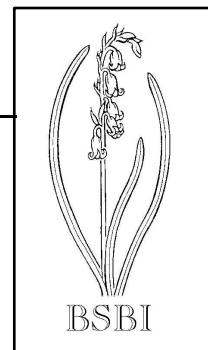


Plant Crib



DRYOPTERIS

1. *Dryopteris affinis* / *D. oreades* / *D. filix-mas*

The Male fern complex may give some difficulty due to the fact that all plants in the *D. affinis* complex are apomictic (called, when used with ferns, apogamous) and like flowering plants with the same breeding mechanism perpetuate populations of minor variants which often become locally common albeit restricted in distribution. The Table below will help recorders to segregate the scaly Male ferns (i.e. taxa of the *D. affinis* complex) and identify plants of the two sexual species, *D. oreades* and *D. filix-mas*.

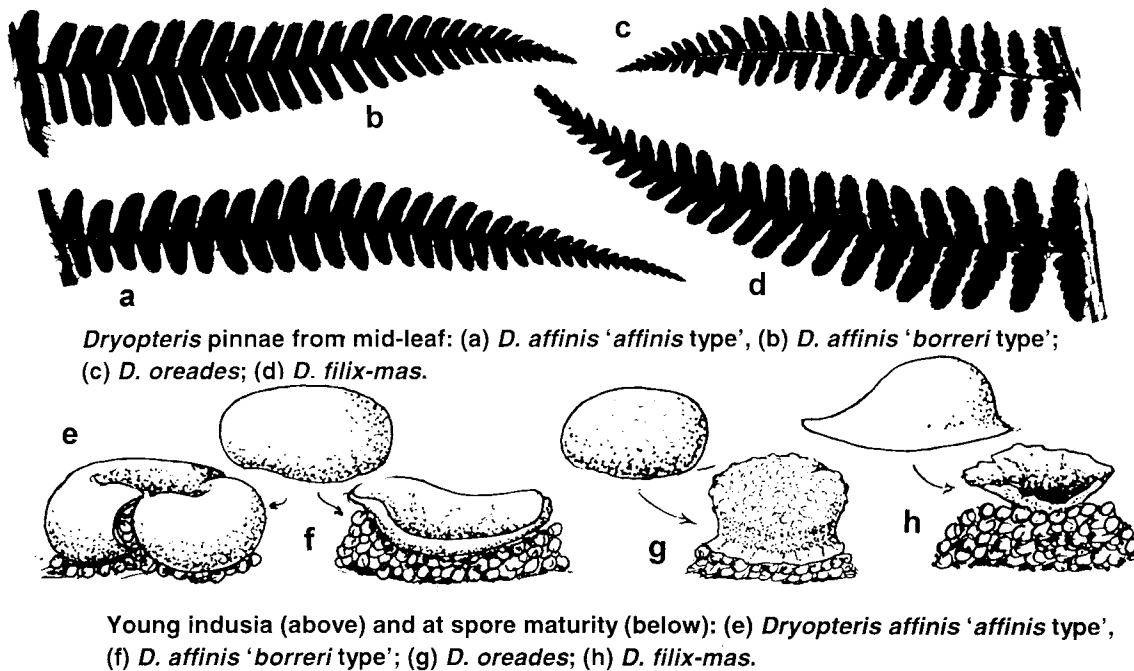
	<i>Dryopteris affinis</i> (Lowe) Fraser Jenk	<i>D. oreades</i> Fomin	<i>D. filix-mas</i> (L.) Schott
Petiole scales	Pale gold or brown to reddish gold with dark bases which remain to give a 'peppered' look if scale rubbed off; mixture of broad and narrow scales; apex acute or with a hair-point	Very pale grey-brown, bases not dark; all \pm equal width; apex acute but not hair-pointed	Pale brown to straw-coloured, bases not dark; mixture of broad and narrow; apex hair-pointed
Pinna midrib	With a conspicuous dark mark on the underside at junction with rachis (may be faint at very apex of leaf or fade with drying)	Without a dark mark on the underside at junction with rachis (see Note 1)	Without a dark mark on the underside at junction with rachis (see Note 1)
Leaves (adult fertile plant)	Length up to 100 (-200) cm, base \pm tapering or abruptly truncate; upper surface of lamina mid-green to yellow-green	Length 40-50 (-80) cm, base \pm tapering; upper surface of lamina grey-green to mid-green	Length c. 35-150 cm, base \pm tapering; upper surface of lamina grey-green
Pinnules	Margins lying flat (see Note 2), ranging from unlobed to having rounded to acute teeth, <i>or</i> with rectangular lobes bearing teeth which are prominently longer at the distal corners; apex variable - square-truncate, rounded or pointed (Figs a, b); glands absent	Margins 'crisped' (turned up and wavy) giving a concave effect; lobes at sides blunt but teeth at rounded apex broad and divergent (Fig. c); glands present	Margins \pm flat; lobes at sides \pm acute; teeth at rounded apex acute, pointing towards obtusely-pointed apex (Fig. d); glands usually absent
Sori	Whole pinnule fertile	Usually only proximal half of pinnule fertile	Whole pinnule fertile
Indusia of immature sori	Margins tucked well under; unicellular glands absent or very sparse	Margins tucked well under; unicellular glands frequent (best seen on margins)	Margins lying flat on the lamina surface; unicellular glands absent
Mature indusia	<i>Either</i> : thick, surface smooth, margins remaining well tucked-	\pm thick, surface granular, 'egg-shell' appearance,	Thin, surface smooth, margin initially

Plant Crib

indusia	under as sporangia mature and lift slightly, occasionally splitting radially on maturity (Fig. e), not overlapping neighbouring indusia; persistent (mostly still present on last year's leaves) [<i>affinis</i> forms] <i>Or</i> : thinner, shrivelling and lifting to form a ± flat or wavy disc, then later rising to a 'chanterelle' shape (Fig. f), without radial splits, separate from neighbouring indusia; rarely still present on last year's leaves [<i>borreri</i> forms] (see Note 3)	becoming cinnamon coloured, usually glandular, with margins tucked under at first, developing to give a constricted 'mob-cap' shape (Fig. g) which usually persists until spores are shed, not overlapping neighbouring indusia; rarely found on previous year's leaves	flattened and spreading, often overlapping neighbouring indusia, shrivelling to form a 'chanterelle' (Fig. h); often shed before the spores; mostly absent on previous year's leaves
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Notes to table on previous page

1. If coloration very pale check spores for sterility.
2. Morphotype '*cambrensis*' has segments lying at an angle to plane of pinna.
3. Morphotype '*cambrensis*' again has intermediate characters between *D. affinis* and *D. oreades* and a rather tall indusium of medium thickness but thin at the edges, maturing to form a 'pie-crust', sometimes splitting radially, some still present on last year's leaves.



2. A note on the *Dryopteris affinis* problem

Apogamous ferns contain 32 spores in a sporangium (instead of the usual 64 found in sexual species), with each spore (and resulting prothalli and gametes when formed) containing the same genetical material as the parent fern plant (sporophyte) producing it. Furthermore a new generation of sporophyte is produced directly from the prothallus without the usual fusion of gametes, a process that produces a new generation of clones (identical individuals). Any minor mutation will be passed on to future generations by the same process and thereby form a new population, morphologically distinct although with a very limited distribution (Manton 1950).

Plant Crib

The ancestry of *D. affinis* agg. is complicated and thought to involve an unknown species and two sexual diploids, *D. oreades* and the non-British *D. caucasica* (A. Braun) Fraser-Jenk. The common Male Fern, *D. filix-mas*, which has evolved through hybridisation between the latter two species, hybridises freely with all forms of *D. affinis* (see below) and through this process can introduce the genomes (and thereby characters) of those species into the *affinis* complex.

For the reasons stated below, the *Dryopteris affinis* complex shows a wide range of morphologies of leaf shape, teeth and lobes of pinna segments, indusium shape and texture and degrees of scaliness. All morphotypes have indusia with the margin tucked under to enclose the developing sporangia in the youngest stages (as has *D. oreades*). As the sporangia mature, so do the indusia – in various and distinctive ways characteristic of the different morphotypes. But not all sori, even on the same pinna segment, develop at the same rate and this is reflected in the variety of form of the indusia seen on any one pinna or leaf. Thickness, especially of the margin, and texture are also important features of the indusium in this group of ferns. The table below distinguishes these apogamous plants from the sexual species with which they can be confused.

Such a situation is a challenge to field botanists, and those who want to study the variation seen in their vice-county in some detail may find published work on the group lacking in the taxonomic clarity needed for precise identification. Even those who have worked on the group for some time find some specimens, albeit often distinct at the individual level and possibly, occasionally, at the population level also, that are almost impossible to assign to any taxonomic unit (conventional or otherwise) presently recognised. **We therefore recommend that for the Atlas 2000 database records of the aggregate species only are submitted.**

However, work continues on the group and more field data and specimens are needed and the authors of this note are keen to see as much material as possible. A detailed appraisal of the *D. affinis* complex thus gained over the next three years will be published by the British Pteridological Society in a revision of the Fern Atlas. Some botanists have already embarked on regional or county surveys (e.g. Cornwall, Cards, Cumbria, NE Yorks, Arran) that have proved of considerable interest, and these and any further collaborators will be fully acknowledged. As a background to this study we provide some introductory text below. Whilst recording for Atlas 2000 we strongly recommend that those undertaking fieldwork make pressed vouchers for later determination by the undersigned, or send fresh material to ACP as below. Material should be fertile, showing black but undehiscent sporangia and firm indusia and show a complete leaf (including petiole) if possible. Fresh material to be sent to Anthony Pigott at Kersey's Farm, Mendlesham, Stowmarket, Suffolk IP14 5RB, by first class post and marked 'Affinis'. **Dried vouchers** should be sent to BPS Affinis Watch, c/o Botany Department, The Natural History Museum, Cromwell Road, London SW7 5BD.

A note on 'hybrids'

The prothalli of any genotype within the complex, whilst unable to form viable egg-cells, can nevertheless form functional male gametes which can cross-fertilise other sexual species (e.g. *D. filix-mas*, *D. oreades*) and hybrids can thus be formed. Early generations of such hybrids will show a very high proportion of abortive spores but some sporangia will contain some well-formed spores which will germinate and produce, apogamously, further plants exhibiting hybrid characters. When *D. filix-mas* is the sexual parent, the resulting hybrids are called *D. × complexa* Fraser-Jenk. (*D. × tavelii* auctt.). The plants are usually more like *D. filix-mas* but always have a black spot (sometimes faint) at the pinna-rachis junction and have a high percentage of spore abortion. There is evidence (K. Trewren, pers. comm.) that the percentage of abortions in populations of such plants can vary from 35% to 75% and it is a possibility that each successive generation has fewer abortive spores than the last. Furthermore, they occur usually as solitary plants, whereas morphotypes (i.e. established apogamous forms of *D. affinis* that may look similar (and often do), occur usually as sizeable populations. Fraser-Jenkins subsequently (in Derrick *et al.* 1987) described three nothosubspecies depending on which subspecies of *D. affinis* (see below) is involved in the crossing. Morphology is significant but the chromosome number is the only way to check such origins: those involving subsp. *borreri* (nothosubspecies *critica* Fraser-Jenk.) and *cambrensis* (nothosubspecies *contorta* Fraser-Jenk.) will be pentaploid (5x); and that with subsp. *affinis*, tetraploid (4x). Fraser Jenkins, an undisputed expert in the group, gave (*loc. cit.*, xii) a detailed description of nothosubspecies *contorta* in which he presumed the plant to be pentaploid (because of the morphology and the parentage proposed). When the type specimen was later counted (M. Gibby, pers. comm.) it was found to be tetraploid. As these nothosubspecies are so difficult to identify, ***D. × complexa* should not be recorded to the nothosubspecies level.** However, vouchers should be made of any suspected plants which have 60% or more abortive spores.

Hybrids with *D. oreades* are more difficult to detect but will similarly have a high percentage of abortive spores. They have so far not been specifically named and given binomials as hybrids but it is possible that *D. affinis* subspecies/morphotype *cambrensis* (a triploid) is the result of *D. oreades* crossing with the diploid subspecies/morphotype *affinis* or something similar. Whatever their origins, such specimens will have sufficient characters of *D. affinis* to place and record them within that complex. However, any with a high proportion of abortive spores should be collected for further determination.

Plant Crib

A practical approach to the nomenclature of the *Dryopteris affinis* complex

Formal botanical names have been given to many units of the variation seen in this complex, including plants with intermediate morphology with related sexual species, but the usefulness of naming within a formal taxonomic framework is questionable until detailed analysis has been carried out. Some British floristic accounts (e.g. CTM 1987; Page, 1997, and Stace, *New Flora*) have divided the aggregate into three subspecies: *affinis*, *borreri* (Newman) Fraser-Jenk. and *cambrensis* Fraser-Jenk., based on Fraser-Jenkins (1980 1996) with varied attempts at definitive descriptions. Beitel & Buck (1988) discussed the use of subspecies rank for these taxa and recommend specific rank to reflect the biological situation. The present authors prefer to have an open mind as to the affinities of the wider range of morphological/taxonomic 'units' for the present exercise and prefer the term '**morphotypes**', a term without rank not governed by the *Code of Botanical Nomenclature* thereby nullifying the problems of potential nomenclatural changes. This terminology also avoids the necessity of showing relationships within a hierarchy of formal names. The final presentation on the distribution and ecology of the 'morphotypes' studied will be put eventually into a formal nomenclatural context.

More detailed descriptions of these morphotypes, based on work done by A. C. Pigott (unpublished), were published in Jermy & Camus *Field Guide* where five of the most commonly seen and easily distinguished types were described. This approach has been elaborated by Pigott (1997) who has described in tabular format nine morphotypes within the complex.

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Authors A. C. Jermy, A. C. Pigott & J. W. Merryweather, January 1998.

3. *Dryopteris aemula* / *D. dilatata*

Once known these two species are rarely confused but the following may help:

D. aemula (Aiton) Kuntze: Leaves mid apple-green, highly glandular on lamina and veins (smelling of hay when dried), remaining green through winter, lamina margins turned up (even from very young stage), giving a characteristic appearance which pteridologists term 'crispy'; petiole purple-red on all faces, pruinose; scales pale brown, concolorous, narrowly triangular; rhizome erect, the growing point flat.

D. dilatata (Hoffm.) A. Gray: Leaves, deep, almost bluish-green, not glandular except on axes when young, mostly dying down in winter, lamina margins turning down; petiole orange-brown on abaxial side, paler often greening on inner (abaxial) face; scales pale, with wide dark brown central stripe, broadly triangular-ovate; rhizome erect, the growing point domed.

4. *Dryopteris carthusiana* / *D. dilatata* / *D. expansa*

In their typical forms these three species present no problem but shade forms of *D. dilatata* can have the flat leaf blade of the other two species and then pinnule cutting and spore sculpturing may be used to help identification. Both *D. dilatata* and *D. expansa* can spread by short (up to 40 cm long) stolons which end in a rosette of leaves bearing on their petioles pale concolorous scales more typical of *D. carthusiana*. Young leaves of all three species are triangular in outline and should not be confused with *D. aemula*, the leaves of which are of a fresh yellow-green and have their margins upturned.

Hybrids between all three species can occur and are best detected by examination of sporangia that do not dehisce and contain abortive spores. That between *D. carthusiana* and *D. dilatata* (*D. × deweveri* (J. T. Jansen) Wacht.), frequent where both parents grow together, has the leaf cutting of *D. carthusiana* but an erect rhizome, and the scales are orange-tinged with only a

Plant Crib

faintly darker centre. That between *D. dilatata* and *D. expansa* (*D. × ambroseae* Fraser-Jenk. & Jermy) is also usually present where the two parents grow together but is more difficult to detect. Its more yellow-green, erect and more finely cut leaves may suggest it but abortive spores will be the best confirmation. *D. carthusiana* × *expansa* (*D. × sarvelae* Fraser-Jenk. & Jermy) is a rare hybrid found in west Scotland (V.c. 97 & 101) where in one site it forms a large distinct population. It is characterised by a mat, almost glaucous tinge to the erect leaf. If growing with *D. expansa* it is seen to die back slightly earlier (i.e. it is less frost-resistant).

	<i>D. carthusiana</i> (Vill.) H.P. Fuchs	<i>D. dilatata</i>	<i>D. expansa</i> (C. Presl) Fraser-Jenk. & Jermy
Habit	Plant with few, erect leaves on a creeping, occasionally branched rhizome, not forming a 'shuttlecock'; growing point flat, with 4 bright green croziers (upper, lower, and two at side); leaves dying rapidly after frost	Plant with leaves arching and clustered in a 'shuttlecock' on a short, ± erect rhizome (see Note 1); growing point domed, young croziers usually more than 4, radially spaced, colourless; leaves staying green through the early part of winter	Plant with leaves only slightly arching and forming a sparse 'shuttlecock' from a ± erect rhizome (see Note 1); growing point domed, young croziers as in <i>D. dilatata</i> ; leaves soon dying down in winter except in very sheltered sites
Leaves (see note 2)	Narrowly lanceolate, pale to yellowish-green	Triangular-ovate, dark bluish-green	Triangular-ovate, mid- to pale green
Petiole scales	Sparse, almost colourless when on young croziers, becoming pale brown with ageing, without a central dark stripe, appressed to petiole, broadly lanceolate, hair-pointed	Dense, at least near base, pale brown with a broad dark central stripe even when on young croziers (but see Note 1), usually flat, appressed to petiole, broadly ovate-deltate apex long acuminate	Dense, at least near base, typically uniform brown-ginger, even when on young croziers, occasionally with a darker central stripe (but see Note 1), often patent or bullate, broadly ovate-deltate, with apex often abruptly acuminate
Pinnules	With edges flat in plane of lamina, segment margins with conspicuous long, incurving, spinulose-tipped teeth	With margins turning under, segments linear-oblong, not cut to midrib, with short spinulose-tipped teeth	With edges flat in plane of lamina, segments ± oval, cut ± to midrib (giving leaf a lacy appearance), with short spinulose-tipped teeth
Spore sculpturing	Rugose with wings less well formed and scattered, sometimes spiny, tubercles	Winged, with ± dense spines or tubercles, darker than those of <i>D. expansa</i> (see Note 3 below)	Winged, with sparse spines or tubercles, paler than those of <i>D. dilatata</i> (see Note 3)

Notes

1. Some plants have stolons originating from leaf axils which creep until 20-30 cm from parent plant when they become erect. They should not be confused with the thick rhizomes of *D. carthusiana*.
2. Leaves on stolons may be distinctly triangular.
3. The best way to know this comparative colour is to mount spores of both species (having confirmed identity on other characters) on the same slide.

Authors

A. C. Jermy & M. Gibby, January 1998.