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Two new hybrids in the *Dryopteris villarii* aggregate
(Pteridophyta, Dryopteridaceae),
and the origin of *D. submontana*

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RÉSUMÉ

FRASER-JENKINS, C. R. & M. GIBBY (1980). Deux hybrides nouveaux dans le complexe *Dryopteris villarii* agg. et l'origine de *D. submontana*. *Candollea* 35: 305-310. En anglais, résumé français.

Description de deux nouveaux hybrides dans le complexe *Dryopteris villarii* agg., soit *D. × vidae* Fraser-Jenkins & Gibby (*D. pallida × villarii*) et *D. graeca* Fraser-Jenkins & Gibby (*D. pallida × submontana*). La cytologie du premier de ces hybrides a été examinée par Gibby; c'est un diploïde qui présente de 0 à 4 bivalents (en moyenne 1.3) et 82 à 74 univalents. Ce résultat montre que les deux parents diploïdes sont génétiquement distincts et permet d'affirmer l'origine allopolyploïde de l'espèce tétraploïde, *D. submontana*.

ABSTRACT

FRASER-JENKINS, C. R. & M. GIBBY (1980). Two new hybrids in the *Dryopteris villarii* aggregate (Pteridophyta, Dryopteridaceae), and the origin of *D. submontana*. *Candollea* 35: 305-310. In English, French abstract.

Two new wild hybrids in the *Dryopteris villarii* aggregate are described, namely *D. × vidae* Fraser-Jenkins & Gibby (*D. pallida × villarii*) and *D. × graeca* Fraser-Jenkins & Gibby (*D. pallida × submontana*). The former has been cytologically investigated at meiosis by Gibby and found to be diploid with from 0-4 bivalents (mean 1.3) and 82-74 univalents, an important result as it shows that its two diploid parents are genomically distinct, and thus demonstrates the allopolyploid origin of the tetraploid species, *D. submontana*.

The *Dryopteris villarii* (Bell.) Woynar ex Schinz & Thell. aggregate consists of three species: two dissimilar diploids, *D. villarii* and *D. pallida* (Bory) Fomin, the latter having fragmented into a number of more-or-less distinct geographical subspecies, and a tetraploid, *D. submontana* (Fraser-Jenkins & Jermy) Fraser-Jenkins, which being morphologically intermediate between the two diploids above mentioned, has somewhat obscured the morphological boundaries within the group and caused them to be treated as an aggregate entity in the literature. *D. villarii* is an alpine species, *D. pallida* a central and Eastern Mediterranean one, and *D. submontana* a submontane one with a distribution that is in general wider than the other two, though absent from parts of their ranges. Details of the morphology, taxonomy, distribution and discovery of the relationships within the group have been given in an earlier paper by FRASER-JENKINS (1977). We need say here only that the two triploid hybrids, *D. submontana* × *villarii* and *D. pallida* × *submontana*, have been artificially synthesised (PANIGRAHI, 1965 and ROY, 1967) and cytologically investigated, while the diploid hybrid, *D. pallida* × *villarii*, has not; and although it seemed almost certain that *D. submontana* was derived from the two mentioned diploids, this could not be proven solely from the evidence of there being equal numbers of bivalents and univalents at meiosis in the triploid hybrids. The bivalents could represent either allosyndetic pairing or autosyndetic pairing, and multivalent suppression may also occur. This situation is well known, having been demonstrated in wheats by RILEY (1960) and in ferns by numerous authors, notably LOVIS & al. (1969), VIDA (1970) and see LOVIS (1977).

Furthermore, as has recently been shown by FRASER-JENKINS (1976) in *D. filix-mas* (L.) Schott, it is quite possible that a taxon long presumed to be allopolyploid may turn out to be a segmental allopolyploid on investigating the genomic relationships between its diploid parents; a similar case may be that of *Asplenium trichomanes* subsp. *quadrivalens* (LOVIS, 1977). To investigate such a situation, evidence is required either from a reduced (i.e. polyhaploid) plant derived from the tetraploid, or better, because polyhaploids may show suppression of pairing behaviour (LOVIS, 1977: 342 fn. and 364 fn.), from the diploid hybrid between the two parents. Evidence for the nature of autopolyploids may also be derived from the pairing behaviour in a wide cross. The discovery of a plant, described below, which appeared to be the diploid hybrid between *D. pallida* and *D. villarii* was therefore of considerable importance, and further investigation was carried out.

***Dryopteris* × *vidae*¹ Fraser-Jenkins & Gibby, **hybrid nova**
(*D. pallida* subsp. *pallida* × *D. villarii* subsp. *villarii*)**

¹Named after Professor Dr. Gabor Vida of the Department of Evolution and Genetics, Eötvös Loránd University, Budapest, Hungary, who discovered *D. submontana* in continental Europe, and was the first to elucidate clearly its proposed origins (VIDA, 1969), and the relationships of the subspecies of *D. pallida*.

Planta intermedia in morphologia inter parentes et eximie simil ad *D. submontana*; a frondibus deltatis multum glandulosis et dentibus ad apice pinnularum longibus, eis ad margines pinnularum exigubus. Sed sporae abortivae et cytotypus diploideus.

Holotypus: Jugoslavia, Montenegro, Lovcen. Coll. Aug. 1957, A. H. G. Alston No. 177--. Ex hort Chelsea Physic Garden (CPG 2520). Comm. C. R. Fraser-Jenkins, 9 May 1979, sub No. 9416 (BM).

The plant is very close in morphology to *D. submontana*, as might be expected, with a deltate and glandular lamina, long apical teeth to the pinnule and few lateral ones, but with abortive hybrid type spores and a diploid cytotype. It was first noticed by Fraser-Jenkins in Winter 1970, growing in a pot at the University Botanic Garden, Leeds, labelled as having been collected by Alston in Montenegro. What brought it to attention was a second label, "showed 82 univalent only in meiosis; summer 1964 — S. K. Roy 1964", Dr. Roy having been a research student at Leeds who made some preliminary investigations into the *D. villarii* aggregate while there. In 1978, some fern plants from Leeds were given to the British Museum (Natural History), and taken to the Chelsea Physic Garden and among them was the Alston plant, still bearing the same labels. It was apparent from its frond morphology, particularly the deltate, highly glandular lamina and narrowly acute teeth on the pinnule apices, that it strongly resembled *D. submontana*, which was to be expected if indeed it was the diploid hybrid that Roy's label indirectly suggested. Accordingly, cytological fixations were made of developing sporangia and clear preparations were obtained, showing a large number of univalents (Fig. 1), the actual number varying from 82-74 univalents with the corresponding 0-4 bivalents. The mean number of bivalents was 1.3. Thus, the plant must indeed represent a natural occurrence of the diploid hybrid *D. pallida* × *villarii*. The significance of this result is not merely that it represents a new hybrid, but also that it demonstrates conclusively for the first time that *D. pallida* and *D. villarii* are genomically as well as morphologically distinct, and thus that the origin of *D. submontana* is clearly an allopolyploid one, its derivation being from *D. villarii* and *D. pallida* as suggested by the two sterile triploid backcross hybrids. *D.* × *vidae* may be presumed to be the original hybrid from which *D. submontana* arose, and in fact may still be arising today in the places where the two parents grow close to each other (the Abruzzi in Italy, the Dalmatian coastal mountains of Jugoslavia and Albania, and the Pindhos mountains of Greece). The two parents are more-or-less ecologically isolated, *D. pallida* being on the lower levels, up to ca. 1500 m, and *D. villarii* being on the mountain-tops, down to ca. 1200 m — thus occasionally overlapping in the middle regions where *D. submontana* is also commonest. Although the spores of *D.* × *vidae* appear abortive with thickened and disorganised perispore and many fragments, it is possible that a few diplospores may occur spontaneously, and sowings will be tested for viability.

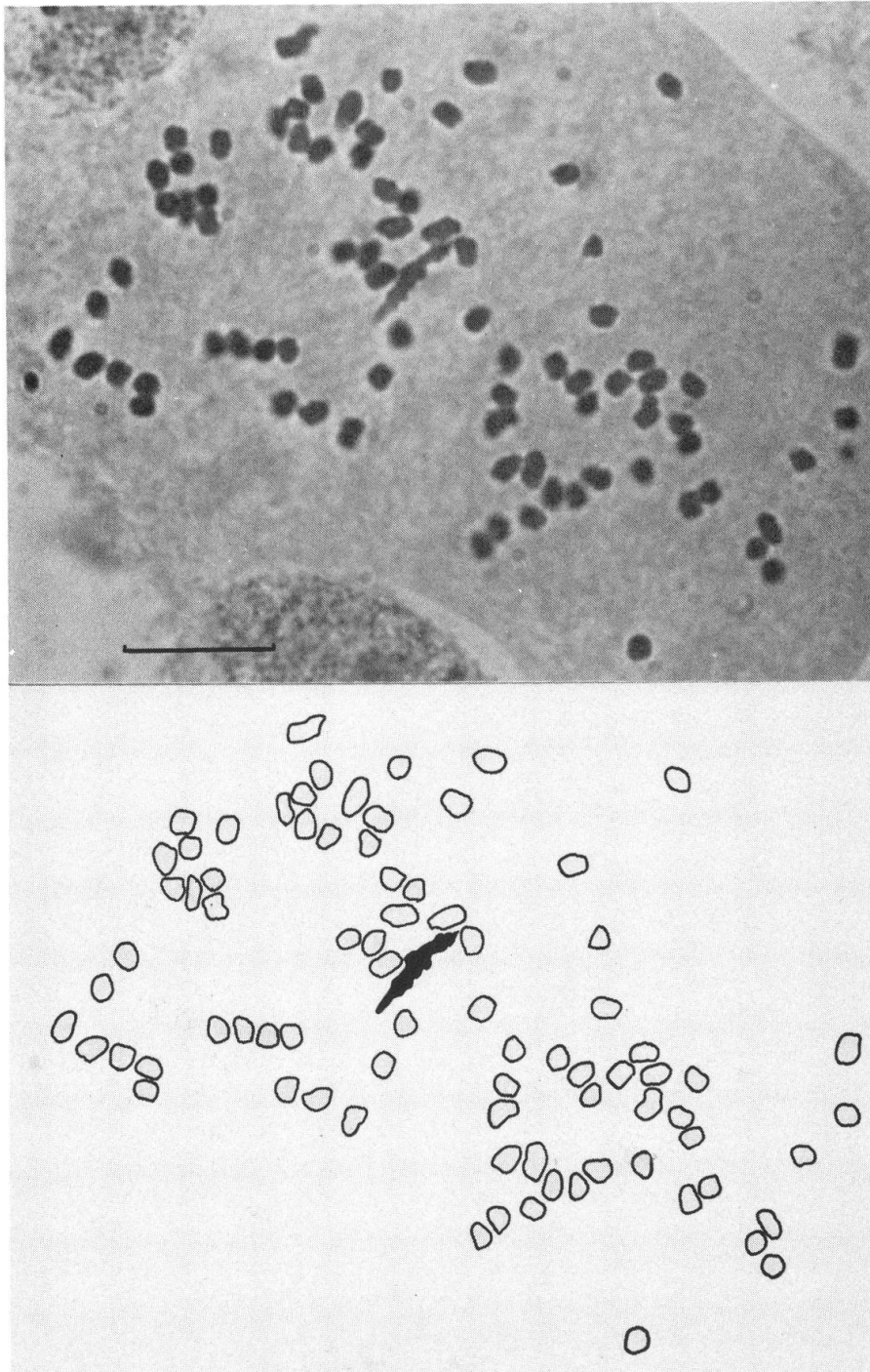


Fig. 1a. — First metaphase of meiosis in *Dryopteris* × *vidae*, permanent acetocarmine preparation, showing one bivalent and 80 univalents. Bar represents 10 μ m.
Fig. 1b. — Explanatory diagram of 1a, bivalent in black, univalents outlined.

Dryopteris × **graeca** Fraser-Jenkins & Gibby, **hybrid nova**
(*D. pallida* subsp. *pallida* × *D. submontana*)

Planta intermedia in morphologia inter parentes, simil ad *D. pallida* a pinnis infinis et eorum pinnulis infimis longibus, sed dentes ad apices pinnulorum longiores, pinnulae minus profunde lobatae et sporae abortivae.

Holotypus: In reg. abietina montium elatiorum Graeciae, alt. 4-7000'. In m. Parnasso (Kaskasia), 4500'. Coll.: De Heldreich 24 Aug. 1856, No. 556 (C). Left hand specimen only: right hand one is *D. submontana*. Issued as *Nephrodium pallidum* in the series "Herbarium graecum".

Isotypus: ditto in G.

Similar to *D. pallida* in its long lowest pinnae and pinnules, but with long-acute teeth at the pinnule apices, and less deeply lobed pinnules. Spores abortive. This specimen cannot be investigated cytologically, but is presumed to be triploid. A plant of almost identical morphology and of the parentage suggested here was synthesised by Roy at Leeds and showed ca. 41 bivalents and 41 univalents at meiosis (ROY, 1967). As with other triploid backcross hybrids in European *Dryopteris* (e.g. the *D. filix-mas* and *D. dilatata* (Hoffm.) Gray aggregates), it may be presumed to be relatively common where the parents grow together, though *D. submontana* itself is seldom in great abundance.

The hybrid between *D. submontana* and *D. villarii* should be equally common, but has not yet been found in the wild. Synthesised specimens made by Panigrahi, again while temporarily studying at Leeds, showed ca. 41 bivalents and 41 univalents at meiosis (PANIGRAHI, 1965).

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