Chromosome numbers in *Hieracium* L. section *Alpina* (Fries) F. N. Williams

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ABSTRACT

Cytological study of 34 of the 35 named British taxa of *Hieracium* section *Alpina*, plus two un-named taxa, showed that 24 are tetraploids (2n = 36), six are triploids (2n = 27), one is a pentaploid (2n = 45), one (*H. macrocarpum*) is a tetraploid or hypertetraploid (2n = 36 or 37), and four occur as both triploids and tetraploids. Of the latter four, *H. tenuifrons* is represented by a western tetraploid, a central triploid and an eastern tetraploid race; *H. insigne* f. *celsum* is represented by a triploid western and a tetraploid eastern race (but only one plant of the former was counted); and material of the other two taxa was insufficient to draw any firm conclusions. The pentaploid taxon (un-named, from An Teallach, W. Ross, v.c. 105) appears to be the first count for any taxon of *Hieracium* sensu stricto above the level of tetraploid.

KEYWORDS: apomixis, hawkweeds, polyploidy, Britain.

INTRODUCTION

TAXONOMY

The genus *Hieracium* L. (Asteraceae) is well known as one in which apomixis is widespread, giving rise to a very large number of variants that have been described as species and to a lesser extent at other ranks. In the older literature the genus was divided into subgenus *Hieracium* and subgenus *Pilosella* (Hill) Gray, but most modern works now treat the latter as the separate genus *Pilosella* Hill. This separation is based on a range of morphological, biochemical, cytological and genetical characteristics. Nevertheless, in most of the literature the generic name *Hieracium* remains ambiguous; it might or might not include *Pilosella*, or indeed concern *Pilosella* alone. An idea of the number of taxa in these two genera is provided by the fact that under *Hieracium* and *Pilosella* there are 11,827 entries in *Index Kewensis* (CD-ROM version, 1993).

British hieraciologists have traditionally divided *Hieracium* sensu stricto into up to 16 sections. The latest work (Kent 1992) recognized twelve, which follows the views of Sell & West (1968). Section *Alpina* (Fries) F. N. Williams is relatively easily recognized by its short scapose stems bearing usually only a single terminal capitulum. The species in Britain mostly occur in rock crevices and on rock ledges and other rather bare rocky places at over 600 m altitude. Sell & West (1976), in their account of *Hieracium* (incl. *Pilosella*) for *Flora Europaea*, did not divide the genus into sections, but instead recognized 260 main taxa at the level of species or species groups. Section *Alpina* in the sense of British authors corresponds with Sell & West's '*H. alpinum* group' and '*H. nigrescens* group' (nos. 158 and 159).

Kent (1992) listed 19 microspecies within section *Alpina*, to which must be added the eleven new species and five extra formae described by Sell *et al.* (1995). There still remain about half a dozen other variants in Scotland that merit names (D. J. Tennant, pers. comm., 1994). The 35 named taxa are distributed as follows: 28 are endemic to Scotland; *H. subgracilentipes* is endemic to the English Lake District; five species (*H. alpinum*, *H. calenduliflorum*, *H. eximium*, *H. globosiflorum* and *H. tenuifrons*) occur in Scotland and European mountains, the first-named extending to Greenland; and *H. holosericeum* occurs in Scotland, the English Lake District, Snowdonia and the European mountains.

TABLE 1. SUMMARY OF CHROMOSOME COUNTS OF SPECIES OF *HIERACIUM* AND *PILOSELLA*

Ploidy Level	No. of Taxa
Diploid (2n = 2x = 18)	83
Triploid (2n = 3x = 27)	110
Tetraploid (2n = 4x = 36)	66
Pentaploid (2n = 5x = 45)	21
Hexaploid (2n = 6x = 54)	6
Heptaploid (2n = 7x = 63)	4
Octoploid (2n = 8x = 72)	1
Nonaploid (2n = 9x = 81)	1
Decaploid (2n = 10x = 90)	2

See text for sources. Aneuploid counts have been rounded off to the nearest euploid level.

CHROMOSOME NUMBERS

We have carried out a literature survey of the chromosome numbers of the genera *Hieracium* and *Pilosella* reported in the standard abstracting references, covering the years up to 1989, to which we have added relevant data in *The cytological catalogue of the British and Irish flora* (Bailey & Gornall ined.). The results are summarized in Table 1. The total number of taxa cannot be obtained by summing the totals, because some occur at more than one ploidy level. Species of both *Hieracium* and *Pilosella* contribute to the diploid, triploid and tetraploid totals, but we have been unable to separate the totals for these two genera. However, in the pentaploid and higher levels all reports but one refer to the genus *Pilosella*. The single exception is actually somewhat spurious, since it refers to the presence of 54 chromosomes in certain pollen mother cells of a plant of *H. umbellatum* with 2n = 27 (Rosenberg 1927b). It is thus the case to date that all known chromosome numbers of *Hieracium* sensu stricto are diploid, triploid or tetraploid (with some aneuploids). As far as we are aware, the diploids represent sexual and the triploids and tetraploids apomictic plants (Rosenberg 1927a).

There have been relatively few chromosome studies of British or Irish *Hieracium* sensu stricto. Mills & Stace (1974) reported counts for 21 and Morton (1974) for twelve taxa, only one being common to the two lists. We know of British counts for only two other species (Bailey & Gornall ined.). These 34 taxa cover eleven of the twelve sections of the genus. Eleven of the species are tetraploid and 21 triploid; the other two taxa (*H. umbellatum* L. subsp. *umbellatum* and subsp. *bichlorophyllum* (Druce & Zahn) Sell & C. West) exist as both diploid and triploid cytotypes. Hence in the British Isles only the two subspecies of *H. umbellatum* are known to be sexual.

In section *Alpina* there have hitherto been only two British counts. Mills & Stace (1974) found *H. hanburyi* to be tetraploid (2n = 36) and Morton (1974) reported the same for *H. calenduliflorum*. Elsewhere there are counts for *H. alpinum* (2n = 27 for material from Greenland, Iceland, Fennoscandia, Komi ASSR, Siberian Arctic, Poland, Slovakia and Switzerland) and for the non-British *H. nigrescens* Willd. (2n = 27 from Komi ASSR).

As part of a molecular genetic investigation of section *Alpina*, we have made a detailed cytological investigation of our material. Here we report the chromosome numbers of 152 plants (34 of the 35 named taxa, plus two un-named ones and four 'intermediates') and discuss their significance.

MATERIALS AND METHODS

Mr D. J. Tennant has made a detailed study of *Hieracium* section *Alpina* over the past 25 years. Uniquely, he has seen all the taxa in their native situation, and has grown them all in his Yorkshire garden. Most of his collection (c. 150 pots), including all but two of the 35 taxa, was transferred to Leicester in 1993 and 1994 for safe-keeping, propagation and study. This has been supplemented by some of our own collections, plants having been grown from wild-collected seed, and by F_1 plants grown from seed produced by Mr Tennant's plants. The collection now contains all the 35 named taxa except *H. optimum* Sell & C. West, as well as six other problematical un-named taxa (Table 2). All determinations have been made by Mr D. J. Tennant. At present the vouchers are the living plants, which are too valuable to press. However, F_1 plants are being grown as vouchers.

Plants are kept in an unheated greenhouse, being grown in 12·5 cm pots containing equal parts of potting compost and terrace gravel (derived from granite) collected in the Cairngorms, Scotland. Seed is germinated on 1% agar after two weeks in tap-water at 4°C. Plants are transferred to pots in compost as soon as they are large enough to move from the agar, and potted on into the compost-gravel mixture when they are fully established.

Cytological studies were made on the pot-grown plants. Actively growing roots were placed into a pretreatment solution of 0.002M 8-hydroxyquinoline and kept at 4°C for 24 hours. Subsequently the pre-treatment solution was replaced by fixative (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). Roots were hydrolysed for 10 minutes at room temperature in 5M HCl, which was then removed and replaced by 70% IMS (industrial methylated spirit).

Dissection of the root was carried out in a drop of 40% acetic acid on a microscope slide. The removed root tip was then transferred into a drop of 2% certified aceto-orcein. Epidermal tissue was removed and discarded thus revealing the meristematic regions, which were then macerated and finally squashed.

The resultant slides were viewed under a high power microscope for suitable, countable metaphases. Chromosome counts were made from at least three root tips for each accession.

RESULTS

The chromosome counts made for 152 plants are listed in Table 2. These cover 34 named taxa, plus:

1. Plants apparently intermediate between *H. eximium* and *H. calenduliflorum*, now thought by Mr Tennant to be a variant of *H. leptodon* (EXI/CLD-1);
2. Plants apparently intermediate between *H. eximium* and *H. memorabile* (EXI/MEM-51, 52 & 53);
3. Plants apparently intermediate between *H. hanburyi* and *H. tenuifrons* (HAN/TNF-1 & 2);
4. Plants apparently intermediate between *H. tenuifrons* and *H. memorabile* (TNF/MEM-51);
5. An un-named, probably new, taxon from Ben Dearg, E. Ross, v.c. 106 (XYZ-2); and
6. An un-named, probably new, taxon from An Teallach, W. Ross, v.c. 105 (XYZ-1).

The first five of these are tetraploids (2n = 36), the last a pentaploid (2n = 45).

Of the 34 named taxa, six are triploids (2n = 27), 24 are tetraploids (2n = 36), and the other four gave both triploid and tetraploid counts. Two plants of *H. macrocarpum* (MAC-24 & 25) were found to be hypertetraploids (2n = 4x + 1 = 37); otherwise all the plants were euploids.

DISCUSSION

The marked prevalence of tetraploid over triploid counts for British species of section *Alpina* (28:10) is in strong contrast to the previously published figures for *Hieracium* (including some *Pilosella* species) overall world-wide (66:110, see Table 1) or for *Hieracium* sensu stricto in Britain alone (13:23). This is particularly surprising since all the previous counts (c. 12) for non-British plants of section *Alpina* (involving two species, *H. alpinum* and *H. nigrescens*) were triploid. Our counts of British *H. alpinum* are also triploid (Fig. 1a).

The existence of a pentaploid (XYZ-1 from An Teallach, W. Ross) is unique (Fig. 1d); we have been able to discover no previous counts for plants of *Hieracium* sensu stricto above the level of tetraploid.

There are many reports of aneuploid counts in the literature. In Table 1 these figures were subsumed into the nearest euploid level. Without detailed population and karyotypic studies it is difficult to be sure of the significance of aneuploids. They could refer to odd individual plants, odd cells of euploid individuals, or simply to errors. On the other hand they might represent whole 'populations' of plants, or whole taxa. Examples of all of these situations are well known in apomicts. For example, most taxa of the *Limonium binervosum* (G. E. Sm.) Salmon aggregate are

TABLE 2. CHROMOSOME NUMBERS IN *HIERACIUM* SECTION *ALPINA*

H. alpinum L.
ALP-1. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 27.
ALP-22. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 27.
ALP-23. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 27.

H. backhousei F. Hanb.
BAC-1. V.c. 90, Angus: Glen South Esk, above Glen Clova, NO/2.7. 2n = 36.
BAC-4. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.

H. calenduliflorum J. Backh.
CLD-1. V.c. 97, Westerness: Ben na' Socaich, Glen Spean, NN/2.7. 2n = 36.
CLD-2. V.c. 92, S. Aberdeen: Lochnagar, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-8. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-13. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-30. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-48. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-65. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-86. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 36.
CLD-150. V.c. 97, Westerness: Ben na' Socaich, Glen Spean, NN/2.7. 2n = 36.
CLD-151. V.c. 90, Angus: Craig of Gowal, head of Glen South Esk, above Glen Clova, NO/2.8. 2n = 36.
CLD-152. V.c. 97, Westerness: Ben na' Socaich, Glen Spean, NN/2.7. 2n = 36.
CLD-153. V.c. 90, Angus: Bachnagairn, head of Glen South Esk, above Glen Clova, NO/2.7. 2n = 36.
CLD-154. V.c. 90, Angus: Loch Brandy, Glen Clova, NO/3.7. 2n = 36.
CLD-155. V.c. 97, Westerness: Ben na' Socaich, Glen Spean, NN/2.7. 2n = 36.
CLD-158. V.c. 97, Westerness: Aonach Mor, Ben Nevis range, above Glen Spean, NN/1.7. 2n = 36.

H. calvum Sell & D. Tenn.
CLV-1. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-2. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-3. V.c. 92, S. Aberdeen: Falls, Coire an Lochain Uaine, Derry Cairngorm, Glen Derry, NO/0.9. 2n = 36.
CLV-4. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-5. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-6. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-7. V.c. 96, Easterness: East side of Cairn Gorm, NJ/0.0. 2n = 36.
CLV-8. V.c. 92, S. Aberdeen: Glen Derry, NO/0.9. 2n = 36.
CLV-9. V.c. 96, Easterness: East side of Cairn Gorm, NJ/0.0. 2n = 36.
CLV-10. V.c. 96, Easterness: East side of Cairn Gorm, NJ/0.0. 2n = 36.
CLV-11. V.c. 96, Easterness: East side of Cairn Gorm, NJ/0.0. 2n = 36.
CLV-12. V.c. 96, Easterness: East side of Cairn Gorm, NJ/0.0. 2n = 36.

H. completum Sell & C. West
COM-1. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
COM-25. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
COM-35. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
COM-36. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
COM-37. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.

H. eximium J. Backh.
EXI-24. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
EXI-54. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 36.
EXI-55. V.c. 90, Angus: Glen Doll, Glen Clova, NO/2.7. 2n = 36. An F_1 plant.
EXI-56. V.c. 90, Angus: Glen Doll, Glen Clova, NO/2.7. 2n = 36. An F_1 plant.

H. eximium f. *tenellum* (J. Backh.) Sell & C. West
TNE-1. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 36. Three F_1 plants.
TNE-2. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 36.

H. eximium/*H. calenduliflorum* intermediate
EXI/CLD-1. V.c. 98, Main Argyll: Allt nan Giubhas, Meall a' Bhuiridh, Glencoe, NN/2.5. 2n = 36.

TABLE 2. *continued*

H. eximium/*H. memorabile* intermediate
EXI/MEM-51. V.c. 92, S. Aberdeen: Coire an Lochain Uaine, Derry Cairngorm, Glen Derry, NO/0.9. 2n = 36.
EXI/MEM-52. V.c. 92, S. Aberdeen: Coire an Lochain Uaine, Derry Cairngorm, Glen Derry, NO/0.9. 2n = 36.
EXI/MEM-53. V.c. 92, S. Aberdeen: Coire an Lochain Uaine, Derry Cairngorm, Glen Derry, NO/0.9. 2n = 36.

H. globosiflorum Pugsley
GLO-1. V.c. 92, S. Aberdeen: Coire an Lochain Uaine, Cairn Toul, Cairngorms, NN/9.9. 2n = 27.
GLO-19. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 27.

H. graniticola W. R. Linton
GRA-1. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 27. Also an F_1 plant.
GRA-3. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 27.
GRA-4. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 27.
GRA-5. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 27.

H. grovesii Pugsley
GRO-1. V.c. 92, S. Aberdeen: Beinn a' Bhuird, Cairngorms, NO/0.9. 2n = 36. Also an F_1 plant.

H. hanburyi Pugsley
HAN-1. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 36.
HAN-23. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.
HAN-26. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.

H. hanburyi f. *atraticeps* (Pugsley) Sell & D. Tenn.
ATR-1. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36. Also three F_1 plants.
ATR-2. V.c. 90, Angus: Above lowest falls, Glen Fee, Glen Clova, NO/2.7. 2n = 36.
ATR-3. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.
ATR-4. V.c. 90, Angus: Glen Fee falls, Glen Clova, NO/2.7. 2n = 36.
ATR-5. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.
ATR-6. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.
ATR-7. V.c. 90, Angus: Head of Glen Fee, Glen Clova, NO/2.7. 2n = 36.
ATR-8. V.c. 90, Angus: Upper falls, Glen Fee, Glen Clova, NO/2.7. 2n = 36.

H. hanburyi f. *pusillum* Sell & D. Tenn.
PUS-2. V.c. 90, Angus: Canness Glen, Glen Isla, NO/2.7. 2n = 36.
PUS-24. V.c. 90, Angus: Canness Glen, Glen Isla, NO/2.7. 2n = 36.
PUS-25. V.c. 90, Angus: Boustie Ley, Glen Clova, NO/3.7. 2n = 36.

H. hanburyi/*H. tenuifrons* intermediate
HAN/TNF-1. V.c. 96, Easterness: Glen Einich, Cairngorms, NN/9.9. 2n = 36.
HAN/TNF-2. V.c. 96, Easterness: Glen Einich, Cairngorms, NN/9.9. 2n = 36.

H. holosericeum J. Backh.
HOL-13. V.c. 92, S. Aberdeen: Allt an Dubh Loch, above Glen Muick, Ballater, NO/2.8. 2n = 27.
HOL-33. V.c. 97, Westerness: Aonach Mor, Ben Nevis range, above Glen Spean, NN/1.7. 2n = 27.
HOL-36. V.c. 96, Easterness: Bynack More, Strath Nethy, Cairngorms, NJ/0.0. 2n = 36.
HOL-47. V.c. 49, Caernarvonshire: Summit of Craig yr Ysfa, south-east of Carnedd Llywelyn, SH/3.6. 2n = 27.

H. insigne J. Backh.
INS-1. V.c. 92, S. Aberdeen: Coire Kander, head of Glen Callater, NO/1.8. 2n = 36.
INS-3. V.c. 92, S. Aberdeen: Coire Kander, head of Glen Callater, NO/1.8. 2n = 36.
INS-4. V.c. 92, S. Aberdeen: Coire Kander, head of Glen Callater, NO/1.8. 2n = 36.

H. insigne f. *celsum* Sell & D. Tenn.
CEL-1. V.c. 96, Easterness: Creag an Lethchoin, Lairig Ghru, NH/9.0. 2n = 36.
CEL-2. V.c. 97, Westerness: Ben na' Socaich, Glen Spean, NN/2.7. 2n = 27.
CEL-3. V.c. 92, S. Aberdeen: Coire an Lochain Uaine, Cairn Toul, Cairngorms, NN/9.9. 2n = 36.
CEL-4. V.c. 96, Easterness: Creag an Lethchoin, Lairig Ghru, NH/9.0. 2n = 36.
CEL-5. V.c. 96, Easterness: Coire Garbhlach, Glen Feshie, Cairngorms, NN/8.9. 2n = 36.

TABLE 2. *continued*

H. kennethii Sell & D. Tenn.
KEN-1. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.
KEN-3. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.
KEN-4. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.

H. larigense (Pugsley) Sell & C. West
LAR-1. V.c. 96, Easterness: Creag an Lethchoin, Lairig Ghru, NH/9.0. 2n = 36. An F_1 plant.
LAR-2. V.c. 96, Easterness: Creag an Lethchoin, Lairig Ghru, NH/9.0. 2n = 27.

H. leptodon Sell & D. Tenn.
TND-1. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 36. An F_1 plant.
TND-2. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 36. Also an F_1 plant.
TND-3. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 36.
TND-5. V.c. 88, Mid Perth: Ben More, Crianlarich, NN/4.2. 2n = 36.

H. macrocarpum Pugsley
MAC-1. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 36. Six F_1 plants.
MAC-19. V.c. 106, E. Ross: Carn Liath, Strath Carron, NH/1.5. 2n = 36.
MAC-21. V.c. 92, S. Aberdeen: Coire an t-Saighdeir, Cairn Toul, Cairngorms, NN/9.9. 2n = 36.
MAC-22. V.c. 96, Easterness: Coire Chuirn, south of Dalwhinnie, NN/6.7. 2n = 36.
MAC-23. V.c. 96, Easterness: Coire Chuirn, south of Dalwhinnie, NN/6.7. 2n = 36.
MAC-24. V.c. 96, Easterness: Coire Chuirn, south of Dalwhinnie, NN/6.7. 2n = 37.
MAC-25. V.c. 96, Easterness: Coire Chuirn, south of Dalwhinnie, NN/6.7. 2n = 37.
MAC-27. V.c. 96, Easterness: Outflow shingle, N. end of Loch Einich, NN/9.9. 2n = 36.

H. marginatum Pugsley
MAR-2. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 36. Also an F_1 plant.
MAR-4. V.c. 105, W. Ross: Meall Doire Faid, Braemore, NH/2.7. 2n = 36.
MAR-5. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 36.

H. marginatum f. *chaetocephalum* Sell & C. West
CHA-1. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 36. Also three F_1 plants.

H. memorabile Sell & C. West
MEM-6. V.c. 97, Westerness: Aonach Mor, Ben Nevis range, above Glen Spean, NN/1.7. 2n = 36. An F_1 plant.
MEM-10. V.c. 92, S. Aberdeen: Head of Glen Callater, NJ/1.7. 2n = 36.
MEM-11. V.c. 96, Easterness: Coire Garbhlach, Glen Feshie, Cairngorms, NN/8.9. 2n = 36.
MEM-13. V.c. 92, S. Aberdeen: Head of Glen Callater, NO/1.8. 2n = 36.
MEM-14. V.c. 96, Easterness: Coire Garbhlach, Glen Feshie, Cairngorms, NN/8.9. 2n = 36.
MEM-15. V.c. 96, Easterness: Creag an Lethchoin, Lairig Ghru, NH/9.0. 2n = 36.

H. milesii Sell & C. West
MIL-1. V.c. 90, Angus: Canness Glen, Glen Isla, NO/2.7. 2n = 36.
MIL-2. V.c. 90, Angus: Caenlochan, NJ/1.7. 2n = 36.
MIL-3. V.c. 92, S. Aberdeen: Loch Kander, head of Glen Callater, NO/1.8. 2n = 36.
MIL-5. V.c. 90, Angus: Caenlochan, NJ/1.7. 2n = 36.
MIL-6. V.c. 90, Angus: Caenlochan, NJ/1.7. 2n = 36.

H. mundum Sell & C. West
MUN-1. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 36.

H. notabile Sell & C. West
NOT-1. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 36. Three F_1 plants.
NOT-3. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 36.

H. pensum Sell & C. West
PEN-1. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 36. Also two F_1 plants.

TABLE 2. *continued*

H. perscitum Sell & C. West
PER-1. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36. Also an F_1 plant.
PER-2. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.
PER-5. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.
PER-7. V.c. 105, W. Ross: An Teallach, Dundonnell, NH/0.8. 2n = 36.

H. probum Sell & C. West
PRO-2. V.c. 97, Westerness: Aonach Mor, Ben Nevis range, above Glen Spean, NN/1.7. 2n = 36.
PRO-24. V.c. 87, W. Perth: Stob Binnein, Crianlarich, NN/4.2. 2n = 36.
PRO-25. V.c. 87, W. Perth: Stob Binnein, Crianlarich, NN/4.2. 2n = 36.

H. pseudocurvatum (Zahn) Pugsley
PCU-1. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 27.
PCU-2. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 27.
PCU-3. V.c. 92, S. Aberdeen: Creag an Dail Bheag, Cairngorms, NO/1.9. 2n = 27.

H. pseudopetiolatum (Zahn) Roffey
PPE-1. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 27.
PPE-17. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.
PPE-18. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.

H. subglobosum Sell & C. West
SGL-1. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 27. Also two F_1 plants.
SGL-2. V.c. 106, E. Ross: Coire Ghranda, Ben Dearg, NH/2.8. 2n = 27.

H. subgracilentipes (Zahn) Roffey
SGR-1. V.c. 69, Westmorland: Dollywaggon, Helvellyn, NY/3.1. 2n = 36.
SGR-8. V.c. 69, Westmorland: Rampsgill Head, above Haweswater, NY/4.1. 2n = 36.
SGR-11. V.c. 69, Westmorland: Dollywaggon, Helvellyn, NY/3.1. 2n = 36.

H. tenuifrons Sell & C. West
TNF-1. V.c. 98, Main Argyll: Allt nan Giubhas, Meall a' Bhuiridh, Glencoe, NN/2.5. 2n = 36.
TNF-2. V.c. 88, Mid Perth: Creag Roro, Ben Lawers, Glen Lyon, NN/6.4. 2n = 27. Also an F_1 plant.
TNF-4. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
TNF-44. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.
TNF-45. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.
TNF-46. V.c. 88, Mid Perth: Creag Roro, Ben Lawers, Glen Lyon, NN/6.4. 2n = 27.
TNF-47. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.
TNF-48. V.c. 98, Main Argyll: Allt nan Giubhas, Meall a' Bhuiridh, Glencoe, NN/2.5. 2n = 36.
TNF-49. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
TNF-50. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
TNF-52. V.c. 88, Mid Perth: Ben Heasgarnich, Glen Lyon, NN/4.3. 2n = 36. Two F_1 plants.
TNF-53. V.c. 92, S. Aberdeen: Coire Etchachan, NO/0.9. 2n = 36.
TNF-54. V.c. 97, Westerness: Coire Ardair, Craig Meagaidh, Loch Laggan, NN/4.8. 2n = 27.

H. tenuifrons/H. memorabile intermediate
TNF/MEM-51. V.c. 96, Easterness: Coire Garbhlach, Glen Feshie, Cairngorms, NN/8.9. 2n = 36.

Un-named new taxa
XYZ-1. V.c. 105, W. Ross: An Teallach, Dundonnell, NN/0.8. 2n = 45.
XYZ-2. V.c. 106, E. Ross: Summit coire, Ben Dearg, NH/2.8. 2n = 36.

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hypotetraploids (2n = 4x − 1 = 35) (Ingrouille & Stace 1986). One previous count of *H. alpinum* from the Siberian Arctic (Sokolovskaya & Strelkova 1960) is a hypotriploid (2n = 3x − 1 = 26), but must be viewed in the light of the above comments. In the present study two plants of *H. macrocarpum* (MAC-24 & 25) from Coire Chuirn, Easterness, were found to be hypertetraploids (2n = 4x + 1 = 37) (Fig. 1c). Two other plants (MAC-22 & 23) from the same locality were tetraploids (2n = 36).

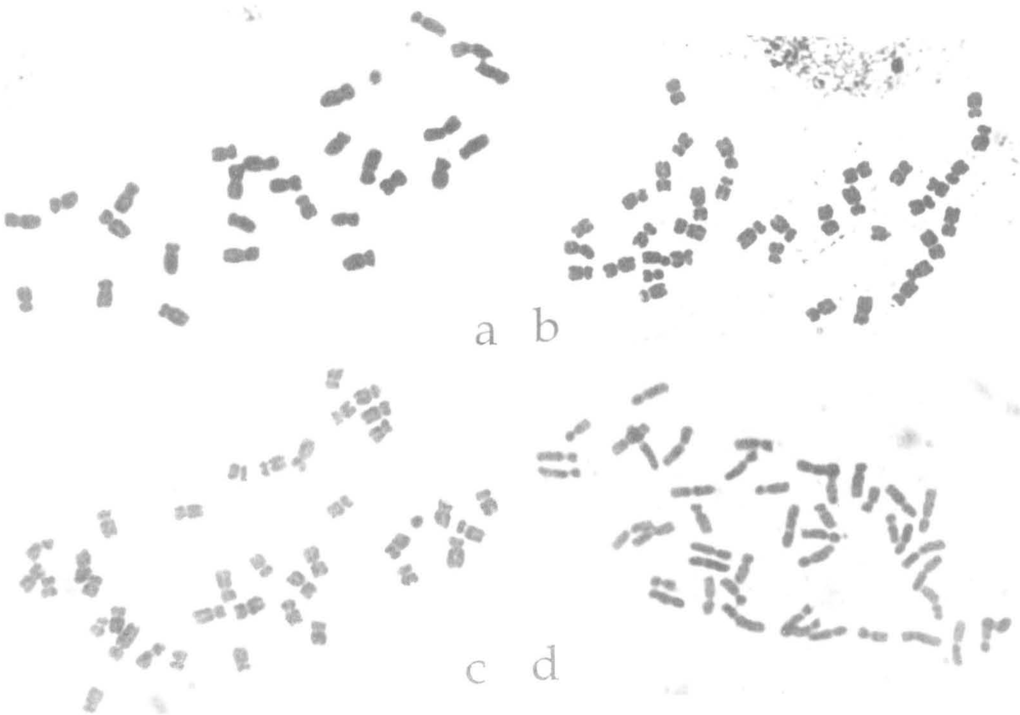

FIGURE 1. Root-tip squashes of (a) *Hieracium alpinum* (ALP-22) from Glen Derry, S. Aberdeen, 2n = 3x = 27; (b) *H. calenduliflorum* (CLD-152) from Ben na' Socaich, Westerness, 2n = 4x = 36; (c) *H. macrocarpum* (MAC-24) from Coire Chuirn, Easterness, 2n = 4x + 1 = 37; and (d) Un-named new taxon (XYZ-1) from An Teallach, W. Ross, 2n = 5x = 45. All × 1250.

The caveats concerning the interpretation of aneuploid counts mentioned above must be repeated when considering taxa in which two ploidy levels have been found. However, in such a highly critical group as *Hieracium* sect. *Alpina*, there are two taxonomic problems as well. Firstly, it is possible that in fact the two cytotypes should be recognized as different taxa, not one. Secondly, pots might have become mislabelled due to clerical or horticultural errors or due to misidentification. The last is a real possibility even when identification has been made by the acknowledged experts in the group, since several of the microspecies are very difficult to distinguish if one or two characters (e.g. style colour) are missing. In section *Alpina* this problem is exacerbated because frequently several (sometimes more than ten) species grow in one locality, and in any one locality only a small proportion of the plants flower in any given year.

Apart from the case of *H. macrocarpum* mentioned above, four taxa were found with two chromosome numbers:

a. *H. tenuifrons*. D. J. Tennant has for long recognized three non-overlapping regional races within this species: a western race found in Westerness (v.c. 97) , Main Argyll (v.c. 98) and just into Mid Perth (v.c. 88); a central race found in W., Mid and E. Perth (v.cc. 87–89) and just into Westerness; and an eastern race found in the Cairngorms (S. Aberdeen and Easterness: v.cc. 92, 96). The chromosome numbers of these three races are 2n = 36 (three plants), 27 (six plants) and 36 (four plants) respectively. In terms of gross morphology, the western race (which includes the type) is far more distinct from the other two than the latter two are from each other (D. J. Tennant, pers. comm., 1994). Although the cytological data do not fully support the morphological data, the two together do provide evidence that the three races of *H. tenuifrons* are distinct entities. Whether they are worth recognizing taxonomically, and if so at what ranks, are moot points.

Chromosome numbers throw no light on the identity of the *H. hanburyi*/*H. tenuifrons*

'intermediate' (HAN/TNF-1 & 2), since it, *H. hanburyi* and the eastern race of *H. tenuifrons* are all tetraploids. The same is true of the *H. tenuifrons*/*H. memorabile* 'intermediate' (TNF/MEM-51).
b. *H. insigne* f. *celsum*. The single triploid (CEL-2) comes from the western area (Glen Spean, Westerness, v.c. 97), while the four tetraploids are from the eastern area (S. Aberdeen, v.c. 92 and Easterness, v.c. 96). These five plants come from four localities which represent much of the total range of this rare taxon. The different chromosome number of the western plant clearly requires further investigation.
c. *H. larigense*. Both plants are from the area of the type locality (Lairig Ghru, Easterness, v.c. 96) and the existence of two ploidy levels in *H. larigense* from this area requires confirmation. A misidentification is one possible explanation, which will be investigated the next time the plants flower at Leicester and by molecular studies.
d. *H. holosericeum*. Although this is the most widespread British species, and is often common in Scottish localities, it is one of the most difficult to keep healthy in cultivation. The single tetraploid and two of the triploid plants come from three rather widely separated Scottish localities. The single Welsh count was also triploid. Clarification of the cytological pattern in this species must await more counts from the same and other localities in Scotland as well as from the Lake District, but clearly the Easterness plant might be misidentified. This will be checked by molecular studies.

Comments on some of the other taxa are also desirable.

H. calenduliflorum is a somewhat variable species. D. J. Tennant recognises two races – a western one from Westerness (v.c. 97) and Main Argyll (v.c. 98), which shows some resemblances to *H. notabile*; and an eastern one from Angus (v.c. 90) and S. Aberdeen (v.c. 92). In addition to this, CLD-151 is an unusually highly pubescent plant, and CLD-158 an unusually small, narrow-leaved plant. All these plants are tetraploids (Fig. 1b), as was the previously counted plant from Lochnagar, S. Aberdeen (Morton 1974). Preliminary results from molecular analyses of the two races have, however, revealed some differences.

The *H. eximium*/*H. calenduliflorum* 'intermediate' plant (EXI/CLD-1) is, like the two species, tetraploid, as is *H. leptodon*, to which D. J. Tennant now refers it. The same is true of the *H. eximium*/*H. memorabile* 'intermediate' (EXI/MEM-51, 52 & 53).

The three plants of *H. eximium* (EXI-51, 52 & 53) from Derry Cairngorm, S. Aberdeen, might represent a distinct taxon, having more coriaceous leaves and being more obviously glandular (D. J. Tennant, pers. comm., 1994), but all have the same chromosome number.

Our plants of *H. hanburyi* are tetraploids, as was the previously counted plant from River Eidart, Easterness (Mills & Stace 1974). The *H. hanburyi*/*H. tenuifrons* 'intermediate' has been commented upon already.

H. macrocarpum is virtually confined to the Cairngorms except for the distant locality in E. Ross, where the plants (MAC-19) differ in some respects from those in the Cairngorms and might represent a different taxon. The chromosome numbers, however, do not differ.

The two plants of *H. pseudopetiolatum* from Westerness differ slightly from that from Coire Etchachan, but not in chromosome number.

Since there are in the main only two ploidy levels involved, it is not surprising that they throw rather little light on taxonomic problems. However, all the five formae newly recognized by Sell *et al.* (1995) have the same chromosome number as the respective type formae, and none of the other variants mentioned above differs in chromosome number from the respective typical species. This indicates that there is in fact rather little (if any) variation in chromosome number within each microspecies as delimited by traditional taxonomists. A corollary of this conclusion is, therefore, that those cases where both triploid and tetraploid counts are found in one microspecies constitute evidence that the two cytological races do, in fact, represent different taxa. This is clearly true of *H. tenuifrons* and perhaps of *H. celsum*. Moreover, it suggests that the pentaploid un-named plant from An Teallach (XYZ-1) is indeed a new species.

The use of chromosome numbers as taxonomic evidence in this way is justifiable in an obligately apomictic group, but much less so in a sexual or facultatively apomictic one. Without the existence of sexual reproduction (i.e. meiosis followed by fertilization) the evolution of a triploid from a tetraploid, or vice versa, although conceivable, is a most unlikely event. It would involve the chance inclusion of 27 chromosomes in a cell destined to become an embryo from a plant with 36 chromosomes, or vice versa. If such an event is at all likely (i.e. if the requisite mechanisms exist), it is surely unlikely that the only new chromosome numbers to arise would be euploids; one would expect aneuploids to be formed at least as frequently (perhaps much more frequently) than euploids. There is no evidence that this occurs; only two of 152 plants so far counted are aneuploids, and none of the F_1 progeny of these 152 plants differed from their parent in chromosome number. A far more likely cause of the existence of both triploids and tetraploids (and higher euploid levels) is their independent origins from sexual events. The only exceptions to this hypothesis would be chromosome number doubling (e.g. triploids giving rise to hexaploids) or the occasional origin of aneuploids, both of which are possible by unexceptional mitotic events.

The published lists used to compile Table 1 show several examples of species represented by more than one ploidy level. Many of these, however, are members of the genus *Pilosella*, in which sexual diploids, tetraploids and hexaploids exist and where mechanisms for the production of plants of different ploidy level (up to decaploid) are well known (Gadella 1991). Of the species of *Hieracium* sensu stricto in which two or more polyploid levels have been recorded, some (e.g. *H. umbellatum* L.) exist as sexual diploids as well and others may well be cases of misidentification (e.g. *H. pulmonarioides* Villars) or varied use of the same name (e.g. *H. murorum* L. and *H. villosum* Jacq.).

Sell & West (1976), in *Flora Europaea*, segregated British *Hieracium* into two species groups (*H. alpinum* group and *H. nigrescens* group), giving chromosome numbers of 2n = 27 and 2n = 36 respectively. The former was based upon the [Continental] counts for *H. alpinum* and the latter upon the British counts for *H. hanburyi* and *H. calenduliflorum* (Moore 1982). The only British species included in the *H. alpinum* group were *H. alpinum* and *H. holosericeum* (both with triploid counts in Britain), while the other 15 British species mentioned were all placed in the *H. nigrescens* group. Besides the special case of *H. tenuifrons* four of these are triploids, and recent counts of *H. nigrescens* from Komi ASSR are also triploid (Lavrenko et al. 1988). Furthermore, one of our three counts of *H. holosericeum* is tetraploid. Hence there is no chromosome number difference between the two species groups, whose descriptions in *Flora Europaea* differ only by few relatively trivial features (viz. leaf width and three characters all prefixed by "often"). Moreover, although Pugsley's (1948) definition of the two species groups was very similar, he placed five of the species that Sell & West included in the *H. nigrescens* group in the *H. alpinum* group (*H. grovesii*, *H. eximium*, *H. calenduliflorum*, *H. macrocarpum* and *H. graniticola*), the first four of these five being tetraploids.

We are carrying out further chromosome studies of *Hieracium* section *Alpina*, including karyotype analyses, in parallel with molecular (DNA and enzyme) methods.

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REFERENCES

Bailey, J. P. & Gornall, R. J. (ined.) *Cytological catalogue of the British and Irish flora.*

Gadella, T. W. J. (1991). Variation, hybridization and reproductive biology of *Hieracium pilosella* L. *Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen* **94**: 455–488.

Ingrouille, M. J. & Stace, C. A. (1986). The *Limonium binervosum* aggregate (Plumbaginaceae) in the British Isles. *Botanical journal of the Linnean Society* **92**: 177–217.

Kent, D. H. (1992). *List of vascular plants of the British Isles.* B.S.B.I., London.

Lavrenko, A. N., Serditov, N. P. & Ulle, Z. G. (1988). Chromosome numbers in some species of Asparagaceae, Asteraceae and Ranunculaceae from the north Urals (Komi ASSR). *Botaničeskij žurnal* **73**: 605–607.

Mills, J. N. & Stace, C. A. (1974). Chromosome numbers of British plants, 2. *Watsonia* **10**: 167–168.

Moore, D. M. (1982). *Flora Europaea check-list and chromosome index.* Cambridge University Press, Cambridge.

MORTON, J. K. (1974). Chromosome numbers of British plants, 3. *Watsonia* **10**: 169.

PUGSLEY, H. W. (1948). A prodromus of the British *Hieracia*. *Journal of the Linnean Society of London (Botany)* **54**: 1–356.

ROSENBERG, O. (1927a). Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. *Hereditas* **8**: 305–338.

ROSENBERG, O. (1927b). Homoeotypic division in uninucleate pollen mother cells. *Hereditas* **9**: 285–288.

SELL, P. D. & WEST, C. (1968). *Hieracium*, in PERRING, F. H. & SELL, P. D., eds. *Critical supplement to the Atlas of the British flora*, pp. 75–131. E. P. Publishing Ltd, London.

SELL, P. D. & WEST, C. (1976). *Hieracium*, in TUTIN, T. G. *et al.*, eds. *Flora Europaea* **4**: 358–410. Cambridge University Press, Cambridge.

SELL, P. D., WEST, C. & TENNANT, D. J. (1995). Eleven new British species of *Hieracium* L. section *Alpina* (Fries) F. N. Williams. Watsonia **20**: 351–365.

SOKOLOVSKAYA, A. P. & STRELKOVA, O. S. (1960). Geographical distribution of polyploid plant species in Eurasian arctic. *Botaničeskij žurnal* **45**: 370–381.

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NOTE ADDED IN PROOF

Recent work on sect. *Alpina* by J. Chrtek jun. in eastern Europe (*Folia geobotanica et phytotaxonomica Bohemoslavaca, Praha* **29**: 91–100 (1994), and unpublished) has shown that:

1. *Hieracium alpinum* sensu stricto from Czechoslovakia, Poland and the Ukraine exists mostly as triploid (2n = 27) but also as diploid (2n = 18) cytotypes. This is the first diploid count for sect. *Alpina*.

2. All the other (non-British) taxa in sect. *Alpina* from these areas are triploids or tetraploids.

3. Continental material named *H. calenduliflorum* and *H. eximium* does not belong to these species but to non-British taxa. It is possible that *H. alpinim* itself is in fact the only British species that is not endemic.

We are grateful to Dr Chrtek for these data.