Three species on the Dryopteris villarii aggregate : Pteridophyta, Aspidiaceae

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Three species in the Dryopteris villarii aggregate (Pteridophyta, Aspidiaceae)

C. R. Fraser-Jenkins

Résumé

Fraser-Jenkins, C. R. (1977). Les trois espèces du complexe Dryopteris villarii (Ptéridophytes, Aspidiacées). *Candollea* 32: 305-319. En anglais.

Révision taxonomique de ce qui fut longtemps considéré comme une seule espèce polymorphe. L'auteur reconnaît deux espèces distinctes au niveau diploïde, *Dryopteris villarii* et *D. pallida*, présentant chacune des différenciations géographiques (c'est-à-dire regroupant chacune 2 à 5 sous-espèces); et une espèce morphologiquement intermédiaire au niveau tétraploïde que l'on nommera *D. submontana*. Une clé des espèces, leur description détaillée et la distribution de tous les taxa sont présentés. Un hybride nouveau entre *D. pseudomas* et un taxon du groupe *D. villarii* est décrit *(D. x cebennae)*. Une nouvelle désignation subspécifique *(D. pallida* subsp. *nigropaleacea)* ainsi que diverses combinaisons nouvelles sont validées.

Abstract

Fraser-Jenkins, C. R. (1977). Three species in the Dryopteris villarii aggregate (Pteridophyta, Aspidiaceae). *Candollea* 32: 305-319. French abstract.

A taxonomic revision for what has often been considered as a single, polymorphic species. The author recognizes two distinct species at the diploid level, *Dryopteris villarii* and *D. pallida*, each showing geographical differentiation (*i.e.*, formed of 2 and 5 subspecies, respectively); and a morphologically intermediate species at the tetraploid level, to be named *D. submontana*. The species are keyed out and described in detail, and the distribution of all taxa is outlined. A new hybrid between *D. pseudomas* and a taxon of the *D. villarii* complex is described *(D. x cebennae)*. One new subspecies name *(D. pallida* subsp. *nigropaleacea)* and several new combinations are also validated.

Introduction

The *Dryopteris villarii* (Bell.) Woynar ex Schinz & Thell. aggregate is a group of strongly calcicole ferns distributed in Europe, N. Africa and Western and Central Asia, with related taxa in the Himalayas and the West Coast States of the U.S.A. The group embraces a rather wide range of form with at least two of the diploid species (*D. villarii* s.str. and *D. pallida* (Bory) Fomin) being noticeably distinct from each other if considered in isolation from the others, though their morphology suggests that they probably diverged from a similar ancestral stock some considerable time ago in the past, and unfortunately the distinction has now become less clear due to the presence of an intermediate tetraploid taxon. The range of form has caused some broad morphological similarities between members of the *D. villarii* aggregate and a number of other species within the genus *Dryopteris;* for example the diploid species in the *D. filix-mas* (L.) Schott aggregate, *D. fragrans* (L.) Schott, *D. barbigera* (Moore) Kuntze, *D. ramosa* (hope) C. Chr., *D. goldiana* (Hooker) A. Gray (= *D. monticola* (Makino) Christ), *D. marginalis* (L.) A. Gray, and *D. aemula* (Aiton) Kuntze. Because of such similarities, Vida (1969) pointed out that the *D. villarii* aggregate probably had a central position in the evolution of most European *Dryopteris* species at the diploid level – even perhaps including the *D. austriaca* aggregate. Partial genomic homology between different diploid species (*e.g.* the *D. filix-mas* aggregate, Fraser-Jenkins 1976) makes this hypothesis seem likely to be correct at least in principle, though a very great deal of hybridisation work remains to be done to investigate it further, and where there turns out to be little or no genome homology, proposed relationships based on morphology will have to remain conjectural, though chemical studies may help.

Through the use of cytotaxonomic methods Professor Manton of Leeds started much of the modern work on *Dryopteris* and other fern Genera and published a large and detailed account of her results (Manton 1950) which set the scene for much of the work to come. As far as the *D. villarii* aggregate is concerned, Manton discovered that *D. villarii* from England is tetraploid, whereas plants from the Swiss Alps are diploid.

Work on this group was continued by Panigrahi (1965), while at Leeds, who synthesized and investigated the triploid hybrid between these two, which showed a high number of bivalents, probably near to 41 (see Vida 1969), and an approximately equal number of univalents. He concluded that the English plant was probably an allopolyploid to which the Alpine plant was part parental, though in fact there was nothing other than the strong morphological evidence to show that it was an allopolyploid and not an autopolyploid; at the time it was not fully realised by some workers that autopolyploids as well as allopolyploids may show only bivalents and not multivalents. Even now final cytological proof of the allopolyploid nature of the tetraploid species is missing.

More cytological evidence came from Dr. S. K. Roy's work, again at Leeds (Roy 1967), where he produced an artificial hybrid between the English tetraploid plant and the diploid *Dryopteris pallida* (Bory) Fomin (as *D. villarii* subsp. *pallida*) which showed 41 bivalents and 41 univalents at meiosis, suggesting that *D. pallida* could also be part parental to the tetraploid taxon.

Later Professor Vida of Budapest discovered the tetraploid taxon in Continental Europe, in Romania, and suggested (Vida 1969) that some Jugoslav plants might be tetraploid, and again pointed out that the tetraploid taxon could be an allopolyploid with the alpine diploid *D. villarii* and the mediterranean *D. pallida* as its original parents. The final cytological proof requires the synthesis of two further hybrids; the first is the diploid hybrid between *D. villarii* and *D. pallida,* in order to discover if they are indeed genomically distinct or partially distinct entities, as would be expected from their morphology. The other hybrid is one between the tetraploid taxon and some completely unrelated sexual diploid (*e.g., D. assimilis* or *D. crassirhizoma* might be suitable if the hybrids could ever be synthesized

– it would probably require very many attempts because they are likely to show a high degree of incompatibility, being so distantly related). The latter is needed in order to prove that the tetraploid is an amphidiploid or at least a segmental allopolyploid, and not an autopolyploid. An autopolyploid involved in such a hybrid would show equal numbers of bivalents and univalents at meiosis due to autosyndetic pairing, whereas an amphidiploid would show univalents only, due to lack of genomic homology. In the case of a segmental allopolyploid, which might well be expected, a fairly low number of bivalents (approximately half a set, or below might occur, but this would still not preclude the origin of the tetraploid from *D. villarii* and *D. pallida,* especially when the morphological evidence is considered.

The most recent work on the *D. villarii* aggregate involves the opening of a new chapter of methodology for investigating fern taxonomy, and adds a new type of evidence which must be considered alongside the cytology, morphology and other taxonomic factors. This is the chemotaxonomic work of Widén & al. (1971, 1973) in analysing the phloroglucides present in the rhizomes and stipe bases. The results, when combined with all the other evidence, suggest very strongly that the tetraploid plant is indeed an allopolyploid derived from the two previously mentioned diploids, *D. villarii* and *D. pallida,* on a simple additive basis of the compounds present. Several recent authors have assumed that this is probably the case (*e.g.* Fraser-Jenkins & al. 1975; Nardi 1976), and the situation is now sufficiently well understood to need only nomenclatural and classificatory clarification, as given below, before attention can be safely turned elsewhere.

In addition to the polyploid series, investigation has revealed that there appears to have been a good deal of evolution at the diploid level in the group: *D. pallida* has fragmented into a number of different geographical races morphologically more or less distinguishable from each other, and the alpine diploid is also mirrored by a probable corresponding taxon from Central Asia.

Classification

In the light of all this work on the group it has become necessary to produce a clear definitive classification, with up to date distribution data and figures of the taxa concerned. The following is therefore intended to clarify the situation and be a guide for the taxonomic treatment of this confusing group. The author feels strongly that the three major taxa in the popyploid series should be treated as species, but recognises that following Heywood (1964) in "Flora europaea" they have usually been treated as subspecies of *D. villarii* and that to avoid changes of rank some authors may prefer to leave them as subspecies; but in this author's view this is highly unsatisfactory as it does not cater well for the different races of *D. pallida,* besides which the three major taxa, *D. villarii, D. submontana,* and *D. pallida* are normally readily distinguishable and in addition to their reproductive isolation from each other, have distinct distributions and ecology.

Key[1]

Ferns of limestone regions, fronds with pale concolorous scales on the stipe. Lamina of a somewhat stiff or hard texture, glandular at least near the axes of the pinnae and pinna-segments, sometimes densely so even on both sides of the lamina; twice pinnate and sometimes a third time pinnatisect in lower parts of the frond. Pinnules on the acroscopic side of the pinnae more or less equal in length to those on the basiscopic side, except sometimes in the lowest pinnae where the basiscopic pinnules may be as much as $1^1/_2$ times as long as the acroscopic ones. Pinna segments lobed at the sides, lobes and tips of the pinna-segments bearing acute tipped teeth. Indusium glandular, more or less leathery, inflected when young
D. villarii aggregate (only on calcareous rock) and
D. tyrrhena (only on non-calcareous rock)

1a. Lowest two pairs of pinna-segments on pinnae not fully petiolate, though lowest pair approaches that condition. All other pinna-segments noticeably adnate, as in the *D. filix-mas* aggregate. Lateral margins of pinna-segments shallowly lobed, only those at very base of lamina more deeply lobed. Segment teeth curved inwards at the apex of the segments tetraploid . . . . *D. tyrrhena* (see Fraser-Jenkins & al. 1975)

1b. Lowest two pairs of pinna-segments on pinna fully petiolate, though the second pair sometimes scarcely reaches that condition. Other pinna-segments not all noticeably adnate. Lateral margins of pinna-segments deeply lobed, especially at the base of the lamina. Segment teeth pointing upwards along the axis of each segment (diploid or tetraploid) *D. villarii* agg. 2

2a. Plant of alpine regions (1500-2500 m alt.). Lamina narrowly lanceolate, widest just below the middle; stipe usually not more than one third the length of the lamina, pinnules fully stipitate only at the base of each pinna, up to the second pair (diploid) . . . . *D. villarii*

2b. Plant ranging from the Mediterranean littoral to submontane or subalpine regions. Lamina triangular-lanceolate or triangular, widest at the base; stipe half to two thirds the length of the lamina, pinnules usually fully stipitate up to a quarter of the way up the pinna or more 3

3a. Plant found from 500 m alt., up to 2000 m alt. in the extreme south of its range (Algeria, S. Spain, S. Greece). Lamina densely glandular on both sides. Pinnules not deeply lobed, and sometimes noticeably adnate, pinnule tips furnished with long narrowly acute teeth, lobes with long acute teeth mainly at the side of the lobe which is towards the tip of the pinnule (tetraploid) . . . . *D. submontana*

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[1] It should be noted that in this critical group it is not possible to produce a key which fits all specimens, and a few specimens in herbaria cannot be identified with certainty.

3b. Plant found from shortly above sea-level, up to 1700 m in the extreme south of its range (Turkey and W. Asia; higher in the Himalayas). Lamina sparsely glandular, and even less so on upper side. Pinnules varying from almost unlobed to almost pinnatisect. Pinnule tips and lobes furnished with triangular-acute teeth all over (diploid) . . . . *D. pallida*

1. **Dryopteris villarii** (Bellardi) Woynar ex Schinz & Thell., Vierteljahresschr. Naturf. Ges. Zürich 60: 339. 1915.

= *Polypodium fragrans* sensu Villars, Hist. Pl. Dauph. 1: 292. 1786 et 3: 843. 1789; non L. (1753).

= *Polypodium rigidum* G. F. Hoffmann, Deutschl. Fl. (Bot. Taschenb.) 2: 6. 1795; non Aublet (1775).

= *Polystichum strigosum* Roth, Tent. Fl. Germ. 3: 86. 1800.

= *Aspidium rigidum* Swartz in Schrader, J. Bot. 1800/2: 37. 1802.

= *Polypodium odoratum* Poiret in Lam., Encycl. Méth. Bot. 5: 541. 1804.

= *Polystichum rigidum* (Swartz) DC. in Lam., Fl. Franç. ed. 3, 2: 500. 1805.

= *Aspidium fragrans* S. F. Gray, Nat. Arr. Brit. Pl. 2: 9. 1821; non Swartz (1801).

= *Nephrodium rigidum* (Swartz) Desv., Mém. Soc. Linn. Paris 6: 261. 1827.

= *Aspidium rigidum* var. *alpinum* Tenore, Fl. Neap. Syll.: 139. 1830.

= *Lastrea rigida* (Swartz) C. B. Presl. Tent., Pteridogr.: 77. 1836.

= *Aspidium rigidum* forma *fallax, major, minor* et lus. *daedaleum* Milde, Verh. Zool. Bot. Ges. Wien 14: 12. 1864.

= *Aspidium rigidum* "forma *bipinnatisecta*" et "subforma *germanica*" Milde, Fil. Eur.: 127. 1867; nom. inval., pro parte

= *Polystichum rigidum* var. *vulgare* et *hypodematium* Trevisan, Atti Soc. Ital. Sci. Nat.: 230-231. 1874; pro parte

= *Aspidium rigidum* f. *pusillum* Goiran, Nuovo Giorn. Bot. Ital. 14: 46. 1882.

= *Dryopteris rigida* (Hoffm.) Underw., Our Native Ferns, ed. 4: 116. 1893; non A. Gray (1848).

= *Nephrodium rigidum* var. *typicum* Fiori in Fiori & Paol., Fl. Anal. Ital. 1: 9. 1896.

= *Aspidium villarii* (Bellardi) Borbas, Balaton Fl.: 313. 1911.

= *Dryopteris burnatii* Christ & Wilczek, Annuaire Conserv. Jard. Bot. Genève 15-16: 345-346. 1913; pro hybr.

= *Nephrodium villarii* (Bellardi) Beck, Glasn. Zemaljsk. Muz. Bosni Hercegovini 28: 382. 1917.

= *Nephrodium villarii* var. *rigidum* (Swartz) Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30/1: 26. 1924.

Basionym

Polypodium villarii Bellardi, Mém. Acad. Roy. Sci. (Turin) 5: 255. 1792.

Rhizome divided into several crowns crowded together, clothed with pale or pale-brown concolorous scales. Fronds upright, up to 40 cm high; stipe not usually more than a third the length of the lamina, but longer when growing through fallen rocks, densely glandular and densely clothed, especially near the base, with pale or pale-brown concolorous scales, ovate-lanceolate below, but becoming narrow further up and on the rachis, lamina narrowly lanceolate, widest about or just below the middle (some plants from the French Alps, W. Switzerland, S. Germany and elsewhere may be unusually wide and well developed, but do not normally become triangular-lanceolate. Such a plant has been described as *D. burnatii* Christ & Wilczek, mistakenly thought to be *D. villarii* x *D. austriaca*), mat blue-green above, paler below, well furnished on both sides and on the axes with stalked glands which impart a sweet scent of lemons to the plant and make the fronds sticky except when old; twice pinnate, pinnae pointing upwards in the top half of the frond and crowded together, triangular or triangular-lanceolate, pinnules fully stipitate only at the base of each pinna, deeply lobed with small lobes and a few narrowly acute teeth at the side of each lobe nearest to the pinnule tip, and more teeth, longer and more acute at the tip of each pinnule, sometimes with slightly mucronate tips; pinnule apices usually somewhat rounded. Sori with rather thin but persistent indusia, curved downwards at the edges, lifting somewhat when ripe, furnished with stalked glands. Spores dark reddish-brown with irregular wavy ridges on the perispore, ripe from late July to September. Diploid with 41 bivalents at meiosis ($n = 41$; cf. Manton 1950).

Open high alpine limestone rocks and screes from (1500-)1700-2500 m altitude.

1a. **Dryopteris villarii** subsp. **villarii**

Description and ecology as for the species. Diploid. Described from Mt.-Cenis, Savoie, France. Type in Torino (TO), not seen.

Distributed in Central Europe: France, Switzerland, Italy, Austria, W. Germany, Jugoslavia, Albania and Greece.

Detailed distribution:[1] The Jura of France and Switzerland, French Alps, Alpes-Maritimes, Swiss Alps, Italian Alps from Piémont and Aosta to the Dolomites and Julien Alps, the Northern Appenines, Apuanian Alps and Abbruzzi, the Bayerische Alps of S. Germany, the Austrian Alps East to Steiermark, Niederösterreich and the Karawanken, the higher mountains of the Dalmatian shield in Jugoslavia, Albania, Mt. Olympos and the Pindhos Mountains of N. Greece and as far south as Mt. Parnassos.

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[1] All distribution data in this paper are based on specimens seen by the author in examining the material of the follow herbaria over the last 10 years: ABN, B, BAS, BERN, BM, BP, BPU, BR, BRNM, BSD, BUC, BUCA, BUGG, C, CGE, CL, CLA, CLF, DUB (now DBN), DD, DE, E, FI, FI-W, G, G-DC, G-BOIS, G-BU, GB, GFW, GOD, H, I, ICEL, ISTF, JE, K, KR, KRA, KRAM, L, LAU, LD, LDS, LE, LTR, MA, MANCH, NMW, O, OAC, ODU, OXF, P, PAN, P-LA, PECS, PR, PRC, RAW, S, SIB, SZE, TBI, TGM, UME, UPS, W, WSY, WU, Z, ZT. Univ. La Laguna, Tenerife; Akureyri, Iceland; Ariamehr, Iran; Budapest Univ. Bot. Garden; Budapest Horticultural Univ., Szeged University; herbs: D. M. Britton, T. Reichstein, G. Vida, K. H. Rechinger (Greek), D. E. Meyer, R. Deschatres, F. Badré, J. Vivant, W. Greuter, A. Sleep, J. D. Lovis, H. V. Corley and C. R. Fraser-Jenkins.

1b. Dryopteris villarii subsp. **mindshelkensis** (Pavlov) Fraser-Jenkins, **comb. nova**

Basionym

Dryopteris mindshelkensis Pavlov, Vestn. Akad. Nauk Kazahsk. SSR 8: 129. 1954.

Differs from the type in its longer stipe and in the lamina being more triangular-lanceolate, often widest near the base, with pinnules less deeply dissect, and with fewer, longer, very acute teeth, longer still at the pinnule apex, pinnules sometimes narrowing a little towards the base.

Alpine regions at c. 2000 m altitude or above, on limestone. Described from the Karatau in Kazakhstan. Holotype in Tashkent, isotype in Leningrad (LE!).

Distributed in West Central Asia: Iran and U.S.S.R.

Detailed distribution: Mindshelke in the Karatau, Kazakhstan; North Alaysky Khrebet, Kirgizia; the Gissarsky Khrebet, Tadzhikistan and Kopet Dagh, N.E. Iran and Turkmenia.

2. Dryopteris submontana (Fraser-Jenkins & Jermy) Fraser-Jenkins, **comb. nova**
= *Aspidium rigidum* "forma bipinnatisecta" et "forma meridionalis" Milde, Fil. Eur.: 127. 1867; nom. inval. pro parte
= *Polystichum nivale* Miégeville, Rev. Cath. Diocese Tarbes 41: 763-764. 1873; nom. provis. (inval.)
= *Polystichum rigidum* var. *bertolonii* et var. *hypodematium* Trevisan, Atti Soc. Ital. Sci. Nat.: 230-231. 1874.
= *Aspidium rigidum* var. *cuneilobum* Borbás ex Luerssen, Farnpfl. in Rabenhorst, Kryptogamenfl. Deutschl. ed. 2, 3: 411. 1886.
= *Aspidium pallidum* lus. *furcatum* Bicknell ex Fiori, Fl. Ital. Crypt. 5: 113. 1943.

Basionym

Dryopteris villarii subsp. *submontana* Fraser-Jenkins & Jermy, Fern Gaz. 11: 338. 1977.

Holotypus

Dryopteris villarii Mid West York, v.c. 64, Ingelborough, on limestone outcrop, *I. Manton* ex Leeds University Botanic Garden (BM!).

Frondes erectae, ad 50 cm altae; petiolus plerumque c. 1/2 laminae aequans; lamina triangulari-lanceolata, bipinnata, griseo-luzulina, impolita, utrinque dense glandulis ornata; pinnae infimae dimensionem maximam plerumque habent; pinnulae ± profunde lobatae, praesertim apicem versus dentes acutos angustos ferentes. Cytotypus tetraploideus.

Rhizome divided into several crowns more or less crowded together clothed with pale or pale-brown concolorous scales. Frond morphology exactly intermediate between *D. villarii* and *D. pallida;* fronds upright, up to 60 cm high; stipe usually half the length of the lamina, or a little longer, densely glandular and clothed with pale concolorous scales, ovate-lanceolate below, but becoming narrow further up the rachis; lamina triangular-lanceolate, widest at the base, mat blue-green above, paler below, well furnished on both sides and on the axes with stalked glands, sometimes very densely so, which impart a sweet scent of lemons to the plant and make the fronds sticky; twice pinnate, pinnae pointing upwards in the top part of the frond and crowded except near the base, triangular-lanceolate, pinnules fully stipitate only at and shortly above the base of each pinna, ranging from virtually unlobed in some populations (S.W. Jugoslavia: Montenegro, where the plant can resemble the *D. filix-mas* aggregate) to fairly deeply lobed with narrowly acute teeth on the lobes, more prominent at the side of each lobe nearest to the pinnule tip, and more teeth, longer and more acute at the tip of each pinnule, sometimes with slightly mucronate tips; pinnule apices usually acute. Sori with rather thin but persistent indusia, curved downwards at the edges, lifting when ripe, and furnished with stalked glands. Spores dark reddish-brown with irregular wavy ridges on the perispore, ripe from late June to August. Tetraploid with 82 bivalents at meiosis ($n = 82$; cf. Manton 1950).

In crevices of open limestone rocks and screes in submontane areas, from 500 m upwards to 2000 m altitude in the extreme south of its range (Algeria; Sierra Nevada, Spain; Mt. Parnassos, Greece). Described from northern England. Holotype in BM, isotypes in G, LE, LTR and herb. G. Vida & T. Reichstein.

Distributed in Western and S. Central Europe and Western Asia, especially where the ranges of *D. villarii* and *D. pallida* overlap, but also outside the ranges of either, possibly due to its having intermediate ecological requirements: Britain, Spain, Algeria, France, Italy, Jugoslavia, Albania, Greece, Romania, U.S.S.R.,? Bulgaria (Plants from Algeria, Italy, Albania, Greece and U.S.S.R. have not yet been confirmed cytologically, but identified by the author).

Detailed distribution: The Lake District (rare or extinct), the Central and Western Pennines and the Peak District of Derbyshire, (rare and possibly introduced in the latter), England, and Snowdonia (rare or extinct) Montgomery & Denbighshire, N. Wales, in Britain; the Pyrenees and Alpes Maritimes in France; the Pyrenees, Picos de Europa, Sierra de Segura, Sierra Tejeda and Sierra Nevada in Spain; the coastal mountains of Blida and Djurdjura in Algeria; Liguria, the Alpi Apuani and the Abruzzi in Italy; the Dalmatian coastal mountains from Northern Istria south to Montenegro and Kosovo-i-Metohija in Jugoslavia; N. Albania; the Pindhos Mts., Vardhousia and Parnassos, and also further north towards Albania on Mt. Timfi, in Greece; South West Romania, nr. Baile Herculane; Western Abkhazia, Adygeya and Southern Krasnodarsky Kray in the Western Caucasus, U.S.S.R. Reports from the Pirin Planina, Bulgaria, by Hayek (1927) and Jordanov (1963) may refer to this species, but specimens have not been seen.

3. **Dryopteris pallida** (Bory) Fomin, Věstn. Tiflissk. Bot. Sada 20: 32. 1910.
= *Aspidium oenopteris* Tenore, Prodr. Fl. Neap.: LVIII. 1811; nom. nudum (a misprint and misidentification)
= *Aspidium rigidum* var. *australe* Tenore, Atti Real Ist. Incoragg. Sci. Nat. Napoli 5: 144, tabl. 2. 1832.
= *Aspidium pallidum* (Bory) Link, Fil. Sp.: 107. 1841; non Blume (1828).
= *Aspidium nivale* Bory ex Fée, Mém. Fam. Foug. 5: 298. 1852; pro syn.

= *Hypodematium nivale* Fée, Mém. Fam. Foug. 5: 298. 1852; nom. nudum
= *Lastrea nivalis* Moore, Index Filicum: 98. 1858; nom. nudum
= *Polystichum pallidum* (Bory) Todaro, Syn. Pl. Acotyl. Vasc. Sicil.: 35. 1866.
= *Polystichum pallidum* var. *intermedium* Todaro, Syn. Pl. Acotyl. Vasc. Sicil.: 35. 1866.
= *Aspidium rigidum* "forma bipinnatisecta", "forma meridionalis" et "forma tripinnatisecta" Milde, Fil. Eur.: 127. 1867; nom. inval., pro parte
= *Aspidium viscosum* F. Muller ex Trevisan, Atti. Soc. Ital. Sci. Nat. 17: 231. 1874; pro syn., non *Dryopteris viscosa* (J. Smith) Kuntze (1891).
= *Aspidium rigidum* subsp. *pallidum* (Bory) Christ, Fougères Alpes-Marit.: 24. 1900.
= *Aspidium rigidum* f. *eglandulosum* Rohlena, Sitzungsber. Königl. Böhm. Ges. Wiss. Prag., Math.-Naturwiss. Cl. 39: 36. 1902.
= *Polystichum pallidum* var. *inarimense* Bolle ex Guss. in Béguinot, Ann. Bot. (Roma) 3: 304. 1905; nom. nudum
= *Polystichum meridionale* Lojac., Fl. Sic. 3: 405. 1908; pro parte
= *Nephrodium australe* (Ten.) Guadagno in Fiori & Béguinot, Sched. Fl. Ital. Exsicc. ser. 3: 97. 1917.
= *Dryopteris villarii* var. *australis* (Ten.) Maire, Fl. Afrique Nord 1: 32. 1952.
= *Dryopteris villarii* subsp. pallida (Bory) Heywood, Feddes Repert. Spec. Nov. Regni Veg. 69: 44. 1964.

Basionym

Nephrodium pallidum Bory, Expéd. Sci. Morée 32: 287. 1832.

Rhizome often divided into several crowns, seldom crowded together, clothed with pale or pale-brown concolorous scales. Fronds spreading, up to 80 cm high; stipe usually at least two thirds the length of the lamina, sparsely glandular and sparsely clothed with pale concolorous scales, sometimes with dark centres at the base of the stipe (from Greece eastwards, always so in the Himalayas), ovate below, becoming ovate-lanceolate further up the rachis; lamina more or less triangular, widest at the base, noticeably leathery, light green above and paler below, sparsely furnished with stalked glands near the axes, sometimes nearly eglandular, but sometimes rather densely glandular in high mountain populations in the south of its range (Central Sardinia, N. Sicily, and the Pindhos mountains of Greece), sweet scented when fronds young; twice pinnate or often nearly three times pinnate below; pinnae not crowded together, lanceolate; pinnules fully stipitate up to halfway up the pinna except when plant growing in a very dry exposed locality, varying from hardly lobed at all to nearly pinnatisect ("forma tripinnatisecta" Milde), lobes larger than in *D. villarii,* with somewhat triangular-acute teeth over the whole edge of the pinnule, those at the tips being the longest (in high mountain populations of central Sardinia, N. Sicily and the Pindhos Mountains of Greece the apical pinnule teeth are often markedly long and narrowly acute); pinnule apices acute or rounded-acute. Sori with somewhat leathery persistent indusia, curved downwards at the edges but lifting when ripe, furnished with stalked glands. Spores brown with irregular wavy ridges on the perispore, ripe from May to June. Diploid with 41 bivalents at meiosis (n = 41) (Roy 1967).

In crevices of lowland limestone rocks, often below trees, from shortly above sea-level up to 1700 m altitude in the south of its range (S. Turkey and Lebanon; higher in the Himalayas). Does not tolerate atlantic climatic influence.

3a. **Dryopteris pallida** subsp. **pallida**

Description and ecology as for the species. Diploid (Roy 1967). Described from S. Greece. Syntypes in Paris (P!).

Distributed in the Eastern Mediterranean area: Tunisia, Corsica (extinct), Sardinia, Italy, Sicily, Jugoslavia, Albania, Greece, Crete, Turkey.

Detailed distribution: Mistakenly reported from Morocco as *D. rigida* (Hoffm.) Underw. var. *riphea* Pau & Font-Quer, Iter. Marocc. No. 3 (1927), (types (G) = *Athyrium filix-femina*). The Zaghouan and Bargou Mts. of N.E. Tunisia; nr. Corte in Central Corsica (extinct), mistakenly recorded elsewhere in Corsica; throughout Sardinia; mistakenly reported from nr. Trento, N. Italy, found from Rome southwards in Italy; Sicily and Pantelleria; from the Velebit southwards along the Dalmatian coast of Jugoslavia; Albania; throughout Greece and the Aegean Islands; Crete; Bursa and the mediterranean coast of Turkey, from Çanakkale southwards and east along the coast as far as Maraş province (mistakenly reported from Bitlis, specimens (E) = *D. filix-mas*), merging in S. Turkey (Antalya) with subsp. *libanotica.*

3b. **Dryopteris pallida** subsp. **balearica** (Litard.) Fraser-Jenkins, **comb. nova**

= *Aspidium pallidum* var. *balearicum* (Litard.) Sennen & Pau, Butl. Inst. Catalana Hist. Nat. 1911: 16-19. 1912.
= *Aspidium pallidum* subsp. *balearicum* (Litard.) Colom, Biogeogr. Balear. 1957.
= *Dryopteris villarii* var. *balearica* Widén & al., Helv. Chim. Acta 54: 2836. 1971; nom. nudum
= *Dryopteris balearica* (Litard.) Nardi, Webbia 30: 28. 1976.

Basionym

Dryopteris rigida var. *balearica* Litard., Bull. Acad. Int. Géogr. Bot. 21: 23. 1911.

Differs from subsp. *pallida* in its smaller size (fronds up to 25 cm long); stipe thin, as long as lamina or often longer; lamina densely glandular, deltoid-triangular, twice pinnate, lowest pair of pinnae deltoid triangular with markedly long lower pinnules, others triangular-lanceolate; pinnules mainly adnate at their bases, fully stipitate only at the base of the lowest pair of pinnae, somewhat shallowly lobed with rather irregularly shaped lobes and elongated lowest pairs of lobes; lobes with acute teeth mainly at the side nearest to the pinnule apex, teeth at the pinnule tips long and acute. Diploid (Vida 1969).

In crevices of limestone rocks from 100-1400 m altitude. Described from the Balearic Island of Mallorca. Type in Paris (P!).

Distributed only in the Balearic Islands: endemic to the Island of Mallorca.

In some respects intermediate in morphology between *D. villarii* and *D. pallida* though it has features special to itself and is clearly closer to *D. pallida.* It may represent a more ancient stock of *D. pallida.* Populations of *D. pallida* subsp. *pallida* from the mountain regions of Central Sardinia, N. Sicily and the Pindhos mountains of Greece which have small densely glandular fronds, long acute pinnule-teeth and more adnate pinnule bases may also be more ancient than lowland populations of subsp. *pallida,* and approach subsp. *balearica* to a certain extend, though obviously closer to subsp. *pallida.* The relationship between subsp. *balearica* and subsp. *pallida* has been investigated by Vida (pers. comm.), who has produced the artificial diploid hybrid between the two. This shows complete pairing of its chromosome complement but the spores appear abortive, probably due to genetic incompatibility.

3c. **Dryopteris pallida** subsp. **libanotica** (Rosenstock) Fraser-Jenkins, **comb. nova**
= *Dryopteris libanotica* (Rosenstock) C. Chr., Ind. Fil.: 275. 1905.

Basionym

Aspidium libanoticum Rosenstock, Mém. Herb. Boissier 9: 1. 1900.

Very close to subsp. *pallida,* and differs only in having marginal sori. Diploid (Vida, in Widen et al. 1971). Described from the Lebanon.

Distributed in S.W. Asia: Turkey, Cyprus, Syria, Lebanon and Israel.

Detailed distribution: Antalya and Mersin provinces of S. Turkey, and the Amanus mountains of Antakya province (previously in Syria) – in all these three provinces along with subsp. *pallida* and fertile intermediates, probably indicating that introgression is occurring between the two, which must originally have diverged in isolation from each other; the mountains of N.W. Syria; Liban mountains of the Lebanon; and the north tip of Israel.

3d. **Dryopteris pallida** subsp. **raddeana** (Fomin) Fraser-Jenkins, **comb. nova**
= *Dryopteris raddeana* (Fomin) Fomin, Fl. Cauc. Crit. 1/1: 57. 1913.

Basionym

Nephrodium raddeanum Fomin, Věstn. Tiflissk. Bot. Sada 12: 8, tab. 2. 1908.

Differs from subsp. *pallida* in its larger size (fronds up to 100 cm long) and in having caudate pinna apices; pinnules varying from mostly adnately based and unlobed (in small fronds from open places) to fully stipitate up to halfway up the pinna and nearly pinnatisect – though usually only shallowly lobed; teeth at the sides of the pinnules few (or even absent) and small, but those at the tip markedly long and somewhat triangular acute, with a long point. Most specimens have dark-centred scales at the base of the stipe. Diploid (Vida, pers. comm.).

On limestone rocks from below sea-level (the Caspian coast) up to c. 600 m altitude, frequently in woods above limestone. Described from near Lenkoran in the Talysch. syntypes in Tbilisi (TBI! and TGM!).

Distributed in Western Asia: U.S.S.R. and Iran.

Detailed distribution: Confined to the south-western Caspian coast; the Talysch of Azerbaijan in S.E. Transcaucasia; the coastal side of the Elburz mountains from Astara as far east as Gorgan in Iran.

3e. Dryopteris pallida subsp. **nigropaleacea** Fraser-Jenkins, subsp. **nova**

= *Nephrodium rigidum* sensu Clarke, Trans. Linn. Soc. London Bot. 1: 523. 1880; non (Swartz) Desv. (1827).

= *Nephrodium odontoloma* sensu Hope, J. Bombay Nat. Hist. Soc. 14: 736, tab. 31. 1903; pro parte max., non Moore (1858), nom. nudum, nec Moore ex Bedd. (1863).

= *Dryopteris odontoloma* sensu Stewart, Bull. Torrey Bot. Club 72: 405. 1945; pro parte max., non (Moore ex Bedd.) C. Chr. (1924).

= *Dryopteris odontoloma* "diploid" sensu Mehra & Loyal, Caryologia 18: 461-498. 1965; non (Moore ex Bedd.) C. Chr. (1924).

Holotypus

"*Dryopteris odontoloma* (Moore) C. Chr.: Mussoorie coll.: Loyal 1953" (BM!).

Similis *D. pallidae* subsp. *pallidae,* sed pinnulae minus profunde lobatae et apice longius dentatae. Differt a *D. odontoloma* (Moore ex Bedd.) C. Chr. apice pinnularum acutiore. Paleae ad basim petioli sitae omnino nigrae, lucentes, altius in petiolo margine pallidae dein in costâ pallidae. Cytotypus diploideus.

Similar to subsp. *pallida,* but differs in having less deeply lobed pinnules with longer teeth at their apices – tending towards subsp. *raddeana.* Differs from *D. odontoloma* in having more acute pinnule apices and narrower pinnules. Fronds less glandular and the scales at the base of the stipe are entirely black, while those higher up have pale edges, and those on the rachis and top of the stipe are completely pale. Diploid (Mehra & Loyal 1965) (*D. odontoloma* is triploid).

Crevices in open calcareous rocks, or more often under trees, from 1000 m to 3000 m altitude.

Distributed in E. Afghanistan and the N. West Himalayas: Afghanistan, China?, Tibet, Pakistan, India, Nepal.

Detailed distribution: Kurram, Konar and (?) Wakhan in E. Afghanistan; Waziristan, Dir, Chitral, Gilgit, Hunza, Baltistan, Kalam, Swat, Murree and Hazara in Pakistan; Kashmir, Poonch, Jammu, Ladak, Chamba, Dharmsala, Simla, Dehra Dun, Tehri Garwhal, Kumaun and Nainital in N.W. India; Western Tibet; West Nepal; (?) S.W. Sinkiang nr. the Pakistan border in China; recorded in error for *D. odontoloma* from the East Himalayas and South India.

A related diploid taxon which is sufficiently distinct from *D. pallida* to be recognised as a species is *D. arguta* (Kaulf.) Watt of the West Coast States of the U.S.A. and Canada (California, Oregon, Washington and British Columbia); it seems to vary considerably, some plants being very close to *D. pallida* while others have more rounded and less lobed pinnules, with more mucronate teeth.

Hybrids

It should be possible to find naturally occurring hybrids of the *D. villarii* aggregate in places where two or more of the species occur together – in particular the Abruzzi of S. Italy, Jugoslavia, Albania and Greece, and the Alpes-Maritimes of S. France. The hybrids should be recognisable by their intermediate morphology and abortive spores; however a collection made by the author on Korax Oros, Vardhousia Ori, S. Greece, contains some specimens with abortive spores (CRFJ no. 4120, BM) which are probably not hybrids, even though *D. submontana* and *D. villarii* were both growing in the vicinity. The sporangia contained spores with thick black deposits of sporopollenin and of irregular shape, but which were fully mature. However a very few sporangia from elsewhere on the same fronds contained good spores and the morphology suggested only *D. villarii.* The abortive spores may have been the result of some infection; when the sporangia fail to develop properly due to environmental factors, the spores appear as misshapen, transparent objects, as if they were immature. These Greek specimens show that hybrid-type abortive spores alone cannot always be regarded as an absolutely reliable indication of hybridity in *Dryopteris* even though the author has not come across this in any other specimens of the many thousands he has both collected himself and examined in many European herbaria. If the morphology leaves any doubt then a chromosome count may be the only way to be certain of a plant's hybrid nature.

However specimens in Copenhagen (C) and Wien (W) collected along with *D. pallida* and *D. submontana,* by Heldreich (no. 556) on Mt. Parnassus, Greece, at 4500′, with abortive spores, are intermediate in morphology between *D. pallida* and *D. submontana* and are almost certainly that hybrid – all three species grow on Mt. Parnassus. The triploid hybrid between *D. villarii* and *D. submontana* should be relatively common, though the diploid hybrid *D. villarii* x *D. pallida* is likely to be a good deal rarer.

A specimen (in MANCH) collected by Revol in the Ardèche Valley of Southern France, at Pont de Labeaume and reported as "*D. abbreviata*" (= *D. oreades* Fomin) in Revol (1910) and again in Berthet & Bange (1960) is not this species, but appears at first sight to be close to *D. tyrrhena* Fraser-Jenkins, Reichstein & Vida, or a hybrid of *D. villarii.* Careful examination of the spores shows that there is a mixture of good and abortive spores, and in fresh specimens from a plant collected by the author in 1972 (*Fraser-Jenkins 3602,* BM) it has been possible to count the number of spores in undehisced sporangia. There are 32 instead of the usual 64, which indicates that the plant is apogamous. It is tetraploid (Vida, pers. comm.), and has been found in two localities south of the Massif Central. It seems to constitute a hybrid of which the parentage on morphological grounds was probably *D. pseudomas* ($3x$) x *D. villarii,* or *D. pseudomas* ($2x$) x *D. submontana.* Further work remains to be done to discover which species in the *D. villarii* aggregate was involved, and the ploidy of the *D. pseudomas* parent; however this new hybrid is described below and named after the Cevennes mountains where it occurs:

Dryopteris x cebennae Fraser-Jenkins, **hybr. nova**

Holotypus

"*Polystichum filix-mas* var. *abbreviatum*, rochers basaltiques au cirque du Pont-de-Labeaume, Ardèche, France, *J. Revol*, 1910" (MANCH).

Intermedia inter *D. submontana* et *D. pseudomas*. Frondes usque ad 50 cm longae; petiolus mediâ longitudine laminae, paleis angustis uniformibus pallide fulvis costam versus angustissimis piliformibus parce obsitus; lamina triangulari-lanceolata, ad axes glandulis crebre obsita, simpliciter pinnata sed par inferius pinnularum cujusque pinnae iterum pinnatum; pinnulae basi latâ sessiles, pari infimo cujusque pinnae excepto quod bene petiolulatum; pinnula infima basiscopica paris infimi pinnarum longissima et ad marginem aliquanto lobata; latera pinnularum aliarum parallela parce tantum dentata nisi apicem versus, apices rotundati et dentibus longis valde acutis interdum mucronatis ornati. Indusia cinerea, margine leviter inflexo. Sporae partim abortivae, partim bene evolutae. Cytotypus tetraploideus, apogamus.

Intermediate between *D. submontana* and *D. pseudomas* in morphology and close to *D. tyrrhena*. Fronds up to 50 cm long; stipe half the length of the lamina, sparsely clothed with narrow uniform pale brown scales which extend up the rachis becoming very narrow and hair-like; lamina triangular-lanceolate well furnished with glands on the axes; once pinnate, a second time pinnate at the basal pair of pinnules of each pinna; pinnules adnate with wide bases except the lowest pair on each pinna which are fully petiolate, the lowest basicopic pinnules of the lowest pair of pinnae being the longest and somewhat lobed at the sides; sides of the other pinnules parallel and only slightly toothed except near their apices, apices rounded and furnished with long and very acute teeth, sometimes mucronate. Indusia grey with edges slightly curved down. Spores partially abortive. Cytotype tetraploid, apogamous.

Distributed in the Cevennes, S. Central France at c. 500 m altitude on silicaceous rocks.

Other specimens seen:

1. Ardèche: Pont-de-Labeaume, France, 1.9.1965, *Bange* (P) – along with *D. pseudomas*. Berthet & Bange (1960) report the original specimen of Revol and two other specimens (*Bange 248* and *Vanden Berghen*, 1956) as *D. abbreviata*, however the two specimens they quote are in Paris and are not *D. oreades* (= *D. abbreviata* auct., non DC.) but *D. filix-mas* and *D. pseudomas*. *D. oreades* does however grow in Ardèche, at Borée, *Deschatres*, 1973 (BR) and Mt. Gerbier de Jonc, *Deschatres* (CLF) also in Lozère at Mt. Lozère, *Deschatres*, 1973 (BR), and in Aveyron at La Croix-Barrex, *Carbonet*, 1934 (BR). It has been recorded from a large number of places in France by Jalas & Suominen (1972) and other authors, but having checked most of the specimens concerned and examined the collections of most of the major European herbaria, the author can now state that in France *D. oreades* only occurs in the Departments of: Basses-Pyrénées, Hautes-Pyrénées, Haute-Garonne, Ariège, Andorra, Pyrénées-Orientales, Corse, Corrèze, Cantal, Puy-de-Dôme, Loire (Forez and (?) Pilat),

Haute-Loire, Ardèche, Lozère, Aveyron and Hérault. Reports from the Vosges and Northern France are erroneous.

2. Ardèche: Pont-de-Labeaume, France, 1953, *Denizot* (P).
3. Villefort-Les-Vans, Chassezac, Ardèche, France, 17.1.1972, *Fraser-Jenkins 3599 & 3600* (BM).
4. Above Pont-de-Labeaume, nr. Aubenas, Ardèche, France, 17.1.1972, *Fraser-Jenkins 3602* (BM – tetraploid).

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