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Cytotaxonomic studies on the *Cochlearia officinalis* L. group from inland stations in Britain

J. J. B. GILL

Department of Genetics, University of Liverpool

H. A. McALLISTER

University of Liverpool Botanic Gardens, Ness, Neston, Wirral

and

G. M. FEARN

Department of Chemistry and Biology, Sheffield City Polytechnic

ABSTRACT

The results of a cytotaxonomic survey of *Cochlearia Officinalis* L. *sensu lato* from inland sites in Britain are reported. One diploid and two tetraploid cytotypes exist. The diploid ($2n = 12$) occurs at moderate altitudes and appears to be restricted to base-rich habitats. It corresponds both ecologically and cytologically with *C. pyrenaica* DC. and, although, in the authors' experience, it cannot be readily distinguished from the tetraploid *C. officinalis* L. *sensu stricto* on morphological grounds, it is most meaningfully regarded as forming an extension to the range of *C. pyrenaica*. The two tetraploids are distinguishable from each other both morphologically and cytologically and usually occur at higher altitudes than the diploid, although the $2n = 24$ cytotype occasionally is found at lower altitudes. The $2n = 24$ cytotype, which frequently contains B chromosomes, is assigned to *C. officinalis* L., while the cytologically constant $2n = 26$ cytotype represents *C. micacea* Marshall. On the basis of the ecology and chromosome numbers of the above three species, it is suggested that *C. alpina* (Bab.) Wats. is best regarded simply as an inland ecotype of *C. officinalis* L.

The probable post-glacial history of the genus is discussed.

INTRODUCTION

The genus *Cochlearia* L. is widely distributed in the British Isles, where it occurs in both maritime and inland-upland habitats. It is generally agreed that the coastal populations fall into three or possibly four species. These are *C. officinalis* L., *C. danica* L., *C. anglica* L. and possibly *C. scotica* Druce. The first three are common round much of the coasts of the British Isles, except that *C. anglica* is apparently absent from Orkney and Shetland. *C. officinalis* is an extremely common plant of sea-cliffs and the drier parts of salt-marshes, and it also occurs inland; *C. danica* is common on the drier parts of sea-cliffs and in sandy places by the sea and occurs rarely inland; and *C. anglica* is locally abundant on muddy salt-marshes. *C. scotica* is a plant of the north and west, although it may possibly occur as far south as Berwick in the east. Gill (1971) has, however, cast some doubt on the reported distribution of *C. scotica*.

The inland-upland populations have been recognized as belonging to *C. alpina* (Bab.) Wats., *C. pyrenaica* DC., *C. officinalis*, or *C. micacea* Marshall. It has, however, been suggested that neither *C. alpina* nor *C. micacea* are entirely montane plants but may descend nearly to sea-level at least in the islands of northern and western Scotland (Druce 1932). The status of the inland populations of *Cochlearia* have been much disputed, with even the same author recognizing the taxa at different levels at different times—Clapham (1952) recognized both *C. alpina* and *C. micacea* but in 1962 submerged both in *C. officinalis* as *C. officinalis* L. subsp. *alpina* (Bab.) Hook. Chater & Heywood (1964) included

C. alpina in *C. pyrenaica*. Like Clapham (1962), these authors did not distinguish *C. micacea*, regarding it only as a narrow-fruited variant of *C. pyrenaica*. In their treatment of *C. officinalis*, Chater & Heywood included a note—'Plants from Scotland approach the following species' [*C. pyrenaica*].

At least some of the taxonomic confusion which exists in *Cochlearia* has arisen because the characters which are used to distinguish between the taxa are mostly quantitative or plastic, or both. The literature abounds with comparisons such as leaves *fleshy* versus leaves *not* or *hardly fleshy* (Clapham 1952), silicula *ovoid to globose* versus silicula *ovoid-ellipsoid* (Chater & Heywood 1964) or pedicels *usually longer* than silicula versus pedicels *equalling or shorter* than the silicula (Chater & Heywood 1964). Occasionally there occurs absolute contradiction between the keys and the descriptions of the species; Clapham (1952) separated *C. alpina* and *C. micacea* from the rest of the genus by

'Inland, usually alpine plants with leaves not or hardly fleshy'—*C. alpina* or *C. micacea*
'Maritime plants with fleshy leaves'—other species including *C. officinalis*,

yet his description of *C. officinalis* states 'reaches 2,800 ft on Ben Creachain'.

The taxonomic uncertainties which exist are to some extent reflected in the various chromosome numbers which have been reported for these species (Table 1).

TABLE 1. PREVIOUSLY PUBLISHED BRITISH COUNTS FOR *COCHLEARIA ALPINA, C. OFFICINALIS* AND *C. MICACEA*

Species	Locality	Author	2*n*
C. alpina	Scotland	Crane & Gairdner 1923	28
	Malham, Mid-W. Yorks, v.c. 64	Gill 1965	12 (+0–2 B)
	Helvellyn, Cumberland, v.c. 70	Gill 1965	12 (+0–1 B)
C. officinalis	St Davids, Pembs., v.c. 45	Crane & Gairdner 1923	28
	Teesdale, Durham, v.c. 66	Saunte 1955	24
	Ben Bulben, Sligo, v.c. H28	Saunte 1955	24
	Black Head, Clare, v.c. H9	Saunte 1955	24
	Lauragh, S. Kerry, v.c. H1	Saunte 1955	24
	Birdsay, Orkney, v.c. 111	Gill 1973	24
	Yecansby, Orkney, v.c. 111	Gill 1973	24
	Wick, Caithness, v.c. 109	Gill 1973	24 (+0–2 B)
	Coast of Isle of Skye, Mid Ebudes, v.c. 104	Gill 1973	24
	Banff, Banff., v.c. 94	Gill 1973	24 (+0–1 B)
	Carnoustie, Forfar, v.c. 90	Gill 1973	24
	Lamlash, Arran, Clyde Is., v.c. 100	Gill 1973	24 (+0–1 B)
	Caernarvon, Caerns., v.c. 49	Gill 1973	24
	Hook Farm, Pembs., v.c. 45	Gill 1973	24
	Parkgate, Cheshire, v.c. 58	Gill 1973	24
C. micacea	Scotland	Crane & Gairdner 1923	34–36
	Ben Lawers, Mid Perth, v.c. 88	Gill 1973	26
	Meall nan Tarmachan, Mid Perth, v.c. 88	Gill 1973	26
	Beinn Heasgarnich, Mid Perth, v.c. 88	Gill 1973	26
C. sp. (Probably *C. officinalis*)	Various coastal localities in the northern and western Scottish islands	Gill 1971a	24

As orthodox taxonomic methods had failed to produce any agreement on the status of the inland populations of *Cochlearia*, the present work was initiated to determine the extent of the morphological and cytological variation in the group.

METHODS

Material was collected in the wild and identified on morphological criteria as either *C. officinalis* or *C. micacea* (for criteria see Discussion). The majority of the plants were grown on at the the University of Liverpool Botanic Gardens until root-tips and/or flower-buds could be taken for the determination of

chromosome numbers. These chromosome counts were made by J.J.B.G. who was kept ignorant of both the taxonomic identities and localities of collection of the material until after the chromosome numbers were determined. Chromosome counts were also made by G.M.F. on flower-buds collected in the field or on root-tips and/or flower-buds from plants grown on at the University of Sheffield Experimental Garden. Chromosome counts were made by the methods previously described (Gill 1965, Fearn 1971).

RESULTS

Of all the populations examined only those from Beinn Dearg and Glas Maol were initially identified as *C. micacea*. These were also the only populations which gave a constant chromosome count of $2n = 26$, thus agreeing with the chromosome number for *C. micacea* previously published by Gill (1973). All the other populations were originally identified as *C. officinalis* but formed two cytotypes. The $2n = 24$ cytotype, which frequently contains B chromosomes, corresponds with *C. officinalis sensu stricto* and was collected from high-altitude stations (above 800m) and from a single low-altitude locality at Cheddar Gorge. All the high-altitude stations were well flushed and presumably relatively base-rich. The $2n = 12$ cytotype, one population of which contains B chromosomes, was collected exclusively from highly base-rich habitats at intermediate altitudes (150–750m).

All the chromosome numbers determined in this investigation are summarized in Table 2 and are included with all previously published counts in Fig. 1.

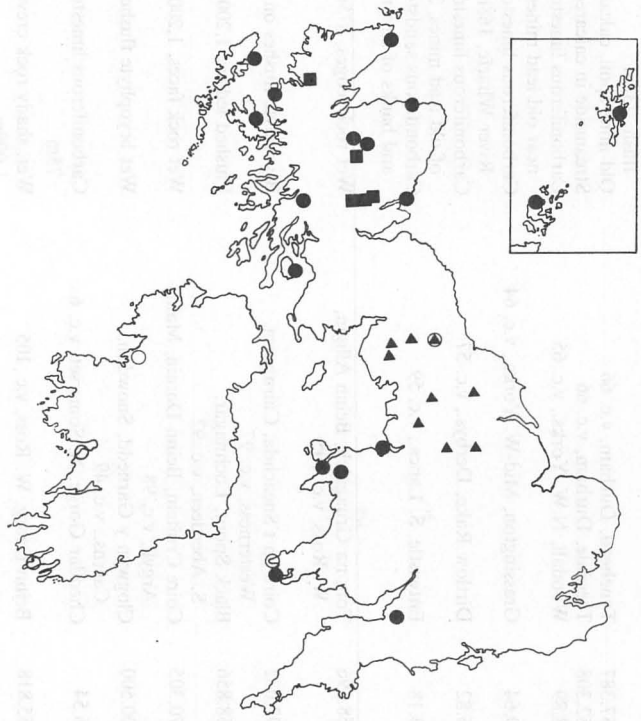

FIGURE 1. Map showing all published chromosome counts in *Cochlearia* together with those reported in this paper (all counts made by the present authors blacked in).

△ = $2n$ = 12(+ 0–2B)
○ = $2n$ = 24(+ 0–5B)
□ = $2n$ = 26

TABLE 2. CHROMOSOME COUNTS OF *COCHLEARIA* SPECIES MADE IN THIS INVESTIGATION

Species	Grid Reference	Locality	Habitat notes	No. of plants	2*n*
C. pyrenaica	35/71.31	Green Castle, Westmorland, v.c. 69	Carboniferous limestone. High altitude flush, 732m	2	12
	35/757.387	Tynehead, Durham, v.c. 66	Old mine spoil, calcareous, 480m	14	12
	35/852.308	Teesdale, Durham, v.c. 66	Streamside in calcareous meadow, 420m	7	12
	34/98.89	Woodall, N.W. Yorks., v.c. 65	Carboniferous limestone Streamside near old lead mines, 214m, pH 6·7	several	12
	34/99.64	Grassington, Mid-W. Yorks., v.c. 64	Carboniferous limestone. Mud banks of River Wharfe, 168m, pH 7·0	1	12
	43/15.82	Dirtlow Rake, Derbys., v.c. 57	Carboniferous limestone. Spoil heaps of old lead mines, 336m, pH 7·4	several	12
	34/73.18	Entwistle, S. Lancs., v.c. 59	Carboniferous sandstone. Shingle bed and banks of stream, 198m, pH 7·3	3	12 12(+ 2B)
C. officinalis	18/858.596	Tom na Gruagaich, Beinn Alligin, W. Ross, v.c. 105	Wet rock ledges, 875m	4	24 24(+ 1B) (2 plants) 24(+ 2B)
	28/992.032	Coire an t'Sneachda, Cairngorm, Westerness, v.c. 97	Bryophyte flushes on cliff, 1,200m	2	24(+ 1B) 24(+ 2B)
	37/258.856	Black Spout, Lochnagar, S. Aberdeen, v.c. 92	Flushed ledges, 1,200m	3	24 (2 plants) 24(+ 5B)
	27/070.305	Coire Cruitein, Beinn Dorain, Main Argyll, v.c. 98	Wet rock faces, 1,200m	2	24(+ 4B) 24(+ 5B)
	23/600.500	Clogwyn y Garnedd, Snowdon, Caerns., v.c. 49	Wet bryophyte flushes, 1,100m	5	24, 24(+ 1B), 24(+ 2B) 24(+ 3B) (2 plants)
	31/46.54	Cheddar Gorge, N. Somerset, v.c. 6	Carboniferous limestone. Roadside verge, 75m	5	24
C. micacea	28/255.818	Beinn Dearg, W. Ross, v.c. 105	Wet, shady rock crevices in N. facing cliffs, 1,000m	5	26
	37/16.77	Glas Maol, Forfar, v.c. 90	Granite. Damp hollow, 839m, pH 5·6	3	26

DISCUSSION

It is apparent from Table 2 that in Britain there exist inland populations of *Cochlearia* with chromosome numbers of $2n = 12 (+ 0$ or 2B), $2n = 24 (+ 0 - 5B)$ and $2n = 26$. These numbers agree with those already published by Gill (1965, 1971a, 1973) for British populations identified as *C. pyrenaica, C. officinalis* and *C. micacea* respectively. The counts of $2n = 28$ for *C. alpina* and $2n =$ 34–36 for *C. micacea* reported by Crane & Gairdner (1923) were not corroborated, so these early counts must remain very doubtful.

The count of $2n = 28$ for *C. alpina* has been discussed by Saunte (1955), who has pointed out that, in Crane & Gairdner's drawing of the somatic chromosomes of this species, there are apparent four chromosomes which are smaller than the others. Saunte interpreted these as being accessory chromosomes and therefore regarded the count as in reality $2n = 24 + 4B$. This interpretation of course gives Crane & Gairdner's material the same chromosome number as *C. officinalis* (Saunte 1955, Gill 1973) and indeed Saunte, who was unaware of the existence of the diploid ($2n = 12$), did not regard the British inland material known to her as being other than *C. officinalis*. It has been well established by both Saunte (1955) and by Gill (1971a, 1973) that specimens of *C. officinalis* containing four B chromosomes, and thus giving chromosome counts of $2n = 28$, are common. Crane & Gairdner's count appears to have been derived from only a single specimen and it is therefore quite possible that it represented an atypical individual from a population of *C. officinalis*. Crane & Gairdner do not give the locality for the collection of their material and it has not proved possible to trace either this or their voucher specimens, so that no direct check of their count can be carried out. The type locality for *C. alpina* is Lochnagar (Druce 1904) and our three plants from this locality had chromosome numbers of $2n = 24$ (2 plants) and $2n = 29$. It would thus appear that our population from the type area was a population of plants with $2n = 24 + 0–5B$ chromosomes. The situation in *C. alpina* is further complicated by the fact that in Smith's (1811) description of Don's material from Lochnagar the plant is said to have extremely fleshy basal leaves, while Clapham (1952) separated *C. alpina* from *C. officinalis* on the absence of fleshiness in the leaves of the former species. Although the absence of fleshiness in the basal leaves was used by Gill (1965) to separate the diploid material from Malham and Helvellyn from the *C. officinalis* populations then known to him, it was found that many of the inland $2n = 24 (+ 0–5B)$ populations also had non-fleshy basal leaves. It is perhaps worth noting here that the fleshiness or non-fleshiness of the leaves is one of those quantitative characters much used in *Cochlearia* but extremely difficult to apply objectively.

Of all the tetraploid counts only three are from low or moderate altitudes. Two of these (Ben Bulben and Cheddar Gorge) are near to the coast and may be interpreted as being remnant coastal populations of *C. officinalis*, isolated as inland populations with the falling of the sea-level during the post-glacial period. The count of $2n = 24$ from Teesdale (Saunte 1955) should be treated with some suspicion as, despite extensive sampling in that area, the present authors are able to report only diploid counts.

The results suggest, therefore, that the diploid is confined in Britain to apparently base-rich habitats at moderate altitudes (cliffs, streamsides, old mine spoil-heaps), but that near the sea, even on base-rich soils, it may be replaced by the tetraploid. At high altitudes the tetraploid occurs in areas which may or may not be base-rich. Confirmation of such distributions must, however, await more extensive sampling of upland calcareous areas in Scotland and a general survey of upland populations in Ireland.

The status of *C. alpina* is still difficult to ascertain. The authors are conscious that despite the demonstration that material from the type locality (Lochnagar) is tetraploid they have not yet seen the herbarium specimens of either Don or Crane & Gairdner and therefore cannot with certainty identify *C. alpina*. They would, however, suggest that, as Lochnagar is not a base-rich habitat, it is unlikely that the diploid would occur there and that it is therefore unlikely that Don's material was diploid. The extreme difficulty of separating *C. alpina* from *C. officinalis* on morphological grounds together with the extremely doubtful differentiation on chromosome number leads them to suggest that *C. alpina* should be treated only as an inland ecotype of *C. officinalis*.

The diploid material can be identified, using existing Floras, with equal facility as *C. pyrenaica* or *C. officinalis* and it has the same chromosome number as *C. pyrenaica* (Rohner 1954; Dersch 1962, 1968; Gill 1971b; Kakes 1973). *C. pyrenaica* in Europe has long been recognized as a plant of base-rich habitats (Hegi 1919, Hiemans 1971) and this also appears true of the diploid populations in Britain. It is thus apparent that, despite the lack of morphological distinguishing characters, the $2n = 12$

populations in Britain are best regarded as forming an extension of the known range of *C. pyrenaica*. The tetraploid $2n = 24(+ 0–5B)$ populations are best treated as inland populations of *C. officinalis*.

Those populations which gave a constant count of $2n = 26$ as well as comprising a unique cytotype also form a morphological entity and can, in the experience of the authors, be taxonomically distinguished as *C. micacea*. The chromosome number of this species has been discussed by Gill (1973). The characters which are used to define *C. micacea* are the much darker green of the foliage of this species when compared with the rest of the inland plants, together with the low-growing habit and strong tendency to produce a perennating woody rootstock with some slight vegetative reproduction by lateral shoots. These characters are, however, all comparative characters and, to use them successfully, it is necessary to be well acquainted with the other inland plants. When, however, these characters are combined with the chromosome number and the known genomic constitution of the taxon (Gill 1973), the authors can see no conclusion other than the maintenance of *C. micacea* as a separate species. Such a conclusion agrees with that of Pobedimova (1971) and is supported by the constant distinction of *C. micacea* from *C. alpina* by McVean & Ratcliffe (1962). The details of the distribution of *C. micacea* must await further investigation but it appears to be a plant of high altitudes usually above 800m. It may indeed be a British endemic but there is some suggestion that it may also occur in Scandinavia (Hylander 1945).

The extreme morphological similarities of the three species recognized here and the difficulties experienced by orthodox taxonomists are to be expected if the evolutionary relationships between the different chromosome levels are as suggested by Gill (1973). He demonstrated that *C. officinalis* is essentially an autotetraploid of *C. pyrenaica* and that *C. micacea* may be regarded as a primary tetrasomic of *C. officinalis*. These relationships would result in the only unique genes or alleles possessed by any of the species being those which arose by mutation shortly after speciation. Such mutations would be very rare and, therefore, if the evolutionary pathways suggested by Gill are accepted, it would be expected that the differences between *C. pyrenaica, C. officinalis* and *C. micacea* would be those arising from the differing number of gene copies in the three species. Such differences would almost certainly be quantitative rather than qualitative but must account for the differing ecological amplitudes of the taxa.

The tetraploid *C. officinalis*, if it originated from a highly heterozygous diploid, would have a greatly increased variance for many loci and could, therefore, be much superior to the diploid in its ability to colonize new habitats. The inland distribution of *Cochlearia* is typical of one much affected by glaciation and it is tempting to suggest, because of the existence of the Polish endemic *C. polonica* Borb. and the possible endemic status of *C. micacea*, that much of the speciation in the European members of the genus occurred either during or at the end of the last glaciation. The great number of new habitats made available by the retreating ice would have produced a selective regime in which increased variance would be of considerable advantage. Such a situation would seem to be ideal for the establishment and spread of an autotetraploid species such as *C. officinalis*. The diploid parent of any autotetraploid would almost certainly be in competition with its tetraploid offspring, but the continued existence of both may also be due to the differences in copies of gene loci between them. The diploid, because of the small number of copies of each locus present, would be able to fix a genetic trait much more quickly than the tetraploid and, in the face of competition from the tetraploid, could retreat into some extreme or relict environment similar to that to which it has already been exposed. In this extreme environment the relative lack of variance of the diploid could well enable it to compete successfully against the tetraploid and eventually, by the accumulation of new mutations, to become so highly and specifically adapted to the particular extreme habitats into which it had retreated that competition from the tetraploid ceased. The habitats at present occupied by *C. pyrenaica* in northern England would appear to be sufficiently extreme to be accountable for by the events suggested above.

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