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# Chromosome elimination in *Hordeum vulgare* × *H. bulbosum* hybrids

## 2. Chromosome behaviour in secondary hybrids

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**Summary.** The hybrid progeny from a stable amphidiploid of *H. vulgare* × *H. bulbosum* involving the cultivar 'Vada' and an unstable amphidiploid involving the cultivar 'Emir' were studied. The genotypes examined contained two genomes from 'Vada' or one from 'Vada' and one from 'Emir', with one or two genomes from *H. bulbosum*. Comparisons between the chromosome numbers in root-tips and anthers revealed that there was no chromosome elimination in most plants, whether there was one or two Vada genomes present. The one plant in which chromosome elimination was positively identified had 'Emir' as opposed to 'Vada' cytoplasm. It also had a high incidence of degraded or fragmented chromosomes in the PMCs. Differences in stability between a 27 chromosome plant and other hypotetraploids suggest that 'Vada' contains both elimination genes and elimination suppressor genes. Upon selfing, again irrespective of the number of 'Vada' genomes present, circa triploid hybrids gave rise to diploid *H. vulgare* offspring while hypotetraploids produced hybrid-like plants. These included diploids, triploids and tetraploids. There was evidence that suggested that *H. vulgare* as well as *H. bulbosum* chromosomes had been eliminated.

**Key words:** *Hordeum* – Stable hybrids – Chromosome elimination – Chromosome stability – Gene balance

### Introduction

In crosses between *H. vulgare* and *H. bulbosum,* the *H. bulbosum* chromosomes are usually eliminated during the early development of the embryo (Bennett et al. 1976). When hybrid plants are produced the *H. bulbosum* chromosomes are steadily lost during plant development and by meiosis many PMCs do not contain the full complement of *bulbosum* chromosomes (Lange 1971). The opportunities of obtaining recombinant chromosomes is thus greatly reduced. Only rarely are *H. bulbosum* chromosomes transmitted to subsequent generations though Lange and Jochemsen (1976) did obtain some plants with hybrid morphology from triploid and tetraploid hybrids. They subsequently found that no *bulbosum* characters had been transferred to the *vulgare* germplasm; the presence of whole *bulbosum* chromosomes probably accounted for the appearance of the morphological characters.

Retention of the *bulbosum* chromosomes in hybrids is clearly vital to the transfer of *bulbosum* characters into the *H. vulgare* germplasm. In a previous paper (Thomas and Pickering 1983) we describe an amphidiploid between *H. vulgare* cv. 'Vada' and *H. bulbosum* that produced 674 seeds, 579 (85.9%) of which had hybrid morphology. *H. bulbosum* characters were also transmitted when reciprocal crosses were made between this hybrid and a second, unstable amphidiploid involving the cultivar 'Emir'. The progeny from these crosses consisted of diploid *H. vulgare* and hypotriploid and hypotetraploid hybrids.

In the unstable amphidiploid (Emir VB10) chromosomes were eliminated during plant growth, during gamete formation and in the developing zygotes. The stable amphidiploids (Vada VB1) produced mainly hybrid gametes which, when combined with either hybrid or haploid *vulgare* gametes from Emir VB10, could prevent chromosome elimination in the subsequent embryogenesis. It was proposed that 'Vada' carries a gene(s) that may cancel the effect of the elimination genes present in *H. vulgare* (Thomas and Pickering 1983).

This paper describes the chromosome behavior of the secondary hybrids i.e. hybrid progeny from the two amphidiploids and examines the status of the seeds harvested from them.

## Material and methods

The hybrid plants studied are presented in Table 1 with their origin and presumed genomic constitution. The basis for assuming this constitution is explained in the first paper of the series (Thomas and Pickering 1983). The plants studied represent both circa triploid and circa tetraploid hybrids. As the 14 chromosome plants produced from crossing and from selfing the original amphidiploids resembled *H. vulgare*, they are not included in this study.

Seeds were germinated on moist filter paper at 21 °C. Root-tips were removed, pre-treated for 24 h in distilled water at 1 °C and fixed in ethanol : acetic acid (3 : 1). They were stained in Feulgen and squashed in 1% aceto-carmine. Only slight pressure was applied when squashing to avoid breaking the cells. Chromosome counts of mature plants were made on roots taken from soil. For meiotic analysis inflorescences were removed before emergence, fixed in Carnoy (6 : 3 : 1) solution and anthers squashed in 1% aceto-carmine.

Plants were maintained in a heated glasshouse with daylight supplemented in winter with high pressure mercury fluorescent bulbs.

## Results

Chromosome counts were made in all plants at the seedling stage (Table 2). Where possible, a total of 25 cells from three root tips were examined. Chromosome counts were again made in 6 of the plants 10 months later and variable numbers of chromosomes were found (Table 2).

### *The selfed progeny of 'Vada' (VB1/n)*

In VB1/28 there was a significant difference ($P < 0.02$) between chromosome numbers in seedling root-tips (Table 2) and PMCs (Table 3). However, if the three cells with less than 14 chromosomes in the root-tips were left out of the analysis there was no significant difference. As only 5 cells were counted at the 10 month stage these were not included in the analysis. Of the PMCs, 14.3% contained either degraded chromosomes or chromosome fragments, and although seed set was good all the progeny were diploid *H. vulgare* (Table 6).

No counts were made of VB1/32 root-tips after 10 months. At the seedling stage the chromosome number was variable (Table 2); the modal class was 27, other cells had 18–24 chromosomes. All PMCs scored had 27 chromosomes and no degraded chromosomes or chromosome fragments were found in the PMCs. Two seeds were obtained one of which germinated and the seedling was hybrid-like with a mean chromosome number of 23.5 (Table 6).

There was no significant difference between the chromosome numbers of the seedling root-tips and the chromosome numbers of the PMCs in VB1/34 (Tables 2 and 3). The 6 cells counted after 10 months (Table 2) were not included in the analysis. Just one PMC contained a chromosome fragment. Two seeds were obtained and both produced hybrid-like seedlings with mean chromosome numbers of 23.3 and 25.7 respectively (Table 6).

**Table 1.** The hybrids studied. Genome symbols: $V^{Va}$ = 'Vada', $V^{Em}$ = 'Emir', $B$ = *H. bulbosum*

| Origin | Plant no. | Mean chromosome no. | Assumed genomic constitution |
|---|---|---|---|
| Selfed progeny of Vada VB1 | VB1/28 | 23.1 | $V^{Va}V^{Va}B$ |
| | VB1/32 | 24.8 | $V^{Va}V^{Va}BB$ |
| | VB1/34 | 26.6 | $V^{Va}V^{Va}BB$ |
| Emir VB10 (♀) × Vada VB1 (♂) | VB14/1 root 1[a] | 20.2 | $V^{Em}V^{Va}B$ |
| | VB14/4 | 18.9 | $V^{Em}V^{Va}B$ |
| Vada VB1 (♀) × Emir VB10 (♂) | VB15/1 | 23.8 | $V^{Va}V^{Em}BB$ |
| | VB15/3 | 14.8 | $V^{Va}V^{Em}B$ |
| | VB15/5 | 26.1 | $V^{Va}V^{Em}BB$ |

[a] Second root had 14 chromosomes/cell

### *Progeny of Emir VB10 (♀) × Vada VB1 (♂) (VB14/n)*

The PMCs in VB14/1 consistently had 14 chromosomes (Table 4). The 2 root-tips counted differed, one consistently had 14 chromosomes while the other had a range of 14–21 (Table 2). The plant subsequently produced *vulgare*-like and hybrid-like parts and it is possible that the inflorescence analysed came from a *vulgare*-like part of the plant. One PMC contained a chromosome fragment. The seed set was good but all the progeny were diploid *H. vulgare* (Table 6).

The difference between the chromosome numbers in root-tips of the seedling (Table 2) and the PMCs in VB14/4 was highly significant ($P < 0.001$), though there were still some PMCs with 20 chromosomes (Table 4). In this plant, 64% of the PMCs scored had degraded or fragmented chromosomes. Three seeds were obtained and germinated to give diploid *H. vulgare* seedlings.

### *Progeny of Vada VB1 (♀) × Emir VB10 (♂) (VB15/n)*

For the three VB/15 hybrids, chromosome numbers from the 10 month root-tip count were included in the analyses. In VB15/1 the difference between the 3 chromosome counts, i.e. seedling and mature plant root-tips (Table 2) and the PMCs (Table 5) was highly significant ($P < 0.001$). This was due to the absence of

**Table 2.** Chromosome distribution in seedling root-tips, and adult plant root-tips at ten months (in brackets)

| Plant no. | No. of cells with chromosome numbers | | | | | | | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 29 | 28 | 27 | 26 | 25 | 24 | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13> | |
| VB1/28 | | | | | 8 | 16 (1) | 1 (3) | (1) | | 1 | 1 | | | 2 | 2 | 2 | 3 | 36 |
| VB1/32 | | | 15 | | | 2 | 1 | 4 | 1 | | | 2 | | | | | | 25 |
| VB1/34 | 4 | 5 (4) | 9 (2) | 2 | 1 | 1 | 1 | | 2 | | | | | | | | | 25 |
| VB14/1 root 1 | | | | | | | | | 17 | 6 (4) | (1) | | | | | 2 | | 25 |
| root 2 | | | | | | | | | | | | | | | | 8 | | 8 |
| VB14/4 | | | | | | | | | | 7 | 6 | 1 | 1 | 2 | | | | 17 |
| VB15/1 | (4) | (2) | 1 (1) | 3 (2) | 3 (1) | 6 (1) | 8 | | | 1 | 1 | | | | | | | 23 |
| VB15/3 | | | | | | | | | (1) | (8) | (1) | | 1 | 3 | 6 | 9 | | 19 |
| VB15/5 | | 3 (3) | 13 (7) | 3 | 1 | 4 | | | | | 1 | | | | | | | 25 |

**Table 3.** Number of PMCs with different chromosome numbers, with mean frequencies per cell of chromosome configurations, extra chromatin (*d* = degraded chromosomes, *f* = chromosome fragments), and chiasmata in the selfed progeny of Vada VB1

| Hybrid | No. of chromosomes/ cell | No. of cells | Mean configuration/cell | | | | Extra chromatin/cell | | Chiasmata/ cell |
|---|---|---|---|---|---|---|---|---|---|
| | | | IV | III | II | I | d | f | |
| VB1/28 | 25 | 4 | 0.25 | – | 7.75 | 8.50 | – | – | 13.50 |
| | 24 | 8 | 0.13 | 0.13 | 6.75 | 9.63 | 0.13 | 0.13 | 13.50 |
| | 23 | 10 | – | 0.30 | 7.30 | 7.50 | 0.1 | – | 12.80 |
| | 22 | 2 | – | – | 8.0 | 6.0 | – | – | 12.00 |
| | 21 | 3 | 0.33 | 0.33 | 6.0 | 5.33 | 0.33 | – | 15.00 |
| | 20 | 1 | – | – | 7.0 | 6.0 | – | – | 11.00 |
| VB1/32 | 27 | 25 | 0.64 | 0.16 | 10.68 | 2.6 | – | – | 19.56 |
| VB1/34 | 28 | 25 | 0.64 | 0.13 | 9.88 | 5.12 | – | – | 19.88 |
| | 27 | 2 | 0.50 | 1.00 | 8.50 | 5.00 | – | – | 17.00 |
| | 26 | 2 | 0.50 | – | 10.50 | 3.00 | – | – | 19.50 |
| | 14 | 1 | – | – | 3.00 | 8.00 | – | 1.00 | 4.00 |

**Table 4.** Number of PMCs with different chromosome numbers, with mean frequencies per cell of chromosome configurations, extra chromatin (*d* = degraded chromosomes, *f* = chromosome fragments), and chiasmata in progeny of Emir VB10 × Vada VB1

| Hybrid | No. of chromosomes/ cell | No. of cells | Mean configuration/cell | | | | Extra chromatin/cell | | Chiasmata/ cell |
|---|---|---|---|---|---|---|---|---|---|
| | | | IV | III | II | I | d | f | |
| VB14/1 | 14 | 10 | – | – | 7 | – | – | 0.1 | 13.80 |
| VB14/4 | 20 | 8 | 0.13 | – | 6.88 | 5.75 | – | – | 13.88 |
| | 19 | 6 | – | – | 7.0 | 5.0 | 0.1 | – | 12.33 |
| | 18 | 8 | – | – | 7.0 | 4.0 | 0.88 | 0.25 | 14.00 |
| | 17 | 5 | – | – | 7.4 | 2.2 | 1.2 | – | 15.00 |
| | 16 | 5 | 0.2 | – | 6.6 | 2.0 | 1.0 | – | 13.80 |
| | 15 | 6 | – | – | 7.0 | 1.0 | 0.83 | 0.67 | 14.00 |
| | 14 | 10 | – | – | 7.0 | – | 1.4 | 0.4 | 14.00 |
| | 12 | 1 | – | – | 5.0 | 2.0 | 1.0 | 1.0 | 10.00 |

cells with lower chromosome numbers in root-tips counted at 10 months and the PMCs. Of the PMCs, 19.6% contained either degraded or fragmented chromosomes. Three seeds germinated to produce hybrid-like seedlings; one had a range of chromosome numbers approaching the tetraploid level, while the other two had constant chromosome numbers of 14 and 27 respectively (Table 6).

In VB15/3 also, the difference between the 3 chromosome counts was highly significant but there was no difference between the chromosome numbers of the root-tips at 10 months (Table 2) and the PMCs (Ta-

**Table 5.** Number of PMCs with different chromosome numbers, with mean frequencies per cell of chromosome configurations, extra chromatin (*d* = degraded chromosomes, *f* = chromosome fragments), and chiasmata in progeny of Vada VB1 × Emir VB10

| Hybrid | No. of chromosomes/ cell | No. of cells | Mean configuration/cell | | | | Extra chromatin/cell | | Chiasmata/ cell |
|---|---|---|---|---|---|---|---|---|---|
| | | | IV | III | II | I | d | f | |
| VB15/1 | 30 | 1 | – | 1 | 9 | 7 | – | – | 17 |
| | 29 | 1 | 2 | – | 9 | 3 | – | – | 20 |
| | 28 | 18 | 0.22 | 0.56 | 9.78 | 5.61 | 0.06 | – | 17.16 |
| | 27 | 4 | 0.25 | 0.50 | 10.00 | 4.50 | 0.25 | – | 18.25 |
| | 26 | 13 | 0.38 | 0.15 | 9.46 | 5.08 | 0.38 | – | 16.85 |
| | 25 | 5 | 0.2 | 0.2 | 8.2 | 6.60 | – | – | 13.80 |
| | 24 | 4 | 1.0 | – | 8.5 | 3.00 | 0.75 | 0.25 | 17.00 |
| VB15/3 | 27 | 1 | – | – | 9 | 9 | – | – | 17 |
| | 26 | 1 | – | – | 9 | 8 | 2 | – | 17 |
| | 23 | 1 | – | 1 | 6 | 8 | – | – | 13 |
| | 20 | 40 | – | 0.03 | 7.0 | 5.88 | – | – | 13.25 |
| | 19 | 6 | – | 0.17 | 6.67 | 5.67 | – | – | 13.27 |
| VB15/5 | 27 | 20 | 0.15 | 0.1 | 11.0 | 4.0 | – | – | 17.6 |
| | 26 | 5 | – | – | 10.6 | 4.8 | 0.2 | – | 17.0 |
| | 25 | 2 | – | 0.5 | 10.0 | 3.5 | – | – | 17.5 |
| | 24 | 2 | – | – | 8.5 | 7.0 | 1.5 | – | 12.5 |

ble 5). Only one PMC was found containing degraded chromosomes. Several seeds were produced upon selfing but all those grown were diploid *H. vulgare*.

In VB15/5 the difference between the 3 chromosome counts was significant ($P < 0.2$) but there was no significant difference between seedling root-tips (Table 2) and PMCs (Table 5). Of the PMCs, 6.9% contained degraded chromosomes. The seed set was good and all those germinated (Table 6) gave hybrid-like seedlings, three with variable chromosome numbers, one with 21 chromosomes and one with 14 chromosomes.

Meiosis in most hybrids was characterised by large cell to cell variation in the number of chromosomes paired. The exceptions were VB15/3 and VB14/4 where pairing was relatively uniform. Comparisons of hybrids is difficult because in those chromosome classes common to more than 2 plants only a few cells were scored (Tables 2, 3 and 4).

**Table 6.** Chromosome number and morphology of selfed progeny of the secondary hybrids

| Secondary hybrids | No. of plants | Chromosome no.[a] | | Morphology |
|---|---|---|---|---|
| | | Mean | Range | |
| VB1/28 | 5 | 14 | – | *Vulgare*-like |
| VB1/32 | 1 | 23.5 | 22 – 25 | Hybrid-like |
| VB1/34 | 1 | 23.3 (14) | 22 – 26 | Hybrid-like |
| | 1 | 25.7 | 22 – 28 | Hybrid-like |
| VB14/1 | 5 | 14 | – | *Vulgare*-like |
| VB14/4 | 3 | 14 | – | *Vulgare*-like |
| VB15/1 | 1 | 14 | – | Hybrid-like |
| | 1 | 27 | – | Hybrid-like |
| | 1 | 25.4 | 22 – 27 | Hybrid-like |
| VB15/3 | 5 | 14 | – | *Vulgare*-like |
| VB15/5 | 1 | 14 | – | Hybrid-like |
| | 1 | 21 | – | Hybrid-like |
| | 1 | 19.8 | 18 – 21 | Hybrid-like |
| | 1 | 20.7 | 20 – 22 | Hybrid-like |
| | 1 | 27.0 | 24 – 28 | Hybrid-like |

[a] 10 cells counted per plant

## Discussion

### *Chromosome elimination within the secondary hybrids*

Comparisons between chromosome numbers in root-tip cells and in PMCs can indicate the extent of chromosome elimination during plant development. In most of the hybrids studied no significant differences were found between the two sets of chromosome numbers.

In VB1/28 a significant difference between the 2 sets was in fact due to the presence of cells with less than 14 chromosomes in the root-tips. In the PMCs the lowest chromosome number was 20. Clearly, therefore, no chromosomes had been eliminated in the somatic tissue, although one dicentric chromosome and a telocentric chromosome found in seedling root-tip cells were not found in the later stages.

In VB1/32 the root-tips contained, in addition to the 27 chromosome cells, cells with between 18 and 24 chromosomes; however all PMCs had 27 chromosomes. The absence of cells with lower chromosome numbers in the anthers could be due to superior viability of the

27 chromosome cells. With no PMC to PMC variation in chromosome number and little variation in chromosome pairing, this genotype contrasted sharply with the other genotypes.

Kasha and Sadasivaiah (1971) found a relatively stable 27 chromosome hybrid. Since Barclay et al. (1972) and Ho and Kasha (1975) reported that chromosome elimination was controlled by genes on chromosomes 2 and 3 of *H. vulgare* and stability was dependent on the balance of these genes with genes in *H. bulbosum*, it is likely that Kasha and Sadasivaiah's hybrid lacked chromosome 2 or 3, and that the same stable balance occurred in VB1/32. This means that elimination genes on at least one of the chromosomes 2 and 3 are present in 'Vada', as the lack of one particular chromosome has an effect over and above the 'Vada effect' (Thomas and Pickering 1983) on chromosome stability.

As there was no significant difference in the range of chromosomes found in the root-tips of VB1/34 and that found in the PMCs, there was no evidence of chromosome elimination during the plant's development.

In VB14/1 it is not possible to ascertain whether the 14 chromosome PMCs were derived from the diploid sector of the seedling or from the hybrid sector following chromosome elimination, though the uniformity of the PMCs suggests the former. However, the chromosome numbers of VB14/4 PMCs had a wide range but were nevertheless significantly different from the root-tips. Though there were still cells with 20 chromosomes in the anthers, chromosome elimination had clearly taken place in this hybrid, the modal chromosome number now being 14.

There were degraded chromosomes or chromosome fragments in 64% of the PMCs in VB14/4. In the original tetraploid hybrid, Emir VB10 had degraded or fragmented chromosomes in 51% of PMCs and again chromosome elimination had taken place between root-tip and anther (Thomas and Pickering 1983). In the present hybrids VB15/5 had the next highest number of PMCs with degraded and fragmented chromosomes at 19.6%. So on the evidence of this small number of plants the high incidence of degraded or fragmented chromosomes seems to be associated with earlier chromosome elimination.

There was no significant loss of chromosomes in any of the VB15 hybrids between root and anther. In these plants the root-tip chromosome counts made at ten months were also included in the analyses. In VB15/1 and VB15/3, cells with chromosome numbers at the lower end of the range found in seedling root-tips were not found in root-tips at 10 months. This, and the slightly higher top-end of the range could be explained by differences between the various sectors of the plants. However, the considerable loss of cells at the bottom end of the range could more likely be explained in terms of relative viability of cells with different chromosome numbers.

In *Hymenocallis calathinum*, Snoad (1955) found a range of chromosome numbers in both root-tips and anthers caused by mitotic spindle abnormalities. While the modal number was the same in both, the chromosome number ranged from 23 to 83 in the root-tips but from 69 to 86 in the anthers. The lower chromosome numbered cells would have been less balanced than the higher numbered and would not have propagated themselves as efficiently. In previously reported *H. vulgare* × *H. bulbosum* hybrids (Lange 1971; Kasha and Sadasivaiah 1971) the lower chromosome numbered cells survive to meiosis. In the present material, in the absence of active chromosome elimination, only cells with higher chromosome numbers, near tetraploid in VB15/1 and near triploid in VB15/3 develop further. There was no significant change in chromosome number from root-tips at 10 months to the anthers subsequently fixed.

The slight difference in chromosome numbers between the seedling and mature plant in VB15/5 was not apparent at meiosis; here the chromosome number was closer to that of the seedling.

Elimination between root and shoot was positively identified in only one hybrid. This hybrid (VB14/4) had 'Emir' cytoplasm while those hybrids which had 'Vada' cytoplasm did not display chromosome elimination during plant development. It should be remembered, however, that for these hybrids to have arisen, elimination was suppressed during embryogenesis in both cytoplasms. It may be that VB14/4, which had a maximum chromosome number of 20, had lost a chromosome that carried an elimination suppressor. However, the possible effect of Vada cytoplasm needs to be examined further.

*Chromosome elimination on selfing the secondary hybrids*

On selfing the hybrids we found that the progeny of the 4 circa triploids (VB1/28, VB14/1, VB14/4 and VB15/3) had reverted to diploid *H. vulgare*, though in VB1/28 and VB15/3 there had been no chromosome elimination between root and anther. It was presumed that these 4 hybrids had two *vulgare* genomes and one *bulbosum* genome. In VB1/28 both *vulgare* genomes would have come from 'Vada' while in the others there would have been one from 'Vada' and one from 'Emir'.

The *bulbosum* chromosomes were eliminated irrespective of the number of 'Vada' genomes present, but it may be that in the triploids insufficient *bulbosum* chromosomes paired and they were left as laggards. Circa triploid cells predominantly contained just seven bivalents, the remaining chromosomes being unpaired. It may also be that the 'Vada effect' is not sufficient to prevent elimination during gamete formation when two *vulgare* to one *bulbosum* genomes are present.

Taking the highest chromosome number found in the seedling root-tip as probably being closest to the zygote number, the progeny of VB1/32 and VB1/34 were 25, 26 and 28, suggesting that very little elimination occurred during gamete formation. The progeny of VB15/1 and VB15/5 present a more confusing picture.

All were hybrid-like and, based on the highest chromosome number, may be grouped as 2 diploids, 3 triploids and 3 tetraploids. The presence of 2 diploid hybrids indicates the elimination of *H. vulgare* chromosomes as well as *H. bulbosum* chromosomes, though these may be further examples of plants with both *vulgare* and hybrid sectors. One of the triploids from VB15/5 had a constant chromosome number of 21 suggesting that it may be a VBB triploid.

## Conclusion

The presence of 'Vada' chromosomes is able to suppress the elimination of *bulbosum* chromosomes in tetraploid (VVBB) and triploid (VVB) hybrids irrespective of whether 2 sets of 'Vada' chromosomes are present or 1 set of 'Vada' and one of 'Emir'. However, upon selfing, no *bulbosum* chromosomes were transmitted in the triploid hybrids, again irrespective of the number of 'Vada' genomes present.

Although there is some pairing between *H. vulgare* and *H. bulbosum* chromosomes, with a mean of 0.77 multivalents in 28 chromosome cells in VB1/34 and 0.78 multivalents in 28 chromosome cells in VB15/1, recombinant chromosomes have yet to be identified. With the 'Vada' genome present, a much larger proportion of PMCs contain *H. bulbosum* chromosomes, and it is possible to maintain the *bulbosum* chromosomes through several sexual cycles so that the chances of obtaining recombinants from this material are much greater than from other *H. vulgare* × *H. bulbosum* hybrids.

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