CIRCAEA IN THE BRITISH ISLES

By PETER H. RAVEN
Division of Systematic Biology, Stanford University, California, U.S.A.

Although the three European taxa of *Circaea* — *C. alpina* L., *C.* × *intermedia* Ehrh. and *C. lutetiana* L. — have in general been well understood on the Continent, the distinction between *C. alpina* and *C.*×*intermedia* has been a persistent source of confusion and subject of discussion in the British Isles (Baker 1951, p. 306). The result of this confusion has been the classification of a number of individuals of *C.* × *intermedia* as *C. alpina* and the consequent obscuring of some remarkable patterns of distribution. It is the aim of this paper to re-examine the British distribution of *C. alpina* and its relation to the hybrid origin and spread of *C.*×*intermedia.*

CHARACTERS DISTINGUISHING THE THREE ENTITIES

Although the three taxa of *Circaea* considered here (Figs. 1-3) are usually quite distinct, there has in the past been some confusion among them, particularly, as noted above, in Britain. Early in the course of the present study, it was discovered that the most useful character separating *C. alpina* from the others was the nature of its inflorescence. In *C. alpina* the rachis of the inflorescence does not elongate until after the open flowers have dropped; consequently, all of the open flowers are clustered at the stem apex (Fig. 1a). In *C. lutetiana* on the other hand the rachis elongates before the flowers open, and the open flowers are well spaced (Fig. 1g). In *C.*×*intermedia*, the spacing of the flowers is similar to that of *C. lutetiana*, but the inflorescence is somewhat more contracted (Fig. 1d). This character is well shown by Ross-Craig (1958, plates 35-37). When its importance was realised, it was found to be correlated with a number of other features, some stressed in earlier descriptions. Many of them are enumerated in the following table on p. 263.

Comment is necessary on some of these characters. Bracteoles are found with a very low frequency in *C. lutetiana*, but I have not seen them in British or Irish specimens. The disc, which is shown in *C. lutetiana* in Fig. 1h, is a prominent, elevated, nectar-secreting ring at the apex of the hypanthium. The flowers of this species are frequently visited by small flies, and, as the anthers are held away from the stigma, self-pollination is probably a relatively exceptional event, although Mr. P. M. Benoit informs me that the plants of this species he tested were self-compatible. In fine weather the anthers of *C. lutetiana* begin to shed pollen an hour or two after the flowers open. In *C. alpina*, on the other hand, no disc is present, and consequently no nectar, and the anthers often deposit pollen on their own stigma before the buds open, which doubtless causes a high degree of self-pollination. In fact, it is common for the later flowers of *C. alpina* not to open; instead, the buds become large and pale and eventually produce fruit cleistogamously. In *C.*×*intermedia* the disc is usually present but low and obscure.

Evidence of the hybrid nature of *C.*×*intermedia* is found in its complete morphological intermediacy between the two parents, as shown by the preceding table. In addition it is absolutely sterile. The anthers of *C.*×*intermedia* often fall undehisced, and I have never seen a single well-filled, morphologically normal, pollen grain in a plant of this taxon. Likewise, plants of *C.*×*intermedia* fail to produce mature fruit. On the other hand, the plants of *C. alpina* and *C. lutetiana* generally set full complements of seed, and those that I examined, with the exception noted below, were consistent in having pollen more than 90 per cent fertile.

	lutetiana	× *intermedia*	*alpina*
Rhizomes	thick	intermediate	slender, forming terminal tubers in autumn
Overwintering portion	entire rhizome	most of rhizome	only tubers
Stolons from lower axils	absent	present	present
Stem height	15–60 cm	10–45 cm	5–30 cm
Stem pubescence	dense, appressed below	more sparse	absent below
Petioles	hairy all round	hairy above, subglabrous below	glabrous
Leaf base	truncate or slightly cordate	shallowly cordate	cordate
Leaf apex	acuminate	abruptly acuminate	subacuminate or acute
Leaf margin	mostly remotely denticulate	dentate	deeply dentate
Leaf pubescence	strigulose along veins and margins	subglabrous	glabrous
Inflorescence elongation	before flowers fall	before flowers fall	after flowers fall
Bracteoles	absent	present, setaceous	present, setaceous
Pedicels	densely glandular-pubescent	sparsely glandular-pubescent	glabrous
Hypanthium	.–1·2 mm long, about equal to ovary in length	0·5–1·2 mm long, shorter than ovary	0·1–0·2 mm long, much shorter than ovary
Disc	conspicuous, dark, 0·2–0·4 mm high	shallow, rarely to 0·2 mm high	absent
Sepals	pale green; densely glandular-pubescent	whitish; sparsely glandular-pubescent	white; glabrous
Petals	2–4 × 2·2–5 mm, deeply notched	1·8–4 × 2–3·5 mm, deeply notched	0·6–1·4 × 0·4–0·9 mm, often shallowly notched
Petal base	truncate to rounded	rounded to cuneate	cuneate
Filaments	2·5–5·5 mm long	2–5 mm long	1–1·5 mm long
Pollen	fertile	sterile	fertile
Fruits	3–4 × 2–2·5 mm, bilocular	up to 2 × 1·2 mm, falling immature	2 × 1 mm, unilocular
Fruit hairs	0·7–1·1 mm long, dense	0·5–0·6 mm long, dense	0·1–0·5 mm long, more sparse

Fig. 1 a–c. *Circaea alpina:* a, inflorescence; b, flower; c, bud. d–f, *C.* × *intermedia:* d, inflorescence; e, flower; f, bud. g–i, *C. lutetiana.* g, inflorescence; h, flower; i, bud. Inflorescences, × 1; flowers and buds, × 6.

A few British collections, morphologically referable to *C. lutetiana* f. *cordifolia* Lasch, are intermediate between *C. lutetiana* and *C.* × *intermedia* in their cordate leaf-bases and in being relatively glabrous. Although these plants often appear to have full seed set, some of them had only about 50 per cent normal pollen. They may have originated from hybridisation between *C.* × *intermedia* (presumably as the seed parent) and *C. lutetiana*, and this possibility should be investigated further by those in a position to do so. On the other hand, a single plant from Goat Fell, Arran, collected in 1883 (collector unknown; herb. Edinburgh), had the floral characteristics of *C.* × *intermedia* but fruit like that of *C. alpina* and might have been of hybrid origin between them.

Some of the characters used to distinguish the species of *Circaea* in Britain are of little or no value. Amongst them may be mentioned the winged petioles supposed to be found in *C. alpina* and the distinctions in the stigmas described for these species. As shown, for example by Ross-Craig (1958, plate 37), even *C. alpina* may have a two-lobed stigma. Mr. P. M. Benoit has informed me that when the flowers of *C. lutetiana* are not fertilised, the papillose stigmas become swollen and up to 1·5 mm in diameter; stigmas of this sort are frequent in the sterile *C.* × *intermedia*. The seed in one cell of the fruit of *C.* × *intermedia* often begins to develop (as shown by Ross-Craig 1958, plate 36); however, as mentioned above, fruits in this species are not known to reach maturity. It may be added at this point that the plants illustrated by Roles (Clapham, Tutin & Warburg 1960, fig. 722), Butcher (1961, fig. 699), and by Fitch & Smith (1924, fig. 354) as *C. alpina* are in fact small plants of *C.* × *intermedia*.

CHROMOSOMES

The chromosome numbers of the taxa involved have been determined a few times from Continental plants (cf. Löve & Löve 1961), and I have been able to confirm them using British material. All plants of *Circaea* that have been examined to date have had the same chromosome number, $2n = 22$. I determined this number in root-tips of a plant of *C. alpina* from Pennant Dyfi, Merioneth. Some cells in these root tips were tetraploid, with $2n = 44$, but were obviously exceptional in a diploid individual. Meiosis was studied in dividing pollen mother cells of *C. lutetiana* from Llanbedr, Merioneth (*Raven & Benoit* 16301 (**BM**); Fig. 2a), and was regular, with a gametic chromosome number of $n = 11$. Finally, what I believe to be the first observations of meiosis in *C.* × *intermedia* were obtained from plants collected along the roadside in *Fraxinus-Acer* woodland ¼ mile north of Llanymawddwy, Merioneth (*Raven & Condry* 16297 (**BM**); Fig. 2b). Pairing and division of the chromosomes in the plant examined, however, appeared completely normal, with 11 bivalents. In view of the hybrid origin of *C.* × *intermedia*, part of its sterility might have been associated with the presence of meiotic irregularities. The only aspect

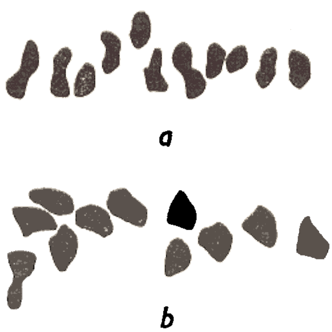

Fig. 2. Meiotic chromosomes of *Circaea* at metaphase I, spaced. a, *C. lutetiana;* b, × *intermedia.* Both × 2000.

in which the meiosis of this plant differed from that of *C. lutetiana*, however, was that two of its bivalents were clearly heteromorphic (one of them is visible in the cell drawn in Fig. 2b), indicating that size differences present in the chromosomes of the parents may have been partly preserved in the hybrid. It does appear from the illustrations of mitotic chromosomes in the three taxa presented by Uddling (1929, Figs. 1–5), that the chromosomes of *C. alpina* are in fact somewhat smaller than those of *C. lutetiana*. Despite this, it would appear that the sterility of *C.* × *intermedia* must be attributed to genetic factors, and certainly not to the kinds of major chromosomal rearrangements that have been so prominent in the evolution of certain other genera of Onagraceae. This is particularly significant in view of the fact that *C. alpina* and *C. lutetiana* seem to be as completely differentiated morphologically as are any two species of *Circaea*.

Distribution of the taxa in the British Isles

As may be seen from an examination of the maps (Figs. 3, 4 and 5), the woodland species *C. lutetiana* is found nearly throughout the British Isles but becomes rarer northward; the hybrid *C.* × *intermedia* likewise has a wide range in the west and north of Great Britain, the Inner and Outer Hebrides, the Isle of Man and northern Ireland, becoming rarer southward; whereas *C. alpina* occupies a much more restricted area than has heretofore been supposed, being relatively common only in the Lake District and on Arran,

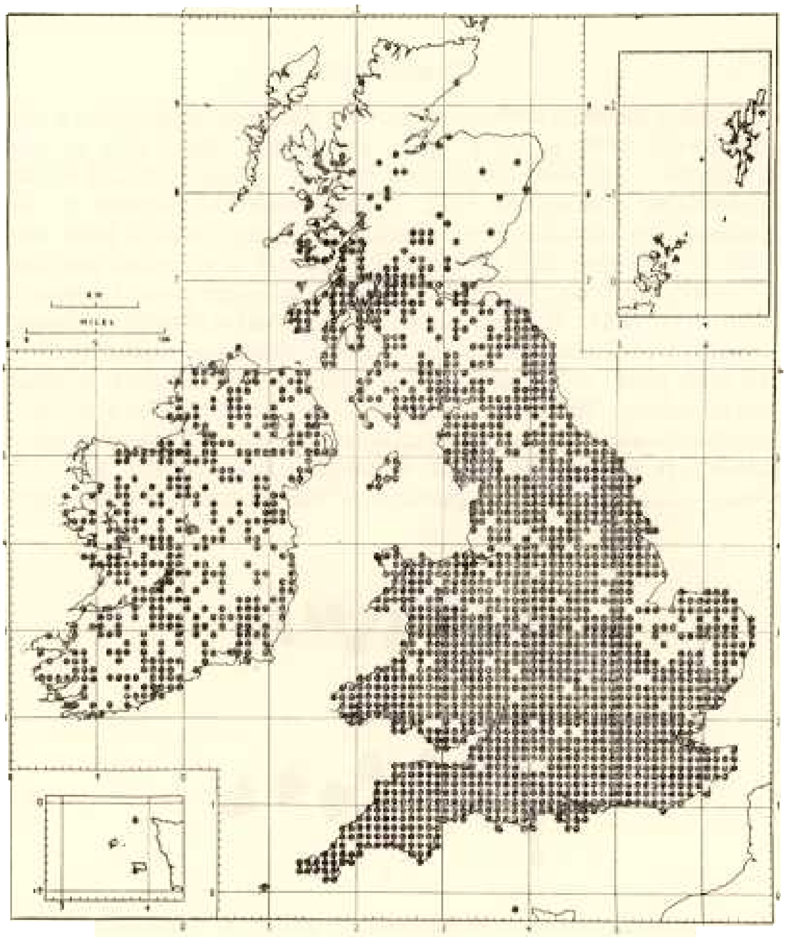

Fig. 3. Distribution of *Circaea lutetiana* L. in the British Isles

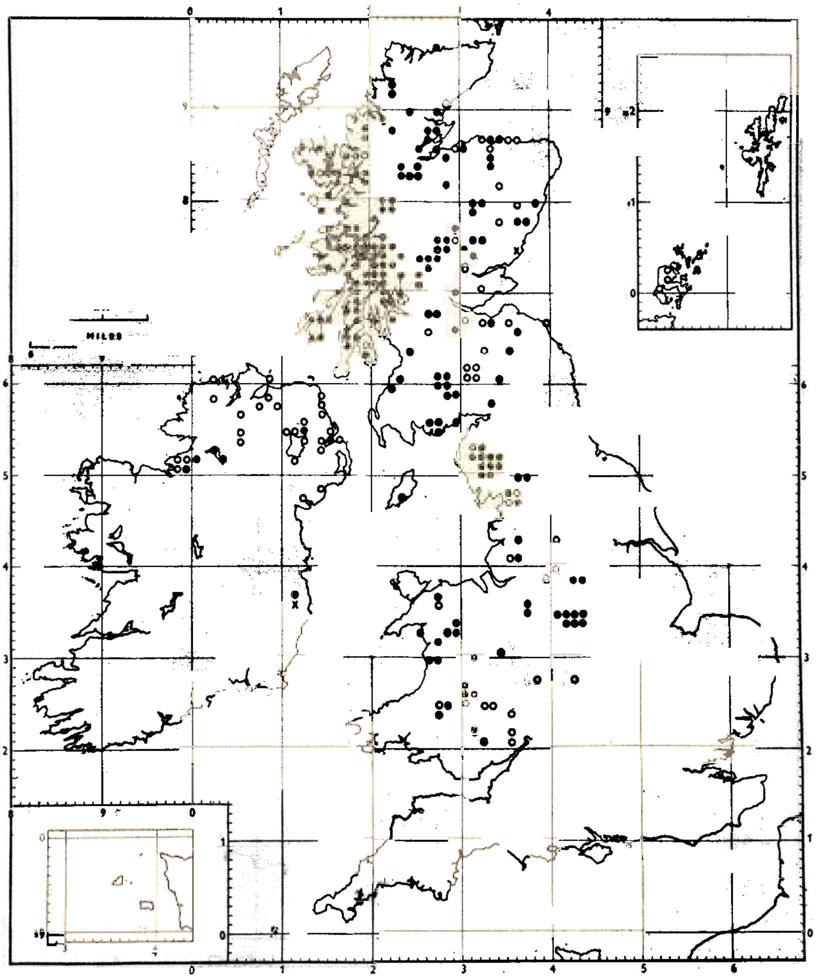

Fig. 4 Distribution of *Circaea* × *intermedia* Ehrh. in the British Isles. Solid dots, 1930 onwards; open circles, before 1930; crosses, introductions.

with scattered localities in Wales and a single station in mainland Scotland (Westerness). Since the restriction of range proposed here for *C. alpina* is so striking, I will amplify my sources in greater detail.

All of the British material labelled *C. alpina* or *C.* × *intermedia* in the following institutions has been examined : Department of Botany, The University, Aberdeen (**ABD**); Department of Botany, The University, Birmingham (**BIRM**); Botany School, University of Cambridge (**CGE**); Department of Botany, National Museum of Wales (**NMW**); National Museum of Ireland (**DBN**); School of Botany, Trinity College, Dublin (**TCD**); The Royal Botanic Garden, Edinburgh (**E**); Department of Botany, University of Glasgow (**GL**); Royal Botanic Gardens, Kew (**K**), including herb. Watson; Department of Botany, British Museum (Natural History) (**BM**); The Manchester Museum, The University (**MANCH**); Druce Herbarium, Department of Botany, University of Oxford (**OXF**); Botanical Department, The University, St. Andrews (**STA**). In addition, material from the private herbaria of J. E. Lousley, R. H. Roberts, N. Y. Sandwith and E. C. Wallace has been examined by kind permission.

The resulting information has been used in drawing up the map of the distribution of *C. alpina* (Fig. 8). As now understood, the species is confined to only 10 vice-counties, all in Great Britain and Arran, instead of the 45 and 11 Irish vice-counties mentioned by

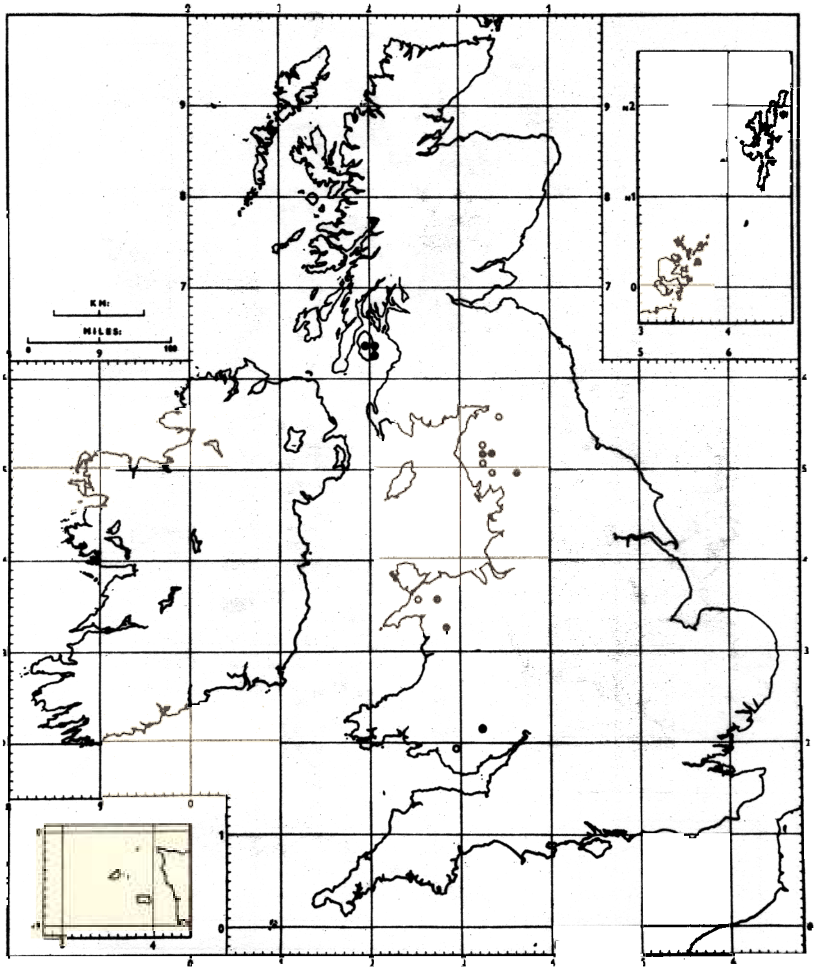

Fig. 5. Distribution of *Circaea alpina* L. in the British Isles. Solid dots, 1930 onwards; open circles, before 1930. Note the isolated Westerness record in grid square 27/07.

Clapham (1952, p. 614). The following list includes all British material of *C. alpina* that has been examined :

V.c. 41, Glamorgan: near a waterfall, west cliffs of the Rhondda Valley, 31 July 1890, *Ley* (**BIRM**; **BM**).

V.c. 42, Brecon: Craig-y-Cilau, 23 July 1952, *Guile* (NMW).

V.c. 48, Merioneth: Cliffs, Llaethnant, Pennant Dyfi, Llanymawddwy, 16 July 1955, *Condry & Richards* (**NMW**; herb. Sandwith); same, 6 July 1961, *Raven & Condry 16294* (**BM**).

V.c. 49, Caernarvon: wooded bank opposite the Dolbadarn Inn (shores of Llyn Peris), 3 July 1832, – (**CGE**); Cobdew Bridge to Capel Curig Lakes, Coed Bryn Engan, 22 July 1948, *E. Roberts 354* (**BM**); woods above Bryn Engan, Capel Curig area, *R. H. Roberts* (herb. R. H. Roberts).

V.c. 60, W. Lancs.: gravel margin of forest in oak wood between Wray Castle and Perry, Windermere, 10 Aug. 1920, *Adamson* (**BM**); gravel stream bank in oak wood, west side of Windermere, 5 Aug. 1920, *Adamson* (**BM**).

V.c. 65, N. W. Yorks.: above Rawthey Bridge near Sedbergh, 1938, *Sledge* (**BM**; **TCD**; herb. Lousley; herb. Wallace).

V.c. 69, Westm.: Glencoyne Dale, Ullswater, 30 July 1937, *Lousley* (**BM**; **K**; **NMW**; herb. Lousley; herb. Wallace); Glencoyne Wood, Ullswater, in large patches on stabilised scree in a good many places throughout the wood, 29 Aug. 1955, *Hervey H1828/1955* (**K**); same, 3 July 1961, *Raven 16222* (**BM**); same, 24 July 1937, *Carter* (**BM**; **K**); Ullswater, 12 June 1893, *Clarke 47531* (**K**); Stybarrow Crag, Ullswater, 19 Aug. 1880, *Slater* (**CGE**); Dungeon Ghyll, Aug. 1870, *Baker* (**BM**); abundant in Rough Crag, Riggindale, 30 July 1910, *Ley* (**BIRM**); rocks of Branstree, above Mardale Green, Aug. 1857, *Watson* (**K**-herb. Watson; **TCD**); Mardale, 1866, *Watson* (**CGE**); Swindale, Sept. 1856, *Watson* (**K**,herb. Watson).

V.c. 70, Cumb.: steep shady bank above Glencoyne Farm, Glencoyne Dale, Ullswater, 1937, *Lousley* (herb. Lousley); Thirlmere, June 1895, *Tennant* (**CGE**); west edge of Thirlmere, 29 Aug. 1881, *Ley* (**BIRM**); damp rocks, Fisher Ghyll between Armboth Fell and Thirlmere, July 1904, *Waterfall* (**K**, **MANCH**); Armboth Fell, July 1904, *Mason* (**OXF**); Lodore Wood, 20 July 1884, *Parsons* (**K**); Lodore Waterfall, Derwentwater, 1806, *Turner* (**K**); Derwentwater, 28 June 1842, *Wright* (**BM**); Troutdale, July 1904, *Waterfall* (**K**); in a moist place in Johnny's Wood, near Rosthwaite, Borrowdale, 8 Aug. 1946, *Whellan* (herb. Lousley; herb. Sandwith); Borrowdale, 31 July 1863, *Hind* (**TCD**); Borrowdale, Glaramara, at bottom of wet gully on north face in very deep shade under large boulder, 1200 feet, 14 June 1953, *Cannon & Herbert 2193* (**BM**); Glaramara, amongst dry overhanging boulders, 1300 feet, 7 July 1951, *Park 215* (**BM**); rocks above Seathwaite, 2000 feet, in wet *Sphagnum*, Aug. 1879,–(**OXF**); mountains, Keswick, July 1860, *Ward* (**MANCH**); plentiful about Stonethwaite, near Keswick, 13 July 1947, *Gerrans 73* (**BM**); Grange Fell, 7 July 1891, *Wolley-Dod* (**BM**).

V.c. 97, Westerness: steep slope of ravine, Coine, 30 June 1957, *McCallum Webster 1012* (**K**).

V.c. 100, Arran, among bracken, Benlester Glen, 300 feet, 3 Aug. 1937, *Mackechnie* (**BM**; herb. Wallace); same, 1000 feet, 8 Aug. 1937, *Mackechnie* (herb. Wallace); same, 1000 feet, 10 Aug. 1933, under *Pteris* (herb. Lousley; herb. Wallace); woodland, Monamore Glen, 300 feet, 23 July 1937, *Mackechnie* (**BM**; herb. Lousley herb. Wallace); Glen Cloy, Aug. 1872, *Craig-Christie 502* (**ABD**); Lamlash, July 1890, *Wilkie* (**GL**); same, Aug. 1928, *Mackechnie* (herb. Wallace); Arran, 29 Aug. 1888, *Thompson* (**BM**).

Not assigned to vice-county: 'North Wales,' *Weiss* (**MANCH**).

One of the more interesting facts that emerges from these maps and the listing of specimens is that *C. alpina* does not have a particularly northern or montane distribution in the British Isles. Rather, while conforming rather closely to the sort of distribution expected of a member of the " Continental Northern " pattern as outlined by Matthews (1955), it occupies a highly fragmented range along the western side of Great Britain. Its extreme rarity on the mainland of Scotland and apparent absence from the Hebrides and from Ireland were entirely unexpected, the more so since *C.* × *intermedia* is common over much of this area. Of equal interest is the occurrence of *C. alpina* in the Rhondda Valley at a locality which is south of the present range of *C.* × *intermedia;* it would be of importance to study this site ecologically if it could be re-located.

A few examples may be given of other species which have ranges in Britain similar to that of *C. alpina* (kindly suggested by Dr. F. H. Perring), but it should be noted that none of them is of the same geographical group when total range is considered. These are *Carum verticillatum* (W. Europe), *Vicia orobus* (W. Europe), *Centaurium littorale* (coasts of W. Europe and inland from Austria to S. Russia) and *Rhynchosinapis monensis* (endemic).

Origin and spread of Circaea × intermedia

On the continent of Europe, *C.* × *intermedia* occurs mostly in or near the zone of contact between *C. alpina* and *C. lutetiana*. In Scandinavia, for example, *C. alpina* is widespread, *C. lutetiana* is present only in the south, and *C.* × *intermedia* is nearly restricted to the area where its two parents overlap (Hultén 1950, maps 1293–1295). As can be seen from an inspection of Figs. 3, 4 and 5, however, the situation is quite different in Britain. *Circaea alpina* doubtless had a wider distribution in the British Isles in cooler times nearer to the last glacial period, but today it is restricted to relatively few localities. On the other hand, *C. lutetiana* is a woodland species that must have mostly expanded its area since the last glacial period. The morphological intermediacy and complete sterility of *C.* × *intermedia*, taken together with the lack of other possible parents, point to the fact that it must be regarded as being of hybrid origin between *C. alpina* and *C. lutetiana*. Despite this, *C. alpina* is now absent from many areas where *C.* × *intermedia* is common, such as Ireland, the Hebrides and much of mainland Scotland. Moreover, *C. lutetiana* also is absent from some of these areas, particularly northern Scotland and Orkney.

These apparent discrepancies may be explained in two ways. Either *C.×intermedia* has achieved its present wide distribution in the British Isles by means of its remarkably vigorous vegetative reproduction, or its distribution reflects the one-time area of *C. alpina* where it came into contact with *C. lutetiana*, or both factors may be important. Correlated with these considerations is the question as to whether *C.×intermedia* in Britain and Ireland originated from a single hybridisation, or whether it is produced with fair frequency whenever its parents come into contact. The latter question may be considered first. Arguing for the fairly frequent production of the hybrid is the sort of situation on which I made observations in Glencoyne Wood, Ullswater, Westmorland, on the 3 July 1961. Here all three species grew in a moist shaded area of woodland dominated by bracken and species of *Carex* and *Juncus*. *Circaea alpina* occurred in two small patches scarcely 3 m across, whereas *C. lutetiana* was more widespread both on this flat and in the neighbouring woods. The individuals of *C.×intermedia* formed a band approximately 2 m across, ringing the small patches of *C. alpina*, and they were in turn surrounded by the abundant *C. lutetiana*. It is extremely probable that these hybrids were produced *in situ*. Furthermore, *C.×intermedia*, as has been remarked by many writers of floras, is very variable in habit, pubescence, flower size, leaf margin and other characteristics. This sort of variability would be most unexpected if all the individuals concerned had been derived by vegetative reproduction following a single hybridisation. Finally, the range of *C.×intermedia*, from Britain to the Caucasus, argues against such an hypothesis. On the other hand, it would be a serious mistake to underestimate the capacity of *C.×intermedia* for vegetative spread, particularly when it is remembered that these plants are often serious garden weeds where they occur. Vegetative reproduction seems to have been important in the spread of certain other well-known plants that occur in gardens, such as *Aegopodium podagraria*, species of *Calystegia* and *Tussilago farfara*; *Circaea × intermedia* has obviously attained part of its present range in the same way. A particularly suggestive example of this, pointed out to me by Professor Webb, is its local occurrence in Co. Wicklow, Ireland, well south of its main area of distribution; here it is exclusively a garden weed and very probably introduced. Also in Merioneth, for example, it is mainly restricted to disturbed areas and man-made habitats, particularly in gardens and along roadsides, and is probably extending its range in connection with cultivation (Benoit & Richards 1961).

Thus, in summary, it does not appear likely that all of the present distribution of *C.×intermedia* in Britain and Ireland can be explained by its admittedly vigorous vegetative reproduction. A more probable hypothesis is that *C. alpina* was more widespread nearer the last glacial maximum. As it contracted from this wider range to the few stations it occupies at the present time, it was often in contact with *C. lutetiana*. Spreading as it must have done with the increase in wooded areas, *C. lutetiana* may eventually have come to occupy an area even more extensive than at present during the warm, dry period approximately 5,000 years ago (Matthews 1955). At the height of this warm, dry period, *C. alpina* may have been even more restricted in range than it is today, judging from the western, oceanic nature of its present range in Britain. As their ranges shifted, hybridisation between *C. alpina* and *C. lutetiana* probably occurred fairly frequently, producing numerous biotypes of *C.×intermedia* with intermediate morphology and ecological requirements. From these centres, the sterile *C.×intermedia* spread by means of its efficient vegetative reproduction and, in some instances, as a ruderal aided by man. It is important to note that the capacity for vegetative spread was already present in one of the parents, *C. lutetiana*, as gardeners will attest, and that it was this pre-determined capacity that allowed the sterile *C.×intermedia* to become established and spread; it is evidently even more vigorous in its spread than *C. lutetiana*. Progressive changes in climate finally led to the apparent extinction of *C. alpina* in Ireland and over much of Scotland and allowed its survival only in those few, particularly favourable localities where it persists to the present day. Its apparent absence from Ireland is particularly interesting in view of its present western oceanic distribution in Britain, which suggests that conditions in at least some portions of Ireland may be suitable for it at the present time. It is possible that the shift to a cooler, more oceanic climate in the past 5,000 years has caused the restriction of *C. lutetiana* in the north and perhaps even allowed *C. alpina* to spread slightly in the Lake District and on Arran. Meanwhile, *C.×intermedia*, apparently well suited to the climatic conditions prevalent in northern Ireland, Scotland, northwest England, and portions of Wales, has flourished in those areas and become locally the commonest or even the only representative of the genus present in some of them, despite its complete dependence on vegetative propagation.

Thus *Circaea×intermedia* presents a truly remarkable example of a sterile hybrid better suited to a particular set of conditions than either parent, and consequently replacing them in certain areas. Two similar examples from the British flora that may be cited are *Nuphar* × *intermedia*, the apparently highly sterile diploid hybrid between *N. lutea* and *N. pumila* (Heslop-Harrison 1953) and *Rorippa* × *sterilis* (*R. nasturtium-aquaticum* × *R. microphylla*), a sterile triploid which occurs locally in the absence of both parents in much the same areas as *Circaea* × *intermedia*. Such patterns of variability are characterized by the ability of hybridisation to produce a large number of relatively uniform genotypes suited to a particular environment correlated with an apparent loss in evolutionary flexibility. Similar patterns occur frequently in the angiosperms but they are usually a product of the spread of fertile allopolyploids rather than of sterile, vegetatively propagated hybrids.

Acknowledgments

The research leading to this paper was completed during the tenure of a United States National Science Foundation post-doctoral fellowship spent in London in 1960–61. I am grateful to Mr. J. E. Dandy, Keeper, Department of Botany, British Museum (Natural History), and to Sir George Taylor, Director, Royal Botanic Gardens, Kew, for the facilities generously extended to me during my stay. I would also like to acknowledge specially the many helpful comments of Mr. Peter M. Benoit, Barmouth, whose perceptive observations on the flora of Merioneth are well known. Thanks are also due Mr. D. E. Allen, London; Dr. H. G. Baker, University of California, Berkeley; Mr. A. O. Chater, Aberystwyth; Mr. W. M. Condry, Machynlleth; Dr. F. H. Perring, Cambridge; Mr. Evan Roberts, Capel Curig; Mr. R. H. Roberts, Bangor; Mr. N. Y. Sandwith, Kew; and Prof. D. A. Webb, Dublin, who aided this study in various ways; to those in charge of the herbaria listed above, for permission to study the material entrusted to their care; and to Dr. C. R. Metcalfe and Dr. K. Jones of the Jodrell Laboratory, Kew, for affording me the facilities to make the cytological studies reported herein. Finally, I would like to thank Miss Gretel W. Dalby, who prepared the illustrations of the plants, and to acknowledge the kind permission of the Distribution Maps Scheme, Botanical Society of the British Isles, for the maps of the three species of *Circaea* to be reprinted here.

References

Baker, H. G. (1951). Hybridization and natural gene-flow between higher plants. *Biol. Rev.* **26**, 302–337.

Benoit, P. M. & Richards, M. (1961). *Circaea*, in A contribution to a flora of Merioneth. *Nature in Wales*, **7**, 95.

Butcher, R. W. (1961). *A New Illustrated British Flora, Part I.* London.

Clapham, A. R. (1952). Onagraceae, in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, Ed. 1, 596–614. Cambridge. Ed. 2 (1962).

Clapham, A. R., Tutin, T. G. & Warburg E. F. (1960). *Flora of the British Isles.* Illustrations, part II. Drawings by S. J. Roles. Cambridge.

Fitch, W. H. & Smith, W. G. (1924). *Illustrations of the British Flora.* Ashford.

HESLOP-HARRISON, Y. 1953). *Nuphar intermedia* Ledeb., a presumed relict hybrid, in Britain. *Watsonia* 3, 7–25.

HULTÉN, E. (1950). *Atlas of the Distribution of Vascular Plants in NW. Europe.* Stockholm.

LÖVE, A. & D. (1961). Chromosome numbers of central and northwest European plant species. *Opera Botanica, Lund* 5, 1–581.

MATTHEWS, J. R. (1955). *Origin and Distribution of the British Flora.* London.

ROSS-CRAIG, S. (1958). Drawings of British Plants, Part 11. Droseraceae – Ficoideae. London.

UDDLING, Å. (1929). Die Chromosomenzahlen von drei *Circaea*-Arten. *Hereditas* 12, 294–296.