morphological, albeit cryptic, character, and in other less obvious ways, we consider it desirable to distinguish them as separate species. We are aware that this decision may be controversial as many would prefer to recognise them as subspecies (cf. Lum & Maze 1989). If *Hedera* were an obscure genus known to few we would perhaps have concurred. However, it is very well-known to botanists and gardeners and there are numerous cultivars, so that the use of subspecies would lead to long clumsy horticultural epithets and possibly to the ignoring of distinction between the subspecies. The level of subspecies is well suited to situations where geographical or ecological variants exist at the same ploidy level, as with *Betula pubescens* Ehrh. (Walters 1964), or where cytotypes are not easily or always distinguishable, as in *Asplenium trichomanes* L. (Crabbe *et al.* 1964) or *Galium palustre* L. (Clapham 1962). However Ehrendorfer & Puff (1976) treat *G. elongatum* C. Presl as a separate species, despite the admission that intermediates occur with *G. palustre* L. We consider that the situation with British ivies is more like that found within the *Dryopteris dilatata* complex, in which northern diploids have been distinguished as *D. expansa* (C. Presl) Fras.-Jenk. & Jermy (*D. assimilis* S. Walker) and are differentiated from the tetraploid, *D. dilatata* (Hoffm.) A. Gray, primarily by a cryptic spore character, but also by a not very easily defined morphology.

Linnaeus' specimens consist of at least four samples of *Hedera helix*, three of which are too mature for certain determination and for this reason specimen 280.2 in LINN, which has a sterile shoot and typical diploid trichomes, is here selected as the lectotype. Thus *H. helix* may be retained for the diploids. The earliest name for the tetraploid is probably *H. hibernica* hortul. (De Candolle 1830), a nomen nudum as there is no description. The first mention with a description is by Kirchner in Petzold & Kirchner (1864) as "*H. helix* var. *hibernica* hort. Schottischer Epheu". In 1914 Bean raised this taxon to specific rank as *H. hibernica* (Kirchner) Bean. Thus *H. hibernica* is the name which now must be used for the tetraploids (McAllister 1981), the cultivated clone becoming *H. hibernica* (Kirchner) Bean cv. *Hibernica*.

Most ivy cultivars are referable to *H. helix*, but some others, as well as cv. *Hibernica*, belong to *H. hibernica*, including 'Digitata', 'Deltoidea', 'Variegata', 'Maculata', 'Albany', 'Hamilton', and 'Helford River' (Lawrence & Schulze 1942; Rose 1980, 1983; Grüber 1983; Sulgrove 1981a & b). The semi-adult nature of *H. hibernica* hort. is paralleled in *H. helix* by a remarkable clone collected at South Glendale in the south-west of South Uist in the Outer Hebrides. This looks superficially like cv. *Hibernica* but has leaves from 6 cm wide by 5 cm long to 12.5 cm wide by 9 cm long; the texture is thinner than that of the Irish Ivy however, and the margins have the typical undulations of maturing juvenile leaves of *H. helix*.

SYNONYMY

The synonymy of most ivies in cultivation and their cultivars is given in Lawrence & Schulze (1942), but is summarised here with *H. hibernica* treated as a distinct species.

1. *H. helix* L., *Sp. Pl.* 202 (1753). LECTOTYPE: sheet 280.2 (LINN), designated here. Common Ivy.
2. *H. hibernica* (Kirchner) Bean, *Trees & shrubs hardy in the Br. Isl.* 609 (1914). Atlantic Ivy.
H. helix var. *hibernica* Kirchner in Petzold & Kirchner, *Arb. Muscav.* 419 (1864).
H. hibernica Carr. in *Rev. Hort.* 71:163 (1890), nomen nudum.
H. helix subsp. *hibernica* (Kirchner) D. McClintock, *Suppl. wild fl. Guernsey* 23 (1987).

We propose the common name Atlantic Ivy for *H. hibernica* in the wild state and suggest restricting the use of Irish Ivy to the cultivar Hibernica.

PHYTOGEOGRAPHY

The distribution of *H. hibernica*, the Atlantic Ivy, is very similar to that of certain heaths, *Erica cinerea* having a slightly more extensive range, while *E. vagans* and *E. mackaiana* have progressively more limited ranges, and *E. ciliaris* extends further south into Morocco. It is interesting that although these heathers belong to totally different types of community from the ivy, all are evergreen and so subject to the same freezing and desiccation stresses in cold winters which presumably limit their eastward spread. They, together with the more widely distributed *H. helix* and *Ilex aquifolium*, are among the very few larger evergreen flowering plants native to northern Europe.

The distribution of the two species in the British Isles shows *H. helix* with an almost continuous distribution and *H. hibernica* in somewhat separate areas on the western coasts. This pattern suggests that *H. hibernica* formerly had a more extensive, continuous range which has been reduced by *H. helix* invading from the south-east. In milder, wetter parts of the country it seems that *H. hibernica* can occupy the available habitats and hold off the advance of *H. helix*. In less mild areas the occasional exceptional cold spell may do sufficient damage to *H. hibernica* to leave niches free for colonisation by the more winter-hardy *H. helix*. *H. hibernica* occurs in the south-west of England, most of southern and western Wales and the northern Welsh coast. There is an isolated record for Silverdale in northern Lancashire and extensive isolated populations occur in the mild coastal parts of Galloway in south-western Scotland. Only *H. hibernica* has been found on the Isle of Man, and the distribution of the two species in Ireland might suggest that *H. helix* has only recently invaded from Scotland, from the Mull of Kintyre, and may be extending its range. The situation on the main island of Great Britain could be expected to have more or less stabilised for present climatic conditions, but it will be interesting to watch what happens following a succession of cold winters.

ORIGIN OF *H. HIBERNICA*

H. hibernica is here classified with *H. helix* and *H. azorica* Carriere (*H. canariensis* 'Azorica' hort.) because it has the same long, white-rayed trichomes. It differs from these diploid species in that its rays lie more or less appressed to the leaf surface, in a similar way to the rays of the other much larger grouping of ivy species, the orange-red, small-haired species of *Hedera*, found mostly to the south and east of the Mediterranean and Black Seas (McAllister 1981). There is the possibility therefore that the tetraploid *H. hibernica* could be an allotetraploid derivative of *H. helix* and a species from the second group. In North Africa, in the Atlas Mountains, there is an as yet undescribed diploid with large five-lobed ivy-shaped leaves and considerable vigour which seems an ideal candidate. *H. hibernica* resembles this species in its capacity to produce larger leaves than those of *H. helix*, in the greater average number of rays per trichome and the fawn to slightly orange colouration of the central boss of the trichomes of some populations, as well as the attitude of the

rays, the sweeter sap odour found in the larger group of ivies and the more luxuriant growth. *H. hibernica* is thus intermediate in several characteristics between *H. helix* and the undescribed species from Morocco.

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