

THE SPECIES AND SUBSPECIES IN THE DRYOPTERIS AFFINIS GROUP

C.R. FRASER-JENKINS

Student Guest House, Thamel, P.O. Box no. 5555, Kathmandu, Nepal
(chrisophilus@yahoo.co.uk)

Key words: *Dryopteris affinis*, Europe, taxonomy, specific rank, subspecies, hybrids

ABSTRACT

Following discussion of the different levels of variation and the ranking of the taxa, "morphotypes" have been replaced with formal names. The main taxa within the *Dryopteris affinis* aggregate in Europe, formerly treated as subspecies of *D. affinis*, are treated as six species, while the former geographical varieties are treated as nine subspecies belonging to three of the species. Seven new combinations are made at the subspecific rank and two new subspecies are described. A new species-name, *D. iranica* Fras.-Jenk. replaces *D. wallichiana* subsp. *coriacea* (Fras.-Jenk.) Fras.-Jenk. Four hybrids between the *D. affinis* agg. and *D. filix-mas* are treated at the nothospecific rank, two of them new and a third a new combination. Two of the hybrids are divided into six nothosubspecies, three of them new. A detailed key and comparative diagnostic descriptions are given, but it is not intended here to discuss the proposed different origins for the taxa and the evidence for those origins.

INTRODUCTION

The European, Macaronesian and W. Asian *Dryopteris affinis* (R.Lowe) Fras.-Jenk. ("*D. paleacea*" auct., *D. borrieri* Newm., *D. pseudomas* (Wollast.) Holub & Pouz.) has long been known as the third member of the *Dryopteris filix-mas* (L.) Schott or Male Fern group, along with two other species, *D. filix-mas*, *D. oreades* Fomin ("*D. abbreviata* Newm." sensu Manton 1950) and, later, a fourth species, *D. caucasica* (A.Braun) Fras.-Jenk. & Corley. *Dryopteris affinis* is an apomictic complex, several of its members presumably derived by hybridisation of various taxa, but in all cases thought to contain a genome in common with or related to the pan-subtropical species, *D. wallichiana* (Spreng.) Hyl. They belong together with the other species with parallel-sided, \pm truncate segments in Sect. *Fibrillosae* Ching, rather than in Sect. *Dryopteris*, where the rest of the Male Ferns belong.

As is well known, apomixis in *D. affinis* means that hybridisation with a sexual species can give rise to a new fertile, apomictic taxon of a different cytotype. Such hybridogenous taxa almost certainly correspond with and are the origin of most of the species within the group (Fraser-Jenkins 1982, as subspecies), though further longer-term study remains to be carried out to add to the known evidence for their proposed origins. However three of the species recognised here (from continental Europe and W. Asia) are insufficiently known as to their origin, but being well known taxa which appear to be of major distinction and having formerly been treated as subspecies, they are now raised to specific rank along with the others.

The other important result of apomixis in *D. affinis* is that any variants that arise within members of the group are preserved by the cloning type of reproduction through

spores. The more major variants have a discrete morphological difference and a partially distinct geographical range and are recognised here as subspecies, which may be of quite ancient origin. They are generally of a similar morphology to the species concerned, but are readily recognisable by their special morphological characteristics. In addition, more minor variants also occur frequently within and between populations, which differ only slightly from the general pattern of the subspecies and can be found here and there in various populations throughout the range of the subspecies. Although they may be partially distinguishable, they are connected by intermediates occurring in other localities and while they may be more-or-less recognised from place to place they merge into one another when all the intermediates from other populations are considered. These more minor variants are therefore understood to be merely part of the variation within the species and are not recognised here as being worthy of nomenclatural distinction. If some of them were needed to be recognised they could be more appropriately treated at the lower ranks of variety or forma, which would not have to be included in general floristic works, including County recording etc.

Detailed study of *D. affinis* throughout its range in Macaronesia, Europe and W. Asia resulted in the present author (Fraser-Jenkins 1980, 1982, 1983, 1987, 1996*a* and *b*, Widén *et al.* 1996, Fraser-Jenkins & Trewren in prep.) separating a number of entities within it. These were initially treated as infraspecific taxa at the rank of subspecies (corresponding to the present species), with varieties (corresponding to the present subspecies) placed within them. This ranking of the group was then considered appropriate because *D. affinis sens. lat.* was widely considered to be of taxonomic equivalence to the other species recognised within the genus and some reluctance to accept further critical taxa within it was brought to the attention of the author at the time. In the author's previous and present treatments the taxa were placed hierarchically in order to reflect their morphological and cytological relationships to each other.

Although following the present author in the taxa recognised, Jermy in Jermy & Camus (1991), chose not to accept his hierarchical taxonomic scheme and placed all the taxa he recognised into the category of "morphotypes". These were intended to be temporary unranked names as a convenient handle to use for any recognisable variant in the complex since the authors had not themselves decided at what rank they would place taxa and did not propose an alternative taxonomy. Morphotypes were thus invalid names outside the standard and universally used hierarchy and Articles of the International Code of Botanical Nomenclature (ICBN 2005) and the authors also took the term morphotype in a different sense from that originally defined by Danser (1950), or Davis & Heywood (1970). In addition the relationships of taxa as reflected in the present author's taxonomic scheme were obscured and no longer recognised. Jermy was followed by Pigott (1997), who added three new morphotype names, two for more minor morphological variants, not recognised here, and the third ("morphotype *arranensis*") being an additional name for a new taxon recognised by the present author and cited by Pigott. The new morphotypes were published as Latin names, but although without a type or type-concept, they have been placed here in the synonymy of the relevant species and subspecies from material kindly made available to the author by Pigott. Morphotypes were advocated again, as the accepted treatment, by Jermy, Pigott & Merryweather (1998) and by Merryweather (2002), though suggesting that up to 70% of specimens were of doubtful identity and that there might be up to 11 possible species in Britain.

Thus until now the group has remained in a state of confusion with the existence of

two alternative types of treatment and the suggestion that it is much more complex than hitherto published or than indicated in Nature and is thus almost intractable to botanists in general. However the relationships and relative placement of the known varieties and subspecies in a formal taxonomic framework have continued to be appraised carefully in the field by the present author and as the present taxonomy has been found to work well, this scheme is again recognised here, as by Fraser-Jenkins (1996a). While it is acknowledged that the taxa in this group, like many others, require further sophisticated study of their origin and that a few of the apparently more minor variants within *D. borrieri* require study as to whether they could be of greater significance, it is hoped that recent confusion can now be laid to rest and the established taxa can be treated in a normal botanical framework.

Part of the reason for recourse to morphotypes was that the authors did not wish to comment on possible relationships and the relative taxonomic significance of the taxa and were studying locally without seeing the larger picture of the taxa throughout their range. Although the vast majority of species have long been described without detailed molecular evidence and continue to be so, the use of morphotypes was also felt appropriate by some authors who sought further genetic, cytological, chemical or molecular proof of the present taxonomic scheme. However no suggestion was made as to where it might be mistaken, or contradicting it, and most workers today have come to accept the main taxa recognised by the present author. Further problems have been caused by the presence of the many minor variants within the subspecies, as following recognition of such variant forms locally, some workers have found it difficult to accept their placement within the species or subspecies. This has also been compounded by prevailing cladistic concepts that a species has to be a single homogeneous entity. But where this has been adhered to with insufficient use of subsidiary and lower ranks to allow for different levels of variation, it has already created enormous practical problems. Thus several now much confused and notorious Angiosperm genera have suffered from excessive separation of unwarranted microspecies unbalanced by practical considerations and have reached a state where almost no one can put a name on a specimen any more. The present scheme has undergone continuing reappraisal for more than 25 years in both field and herbarium and has been successfully used by a number of workers both in Britain and abroad and it is therefore hoped that its clarification here and will help to avoid some of the above difficulties. In particular it is hoped that the temporary and rather unsatisfactory usage of non-standard morphotype names, which have inevitably become the equivalent of formal names, may now be superseded by reverting to standard botanical nomenclature. Doing so will not preclude the recognition of new taxa, should that occur, nor adjustment of rank for individual taxa, should it become necessary, but it is emphasised that the rank of the species and subspecies, particularly in Britain now appears to have reached some stability and general acceptance.

A relatively major and important change in the taxonomy is effected here in altering the rank of the main taxa from subspecies to species. Taxonomic understanding of the group has undoubtedly changed considerably from 25 years ago, when the existence and delimitation of its constituent taxa were little known. Given the fact that the important taxa, the former subspecies, recognised within *D. affinis* by the author are sufficiently distinct and are now generally and widely able to be recognised, they are treated here as species in their own right. The choice of species versus subspecies is always an arbitrary one, and originally the rank of subspecies was chosen as much the

better “middle ground”, with good grounds to support it at the time. But as time has gone on, their distinctiveness and ranges of variation have become much better known to botanists than they were a decade ago, as have their apparent relationships. In general they can be considered to be of roughly the same degree of distinction as the other species of the Male Fern group and, being readily recognisable from their gross morphology alone, it is more appropriate to recognise them as species. This also reflects the biology of the taxa since it is known that most of them have a different individual biological (cytological and genomic) basis, though the mere fact of the existence of such a difference, had it been in the absence of relatively major and readily recognisable morphological separability would in the present author’s opinion be an inappropriate and undesirable basis on its own for recognising species.

As there are few great practical difficulties in the *D. affinis* group, the previous subspecies are recognised in the present paper as species, and in tandem with this the previous varieties are treated in a standard way as geographical subspecies within them. Variant forms below these ranks are not considered to be of sufficient taxonomic significance to be recognised here, though many have already been named in the past as varieties or forms. They are obviously morphologically close to the subspecies concerned and it can readily be recognised as to where they belong; these include two of the new morphotypes of Pigott, one of which has been found (Fraser-Jenkins & Trewren in prep.) to have similar 16 spore-mother-celled chromosome-pairing behaviour and to be chemically similar (Widén *et al.* 1996) to *D. borrieri*, though further study is required into variation within the latter.

TAXONOMIC TREATMENT

The three best known species occurring throughout most of the range of the group, and the only three known so far from Britain, are *D. affinis*, *D. cambrensis* and *D. borrieri*. Fortunately all three names, now well known as subspecies and two of them also as species names, appear to be usable at the specific rank, despite the involved and complicated synonymy of the taxa within the group.

The currently accepted species and subspecies in the *D. affinis* group are as follows (those with an asterisk inserted after the names are present in Britain and/or Ireland):

1. *Dryopteris affinis** (R.Lowe) Fras.-Jenk., *Fern Gaz.* **12**(1): 56 (1979), *non* Newm. (1854) [*nom. inval.* for *Lastrea filix-mas* var. *affinis* Newm.]. Lectotype (Fraser-Jenkins 1980): from Madeira (Ribeiro Frio), *R.T. Lowe*, 1 Nov. 1828 in K!, paratypes: in K! BM! M! B! *etc.* Cytotype: Diploid apomict.

A. subsp. *affinis**. Synonyms: *D. affinis* [subsp. *affinis*] var. *affinis* (in Fraser-Jenkins 1980), *Dryopteris borrieri* var. *subintegra* (Aschers & Graebn.) Tavel (1937) [based on *Aspidium filix-mas* var. *subintegrum* Döll (1857), *non* Boreau (1840)], *D. pseudomas* (Woll.) Holub & Pouzar (1967), *D. mediterranea* Fomin [= *D. wallichiana*] f. *disjuncta* Fomin, *D. affinis* [subsp. *affinis*] var. *disjuncta* (Fomin) Fras.-Jenk. (1980), *Dryopteris resendeana* Rezend.Pinto (1969), *Dryopteris borrieri* subsp. *resendeana* (Rezend.Pinto) Malagar. (1975), *Dryopteris affinis* [subsp. *affinis*] var. *azorica* Fras.-Jenk. (1980). Cytotype: Diploid apomict, the rare 16-smc sporangia showing almost all univalents (Manton 1950, Döpp 1955). Range: Can, Mad, Az, Mor, Lu, Hs, Andorra, Ga, Co, Be, Lux, Ho, Br (Scot., Wales, Engl. [VC. S, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 16, 17, 20, 21, 22, ??23, 24, 27, 29, 30, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 66, 67, 69, 70,

71, 72, 74, 75, 77, 78, 79, 83, 85, 86, 87, 89, 90, 92, 95, 96, 97, 98, 99, 100, 101, 103, 104, 105, 106, 107, 108, 109, 110, ??111, 112), Hb [VC H1, H2, H3, H4, H5, H6, H7, H8, H9, H10, H11, H12, H13, H14, H16, H17, H20, H21, H22, H27, H28, H29, H31, H32, H35, H36, H38, H39, H40], No, Ge (W and E), He, Liecht, It, Elba, Si, Sa, Au, Ju (Slov., Hrvat.), Ro, An, Rs (S) (Caucasus (Karach.-Cherk.), W. Transcaucasus (Gruz., Abkhaz., Adzhar.)). Specimens of this subspecies with more acute teeth and slightly convex pinnae were invalidly named by Pigott (1997) as his “morphotype Convexa”. This taxon is understood here to be one of the minor variant forms within subsp. *affinis*, occurring with intermediates from place to place and not requiring nomenclatural recognition. Some other specimens named as “Convexa” appear to be less lobed or convoluted specimens of subsp. *paleaceolobata* and some are flatter-pinnuled specimens of *D. cambrensis*. In its tothing it is slightly towards subsp. *punctata* and subsp. *paleaceolobata*, but is obviously not as distinct as they are.

B. subsp. *paleaceolobata** (T.Moore) Fras.-Jenk., **comb. nov.**, basionym: *Lastrea filix-mas* var. *paleaceo-lobata* T.Moore, *Handb. British Ferns*, ed. 3: 112 (1857). Lectotype, here designated: from Scotland, Dumbartonshire, “*Lastrea filix-mas paleaceo-lobata*. Tarbet, Dumbartonshire, 1855, *T.M.*” (K-Moore!), isolectotypes (x 3): Ditto: “var. *paleacea* (M) crispy and incised form”, and same loc. and date, “Herbarium Hookerianum 1867” (K! one specimen). Synonym: *D. affinis* [subsp. *affinis*] var. *paleaceolobata* (T.Moore) Fras.-Jenk., **comb. inval.** (1996). Cytotype: Diploid apomict (Manton 1950, identified more precisely in Fraser-Jenkins & Trewren in prep.). Range: Br (Scot., Wales, Engl. [VC. 1, 2, 3, 5, 35, 36, 38, 41, 42, 43, 46, 47, 48, 49, 55, 61, 62, 69, 70, 78, 85, 88, 89, 96, 98, 99, 101, 103, 105], Hb [VC. H1], [Be, adventive], ?Ge (J. Freigang, det. CRFJ, Dec. 2002).

C. subsp. *punctata* Fras.-Jenk., **subsp. nov.**, *facies superiora laminae laevis et paleae stipitis rhachidis angustae ut in subsp. affinis; sed facie superiora pinnularum valde depressa super solum et dentibus acutioribus longioribus flabellatis differt.* Holotype, here designated: Switzerland, Kt. Zürich, above Hutten [N. side of Hohen Rohn mountain], c. 950 m. alt., Leg. E. Oberholzer, 3 Oct. 1962; frond pressed by T. Reichstein 740, 12 Aug. 1974, in BM! (sheet with the lower half of the frond is here designated holotype), isotypes: in BM! Z! ZT! NY! GRU! DUB! Fronds collected by the present author from the type-plant cult. by T. Reichstein in Basel: in BM! FR! BR! G! NMW! *D. affinis* [subsp. *affinis*] var. *punctata* Oberh. & Tavel *ex* Fras.-Jenk. (1980) was probably invalid as it was not indicated which specimen of TR 740, in which herbarium, was the holotype. Thus a new subspecies has been described here, rather than making a new combination. Synonym: *D. affinis* [subsp. *borreri*, *err.*] var. *splendens* (Ehrler 1950, as a subvar.) Fras.-Jenk. (1980). Cytotype: Diploid apomict (Manton 1950, Eschelmüller & Schneller 1980, Reichstein & Schneller 1983 *etc.*). Range: Ga, Ge (W.), He, Au, Ju (Slov., Hrvat.), An.

D. subsp. *kerryensis** (Fras.-Jenk.) Fras.-Jenk., **comb. nov.**, basionym: *Dryopteris affinis* [subsp. *affinis*] var. *kerryensis* Fras.-Jenk. in Widén, Fraser-Jenkins, Reichstein, Gibby & Sarvela, *Ann. Bot. Fennici* **33**: 73 (1996). Holotype: from Ireland, Co. Kerry (Tahilla to Rossdohan, Kenmare), *CRFJ* 15174, 6 June 1988, in BM!, isotype: ditto, in G! Cytotype unknown, but has relatively small, regular spores similar to those of subsp. *affinis*, which almost certainly indicate that it is diploid. Range: Hb [VC. H1, H2, H3, H4, H5, H6, H7, H16].

E. subsp. *jessenii* (Fras.-Jenk.) Fras.-Jenk., **comb. nov.**, basionym: *Dryopteris affinis* [subsp. *affinis*] var. *jessenii* Fras.-Jenk., in Widén, Fraser-Jenkins, Reichstein,

Gibby & Sarvela, *Ann. Bot. Fennici* **33**: 73 (1996). Holotype: from Romania, Judeþ. Oltenia (road above Băile Herculane), *CRFJ* 3503, 27 July 1971, in BM!, isotypes: ditto, in G! H!, paratypes: in Herb. S. Jessen, Chemnitz! BR! G! Z! PRC! Cytotype: Diploid apomict (Jessen 1991). Range: Ju (Srb.), Ro.

2. *Dryopteris cambrensis** (Fras.-Jenk.) Beitel & W. Buck, *Fiddlehead Forum, Bull. Amer. Fern Soc.* **15**(2): 15-16 (1988). Holotype: Britain, Wales, Merionethshire [= Gwynedd] (Bala, below Arennig Fawr), *CRFJ* 12748, 18 Sept. 1986, in BM!, isotypes: B! BP! DUB! E! G! H! K! NMW! NY! P! Z! Synonym: *D. affinis* subsp. *cambrensis* Fras.-Jenk., in Derrick, Jermy & Paul, *Sommerfeltia* **6**: xi [-xiii] (1987). Cytotype: Triploid apomict.

A. subsp. *cambrensis**. Synonym: *D. affinis* [subsp. *cambrensis*] var. *paleaceocrispa* (T.Moore) Fras.-Jenk., *nom. inval.* (1996). Cytotype: Triploid apomict, with the 16-smc sporangia showing 41 bivalents and 41 univalents (Gibby in Fraser-Jenkins 1982). Range: Lu, Hs, Ga, Br (Scot., Wales, Engl. [VC. 1, 2, 3, 35, 36, 40, 41, 42, 43, 44, 46, 47, 48, 49, 55, 57, 62, 63, 65, 66, 67, 69, 70, 72, 73, 74, 75, 76, 77, 78, 81, 85, 86, 87, 88, 89, 90, 91, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112]), Hb [Vc. H2, H7, H8, H9, H10, H16, H20, H39, H40], No, An.

B. subsp. *distans* (Viv.) Fras.-Jenk., **comb. nov.**, basionym: *Aspidium distans* Viv., *App. ad Flor. Cors. Prodr.*: 9 (1825), *non Dryopteris distans* (Hook.) Kuntze. Lectotype (Pichi Sermolli 1960): from Corsica (Ospedale), *S. Serafini*, 1827 in BOLO!, isolectotype: in GE (lost). Synonym: *Dryopteris affinis* [subsp. *cambrensis*] var. *distans* (Viv. ["Fiori"]) Fras.-Jenk. (1987). Cytotype: Unknown. Range: Ga, Co, It. The author (Fraser-Jenkins 1987) initially misidentified the precise identity of the immature type of this name until making a detailed study of the type and type-locality. This subspecies, with a distinct range centred on western France, is consistently intermediate between the eastern French, Mediterranean *etc.* subsp. *insubrica* and the more northerly subsp. *cambrensis*, but is nearer to the latter, yet has reddish scales.

C. subsp. *insubrica* (Oberh. & Tavel *ex* Fras.-Jenk.) Fras.-Jenk., **comb. nov.**, basionym: *D. affinis* [subsp. *cambrensis*] var. *insubrica* Oberh. & Tavel *ex* Fras.-Jenk., in Widén, Fraser-Jenkins, Reichstein, Gibby & Sarvela, *Ann. Bot. Fennici* **33**: 73 (1996). Holotype: from Switzerland, Kt. Ticino (Lugano, Breganzona to Muzzano), *F. von Tavel*, 14 Oct. 1916, in BERN!, isotypes (x 3): in BERN! Cytotype: Triploid apomict with the 16-smc sporangia showing approximately equal numbers of bivalents and univalents, or sometimes slightly fewer bivalents (Vida in Fraser-Jenkins 1980, 1982 and in Fraser-Jenkins & Trewren in prep.). Range: Ga, Co, Be, Lux, Ho, Da, No, Ge (W. and E.), He, It, Elba, Si, Sa, Au, Hu, Cz (Bohem., Morav.), Po, Ju (Slov., Hrvat.), Bu. A further, more minor local variant of subsp. *insubrica* from the Armorican region of S.W. France has more acute pinnule-apices and long teeth, but is not considered sufficiently distinct to be worthy of nomenclatural recognition here.

D. subsp. *pseudocomplexa** Fras.-Jenk., **subsp. nov.**, *planta similis ad D. cambrensi subsp. cambrensi a qua differt paleis stipitis pallidioris, lamina latiora, pinnuli laxioris minoris confertis, apicibus earum acutioribus-rotundis, dentes plus minusve absentis vel brevibus acutos saepe ferrentibus*. Holotype, here designated: Britain, Scotland: Woods in from gate, just south of Dunvegan Castle car-park, N.W. Skye, Inner Hebrides, Scotland, *C.R. Fraser-Jenkins* 12635, 9 Sept. 1986, in BM!; isotypes: Ditto, in H!; paratypes: ditto, nos. 12634, 12636-12640, 12644-12648, in BM!

NMW! H!; woods in from gate just south of Dunvegan Castle car-park, N.W. Skye, Inner Hebrides, Scotland. *CRFJ* 11130-11134, 11136-11141, 11143-11154, 16 Sept. 1984, in BM! NMW! Synonym: *D. affinis* [subsp. *cambrensis*] var. *pseudocomplexa* Fras.-Jenk., *nom. nud.* (1996b) ["form imitating *D. x complexa*" in Widén, Fraser-Jenkins, Reichstein, Gibby & Sarvela: 75 (1996)]. Cytotype unknown, but spores large and a fairly high percentage (up to c. 30%) of abortive spores, similar to those of the triploid apomict subsp. *cambrensis*. Range: Ga, Br (Scot. [VC. 100, 104], Hb [VC. H2, H6], No, ?Au. Also discovered independently by Dr. A. Church on the Isle of Arran, W. Scotland in 1992 and thence published as "morphotype Arranensis" by Pigott (1996), with the comment that it might be the same as the unattributed var. *pseudocomplexa* [from the author's manuscript]. This is now placed within subsp. *pseudocomplexa*.

3. *Dryopteris pseudodisjuncta* (Tavel *ex* Fras.-Jenk.) Fras.-Jenk., *comb. nov.*, basionym: *Dryopteris affinis* [subsp. *borreri*, *err.*] var. *pseudodisjuncta* Tavel *ex* Fras.-Jenk. in Dostál, Fraser-Jenkins & Reichstein, Hegi's *Illustr. Flor. Mitteleurop.*, ed. 2 (Kramer), 1: 147 (1983 ["1984"]). Holotype: from Switzerland, Kt. Zug (Finstersee, Hohen Ron [mountain]), *E. Oberholzer*, in BERN! Synonyms: *Dryopteris affinis* subsp. *pseudodisjuncta* (Oberholz. & Tavel *ex* Fras.-Jenk.) Fras.-Jenk., *Nordic J. Bot.* **16**(1): 4 (1996a); *Dryopteris affinis* [subsp. *cambrensis*, *err.*] var. *setosa* (Christ 1900) Fras.-Jenk. (1987). Cytotype: triploid apomict, with the 16-smc sporangia showing c. 20-24 bivalents and the remainder univalents (Döpp 1963, Schneller in Eschelmüller & Schneller 1980). Its proposed genomic origin is unclear, but is apparently different from that of *D. cambrensis*, from which it shows slightly different pairing behaviour at meiosis, suggesting segmental allopolyploidy, though its phloroglucinol chemistry is similar to subsp. *cambrensis*. Range: Ga, Be, Lux, No, Ge (W.), He, Au.

4. *Dryopteris schorapanensis* Askerov, *Isvest. Akad. Nauk. Azerbaidzhan S.S.R.*, ser. Biol. Med. Nauk, **1978**(4): 4 (1979), *pro hybr.* [omitted by Johns *et al.* 1996] (described as a proposed hybrid of what is now *D. affinis* with *D. caucasica* Fomin). Holotype: [former] U.S.S.R., Gruzha [Georgia] (Schorapani, Mesketskii Khrebet [range], Kavkaz [Caucasus] Mts., N. Georgia), *I. Medvedev*, 18 July 1968, in TBI! Synonym: *D. affinis* subsp. *persica* Fras.-Jenk. (1980). Cytotype: Triploid apomict (Vida in Fraser-Jenkins 1980). Its proposed genomic origin is unclear. Range: ?Ro, ?An, Caucasus (Rs (S) (Krasnodar)) and Transcaucasia (Abkhaz., Georg., Karabakh., Azerbay., Dagest.), Ir. At specific rank what had been called subsp. *persica* must be called *D. schorapanensis*, one of several taxa described as hybrids by Askerov.

5. *Dryopteris pontica* (Fras.-Jenk.) Fras.-Jenk., *comb. nov.*, basionym: *Dryopteris affinis* subsp. *pontica* Fras.-Jenk. in Widén, Fraser-Jenkins, Reichstein, Gibby & Sarvela, *Ann. Bot. Fennici* **33**: 73 (1996). Holotype: Turkey (Anatolia), Ordu Vilhayet (Harçbeli Pass, Kirtibe°, Gölköy), *CRFJ* 14065, 15 Nov. 1987, in BM!, isotypes: ditto, in G! H!, paratypes: ditto, *CRFJ* 14058-14064, 14066-14068, in BM! NMW! Cytotype: Triploid apomict (Gibby in Fraser-Jenkins 1980, Vida in Fraser-Jenkins & Trewren in prep.). Its proposed genomic origin is unclear, but it has a quite distinct morphology with some characteristics in common with *D. schorapanensis* and rectangular lobes similar to *D. borreri*. Range: An, Transcaucasus, Ir.

6. *Dryopteris borreri** (Newm.) Newm. *ex* Oberh. & Tavel in Tavel, *Verh. Schweiz.*

Naturf. Ges. **118**: 153 (1937). Lectotype (Fraser-Jenkins 1980): Britain, England, *E. Newman*, 1879, in BM! Synonyms: *Dryopteris affinis* subsp. *borreri* (Newm.) Fras.-Jenk. (1980), *Lastrea filix-mas* var. *abbreviata* (DC.) Newm (1854), *Dryopteris abbreviata* (DC.) Manton (1950), *non* (Schrad.) Kuntze, *Aspidium blackwellianum* Ten., *nom. provis. inval.*, ??*Polystichum induratum* Schur (1866) (said to be *D. filix-mas* by Christensen (1905); type not found by the author, ?in LW), *Dryopteris affinis* subsp. *stilluppensis* (Sabr.) Fras.-Jenk. (1980), *non sensu* Fras.-Jenk., *D. stilluppensis* (Sabr.) Holub (1986), *non sensu* Holub, *D. affinis* subsp. *robusta* Oberh. & Tavel *ex* Fras.-Jenk. (1980) (holotype, isotype and paratypes: from Switzerland, Kt. Zürich (Hohen Ron [mountain]), *E. Oberholzer*, 28 Sept. 1940, in BERN!), *D. pseudomas* subsp. *robusta* (Oberh. & Tavel *ex* Fras.-Jenk.) Holub (1984), *D. mediterranea* Fomin [= *D. wallichiana*] var. *robusta* (Oberh. & Tavel *ex* Fras.-Jenk.) Holub (1986), *D. x tavelii* Rothm. (1945) (lectotype (Fraser-Jenkins 1987): from Hungary, Vas Comit. (Hámor, Kőszeg (Güns) [= Göszbachtal, Aradopatak valley], *A. Waisbecker*, 10 Aug. 1899, in B!). Many other varietal names also apply to this species. Cytotype: Triploid apomict, with the 16-smc sporangia showing *c.* 123 single chromosomes, or sometimes from 10-18 bivalents (Manton 1950, Schneller 1974, 1975a-b, Manton, Vida and Rasbach in Rube & Heise 1975, in Fraser-Jenkins 1980 and in Fraser-Jenkins & Trewren in prep.). Fraser-Jenkins' (1980) reports of some plants showing approximately equal numbers of bivalents and univalents was made prior to his reidentification of Manton's voucher-specimens, and referred to *D. cambrensis*. Range: Lu, Hs, Andorra, Ga, Co, Be, Lux, Ho, Br (Scot., Wales, Engl. [VC. S, 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 20, 22, 23, 24, 25, 26, 27, 29, 30, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 52, 53, 54, 55, 57, 58, 59, 60, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 108, 109, 110, 111, ??112]), Hb [VC. H1, H2, H3, H4, H5, H6, H7, H8, H9, H10, H13, H15, H16, H20, H21, H23, H25, ?H26, H27, H28, H29, H30, H31, H32, H33, H35, H36, H37, H38, H39, H40], Da, No, [S], Ge (W. and E.), He, It, Elba, Si, Au, Hu, Cz (Bohem., Morav., Slovak.), Po, Ju (Slov., Hrvat., Bosn.-Herc., Crna Gora, Srb., Makedon.), Ro, Bu, Tu, An, Rs (W) (Kalinin., Ukr.), ??Rs (K), Rs (S) (Caucasus (Krasnod., Sev.-Osset.), Transcauc. (Abkhaz., Georg., Dagest., Adzhar., Azerbayd.)), Ir.

D. borreri is morphologically very close indeed to the triploid apomict *D. pseudofilixmas* Rothm. (1945), from Mexico, which may be due to chance convergence following the combination of their ancestors; their chemistry and presumably their origin is different, but further study is required to investigate its relationship to *D. borreri*. There are numerous minor variants of *D. borreri*, which all appear to merge into each other and are probably merely due to less significant variation being preserved through apomictic cloning, as also occurs within the subspecies of the other species. Being obviously below the rank of subspecies these are not recognised here even though many of them have received varietal names, albeit uncritically, in the past. The botanical varietal names have been detailed in Fraser-Jenkins & Trewren (in prep.), but a great many more varietal names given to abnormal cultivars are also valid at varietal rank and apply to the basic more normal plant from which the monstrosities were derived. Any attempt to apply lower ranking names to the minor variants within *D. borreri* or within the subspecies of the other species would therefore be extremely difficult. Applying new names would be still less advisable unless they were for more fundamental entities at the subspecific rank, which the author has not recognised in

Nature so far. It would probably also be of dubious value because whereas individual minor variants can recur frequently in many populations and be more-or-less recognisable from place to place, intermediates occur in other populations and in different regions and it appears doubtful whether any of them represent discrete entities. They have therefore not been recognised nomenclaturally by the present author, even at the rank of forma, though it is evident that further research is required. One such form that occurs frequently with rather small, squarely truncate pinnules similar to the type of *D. borrieri*, has been separated by Pigott (1997) as "morphotype Insolens". It may be directly synonymous with *D. borrieri* itself, or may turn out to be a distinct entity on further investigation. It occurs commonly throughout Britain and in parts of the western European-continental range of the species, whereas in N.E. Europe *D. borrieri* usually has wider and often more lobed pinnules (these forms also occurring in Britain and W. Europe). The present author mistakenly validated one of von Tavel & Oberholzer's many varietal names within this species as *D. affinis* subsp. *robusta*, which was taken up by Holub, Jermy and then Pigott in various slightly different senses, the two latter as "morphotype Robusta". But this name simply referred to plants of *D. borrieri* with slightly long, developed, but hardly lobed lowest basicopic pinnules, with more rounded pinule-apices, which can occur in several of its minor variants and perhaps varies continuously in degree of development, though requiring further study. Subsp. *robusta* has already been sunk by Fraser-Jenkins (1987, 1996b) but the name is still being used in various senses by some authors.

7. *Dryopteris iranica* Fras.-Jenk., *nom et stat. nov.* for *Dryopteris affinis* subsp. *coriacea* Fras.-Jenk., *Willdenowia* **10: 12-113 (1980), *non Dryopteris coriacea* (Brause) Ching [= *Thelypteris (Amphineuron) coriacea* (Brause) Ching]. Holotype: Iran, Talesh, Gilan (above Assalem, S. of Siâdûn, Astara to Bandar-e Pahlavi), *CRFJ* 5933, 30 June 1977, in BM!, isotype: ditto, in BM!; paratypes: ditto, 5926-5932, 5934-5939, BM! NMW! H! G! FR! Synonyms: *D. wallichiana* subsp. *coriacea* (Fras.-Jenk.) Fras.-Jenk. (1996b), *D. affinis* subsp. *coriacea* var. *gigantea* Fras.-Jenk. (1980). Cytotype: triploid apomict (Vida in Fraser-Jenkins 1980). This subspecies, though more closely related to *D. wallichiana* in its long scales and very coriaceous lamina is readily morphologically distinguishable from it in its rounded, flabellately toothed pinule-apices etc. and deserves specific rank. Other subspecies and unnamed variants of *D. wallichiana* in Asia are generally closer to subsp. *wallichiana* itself and are maintained by the author as subspecies, with the exception of *Dryopteris himalaica* (Ching & S.K.Wu) S.G.Lu (syn.: *D. wallichiana* var. *himalaica* Ching & S.K.Wu, *D. wallichiana* subsp. *himalaica* Fras.-Jenk. (1997), the latter fortuitously using the same epithet as Ching's, despite having inadvertently lost track of the earlier name at varietal rank). *D. wallichiana* subsp. *coriacea* var. *gigantea* Fras.-Jenk. (1980) from N. Turkey and N. Iran appears very similar morphologically to *D. himalaica* but was reported as triploid by Gibby, while *D. himalaica* was reported as diploid (Gibby 1985, *CRFJ* 10364).**

HYBRIDS

The cytotypes of the *D. affinis* x *D. filix-mas* hybrids detailed here are tetraploid or pentaploid, whereas the species are diploid or triploid. They are normally distinguishable by their intermediate frond-morphology combined with mostly abortive spores and by not usually forming large populations, but occurring as a few isolated individuals in a population. However the author has seen some considerable

populations of *D. x complexa* nothosubsp. *complexa* in S.W. Ireland, which may have something to do with spore-germination being favoured by the luxuriant, mild and consistently moist climate there, as elsewhere in the west. So far no definite *D. affinis* agg. *x D. oreades* Fomin has been discovered, previous records all being of *D. cambrensis*, which almost certainly had such an origin. Some further candidates have recently been suggested, but are at present of uncertain identity. A further complication is that *D. oreades x D. affinis* would presumably be genomically identical and probably the same as *D. cambrensis*, while *D. oreades x D. borreeri* would presumably be genomically identical to *D. x complexa* and the two origins for both would probably give indistinguishable results. Only *D. cambrensis x D. oreades* should be expected to be a distinctive hybrid worth looking out for, though like any other hypothetical taxa within the group which may or may not exist, it need not be mentioned further until actually discovered in Nature.

The nomenclature of several of the hybrids in the group requires revision now that the subspecies of the *D. affinis* group have been raised to the specific rank. Hybrids within the group known to the author are as follows:-

1. *Dryopteris x complexa** Fras.-Jenk., in Derrick, Jermy & Paul, *Sommerfeltia* 6: x-xiii (1987). *D. affinis x D. filix-mas*. Holotype: from Germany [former W. Germany] (Gaisbrunnen, c. 2 km S.E. of Herrenalb, S. of Karlsruhe), *G. Philippi, H. & K. Rasbach, T. Reichstein & A. Sleep* TR 4020, 14 Aug. 1976, in Z!, isotype: in M! Fronds from type-plant cult. by T. Reichstein in Basel in herb. CRFJ, in BM! NMW! Cytotype: Tetraploid semi-sterile hybrid.

A. nothosubsp. complexa*. *D. affinis* subsp. *affinis x D. filix-mas*. Cytotype: Tetraploid semi-sterile hybrid, with the 16-smc sporangia showing c. 41 bivalents and c. 82 univalents (Manton 1950 and in Fraser-Jenkins & Trewren in prep., Rasbach in Rasbach, Rasbach, Reichstein & Schneller 1983 and in Fraser-Jenkins & Trewren in prep.). Range: Lu, Hs, Ga, Be, Br (Scot., Wales, Engl. [VC. S, 1, 2, 3, 5, 11, 32, 35, 36, 41, 42, 44, 51, 55, 62, 63, 69, 70, 82, 85, 87, 99, 103, 105]), Hb [H1, H2, H3, H6, H8, H10, H20, H22, H28, H29, H32, H39], Ge (W.), He, It, Au, Ro.

B. nothosubsp. contorta* Fras.-Jenk., in Derrick, Jermy & Paul, *Sommerfeltia* 6: x-xiii (1987) (erroneously thought at first to be *D. cambrensis* subsp. *cambrensis x D. filix-mas*). *D. affinis* subsp. *paleaceolobata x D. filix-mas*. Holotype: from Britain, Scotland (Glen Affric, Inverness-shire, *CDFJ* and *ABJ*, 1967 [erroneously thought to have been from Leicestershire, at The Brand, Woodhouse Eaves, *CRFJ*, Oct. 1968]), *CRFJ* 11494, *ex hort.* Newcastle House, Bridgend, 25 Aug. 1985, in BM!; isotypes: ditto, in G! H! NMW! Cytotype: Tetraploid semi-sterile hybrid (Gibby in Fraser-Jenkins & Trewren in prep.). Range: Br (Wales, Engl. [VC. 47, 96]).

C. nothosubsp. eschelmulleri Fras.-Jenk., *nothosubsp. nov. planta similis ad nothosubsp. complexam sed dentibus longioris flabellulatis et facie superiora pinnularum valde depressa super sorum differt. Sporae plerumque abortivae*. Holotype, here designated: Germany [W.], Bayern, south Schwaben, Allgäuer Alpen, Grunten süd, giffelstein, A. Eschelmüller [klon 11] 85/11 (Herb. T. Reichstein no. 6282, Basel, now in Z!); isotypes: A. Eschelmüller [klon 10 and 11] 84/23, 13/8/1984, 84/36 and 84/88, 13/9/1984, 84/87, 13/9/1984 and 85/73, 19/8/1985 (Herb. A. Eschelmüller, Sulzberg-im-Allgäu, now in M!). *D. affinis* subsp. *punctata x D. filix-mas*. Cytotype: Tetraploid semi-sterile hybrid (Bär & Eschelmüller 1985). Range: Ge (W.), He, Ju (Hrvat.), An.

2. *Dryopteris x convoluta** Fras.-Jenk., **nothosubsp. nov.**, *frons angustiora quam in D. x complexa segmenta parviora et pinnulae basiscopicae ad superam curvatae. Par inferum pinnularum quoque pinnae valde longiorum. Paleae stipitis rubricantae. Indusia glandulosa. Sporae plerumque abortivae, sed sporae bene formatae maximae.* Holotype, here designated: Germany [W.], Bayern [= Bavaria], south Schwaben, Südwest seite des Grünten, von Burgberg aufwärts, A. & H. Eschelmüller 85/40, 24/5/1985 (Herb. A. Eschelmüller, Sulzberg-im-Allgäu, now in M!). Plant then grown from spores by A. Eschelmüller, frond coll. AE 88/72, 9/1988 (photo!). *D. cambrensis* x *D. filix-mas*. Cytotype: Pentaploid semi-sterile hybrid.

A. nothosubsp. convoluta. *D. cambrensis* subsp. *insubrica* x *D. filix-mas*. Cytotype: Pentaploid semi-sterile hybrid (Döpp 1941, Bär & Eschelmüller 1989). Range: Co, Ge (W.), He.

B. nothosubsp. occidentalis* Fras.-Jenk., **nothosubsp. nov.**, *planta similis ad nothosubsp. convolutam sed paleae stipitis flavo-fuscae, dentes pinnularum minori. Indusia fere eglandulosa. Sporae plerumque abortivae.* Holotype, here designated: Britain, Scotland (Inverness-shire, road-cutting near top of pass, Shlochd, north of Carrbridge, south of Inverness), CRFJ 11187, 18/9/1984, in NMW. *D. cambrensis* subsp. *cambrensis* x *D. filix-mas*. Cytotype: unknown. Range: Ga, Co, Br (Scot., Wales, Engl. [VC. 47, 49, 62, 69, 74, 87, 96, 104]), Hb [VC. ?H6].

C. nothosubsp. inconspicua Fras.-Jenk., **nothosubsp. nov.**, *planta similis ad nothosubsp. occidentalem sed segmenta minore lobata et dentes insignificanti, paleae stipitis pallidae vel flavae.* Holotype, here designated: France, Haut-Rhin (east-facing woodland scree, c. 1 km along Sentier des Roches foot-path, south-east side of Col de la Schlucht, west of Colmar on Remiremont road, Vosges mountains), CRFJ 13688, 9/8/1987, in NMW (with *D. x sarvelae*. CRFJ 13876, 17 Sept. 1987, NMW). Plant cultivated in hort. M.H. Rickard, Leinthall Starkes, Herefordshire, later transferred to Kyre Park, Ludlow, Shropshire, where it subsequently died. *D. cambrensis* subsp. *pseudocomplexa* x *D. filix-mas*. Cytotype: unknown. Range: Ga, Br (Scot. [VC. 100]) It should be searched for further in Scotland and Ireland, where it is likely to occur more commonly.

3. *Dryopteris x complanata* Fras.-Jenk., **hybr. nov.**, *frondes similes ad D. x criticam sed lamina valde complanata et pinnulis minoris lobatis, apicibus pinnularum cuneato-acutis similis ad D. pseudodisjunctam sed dentes plures. Sporae plerumque abortivae.* Holotype, here designated: Germany [W.], Nordrhein-Westfalen (east Arnsberg, below Ramsbeck waterfall, south of Meschede, north Rothaargebirge, Dortmund to Kassel, wooded slopes across stream), C.R. Fraser-Jenkins 13748, 19/8/1987, in BM!, isotypes (x 8): FR! BR! G! H! Herb. T. Reichstein (no. TR 6862), Basel, now in Z! NMW! K!, paratypes (x 3): Ditto, CRFJ 13749 in NMW. *D. pseudodisjuncta* x *D. filix-mas*. Cytotype: unknown. Range: Ge (W.). Reports of this hybrid by Gätzi (1961: 44) and Döpp, Gätzi & Oberholzer (1963) have been investigated by the author and were in error for *D. filix-mas* and *D. pseudodisjuncta* respectively.

4. *Dryopteris x critica** (Fras.-Jenk.) Fras.-Jenk., **comb. nov.**, basionym: *Dryopteris x complexa* nothosubsp. *critica* Fras.-Jenk., in Derrick, Jermy & Paul, *Sommerfeltia* 6: x-xii (1987). Holotype: from Germany (former E. Germany), Gera (Rudolstadt/Thüringen, zw. Partschefeld und Ühlstädt), I. & S. Jessen 1291, 22 June 1985, in Herb. S. Jessen, Chemnitz [formerly Karl-Marx-Stadt]!, isotype: in JE! *D.*

borreri x *D. filix-mas*. Cytotype: Pentaploid partly sterile hybrid, with the 16-smc sporangia showing a range from nearly all univalents to c. 68-81 bivalents and the rest univalents (Manton 1950, Vida in Rasbach, Rasbach, Reichstein & Schneller 1983, Schneller 1974, 1975a-b, Rasbach in Jessen 1985). Range: ?Hs, Ga, Be, Lux, Br (Scot., Wales, Engl. [VC. 27, 35, 36, 40, 47, 48, 49, 52, 55, 57, 60, 62, 63, 64, 69, 88, 92, 97, 104, 105], Hb [VC. H4, H23, ?H39 and collected by R.L. Praeger], No, Ge (W. and E.), He, It, Au, Hu, Ju (Hrvat.), Cz (Moravia), Ro, Bu, Tu. Some plants of *D. x complexa* were erroneously distributed to various British gardens as being this hybrid from the collection of the late Prof. I. Manton, Leeds, by the late Dr. A. Sleep, the two having become transposed at Leeds University Botanical Garden.

KEY TO THE *D. AFFINIS* GROUP.

Comparative diagnostic descriptions of the various taxa have been provided by Fraser-Jenkins & Trewren (in prep.) and these and the key from that work are provided here. Unfortunately, as with many complex groups in pteridophytes, apparently "diagnostic" characteristics can on occasion vary sufficiently in some individuals so as to be misleading and may have to be overridden in order to place a specimen in its species or subspecies correctly. The key allows for this to some degree concerning the main exceptions likely to be encountered, but it may still be necessary to balance and evaluate a combination of characteristics simultaneously when examining a specimen. Mature specimens are dealt with in this key and both immature ones and occasional extremes may have to be abandoned, at least as far as the key and diagnostic descriptions are concerned (though with experience they can usually be correctly recognised identified more intuitively). Garden-grown specimens can also be particularly difficult when, as often occurs, rather exposed, or not well developed. It is also pertinent to point out that specimens which have been pressed and mounted in such a way that the very important upper (adaxial) surface of the lower part of the frond is covered over or scrunpled up may also be very difficult to identify. The smaller spore-size of *D. affinis* has not been used here as a key-characteristic, partly because many people will not have easy access to a microscope. However it should be pointed out that it can be useful in cases of doubt, as long as the spores are not mostly shed and as long as they are fully mature. Youngish spores in the *D. affinis* group, even after they have become brown and developed their perispore, are normally smaller than mature ones. It takes a little experience to recognise their very slightly paler colour, less wrinkled perispore, greater irregularity in size and partial clumping as being typical of an immature spore-sample, and not of a hybrid, and thus not to rely on their small size in such cases. However it is not uncommon to find specimens of *D. borreri* (which usually has the smallest spores of any of the triploids) with small spores almost approaching those of *D. affinis*, though they are less regular. A chromosome-count is not considered here to be a necessary or normal part of the identification process.

1a. Spores (when ripe and not mostly shed) almost entirely and highly irregularly abortive, with a few very large good ones (c. 5% - 20%) present, including \pm spherical ones. [This characteristic has to be observed in combination with the occurrence of intermediate-type frond-morphology, as on rare occasions spore-abortion alone is not always absolutely reliable in this group.] Plants of sporadic occurrence and not normally forming populations
*D. x complexa**, *D. x convoluta**, *D. x complanata* and *D. x critica**.

1b. Spores (when ripe and not mostly shed) mostly good, or with a majority, or high proportion of good ones mixed with abortives, so that the good spores predominate in the sample **2.**

2a. Rachis-scales markedly long and narrow, strongly exerted from the rachis. Laminar texture very stiffly coriaceous; pinnules or pinna-lobes deeply joined together at their bases (*i.e.* sinus between the pinnules not extending as deeply as in *D. affinis*) in the mid-upper parts of the lamina and pinnae *D. wallichiana* agg.

2b. Rachis-scales shorter and usually wider, clothing the rachis more tightly. Laminar texture often coriaceous, but hardly stiffly coriaceous; pinnules or pinna-lobes not so deeply joined together at their bases (*i.e.* sinus between the pinnules very nearly reaching the costa) in the mid-upper parts of the lamina and pinnae *D. affinis** agg.

3a. Sori tall, indusium \pm thick, only slightly lifting and usually splitting on ripening and not, or only slightly shrivelling. The lowest basicopic pinnule of the lowest pinna usually $\frac{1}{4}$ - $\frac{1}{2}$ adnate to the pinna-costa; lamina considerably glossy above **4.**

3b. Sori not tall, indusium \pm thin, lifting on or after ripening and shrivelling, not splitting [except for *D. affinis*, included under 28a. for comparison]. The lowest basicopic pinnule of the lowest pinna usually fully stalked, or sometimes $\frac{1}{4}$ adnate; lamina not, or only slightly glossy **12.**

4a. Pinnules markedly crowded, some with sloping apices
..... *D. affinis* subsp. *kerryensis**.

4b. Pinnules not markedly crowded, with symmetrical apices **5.**

5a. Scales black, pinnule-apices squarely truncate *D. affinis* subsp. *jessenii*.

5b. Scales pale, reddish, or brown (rarely with very dark bases), pinnule-apices rounded-truncate to rounded-pointed, or pointed **6.**

6a. Lamina with marked "punctate" indentations on the top surface above each sorus *D. affinis* subsp. *punctata*.

6b. Lamina without, or only with shallow and insignificant "punctate" indentations above **7.**

7a. Lamina with a wide base, the lowest basicopic pinnules of the lowest pinna developed and longer than the rest, the lower pinnules on each pinnule markedly lobed with small, neat lobes; stipe and rachis scales all narrow (indusium shrivels more than in other *D. affinis* subspecies) *D. affinis* subsp. *paleaceolata**.

7b. Lamina more-or-less tapering to the narrowed base, the lowest basicopic pinnules of the lowest pinna not usually the longest, lower pinnules on each pinna unlobed, or \pm shallowly lobed with somewhat coarse lobes; stipe and rachis scales narrow or wide..... **8.**

8a. Lamina flat, thickly coriaceous, with veinlets markedly impressed above. Pinnae long; pinnules markedly regular in size, with parallel sides, seldom lobed at the sides apart from a rounded basal auricle on the lowest pair of pinnules on each pinna. Sori large, spores small mostly regular (*i.e.* nearly all good)
..... *D. affinis* subsp. *affinis**.

8b. Lamina not flat as at least some pinnules are normally curved up at their tips, coriaceous, but not thickly so, veinlets not markedly impressed above. Pinnæ short; pinnules often irregular in size as the first opposite-pair of pinnules on each pinna is frequently somewhat longer than the rest, not completely parallel at the sides as they are often slightly spatulate and wider at their apices (sometimes due to the down-rolling of the lower-mid sides), usually lobed at the sides, at least on the lowest pair of pinnules on each pinna. Sori relatively small, spores large with a considerable proportion of abortive spores (sometimes nearly equal to the number of good spores) **9.**

9a. Pinnule side-lobes wedge-shaped and pointed, pinnule-apices with prominent, ± markedly long, acute, markedly flabellate teeth; frond-axes highly glandular, scales markedly reddish-yellow or red in colour..... *D. cambrensis* subsp. *insubrica*.

9b. Pinnule side-lobes not wedge-shaped or pointed, but rounded, pinnule-apices with smallish, ± obtuse to slightly acute, weakly flabellate or non flabellate teeth (or teeth absent); frond-axes mostly eglandular, scales varying from pale or whiteish to red or dark brown in colour **10.**

10a. Scales red coloured *D. cambrensis* subsp. *distans*.

10b. Scales whiteish or brown **11.**

11a. Scales all pale, lamina pale-green, pinnæ long with well separated pinnules and teeth often absent, or, when present, narrowly acute
..... *D. cambrensis* subsp. *pseudocomplexa**.

11b. Scales not all pale (apart from in some exceptional plants), but brown or slightly yellowish-russet brown, lamina mid- to dark-green, pinnæ short, teeth often absent, or, when present, somewhat obtuse, though often with a pointed apex
..... *D. cambrensis* subsp. *cambrensis**.

12a. Pinnule-teeth obviously present **13.**

12b. Pinnule-teeth ± absent **28b.**

13a. Pinnule-apices squarely truncate **14.**

13b. Pinnule-apices ± rounded, or pointed **16.**

14a. Scales black, lamina glossy and thick, pinnule-teeth long, but wide and irregular in length on each pinnule-apex *D. affinis* subsp. *jessenii*.

14b. Scales pale or brown, lamina ± matt and thin, pinnule-teeth long or short, with a ± narrowly acute apex, ± regular in length on each pinnule-apex **15.**

15a. Lower pinnules with a wedge-shaped base, pinnules usually not markedly lobed, laminar upper surface ± glossy; indusia with well curved-down sides and a deep, darkish centre *D. pseudodisjuncta*.

15b. Lower pinnules with a rectangular base, pinnules usually not markedly lobed, laminar upper surface matt; indusia with less markedly curved down sides and a shallow, concolorous centre *D. borrieri**.

16a. Pinnule-teeth ± narrowly acute at the tips of the pinnules **17.**

- 16b.** Pinnule-teeth \pm obtuse at the tips of the pinnules **23.**
- 17a.** Lamina with marked “punctate” indentations on the top surface above each sorus *D. affinis* subsp. *punctata*.
- 17b.** Lamina without, or only with very shallow and insignificant “punctate” indentations **18.**
- 18a.** Lower pinnules with markedly rectangular side-lobes with pointed corners *D. borrieri**.
- 18b.** Lower pinnules \pm without rectangular side-lobes (though often with rounded, or pointed ones) **19.**
- 19a.** The lower pinnules on each pinna lobed with numerous small, neat lobes; stipe and rachis scales all narrow *D. affinis* subsp. *paleaceolobata**.
- 19b.** The lower pinnules on each pinna unlobed or lobed with few, often somewhat coarse lobes; stipe and rachis scales include many wide ones **20.**
- 20a.** Pinnules long and narrow, widely separated *D. cambrensis* subsp. *pseudocomplexa**.
- 20b.** Pinnules not noticeably long and narrow, crowded, or \pm narrowly separated **21.**
- 21a.** Lamina pale-green and matt above, pinnule-teeth wide-based, narrowing \pm abruptly to a long, acute apex; only a weak dark spot present at pinna-axils, or absent altogether; indusium rapidly lifting and shrivelling on sporangial ripening *D. schorapanensis*.
- 21b.** Lamina \pm darker green and \pm glossy above, pinnule-teeth not abruptly narrowed from a wide base, long- or shortly acute; an obvious dark spot present at the pinna-axils; indusium remaining inflected at the sides until shrivelling soon after sporangial ripening **22.**
- 22a.** Scales paler- or brighter reddish in colour, pinnae short, lamina well tapered so that the lowest pinnae are usually the shortest, frond-axes highly glandular; pinnule-apices rounded to somewhat acutely pointed *D. cambrensis* subsp. *insubrica*.
- 22b.** Scales pale, or slightly smokey-yellow in colour, pinnae long, the lowest pinna \pm as long as those above, frond-axes \pm eglandular; pinnule-apices varying from narrowly truncate to narrowly pointed, but frequently lop-sided so that one apical corner is taller than the other *D. pseudodisjuncta*.
- 23a.** Lamina with marked “punctate” indentations on the top surface above each sorus *D. affinis* subsp. *punctata*.
- 23b.** Lamina without, or only with very shallow and insignificant “punctate” indentations **24.**
- 24a.** The lower pinnules on each pinna lobed with numerous small, neat lobes; stipe and rachis scales all narrow *D. affinis* subsp. *paleaceolobata**.
- 24b.** The lower pinnules on each pinna unlobed, or lobed with few, somewhat coarse lobes; stipe and rachis scales include many wide ones **25.**

- 25a.** Lower pinnule-apices narrowly rounded-pointed; scales pale- to mid-brown
..... *D. pseudodisjuncta*.
- 25b.** Lower pinnule-apices obtusely rounded-crenate; scales mid-brown or reddish
..... **26.**
- 26a.** Scales brown *D. cambrensis* subsp. *cambrensis**.
- 26b.** Scales reddish or red **27.**
- 27a.** Pinnule side-lobes wedge-shaped and pointed, pinnule-teeth markedly long, frond-axes highly glandular *D. cambrensis* subsp. *insubrica*.
- 27b.** Pinnule side-lobes rounded or rounded-truncate, pinnule-teeth short, frond-axes hardly or not glandular *D. cambrensis* subsp. *distans*.
- [**28a.** Indusia large, markedly tall, thick, persistent, splitting, scales mostly to almost all narrow, lamina very glossy *D. affinis** (included here for comparison)].
- 28b.** Indusia small, not markedly tall, relatively thin, not splitting, shrivelling later, scales include many wide ones, lamina matt or somewhat glossy **29.**
- 29a.** Pinnule-apices squarely truncate, though often with rounded corners, so becoming truncately rounded **30.**
- 29b.** Pinnule-apices rounded to rounded-pointed **32.**
- 30a.** Indusia ± flat to shallowly curved, but begin slightly inflected at their edges, then shrivel rapidly; pinnule side-lobes (usually present on lower pinnules) square or rectangular with pointed corners **31.**
- 30b.** Indusia markedly curved and begin well inflected at their edges with a central depression before shrivelling later; pinnule side-lobes absent, or wedge-shaped and pointed *D. pseudodisjuncta*.
- 31a.** Stipe-base scales varying from ± concolorous to having vaguely defined darker bases and centres, or if well defined, the dark colour not extending upwards in narrow streaks *D. borrieri**.
- 31b.** Stipe-base scales bicolorous, pale, with glossy blackish streaks extending upwards from a clearly contrasting dark base *D. pontica*.
- 32a.** Pinnules well separated, pinnae long; scales very pale or whiteish
..... *D. cambrensis* subsp. *pseudocomplexa**.
- 32b.** Pinnules crowded, pinnae short; scales reddish or brown **33.**
- 33a.** Scales reddish or red *D. cambrensis* subsp. *distans*.
- 33b.** Scales yellowish brown to brown *D. cambrensis* subsp. *cambrensis**.

COMPARATIVE DIAGNOSTIC DESCRIPTIONS

1. *D. affinis**.

1A. subsp. *affinis**. The “purest” *D. affinis* morphology after *D. wallichiana* and the most reminiscent of *D. wallichiana* in its flat frond, “plasticity” (like a moulded plastic) upper surface, smooth laminar texture and regular, rounded-truncate pinnules.

Fronde usually \pm wide (except when exposed on screens *etc.*), with a relatively short stipe, except in large, luxuriant plants in woods; lamina generally tapering somewhat towards the base. Stipe and rachis densely clothed with somewhat narrow scales which stick out from the rachis, but not as much as in *D. wallichiana*; scales variable in colour, most commonly mid- to deep golden-brown, with darker centres and bases, but in some localised clones deep-brown to blackish, in others pale. Lamina thicker, more highly coriaceous and markedly more glossy above than in the other taxa, of a noticeably plastic-like texture above, with the veinlets impressed in the upper surface, somewhat glaucous below with the veinlets darkened. Variable in colour above, but usually dark-green except when exposed, when becoming yellower. Pinnae not, or hardly tapering throughout most of their length, but extending to a long caudate apex, flat; pinnules more regular in size and shape than in the other taxa, sometimes becoming \pm crowded when growing in open places, though not overlapping, but usually \pm separated, or well separated by a U-shaped gap (or “disjunction”), especially when growing in woods, though when not markedly “disjunct” the pinnules may be slightly more widely attached to each other at their bases than in the other taxa; usually \pm unlobed except for a \pm rounded basal auricle on the lowest-opposite pair of pinnules on each pinna (though occasional plants may have prominently lobed and/or even sharply toothed pinnules), the lowest opposite-pair of pinnules on each pinna usually \pm the same length as the rest, basiscopic pinnules at the bases of the lowest pinnae not usually becoming developed or longer, with the lowest basiscopic pinnule of the lowest pinna either the same size as, or often somewhat smaller than the rest and usually between $\frac{1}{4}$ and $\frac{1}{2}$ attached (or adnate) to the pinna-costa, usually nearly all along the acroscopic side of its stalk with most of the base on the other side free; pinnule-apices rounded to rounded-truncate (rarely more pointed further up the frond in large plants), bearing rather few, obtuse pinnule-teeth. Fronds eglandular. Sori the largest in the group, indusia thick, large, \pm tall, somewhat pale until older, eglandular, markedly curved down and inwardly inflected at the margins until the spores ripen, when the indusia lift slightly at the edges and usually split open radially in one or more places as the sporangia turn black (the splits being difficult to see once the sporangia have dehisced), but hardly shrink and do not normally shrivel up or lift completely (except in a few exceptional specimens), persisting until the fronds begin to die. Spores relatively small and regular, ripening later than in the other taxa. Fronds \pm persistent throughout most of winter.

1B. subsp. *paleaceolobata**. Can be confused with *D. cambrensis* subsp. *cambrensis* because of its lobed pinnules, but the pinnae are longer and more parallel-sided than in *D. cambrensis* and the lamina is more widely lanceolate with a somewhat wide base base or just above it, tapering from there to the apex, more glossy and with more twisted pinnules including their side-lobes, and the stipe-scales are consistently darker and narrower; the pinnule-lobes are also smaller, narrower and neater and the spores are smaller. Appears to be the nearest Atlantic equivalent to subsp. *punctata* but is more lobed and without the “punctate” indentations (apart from very small ones) above the sori. Also similar to subsp. *affinis* but differs somewhat markedly in its pinnules all being lobed at the sides and usually slightly irregularly twisted or tilted up from side-to-side (seldom curved up at the apices as in *D. cambrensis*). The lowest basiscopic pinnule is developed and becomes the longest and most lobed in the frond, and is fully stipitate. However it retains the dense, dark and narrow stipe- and rachis-scales and markedly glossy lamina of *D. affinis*, as well as the eglandular frond and tall

though not as thick, eglandular indusium, which splits, but then, unlike in subsp. *affinis*, shrivels somewhat on ripening. It also has similarly small spores and usually more obtuse teeth, though these often become somewhat acutely deltate (acuminate) and flabellately spread out around the pinnule-apex. The pinnule side-lobes are rounded and not as rectangular as in *D. borrieri*.

1C. subsp. *punctata*. Differs from subsp. *affinis* in having larger, more crowded, often somewhat crinkled pinnules, bearing more side-lobes, including a pair of auricles at their bases, and with less regularly parallel margins and more rounded pinnule-apices; they also bear characteristic longer, more prominent and narrower, but obtuse-tipped teeth splayed out around the pinnule-apices in a fan-like arrangement. The upper surfaces of the pinnules have a marked circular, "punctate" indentation above each sorus, which is highly characteristic, and deeper than the small ones that sometimes occur in subsp. *affinis* etc. The lowest basisopic pinnule on the lowest pinna is more narrowly attached to the costa than is usual in subsp. *affinis*, normally being fully stipitate, and the lower pinnules are usually markedly more lobed. Fronds eglandular. The indusium is eglandular and usually (but not always) splits on sporangial ripening, but is thinner than in subsp. *affinis* and lifts up and normally completely shrivels, except in plants from exposed places, which have thicker and less shrivelling indusia. In its scales, glossy, thick, usually dark-green, flat, regular lamina and large sori, it obviously belongs to *D. affinis*.

1D. subsp. *kerryensis**. Similar to *D. cambrensis* subsp. *cambrensis*, but with a smaller, somewhat diminutive frond, and markedly flatter and dark-green, glossy lamina. Stipe- and rachis-scales narrow, dark-brown to blackish; pinnae flat, or slightly convex from above, with the pinnules often slightly curved down at their edges and apical halves. Pinnules markedly crowded, \pm rectangular, the lowest opposite-pair on each pinna often bearing a few distinctive \pm wedge-shaped, pointed side-lobes and a similar basal auricle. Pinnule-apices varying from rounded to more usually rounded- to square-truncate, often slightly sloping obliquely from one side to the other, bearing somewhat long, acute teeth, but which are slightly wider up to their apices than in *D. borrieri*.

1E. subsp. *jessenii*. Perhaps distantly related to subsp. *punctata*, and like it, has lobed pinnules and usually a fully stalked lowest basisopic pinnule on the lowest pinna (but sometimes when \pm unlobed, becomes half adnate to the costa in exposed plants, or in dry situations), it also has smaller punctate depressions above the sori and somewhat small and thin, but inflected indusia, some of which split before shrivelling; but it differs in its usually markedly darker (usually almost black, at least at their bases) stipe- and rachis-scales, its smaller, more disjunct, and irregularly margined pinnules, and especially in at least the lower pinnule-apices being markedly squarely truncate, while the upper ones in the frond may become pointed, but are not as rounded as in subsp. *punctata*. The pinnule-teeth are characteristically longer and narrower than in the other varieties of *D. affinis*, becoming somewhat finger-like, but not acuminate, with slightly obtuse, if narrow apices, and are curiously irregular in length, slightly reminiscent of a monstrosity or abnormality. Axes, lamina and indusia eglandular.

2. *D. cambrensis**.

2A. subsp. *cambrensis**. Intermediate between *D. affinis* and *D. oreades*, and the nearest triploid to *D. affinis* in morphology. The British plants are usually the least toothed, with the brownest (or occasionally pale) scales, though in places in north Wales and the Cairngorm Highlands of Scotland they may become slightly more toothed, and

with more russet-brown scales, slightly approaching subsp. *distans*. The scales range from pale, to, more usually, mid- to dark-brown, usually with darker bases, and are glossy and usually slightly twisted; the larger ones are wider than in *D. affinis* and sometimes more glossy. Stipe usually relatively short, except when growing in woods, or between boulders. Lamina slightly thinner than in *D. affinis*, smooth, with the veinlets hardly impressed above, glossy above when compared with *D. borneri*, though not as glossy as in *D. affinis*, usually darker-green (darker than in subsp. *insubrica*) though paler or yellowish when in the open, characteristically narrow, \pm tapering towards the base. Pinnæ short compared to *D. affinis*, tapering throughout from their wider bases, seldom flat as at least some of the \pm rounded or narrowly-rounded pinnule-apices, especially the lowest basiscopic ones and lowest opposite-pair on each pinna, are usually curved upwards out of the plane of the frond, and the pinnules sometimes twist irregularly laterally, resulting in a slightly crisped appearance to the frond (but not as markedly as in *D. affinis* subsp. *paleaceolobata*). Lowest opposite-pair of pinnules of each pinna (*i.e.* the lowest acroscopic (upper) and basiscopic (lower) pinnule of a pinna) the longest, and usually overlapping the rachis, the lowest one often deflexed basiscopically (*i.e.* bent slightly towards the base of the pinna) so as to lie slightly over the rachis, the lowest basiscopic pinnule of the lowest pinna is usually fully stalked, or stipitate. The pinnules vary from well lobed with rounded lobes to almost unlobed, the pinnule-apices are rounded and vary from fairly prominently toothed to more frequently small-toothed or \pm untoothed and in either case have shorter and more obtuse teeth than in subsp. *insubrica*. In some specimens there are a few (up to *c.* 30) glands on the edge of the indusium, or the frond-axes are sparsely glandular, but most plants are \pm eglandular. Sori smaller, or nearly the same size as in *D. affinis*, the indusia are somewhat thick, thicker than in *D. borneri*, though with a thinner margin than in *D. affinis*, \pm tall, somewhat pale, or greyish, until old, markedly curved down and inflected as in *D. affinis*, but when the spores ripen the indusia frequently split, then lift up, to lie over the top of the sorus, finally shrivelling considerably and after some time, dropping off, but not shrivelling as much as in *D. borneri* and persisting longer, becoming brown. Spores markedly larger than in *D. affinis* and containing a markedly higher proportion of abortive ones; also somewhat darker brown in colour. Fronds turning brown and dying down in mid Autumn.

2B. subsp. *distans*. Generally intermediate in morphology between subsp. *combrensis* and subsp. *insubrica*, but closer to the former except in scale-colour. Fronds are often taller than in subsp. *insubrica*; pinnules with small, rather insignificant teeth, occasionally becoming longer and slightly flabellate; pinnule-lobes when present rounded, not cuneate. Axes and indusia eglandular or bearing only few, scattered, small glands. Stipe-scales markedly reddish or reddish-brown, thin, often rather twisted. Some British and Norwegian populations of subsp. *combrensis* approach it, but the distinction between the two is less clear in parts of those areas.

2C. subsp. *insubrica*. Strongly reminiscent of the pale russet-scaled, glandular and somewhat narrowly toothed forms of *D. oreades* of Corsica, Sardinia, Elba and northern Italy. More acute-toothed, pointed-lobed and with more reddish-russet coloured scales than in subsp. *combrensis*. The larger stipe- and rachis-scales are wider than in *D. affinis*, more glossy and slightly thicker, often \pm concolorous, ranging from pale yellow (particularly in eastern Europe), to pale-russet, to a more common and characteristic reddish or russet-brown, often with darker, castaneous bases and some dark flecks or streaks in the scales; some of the narrower ones characteristically exerted and

somewhat twisted spirally, particularly on the upper stipe and lower rachis. Stipe usually relatively short except in large, luxuriant plants in woods, or when growing between boulders. Lamina narrow, ± tapering towards the base, slightly thinner and less highly coriaceous than in *D. affinis*, but of a slightly crispaceous texture, ± matt above, veinlets usually slightly impressed in the upper surface. Variable in colour above, but often dark- to mid-green, except when exposed, when yellowish. Pinnae usually short, tapering from their wider bases, ± flat. Pinnules rather irregular in length, crowded and sometimes slightly overlapping, though they may become separated by a ± narrow, V-shaped gap; the lowest opposite-pair on each pinna usually longer than the rest, and usually close to the rachis or somewhat overlapping it, the lowest basiscopic one on each pinna may sometimes be slightly basiscopically deflexed so as to lie partly over the rachis, the lowest basiscopic pinnule of the lowest pinna is usually fully stalked, or stipitate. The lowest opposite-pair of pinnules on each pinna is usually well lobed, with characteristic wedge-shaped, pointed side-lobes. Pinnule-apices rounded to rounded truncate, as in *D. affinis*, but often becoming square-truncate above, bearing prominent, long, ± narrow, but wide-based, usually somewhat acute-tipped teeth, which are flabellate, i.e. splayed out around the apex in the manner of *D. oreades*. Many small, fairly scattered, or dense, white glands on the frond-axes and on the indusia as well. Sori usually smaller than in *D. affinis*, usually also slightly thinner, though thicker than in *D. borrieri*, ± tall, somewhat pale, or greyish, until old, usually glandular near their margins, markedly curved down and inflected as in *D. affinis*, but when the spores ripen the indusia frequently split, then lift up to lie over the top of the sorus, finally shrivelling considerably and after some time dropping off, but not shrivelling as much as in *D. borrieri* and persisting longer, usually remaining paleish to pale-brown until considerably later, when becoming brown. Fronds turning brown and dying down early in Autumn.

2E. subsp. *pseudocomplexa**. Somewhat similar to *D. x complexa*, but with a paler coloured lamina and smaller, narrower, less lobed pinnules, and with a high proportion of good spores. It also differs in forming extensive populations. Generally similar to subsp. *cambrensis*, but with pale to very pale-russet, thin, but slightly glossy, ovate stipe-base scales; the lamina thin, pale- to mid-green, wider and more lax than in subsp. *cambrensis*; pinnules usually rather widely separate, or at least not as crowded, long and narrow, with the side-lobes smaller and neater when present. Pinnule-apices narrowly rounded, often becoming somewhat pointed or rounded-pointed in larger plants, varying from being ± toothless to bearing small, somewhat narrow, often acute teeth, more acute than in subsp. *cambrensis*. Indusia somewhat thin, inflected at first, not as tall as in subsp. *cambrensis* and not, or seldom splitting, soon lifting and shrivelling markedly.

3. *D. pseudodisjuncta*.

Stipe- and rachis-scales ± pale, usually with darker-brown bases; somewhat abundant narrow, hair-like, pale scales present on the costae on the underside of the pinnae. Frond wider than in *D. cambrensis*; lamina slightly glossy; pinna-axils very occasionally without the dark spot (darkened area of the petiole at the junction beneath) ; pinnae long, markedly flat; pinnules ± regular in length, or the first pair slightly the longest in each pinna, usually separated from each other above their bases by a distinctive, quite wide, V-shaped gap or notch, and in mid and upper pinnae somewhat widely attached to each other at their bases, often narrowed to their bases in the lowest pair of pinnules

in the lower pinnae which thus become \pm wedge-shaped below, \pm unlobed (including the lowest basicopic pinnules of the lowest pinnae) apart from \pm rounded (occasionally more rhombic) basal auricles in the basal pinnules of mid and upper pinnae in some plants, the lowest opposite-pair of pinnules of each pinna usually slightly longer than the rest and often somewhat deflexed towards the rachis (which rarely occurs also in *D. borrieri*); the lowest basicopic pinnule of the lowest pinna (i.e. the lowest one of the frond) sometimes becomes longer and developed, but is not usually the longest one, fully stalked or stipitate, pinnules usually sloping towards their narrow apices; pinnule-apices narrow or wedge-shaped, varying in the upper part of the frond from rounded to rounded-truncate (or often somewhat markedly truncate), but characteristically rounded-pointed in the lower pinnae. Fronds eglandular. Indusium tall, eglandular, small, \pm thin, mid- to dark-brown, but greyish when younger, matt, markedly inflected at the margins, with a \pm obvious depression in the centre that becomes noticeable when the indusium begins to lift slightly at the edges on ripening; often splitting before lifting slightly on ripening, though the edges remain downturned and enclosing much of the top of the sorus; only later, after the spores have been shed, do the edges lift up markedly before the indusium shrivels. Fronds turning brown and dying down in mid or late Autumn.

4. *D. schorapanensis*.

Close to *D. filix-mas* and often mistaken for it. Frond \pm wide with a long stipe, tapering slightly to the lamina-base. Stipe and rachis not very densely clothed with scales; scales thin, \pm wide, pale to pale-brown, concolorous, or with a dark base, or sometimes a few dark streaks in the centre. Lamina as thin as in *D. borrieri*, or thinner, hardly coriaceous, \pm matt above, slightly glaucous below, lighter green than in *D. borrieri*, veinlets slightly impressed above, not darkened. Pinna-axils usually without the dark spot normally present in the living state in all the other species and subspecies (but see under *D. pseudodisjuncta*); pinnae flat; pinnules \pm regular in length, or the lowest opposite-pair of each pinna slightly the longest, seldom much separated, often somewhat narrowed towards their bases near the bottom of each pinna, \pm unlobed, or with insignificant shallow, \pm square lobes, the lowest basicopic pinnule of the lowest pinna not usually becoming longer and developed, and not the longest one, fully stalked or stipitate; pinnule-apices truncate to rounded-truncate in the lower part of the frond, often becoming more pointed and wedge-shaped in the upper part of the frond, bearing characteristic subulate, wide-based teeth, somewhat abruptly narrowed to \pm and often rather irregularly long-acute points and spread out around the apex in a flabellate, or fan-like arrangement. Fronds eglandular. Sori similar to *D. borrieri*, the indusium eglandular, pale, starting only slightly curved down and not much inflected at the margins (less so than in *D. borrieri*), until lifting, when it shrinks but does not split, either sitting \pm flat over the top of the ripe sporangia until dropping off, or shrivelling considerably, though more persistent than in *D. borrieri*. Spores large and long, with much abortive material present. Fronds turning brown and dying down early in Autumn.

5. *D. pontica*.

Similar to *D. schorapanensis*, but with the truncate lobes and pinnule-apices of *D. borrieri*. Stipe-base scales with dark bases and prominent, separating, dark, glossy streaks extending upwards into the pale area of the scale. Lamina not markedly glossy.

Pinnules becoming wider towards their bases and somewhat remote towards their apices, with obliquely sloping, truncate-tipped basal lobes on each side and often a few smaller lobes above; pinnule apices varying from obtuse to more usually narrowly truncate, with rather prominent teeth. Indusia thin, beginning well turned down, but lifting and partly shrivelling on ripening. Spores larger than in *D. borrieri*, with a similar proportion of abortive spores to that in *D. cambrensis*. Fronds turning brown and dying down early in Autumn.

6. *D. borrieri*.

Usually nearer in morphology to *D. filix-mas* than are the other taxa (except *D. schorapanensis* and *D. cambrensis* subsp. *pseudocomplexa*). Frond usually \pm wide and, except when exposed, with a relatively long stipe, the lamina not usually tapering much below, or not as much as in the other taxa (excluding *D. schorapanensis*), except in more exposed plants and rarely in some localised clones. Stipe and rachis sometimes less densely clothed in scales than in the other taxa (except *D. schorapanensis* and *D. cambrensis* subsp. *pseudocomplexa*) and the scales often paler (sometimes with dark bases) and wider, though very variable. Lamina relatively thinner (except in exposed plants) than the other taxa (except *D. schorapanensis* and *D. cambrensis* subsp. *pseudocomplexa*), less coriaceous, hardly glossy, but more matt above, and usually lighter green than in *D. affinis*, though the colour varies considerably, veinlets not impressed above or darkened beneath, lamina not glaucous beneath. Pinnae \pm flat; pinnules not as regular in length as in *D. affinis*, adjacent, but not crowded, though seldom much separated (though occasionally so, by V- or rarely U-shaped gaps), the lower pinnules on lower pinnae, particularly the lowest basicopic one of the frond, usually lobed with characteristic \pm rectangular side-lobes, and a larger, rectangular basal auricle (though they can be absent), the lowest opposite-pair of pinnules of each pinna often curved slightly away from the rachis, usually \pm the same length as the rest, except that the basicopic one frequently becomes a little longer, at least in the lower pinnae, the lowest, or second lowest basicopic pinnule of the lowest pinna is usually the longest in the frond, is often markedly developed and lobed with rectangular side-lobes, and is fully stalked or stipitate; pinnule-apices characteristically markedly squarely truncate in the lower parts of the frond, but becoming rounded or pointed, particularly in the upper frond, in many larger specimens, but at least some of the lower- or mid-frond pinnule-apices usually remain truncate, rounded-truncate, or obovate, as opposed to their all being more rounded as in *D. affinis* and in most *D. cambrensis* subsp. *cambrensis* etc.; in normal plants the pinnule-apices bear characteristically long, mostly acute teeth, similar to those in *D. filix-mas*, but some plants are occasionally almost toothless, when they can become difficult to separate from *D. cambrensis* subsp. *cambrensis*; in the truncate-pinnuled plants the teeth may be longer above each corner of the pinnule than in the centre of the apex (the late H.V. Corley's "cat's head" outline - the corner teeth representing the cat's ears). Fronds eglandular. Sori smaller than in *D. affinis* or *D. cambrensis*, and indusia noticeably relatively thin and less tall, whiteish or pale- to mid-brown, eglandular, beginning curved down at the sides (but not inflected, or turned in, as in *D. affinis* and *D. cambrensis*) until the spores ripen, when they lift right up, without splitting, shrivel and shrink markedly to become a very small, inverted, wrinkled cone, or funnel on top of the fully exposed sporangia, and soon drop off. Spores relatively larger and with more abortive material than in *D. affinis* and quite often with as many abortive spores as in *D. cambrensis*, but they are usually more

regular and often noticeably smaller than in the other triploid taxa, and can be considerably smaller than expected. Spores ripen from two weeks to up to nearly a month earlier than in *D. affinis*. Fronds mostly turn brown and die down early in winter, though some persist longer.

The most widespread and commonest member of the group, though absent from Macaronesia, north-west Africa and southernmost mainland Italy and less common in Portugal and Spain than subsp. *affinis*.

7. *D. affinis* agg. hybrids with *D. filix-mas*.

The frond-morphology does not fit in with any of the other taxa in the *D. affinis* agg. and is intermediate between the parents, *i.e.* markedly towards *D. filix-mas* when compared with that of any other members of the *D. affinis* agg., though the lamina clearly has more of the glossiness and darker colour (especially in *D. x complexa*) of *D. affinis* than is normal in *D. filix-mas*. Fronds and segments often very large (though this can also occur sometimes in the rest of the *D. affinis* agg., especially in *D. affinis* subsp. *affinis* and in *D. borrieri* and occasionally also in *D. cambrensis* subsp. *cambrensis*), the lamina is sometimes rather narrow in the lower part of the frond (particularly in *D. x complexa* and *D. x convoluta*). The stipe bears denser, darker and narrower scales than in *D. filix-mas* (but it should be noted that occasionally *D. filix-mas* can also be very densely scaly), which often become more russet-coloured and slightly towards those of *D. cambrensis* subsp. *insubrica*; the pinnules of the lower pinnae have more parallel sides than in *D. filix-mas* and sometimes slightly more rectangular side-lobes, if present, though not as parallel and rectangular as in *D. borrieri*, but they become much more like *D. filix-mas* with more curved and sloping sides and more pointed lobes and pinnule-apices further up the frond. The pinnule-teeth are \pm acute, though less so in *D. x complexa*. The sori (except in *D. x complexa*) have less inflected indusia than in *D. affinis* etc. The spores, which are most important [examined dry at *c.* 100-150 x magnification when ripe, yet not mostly shed and lost], are characteristically highly abortive, without which feature being examinable it is difficult to confirm *D. x complexa* except in very obvious specimens. Apart from the mass of abortive spores there is also a small and variable percentage (*c.* 5-20%, occasionally up to *c.* 50%) of mostly very large, or exceptionally large, sometimes nearly spherical, apparently good spores present. The all-good, very small spores of *D. filix-mas*, by contrast, are instantly separable (and much smaller than in any species or subspecies of the *D. affinis* agg.), while those of the species and subspecies of the *D. affinis* agg. are usually at least 50%, to mainly good, unless nearly all shed. The abortive spores of the hybrids may be many small fragments (possibly confusable with slightly immature spores, but smaller and with more developed and darker perispores), or misshapen spores with an irregular, often darker perispore (not to be confused with shapeless, dark pieces of earth), with occasional unseparated diads or tetrads amongst them and usually with some perispore (sporangial) debris attached to their surfaces, also with dark debris remaining in the sporangia (not to be confused with earth or dust). They are usually more irregular and often with wider wings of perispore than in the less numerous abortive spores of any other members of the *D. affinis* agg. The hybrids occur sporadically, but fairly commonly, as occasional plants among populations of the parents, not forming populations of their own, except some scattered rather small local, probably mostly vegetative ones, and seldom more than 1-5 clumps per local wood, except in a few favoured habitats where the parents have long been together in quantity, or conditions

are very luxuriant, damp and favourable for spore-germination, when the hybrid can become more numerous. Rarely large-sized populations of hybrids may occur, for example, in places in south-western Ireland, and are likely to be discovered occasionally elsewhere in Atlantic Britain *etc.* Hybrids can occur throughout the range of the *D. affinis* agg. as *D. filix-mas* occurs in all the range of the *D. affinis* agg. as well as in its own, wider range. Without being properly familiar with all the taxa of the *D. affinis* agg. it is difficult to recognise, or even accurately guess the presence of genuine hybrids. In the past *D. borrieri* was widely misidentified as being such hybrids and was often reported under the name *D. x tavelii* Rothm.

8. *D. wallichiana* subsp. *wallichiana*.

Morphology like an extreme *D. affinis*. Frond persistent in winter, tall and usually tapering towards the base. Stipe short, except in occasional luxuriant wide-fronded specimens with large segments; stipe and rachis densely clothed with longer, narrower scales than in any of the *D. affinis* agg., which stick out markedly from the rachis. Lamina more highly coriaceous and stiff, more glossy above and glaucous below and more crispaceous than in any of the *D. affinis* agg. Pinnæ flat and regular; pinnules ± crowded, usually markedly squarely truncate at their apices, those in the upper parts of the frond more widely joined together at their bases than in *D. affinis*; pinnule-teeth few, more obtuse and short, though usually with an acute tip at their apex. Fronds eglandular. Sori smaller than in *D. affinis*, with thick, inflected, eglandular indusia that split on ripening and persist for a long time. Spores relatively small and regular (diploid apomict).

A pan subtropical montane taxon. Not in the European (*sens. lat.*) flora, where it is replaced by the W. Asian *D. iranica* (usually with a longer stipe, wider lamina-base, larger segments; triploid apomict, and with larger and less regular spores).

ACKNOWLEDGEMENTS

The author wishes to thank the following for their various help and contributions to this study:

Prof. Mary Gibby, Edinburgh; the late Dr. Trevor Walker, Newcastle; Miss Alison Paul, London; Miss Josephine Camus, London; Mr. Peter Edwards, Kew; the late Prof. I. Manton, Leeds; Mr. Ken Trewren, Egton Bridge; Mr. Anthony Pigott, Mendlesham; Mr. Alfred Eschelmüller, Sulzberg; the late Mr. Hugh Corley, Faringdon; Prof. Gabor Vida, Budapest; the late Dr. Walter Gätzi, St. Gallen; M. Michel Boudrie, Clermont Ferrand; Mr. Mike Taylor, Isle of Skye; Mr. Martin Rickard, Kyre Park; Dr. Jacob Schneller, Zürich; Dr. Stefan Jessen, Chemnitz; Herr Jens Freigang, Germany; Herr Walter Bujnoch, Germany, and above all his colleague of 25 years, the late Prof. Tadeus Reichstein, Basel and Agarone.

The great many correspondents and the staff of nearly 200 herbaria who have assisted in his inquiries have been acknowledged in full in the forthcoming study by Fraser-Jenkins & Trewren (in prep.).

REFERENCES

- BÄR, A. & ESCELMÜLLER, A. 1985. Tetraploide und pentaploide *Dryopteris x tavelii* - - jetzt im Allgäu bestätigt. Mitt. Naturwiss. Arbeitskr. Kempten (Allgäu) 27 (1): 57-68.
- BÄR, A. & ESCELMÜLLER, A. 1989. Beitrag zur Kenntnis von *Dryopteris affinis*

- (Lowe) Fraser-Jenkins und von Bastarden mit *Dryopteris filix-mas*. Mitt. Naturwiss. Arbetskr. Kempten (Allgäu) 29 (1): 25-48.
- BÄR, A. & ESCHELMÜLLER, A. 1990. *Dryopteris x complexa* nssp. *contorta* Fraser-Jenkins - ein seltener Farnbastard in Bayern. Ber. Bayer. Bot. Ges. 61: 91-97.
- DANSER, B.H. 1950. A theory of systematics. Bibl. Biotheor., ser. D, 4: 117-180.
- DAVIS, P.H. & HEYWOOD, V.H. 1970. Principles of Angiosperm Taxonomy: 10. Cambridge.
- DÖPP, W. 1941. Über *Dryopteris paleacea* Christensen (*D. borrieri* Newm.). Ber. Deutsch. Bot. Ges. 59 (9): 423-426.
- DÖPP, W. 1955. Experimentell erzeugte Bastarde zwischen *Dryopteris filix-mas* (L.) Schott und *D. paleacea* (Sw.) C.Chr. Planta, Arch. Wissensch. Bot. 46: 70-91.
- DÖPP, W., GÄTZI, W. & OBERHOLZER, E. 1963. *Dryopteris borrieri* Newman (*D. paleacea* Hand.-Mazz.) var. *pseudodisjuncta* v. Tavel. Ber. Deutsch. Bot. Ges. 76 (4): 99-111.
- ESCHELMÜLLER, A. & SCHNELLER, J.J. 1980. Beitrag zur Kenntnis der Variabilität von *Dryopteris affinis* im Allgäu. Mitt. Naturwiss. Arbetskr. Kempten (Allgäu) 24 (1): 1-12.
- FRASER-JENKINS, C.R. 1980. *Dryopteris affinis*: a new treatment for a complex species in the European Pteridophyte flora. Willdenowia 10 (1): 107-115.
- FRASER-JENKINS, C.R. 1982. *Dryopteris* in Spain, Portugal and Macaronesia. Bolm. Soc. Broteriana, ser. 2a, 55: 175-335.
- FRASER-JENKINS, C.R. 1983. *Dryopteris affinis*, in DOSTÁL, J., FRASER-JENKINS, C.R. & REICHSTEIN, T., in HEGI, G., Illustrierte Flora von Mitteleuropa, ed. 3, 1, pp. 136-169. Berlin.
- FRASER-JENKINS, C.R. 1987. Taxonomic and Nomenclatural notes 5, *Dryopteris*, in DERRICK, L.N., JERMY, A.C. & PAUL, A.M., Checklist of European Pteridophytes. Sommerfeltia 6: x-xiii.
- FRASER-JENKINS, C.R. 1996a. *Dryopteris affinis* subsp. *pseudodisjuncta* (Oberh. & Tavel ex Fras.-Jenk.) Fras.-Jenk., comb. nov., in JONSELL, B. (ed.), Lectotypifications and new combinations for Flora Nordica Vol. 1 (Lycopodiaceae – Papaveraceae). Nordic J. Bot. 16 (1): [3-] 4 [-8]. [not published in Nordic J. Bot. 15 (1995), as stated in Flora Nordica]
- FRASER-JENKINS, C.R. 1996b. A reaffirmation of the taxonomic treatment of *Dryopteris affinis* (Dryopteridaceae: Pteridophyta). Fern Gaz. 15 (3): 77-81.
- FRASER-JENKINS, C.R. & TREWREN, K. in prep. The *Dryopteris affinis* complex and its species, subspecies and hybrids.
- GÄTZI, W. 1961. Über den heutigen Stand der *Dryopteris*-forschung unter besonderer Berücksichtigung von *Dryopteris Borrieri* Newman, zugleich ein Beitrag zur Farnflora des Südbahnges des Tannenbergs. Ber. üb. Tätigkeit St. Gallisch. Naturw. Ges. 77: 1-73.
- ICBN: GREUTER, W. et al. 2000. International Code of Botanical Nomenclature (Saint Louis Code). Regnum Vegetabile 138. Königstein.
- JERMY, A.C. & CAMUS, J.M. 1991. The illustrated Field Guide to Ferns and Allied Plants of the British Isles. London.
- JERMY, A.C., PIGOTT, A.C. & MERRYWEATHER, J.W. 1998. *Dryopteris*, in RICH, T.C.G. & JERMY, A.C. (eds.), The Plant Crib, pp. 29-33. London.
- JESSEN, S. 1985. A reappraisal of *Dryopteris affinis* subsp. *borrieri* var. *robusta* and new records of *D. affinis* subspecies in eastern Europe. Fern Gaz. 13 (1): 1-6.

- JESSEN, S. 1991. Neue Angaben zur Pteridophytenflora Osteuropas. Farnblätter 23: 14-47.
- JOHNS, R.J., EDWARDS, P.J. & PICHI SERMOLLI, R.E.G. 1996. Index Filicum Supplementum sextum. Kew.
- MANTON, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge.
- MERRYWEATHER, J.W. 2002. Identification – British male ferns. Pteridologist 4 (1): 12-14.
- PICHI SERMOLLI, R.E.G. 1960. The identification of *Aspidium distans* Viv. American Fern J. 50 (1): 133-138.
- PIGOTT, A.C. 1997. Affinis Watch Newsletter, Special Issue British Pteridological Society, insert in Pteridologist 3(2).
- RASBACH, H., RASBACH, K., REICHSTEIN, T. & SCHNELLER, J. 1983. Tetraploide *Dryopteris x tavelii* Rothm. im nördlichen Schwarzwald. Farnblätter 10: 1-13.
- REICHSTEIN, T. & SCHNELLER, J. 1983. *Dryopteris affinis* var. *punctata* im Hüllerich-Wald ob Pfaffikon (SZ). Farnblätter 9: 9-21.
- ROTHMALER, W. 1945. Der Formenkreis von *Dryopteris paleacea* (Sw.) Hand.-Mazz. Candollea 10: 91-101.
- RUBE, G. & HEISE, K. 1975. Neufund von *Dryopteris borrieri* Newm. (Dreiwertiger Speuschuppenfarn) in Nördosthessen. Beiträge zur Naturkunde in Osthessen 9-10: 169-173.
- SCHNELLER, J.J. 1974. Untersuchungen an einheimischen Farnen, insbesondere der *Dryopteris filix-mas*-Gruppe 1.Teil. Ber. Schweiz. Bot. Ges. 84 (3): 195-217.
- SCHNELLER, J.J. 1975a. Untersuchungen an einheimischen Farnen, insbesondere der *Dryopteris filix-mas*-Gruppe 2.Teil. Cytologische Untersuchungen. Ber. Schweiz. Bot. Ges. 85 (1): 1-17.
- SCHNELLER, J.J. 1975b. Untersuchungen an einheimischen Farnen, insbesondere der *Dryopteris filix-mas*-Gruppe 3.Teil. Ökologische Untersuchungen. Ber. Schweiz. Bot. Ges. 85 (2): 110-159.
- WIDÉN, C.-J., FRASER-JENKINS, C.R., REICHSTEIN, T., GIBBY, M. & SARVELA, J. 1996. Phloroglucinol derivatives in *Dryopteris* sect. *Fibrillosae* and related taxa (Pteridophyta, Dryopteridaceae). Ann. Bot. Fennici 33: 69-100.