The Distribution of *Dryopteris assimilis* S. Walker in Britain

By J. A. CRABBE*, A. C. JERMY* and S. WALKER**

**British Museum (Natural History), London.*
***Department of Genetics, Liverpool University.*

ABSTRACT

The *Dryopteris dilatata* complex in Britain consists of two allotetraploids, *D. dilatata* (Hoffm.) A. Gray and *D. carthusiana* (Vill.) H. P. Fuchs, and an ancestral parental diploid *D. assimilis* S. Walker. The latter has hitherto been confused with *D. dilatata sensu stricto* and this paper discusses the variation of the characters used to separate *D. assimilis* and gives the known distribution in Britain. In particular the variation of the perispore is discussed in the light of studies made on the scanning electron microscope.

INTRODUCTION

The presence in Europe (in Britain, Norway and Switzerland) of a diploid cytotype of the *Dryopteris dilatata* complex was first pointed out by Manton (1950). Following cytogenetic studies (Walker 1955, 1961), it was proposed that this taxon be regarded as a species, *Dryopteris assimilis* S. Walker (1961: 607), based on *Lastrea dilatata* var. *alpina* T. Moore, which, as long ago as 1845, had been recognised as a distinct variety. *D. dilatata* (Hoffm.) A. Gray and *D. carthusiana* (Vill.) H. P. Fuchs (*D. lanceolatocristata* (Hoffm.) Alston, in Dandy 1958) are both tetraploid species. A survey of material of these three species in the major British and Irish herbaria (by J.A.C. and A.C.J.) showed that *D. assimillis* has a wider distribution than hitherto thought and led to further collecting of living material, which has been examined cytologically by S.W. Diploid plants attributable to *D. assimilis* can now be reported from 23 localities; Roberts (1965) recorded the presence of diploids in Snowdonia, N. Wales.

Since 1961 several papers have dealt with the morphology of and variation within *D. assimilis* (Walker & Jermy 1964; Döpp & Gätzi 1964; Nannfeldt 1966; Widén, Sarvela & Ahti 1967; Simon & Vida 1966). Chromatographic investigation by Hegnauer (1961), Wieffering, Fikenscher & Hegnauer (1965), and Widén & Sorsa (1966) into the intraspecific variation of phenolic and other compounds is proving to have interesting results. The discussion below, of characters found useful in this survey, stresses the similarities and differences between the three species mentioned above; it is summarised in Table 1, p. 6.

Material from the following herbaria has been studied: British Museum (Natural History) (**BM**); Cambridge University (**CGE**); National Museum of Ireland, Dublin (**DBN**); Royal Botanic Garden, Edinburgh (**E**); Glasgow University (**GL**); Royal Botanic Gardens, Kew (**K**); Manchester Museum (**MANCH**); National Museum of Wales, Cardiff (**NMW**); Oxford University (**OXF**); and those of J. E. Lousley and E. C. Wallace.

SPORE ORNAMENTATION AND CHROMOSOME NUMBER

We examined about 1500 specimens for this survey and found that the most reliable identification characters are spore ornamentation and chromosome number and these have therefore been stressed in the list of identifications below. We feel that with a little experience certain vegetative characters can be correlated with this spore type and these and the variation within them will be briefly discussed.

The sculpturing of the perispore of *D. assimilis* differs from that of *D. dilatata* and *D. carthusiana* in density and shape and size of projections. In *D. dilatata*, 50 per cent. or more of the surface is covered with subconical blunt spines, the majority of which are touching and coalescing towards their bases (see Plate 1a). The differences between the spores of *D. carthusiana* and *D. dilatata* are somewhat more subtle; those of the former are possibly more rugose and the projections shorter in relation to their width, many forming rounded papillae rather than spines (see Plate 1b). The perispore of *D. assimilis* is 10–25 per cent. covered with more finely tapered, blunt spines which only rarely are close enough to coalesce at their bases (see Plate 1c and d).

Of the 102 herbarium specimens of *D. assimilis* with mature spores studied, only two populations showed a spore-type which could not immediately be placed in the *assimilis* range. One of these was from Borrowdale (collected by Mr F. Jackson in 1963) and the spores were more rugose and had extremely few spines; this first gathering was tentatively identified (Jermy 1968), on spore and gross morphology, as a hybrid involving the *D. dilatata* aggregate and *D. aemula* (Ait.) Kuntze, a diploid not hitherto regarded as a member of this complex. A further search in the field failed to find this problem plant but similar plants from the same locality proved to be diploid with regular meiosis. These do not show *aemula* characters but are morphologically within the range of *D. assimilis* and are regarded as that species in this paper. However, this population may have been isolated for a long time and the spore morphology is not typical (see Plate 1e); it needs further investigation. It is possible that *D. assimilis* is elsewhere in upland sites in the Lake District; the specimen at Kew collected at 'Keswick' in 1859 by Wright could well be from the same Borrowdale locality, or at least the same valley.

The second is the plant recently found by Mr J. W. Dyce near Cullen, Banffshire (see below) and as yet its chromosome number is unknown. The spines on the perispore are denser and more robust and bear a resemblance to those of *D. carthusiana* (see Plate 1f).

When an investigation into the finer structure of the perispore (perine) using the scanning electron microscope was begun, it was realised that immature stages could well be interpreted as different spore types. A preliminary investigation using ultra-thin sections through developing sporangia suggested that the perispore is laid down within a relatively short time and that the sporopollenin is built up on a predetermined pattern; the density of the projections at least would be obvious, therefore, from the outset of perispore formation (Pettitt, J.M., personal comm., 1968). The degree of rugosity could well be an artifact accentuated on drying, when it would then reflect the thickness of the various walls of the spore. It is concluded that differences seen in the *assimilis* type of spore are real and not arrested stages of the *dilatata* type.

It is said above that the chromosome number ($n = 41$) is a reliable character.

We are aware, however, that other diploid taxa, possibly originating from the same ancestral stock, may well be very close morphologically to *D. assimilis*. Without an investigation into their breeding behaviour these may not obviously disclose themselves.

RANGE OF VARIATION IN SPECIMENS WITH AN *ASSIMILIS* SPORE-TYPE

RHIZOME

The rhizome is basically an erect system which falls into a semi-prostrate condition in old specimens. Large *D. assimilis* plants show a more open-branched rootstock than the compact head of two or three crowns seen in a well-established *D. dilatata*. The side branches of the rhizome of *D. assimilis* may be distinctly creeping thus having a growth-form similar to the hybrid *D. carthusiana* × *dilatata*. In both *D. dilatata* and *D. assimilis* the leaves arise close to each other, thus forming a closed 'shuttlecock' crown; in *D. carthusiana*, the leaves are more widely spaced along a creeping rhizome and never form a closed 'shuttlecock' crown. Widén *et al.* (1967) describe internal secretory hairs in the intercellular spaces of the rhizome (and petiole) which are smaller (60–80 μm) but more frequent in *D. assimilis* than the other two species where they average 80–100 μm long.

SCALES ON RHIZOME AND STIPE

All the scales around the growing apex of all three species are triangular-lanceolate; those on the stipe base are similar, often grading into very narrow, hair-like scales. Also found on the stipe are more ovate scales with acuminate tips and in *D. assimilis* these are frequently bullate (blistered or balloon-like), a condition not seen on the other two species. The colour of the scales of *D. assimilis* is very variable, both concolorous forms and those with a darker centre being found. Pale concolorous scales are found always in *D. carthusiana* and on the stipes of juvenile leaves produced on adventitious side branches in *D. dilatata* (small plants of *D. dilatata* from high altitudes occasionally have pale scales also). Large *carthusiana*-like plants showing a darker median stripe in their scales usually suggest hybridity with *dilatata*. Some populations of *D. assimilis* have concolorous scales of a distinct red-brown colour not seen in the other two species.

FROND HABIT, TEXTURE AND COLOUR

D. assimilis shows the erectness of habit characteristic of *D. carthusiana*; this stiffness is reflected in the pinnae and lamina itself and the blade is flat from the very beginning. In *D. dilatata* the whole frond reposes at an angle of 60° or less and the blade throughout is more flaccid. On the ultimate segments, the lamina tissue itself is reflexed from the midrib (*cf.* Plate 2a, b and c), a condition more marked in young fronds but nevertheless obvious throughout the life of the frond.

The colour of the lamina of *D. assimilis* is a mid- to yellow-green which dries to a yellow-brown green in the herbarium. To some extent *D. carthusiana* has this same character; *D. dilatata*, on the other hand, is a darker, more bluish (olive) green which remains dense in the dried state. Obviously the resulting colour of dried specimens varies to some extent with the method and speed of drying but that of fresh material is not affected by shade or similar habitat conditions.

FROND SHAPE AND SIZE

The ratio of length of stipe to length of lamina ranges from 2:3 to 1:1 in both *D. carthusiana* and *D. assimilis*; in *D. dilatata* it is more often 1:2. *D. assimilis* from woodland sites can attain 1 m in height, as can *D. carthusiana* in similar situations, but *D. dilatata* reaches up to 1·6 m. The range of height of frond is greatest in *D. assimilis*, some smaller specimens 10–15 cm high retaining their low stature after three years in cultivation; *D. dilatata* may also have small fronds at high altitudes and in exposed places.

The shape of the lamina in *D. dilatata* varies from ovate-triangular to lanceolate-triangular; in *D. carthusiana* the frond is narrower, almost linear-lanceolate in outline. *D. assimilis* ranges between the two but more typical specimens are linear-lanceolate; some small specimens and juvenile leaves tend to be ovate or even triangular. The shape of the lowest pinna has been used as a diagnostic character for *D. assimilis* (Walker 1955, Clapham, Tutin & Warburg 1962, Heywood 1964, Simon & Vida 1966); unfortunately this exaggerated lowest basiscopic pinnule, often half as long as the pinna itself, emphasising a triangular outline, can be found in *D. dilatata*. The record of *D. assimilis* for Kerry (v.c. H2) by Vida (1966, p. 281) is based solely on this character (pers. comm.) and as no other Irish specimens have come to light in our search, this record must be taken as extremely doubtful. On the other hand, however, the shape of the median pinnae does point to a distinction and, as Plate 2 shows, *D. assimilis* has a smaller length/breadth ratio than either of the other two.

The degree to which a fern leaf is dissected is difficult to define because two axes of development are concerned; it is, however, so often the basis of the general appearance of a species.

TABLE 1. COMPARISON OF CHARACTERS

D. assimilis	*D. dilatata*	*D. carthusiana*
Rhizome		
erect to semi-prostrate; frond bases forming open shuttlecock	erect or rarely semi-prostrate; frond bases forming dense shuttlecock	creeping; frond bases more distant, not forming distinct shuttlecock
Scales		
concolorous, pale or red-brown, or with darker median stripe; some ballooned scales on stipe	with a darker median stripe (concolorous only on adventitious shoots or at high altitudes); no ballooned scales	concolorous and pale; ballooned scales absent
Frond shape/habit		
erect, ovate-lanceolate to linear-lanceolate, small fronds ovate-triangular; flat; teeth often turned up	lax, ovate-triangular, rarely becoming lanceolate; convex; teeth turned down	erect, (linear-) lanceolate; flat; teeth turned up
Frond dissection		
sinus open, cut ± to costule; teeth obtuse	sinus closed, cut ½ or 2/3 to costule; teeth obtuse	sinus closed, cut ± halfway to costule; teeth acute
Frond colour		
yellow-green	olive-green	yellow-green

In *D. assimilis* the cutting, especially towards the tips of the pinnae, is deep and the segments are distinct; in fact some fronds are so finely dissected that, when the upper half only is seen, the plant may be taken for *Athyrium filix-femina*. In both *D. dilatata* and *D. carthusiana*, the sinus between the segments rarely reaches more than half-way to the midrib (see Plate 2). Furthermore this open pattern is accentuated in *D. assimilis* by the sinus being wide, whereas in the other two species it is closed and the lamina edges often touch.

General comments on the variation

Dryopteris assimilis shows then considerable variation in scale colour, frond shape and the cutting of pinnae but there is insufficient correlation between these characters to warrant any further formal taxonomic separation. Widén *et al.* (1967, p. 5) describe a form from S. Finland with finely dissected pinnae and with distinct red-brown scales, which they compare with *D. dilatata* var. *pseudo-spinulosa* Rosendahl (1916, p. 327), but stress that on morphological and chemical grounds it 'is of no taxonomic importance'. This form is present in W. Scotland also, e.g. *Jermy 6176*, where $n = 41$.

Thomas Moore described many varieties of *Lastrea dilatata* (Moore 1855; 1857), one of which (var. *alpina*) is, of course, the type of *D. assimilis*. Another variety whose gross morphology and spores suggest *D. assimilis* is *L. dilatata* var. *ordeanae* described from a lowland site at Kilmory, Argyll. It has a broader, finely dissected frond with dark-centred scales and is characteristic of the *D. assimilis* found around 1000 m in the Austrian Tyrol. Other specimens in the Moore herbarium at Kew, from Bute and labelled '*L.d.* var. *micromera* T. Moore' are also *D. assimilis*. The type of var. *micromera*, however, is from Devon and other specimens so named are from SW. Wales; this southern element has spores of the *D. dilatata* type and needs further investigation. The well-worked site of Ben Lawers has produced not only the type of *D. assimilis* but also *L.d.* var. *fraseri*, a form with dark-centred scales and an ovate-triangular frond, which is extremely (and abnormally?) finely cut; it has the *assimilis* spore-type.

Two forms that stand out in the field, in cultivation and in the herbarium have not, as far as can be seen, been named. One is a plant with crowded (i.e. overlapping), ascending pinnae and pale reddish-brown scales; one such population of very small plants from Glen Spean (Stirling & Walkinshaw 1 & 2) that keep their small stature in cultivation has been cytologically investigated and found to be diploid. Similar, but larger plants have been detected in the herbarium from other parts of Scotland. The other is a plant collected in fairly dry, acid, dwarf heath near Cullen, Banffshire by J. W. Dyce, now in cultivation. It has distinct creeping rhizomes and pale scales, an ovate-triangular frond with very narrow pinnae and oblong, truncate pinnules (*cf.* the form known as *D. dilatata* var. *collina*: see Moore 1855, tab. 26A). The spines on the perispore are somewhat denser than in normal *D. assimilis* (see Plate 1f) and the plant may turn out to be a form of *D. carthusiana*; it certainly needs further investigation.

Detailed distribution of *D. assimilis*

The distribution of the specimens seen is summarised on the map (Fig. 1); the data is listed below in vice-county order and, within each vice-county, it follows

the numerical order of the National Grid co-ordinates. The overall distribution in Britain is that of an 'arctic-alpine' as defined by Matthews (1955); it follows closely the distribution of such species as *Carex bigelowii* Torr. ex Schwein., *Silene acaulis* (L.) Jacq. and *Saxifraga nivalis* L. and, in England, that of *Woodsia ilvensis* (L.) R. Br. In Europe it is mainly northern in distribution, reaching 71° N. in Norway; in central and southern Europe it is confined to the mountain ranges.

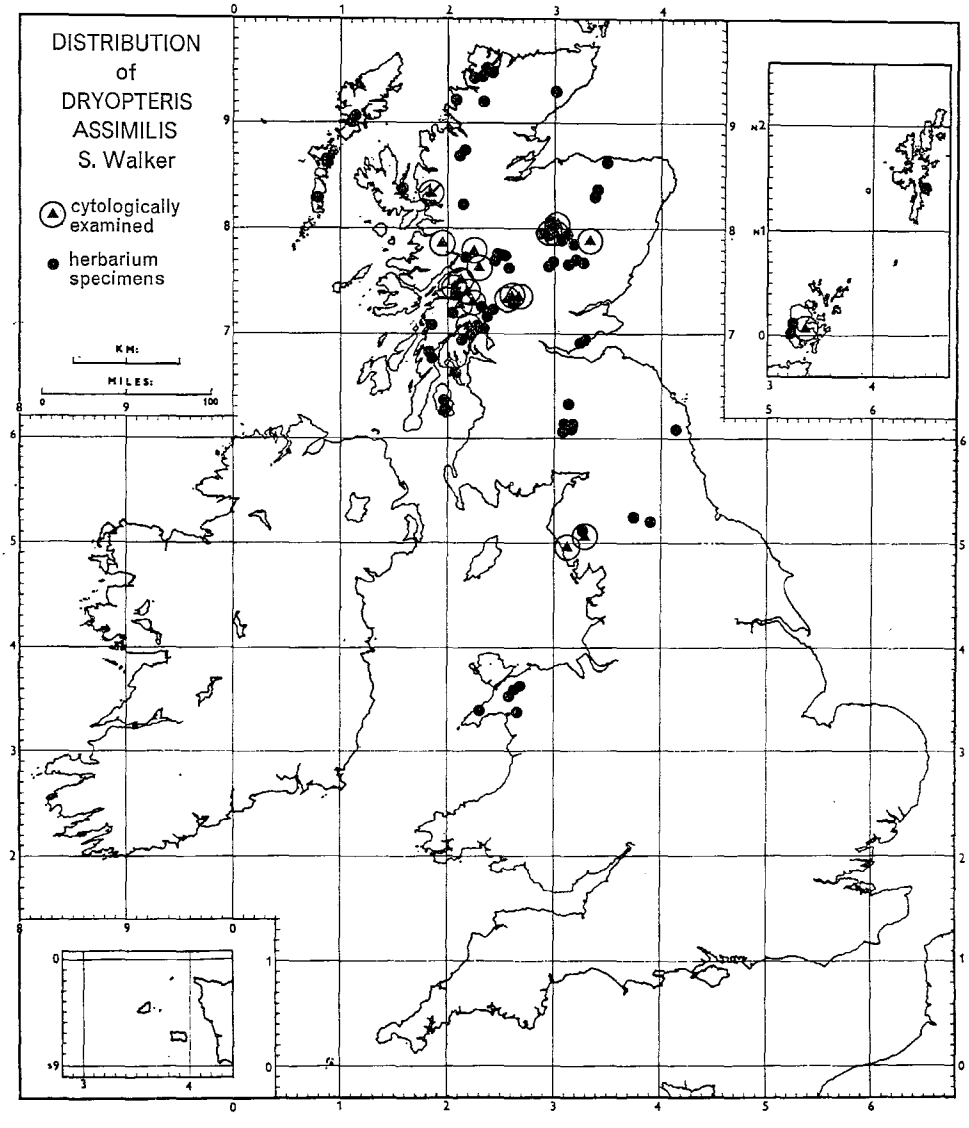

FIGURE 1. Distribution of *Dryopteris assimilis* S. Walker in the British Isles.

Its presence, together with other arctic-alpines, on the higher mountains of Britain suggests it may have been a member of our Late-glacial flora. Its ecology on the other hand is that of a woodland plant, a habitat which it often frequents at lower altitudes (e.g. at almost sea level in western Scotland). Did our mountain form spread from central European woodlands because of its ability to find a niche amongst the bolders of a stable moraine? If so, why did it not return to the lowlands in some quantity to the habitats where we now find *D. dilatata*? We need to know more of the ecology of *D. assimilis* and to decide whether in fact there are two ecological races (and diploid cytotypes).

SPECIMENS OF *DRYOPTERIS ASSIMILIS* IDENTIFIED BY THE AUTHORS

(a) *confirmed by examination of chromosomes (by S.W.)*

V.C. 70 CUMBERLAND: Holmrook, *c.* 200 ft., 34/0799, *H. V. Corley*, 1967 (**BM**); Borrowdale, W slopes of Glaramara, 2000 ft., 35/2512, *F. Jackson 2 & 4*, 1966 (**BM**).

V.C. 88 MID PERTH: Ben an Eachan, *c.* 2500 ft., 27/5638, *A. C. Jermy 3363*, Sept. 1962 (**BM**); Meall na Tarmachan, *c.* 2500 ft., 27/5838, *S. Walker 63103*, 1963 (**BM**); Ben Lawers, *c.* 3000 ft., 27/6341, *S. Walker 63114*, 1963 (**BM**).

V.C. 92 SOUTH ABERDEEN: above Loch Muick, *c.* 2000 ft., 37/2989, *S. Walker 65001*, 1965 (**BM**).

V.C. 96 EASTERNESS: Beinn Braeriach, *c.* 2500 ft., 28/9500, *S. Walker 66002*, 1966 (**BM**); Coire an Lochain, *c.* 3000 ft., 28/9803, *S. Walker 66003*, 1966 (**BM**); Faicaill a' Choire Chais, *c.* 3000 ft., 28/9904, *S. Walker 66004*, 1966 (**BM**).

V.C. 97 WESTERNESS: Stob Coire an Easain, Glen Spean, *c.* 3000 ft., 27/2372, *A. McG. Stirling & D. A. Walkinshaw 1 & 2*, 24 Sept. 1966 (**BM**); Stronanime, Ardgour, 17/9583, *H. V. Corley 674 & 678*, 1967 (**BM**); Beinn na Lap, 27/3769, *H. V. Corley 14*, 1966 (**BM**).

V.C. 98 MAIN ARGYLL: Beinn Fraochaidh, 1600–1750 ft., 27/0251, *A. C. Jermy 6176*, 27 Aug. 1966 (**BM**); Coire Dubh, Beinn Fraochaidh, 27/0252, *H. V. Corley*, 1965 (**BM**); Allt Coire Ghlias, *c.* 3000 ft., 27/1028, *S. Walker 65010*, 1965 (**BM**); Bidean nan Bian, *c.* 1750 & 2250 ft., 27/1354, *S. Walker 65005 & 65006*, 1965 (**BM**); Beinn an Lochain, 27/2208, *H. V. Corley*, 1965 (**BM**); Beinn Laoigh, *c.* 1900 ft., 27/2626, *H. V. Corley*, 1965 (**BM**); Beinn Udlaidh, *c.* 1900 ft., 27/2732, *H. V. Corley 9*, 1966 (**BM**); Coire Daimh, 27/2732, *H. V. Corley 6*, 1966 (**BM**); Beinn Dothaidh, *c.* 3000 ft., 27/3240, *S. Walker 63113*, 1963 (**BM**); Coire an Dothaidh, *c.* 2250 ft., 27/3240, *S. Walker 63112*, 1963 (**BM**).

V.C. 105 WEST ROSS: 2 miles W of Strome Ferry, 18/8032, *S. Walker 63109*, 1963 (**BM**).

V.C. 111 ORKNEY: Naversdale, Orphir, N30/3304, *E. M. Bullard*, Aug. 1966 (**BM**.

(b) *determined by examination of spores (except those marked * where ripe spores were not found) or by other morphological criteria*

V.C. 48 MERIONETH: Moelwyn Bach, Ffestiniog, 23/6644, *R. E. Hughes*, Aug. 1967 (**NMW**)*.

V.C. 49 CAERNARVON: Yr Eifl, 23/3544, *R. H. Roberts*, 22 July 1967 (**NMW**); Cribbyn, 23/65, *H. A. Hyde*, July 1925 (**NMW**)*; Cwm Brynog, 2000 ft., 23/6054, *J. H. Lewis*, 29 July 1875 (**MANCH**); Cwm Glas, 23/6155, *J. E. Griffith* (**NMW**); Cwm Glas Mawr, 23/6155, *R. E. Hughes*, June 1967 (**NMW**)*; Cwm Glas Bach, 23/6156, *R. E. Hughes*, June 1967 (**NMW**)*; Cwm Llafar, 23/6565, *J. E. Griffith*, July 1893 (**NMW**)*.

V.C. 65/66 NORTH-WEST YORK/DURHAM: Teesdale, 35/82, *Mitchinson*, 1860 (K).

V.C. 68 CHEVIOTLAND: Hulne Parks, 46/1912, *W. Richardson*, Aug. 1868 (BM)*.

V.C. 69† WESTMORLAND: High Cup Nick, Murton, 35/7426, *A. H. G. Alston 4293*, 13 July 1939 (BM)*.

V.C. 70 CUMBERLAND: Borrowdale, W slopes of Glaramara, 35/2512, *A. C. Jermy 6424–30*, 23 June 1968 (BM); Keswick, 35/2723, *Wright*, 1859 (K).

V.C. 72 DUMFRIES: Moffat, 36/0805, *J. Anderson*, 1861 (K); Midlaw Burn, Moffatdale, 1500 ft., 36/1205, *E. S. Marshall*, 23 July 1907 (BM, CGE, E)*, 12 Oct. 1907 (K)*; Hartfell, near Moffat, 36/1113, *P. N. Fraser*, 21 Aug. 1861 (E, K); Carrifran Glen, 36/1514, *P. N. Fraser*, 25 July 1860 (E); Loch Skene, 36/1716, *P. N. Fraser*, 15 Sept. 1860 (E), 24 July 1866 (K)*.

V.C. 78 PEEBLES: Mossfennan, 36/1136, *P. N. Fraser*, 13 July 1860 (E).

V.C. 85 FIFE: wood in estate, Balmuto, 36/2289 (introduced?) *J. T. Boswell-Syme*, June 1876 (BM); Kirkaldy, 36/2791, *W. Stewart* (K).

V.C. 86 STIRLING: Ben Lomond, 3100 ft., 27/3302, *B. W. Ribbons*, 23 Oct. 1965 (GL); North Corrie, Ben Lomond, 3000 ft., 27/3602, *R. Mackechnie*, 20 Aug. 1932, (**Herb. Lousley; Herb. Wallace**).

V.C. 87 WEST PERTH: Meall Mor nan Eag, 27/3418, 1650 ft., *H. V. Corley 126*, 27 May 1968 (BM)*; Glen Falloch, *c.* 2400 ft., 27/3622, *E. S. Marshall*, 25 July 1890 (CGE)*.

V.C. 88 MID PERTH: Beinn Oss, 27/2825, *F. M. Webb*, 5 Aug. 1879 (E); An Binnein, Ben More, 3300 ft., 27/4322, *F. J. Hanbury*, 26 July 1889 (BM)*, *E. S. Marshall*, 26 July 1889 (CGE); Killin, 27/5732, *E. Liddell*, 1871 (K); Glen Lyon, 27/5646, *P. N. Fraser*, July 1885 (E)*; Ben Lawers, 3000 ft., 27/6341, *A. H. G. Alston*, ex Univ. Botanic Garden, Leeds, 1952 (BM), *J. H. Balfour* (BM)*, *J. T. Boswell-Syme*, Aug. 1851 (BM), Aug. 1866 (E), *Cleminshaw*, July 1905 (CGE)*, *J. N. Frankland*, Aug. 1949 (BM), *P. N. Fraser*, 5 Aug. 1856 (E), *J. Hardy*, Aug. 1865 (CGE), *C. W. Hope*, 5 Aug. 1856 (E), *T. Moore*, 1855, [LECTOTYPE of *Lastrea dilatata* var. *alpina* T. Moore and HOLOTYPE of *Dryopteris assimilis* S. Walker] (K), *Wilson*, Sept. 1855 (NMW); Ben Lawers E corrie, 27/6341, *A. J. Wilmott*, 21 July 1928 (BM), *R. David*, 25 July 1964 (CGE)*; Ben Lawers SW corrie, 2000 ft., 27/6341, *J. E. Lousley*, 12 Aug. 1932 (**Herb. Lousley**)*; An Stuc above Lochan nan Cat, 3000 ft., 27/6341, *A. C. Jermy 1884 bis* (BM)*, *E. S. Todd 25 & 26*, (OXF); Meall Garbh, 3000 ft., 27/6441, *E. S. Marshall*, 22 Aug. 1887 (CGE); Aberfeldy, 27/8548, *W. H. Forbes*, 8 Oct. 1892 (OXF).

V.C. 89 EAST PERTH: Beinn Pharnagain, on boulder scree, 1750 ft., 27/4562, *K. Trewren 3*, 19 Sept. 1965 (BM); S side of Ben Vrackie, 2600 ft., 27/9563, *J. E. Lousley*, 18 Aug. 1966 (**Herb. Lousley**); below Corrie Cas ea gallach, Ben-y-Glow, 2000 ft., 27/9873, *P. Halligey*, 8 July 1964 (BM)*.

V.C. 90 FORFAR: Glas Maol (Forfarside), 37/1676, *E. F. Linton*, 6 Aug. 1883, (BM)*; Glen Clova, Corrie Winter, 37/2774, *W. A. Shoolbred*, 30 June 1904 (NMW)*; Loch Brandy, E side, 37/3375, *H. & J. Groves*, 25 July 1878 (BM); Corrie Fee, Clova, 2500 ft., 37/2575, *A. C. Jermy 3405*, 22 July 1964 (BM)*; Glen Clova, 37/2575, *E. F. Linton*, 21 Aug. 1884 (OXF), *Wollaston*, 1873 (K).

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† The specimen recorded as *D. assimilis* from Knock Ore Gill (V.C.69) by A. Eddy & D. Welch (*Proc. bot. Soc. Br. Isl.*, **6**: 326 (1967)) is *D. dilatata*.

V.C. 92 SOUTH ABERDEEN: in the higher parts of the Grampians, 27/88, *H. C. Watson* (**BM**)*; Cairn Toul, Coire Lochan Maine, 3000 ft., 27/9697, *E. C. Wallace & R. Mackechnie*, 5 July 1934 (**Herb. Lousley***; **Herb. Wallace**): Pools of Dee, Lairig Ghru, Cairngorms, 28/9503, *W. Edgar Evans*, 31 July 1907 (**E**)*; Derry Cairn Gorm, near Braemar, 37/0198, *F. J. Hanbury*, 23 July 1885 (**BM**)*; Beinn a Bhuird, 3000 ft., 37/0898, *Greville*, 1831 (**E**); Braemar, Castleton, 37/1491, *A. Croall 167*, August 1854 (**CGE, K**); Morone, Braemar, 37/1288, *C. Bailey*, 6 Sept. 1864 (**MANCH**); Glen Callater (highland above Loch Kander), 37/1880, *J. Fraser*, Sept. 1885 (**MANCH**)*; Glen Callater, Braemar, 37/1883, *A. Croall*, 1855 (**K**); *J. F. Duthie*, August 1874 (**BM**)*; rocks below Lochnagar cliffs, 37/2485, *E. C. Wallace*, 8 Sept. 1934 (**NMW**)*.

V.C. 93 NORTH ABERDEEN: 3 miles S of Keith, near Pitgour Farm, 38/4445, *M. McCallum Webster 7891*, 14 Aug. 1962 (**BM**).

V.C. 94 BANFF: Cabrachan, 38/3826, *D. Clarke*, 1864 (**K**); Crannoch Hill, Cullen, *c.* 200 ft., 38/5266, *J. W. Dyce*, Sept. 1966, (**BM**).

V.C. 96 EASTERNESS: north-facing slopes of Coire Garblack, 27/8794, *Proctor & Goodway G3/82*, June 1953 (**CGE**)*; Braeriach, 2800 ft., 27/9599, *J. A. Wheldon*, July 1909 (**CGE, OXF**); Corrie an Lochan, Braeriach, 3300 ft., 27/9599, *E. S. Marshall*, 12 Aug. 1898 (**BM**)*; above Corrie an Lochan, 3500 ft., 38/0004, *J. E. Lousley*, 1 July 1953 (**Herb. Lousley**)*.

V.C. 97 WESTERNESS: Ben Nevis, 2750 ft., 27/1671, *M. S. Campbell*, 16 July 1937 (**BM**)*, *K. Trewren*, 22 Sept. 1965 (**BM**), Herb. Terras, 1887 (**E**); Ben Alder, 27/4971, *E. C. Wallace*, 10 July 1946 (**Herb. Wallace**)*; S side of Coire Ardair, Crage Meagaidh, 2200 ft., 27/4387, *H. V. Corley 124*, 30 Aug. 1967 (**BM**); Coire nan gall, L. Laggan, 27/4886, *F. J. Hanbury*, 28 July 1916 (**BM, E**)*.

V.C. 98 MAIN ARGYLL: Kilmory, 16/78, *A. Brown*, 1862 (**K**); Ormay Woods, 17/8101, *J. W. Dyce 6*, Sept. 1968 (**BM**); above L. Craignish, 200 ft., 17/8204, *H. V. Corley*, May 1968 (**BM**)*; Ben More, Cowal, 26/1090, *A. G. Kenneth*, 7 Apr. 1966 (Herb. Wallace); Tailor's Leap, Glen Nant, 27/0128, *H. J. Bruty*, Sept. 1968 (**BM**); Beinn Fraochaidh, 1600–1750 ft., 27/0251, *A.C. Jermy 6173*, 27 Aug. 1966 (**BM, E**); Beinn nan Aighenan, 3000 ft., 27/1441, *H. McAllister*, May 1961 (**BM**); Sgurr an Ulaidh, 27/1153, *H. V. Corley 10*, Apr. 1966 (**BM**); Fionn Glenn, Glencoe, 27/1557, *R. Mackechnie* (**Herb. Wallace**)*; Ben Donich, near Lochgoyl Head, 2500 ft., 27/2204, *A. G. Kenneth*, 19 Nov. 1966 (**BM**); Ben Laoigh, 3000 ft., 27/2626, *J. W. Dyce*, 1967 (**BM**), *C. I. & N. Y. Sandwith*, 21 July 1936 (**K**)*; Clach Leathad, 3 miles SW of Kingshouse Inn, 27/2449, *E. S. Marshall* (**CGE**)*; Beinn Dhorain, 3000 ft., 27/3238, *G. C. Druce*, Aug. 1898 (**OXF**)*.

V.C. 99 DUNBARTON: Ben Vane, 2800 ft., 27/2709, *J. E. Lousley*, 27 July 1966 (**Herb. Lousley**)*; Ben Vorlich, 27/2912, *P. N. Fraser*, 10 Aug. 1864 (**E**).

V.C. 100 CLYDE ISLES: Arran, 16/26, *J. Anderson*, 1857 (**K**); head of Glen Dubh, Arran, 16/9833, *J. W. Dyce 5*, Sept. 1968 (**BM**); Bute, 26/06, *E. Liddell*, 1869 (**K**)*.

V.C. 101 KINTYRE: Ballenach, Lochgilphead, 16/8491, *J. Anderson*, 1860 (**K**), *E. Greatorex*, 1861 (**K**); Erine, Lochfyneside, 16/8576, *A. G. Kenneth*, Oct. 1966 (**BM**); Cam Loch, near Lochgilphead, 16/8286, *H. V. Corley*, May 1966 (**BM**)*; Ardrishaig, Loch Fyne, 16/8585, *F. Griffith*, 1858 (**K**).

V.C. 104 NORTH EBUDES: Hallaig, Raasay, 18/5436, *M. McCallum Webster*, 20 June 1957 (**BM**)*.

V.C. 105 WEST ROSS: SW side of A'Chailleach, 28/1371, *A. G. Kenneth*, 19 July 1967 (**BM**)*; Meall a Chrasgaidh, Fannich Forest, 28/1873, *E. C. Wallace*, 22 July 1948 (**Herb. Wallace**)*, *A. G. Kenneth*, 4 July 1967 (**BM**)*.

V.C. 106 EAST ROSS: Coire Dombain, Carn Eige, Glen Cannich, 28/1326, *E. C. Wallace*, 18 July 1947 (**Herb. Wallace**).

V.C. 107 EAST SUTHERLAND: Ben More Assynt, 2300 ft., 29/3120, *F. J. Hanbury*, 12 July 1890 (**BM**)*, *E. S. Marshall*, 12 July 1891 (**CGE**).

V.C. 108 WEST SUTHERLAND: Achmelvich, 250 ft., 29/0524, *J. Anthony*, 25 July 1955, (**E**); Ben Stack, 29/2642, *A. G. Kenneth*, 8 July 1967 (**BM**)*; NW. end of Foinaven, 29/3149, *A. G. Kenneth*, 10 July 1967 (**BM**)*; Cranstackie, 29/3555, *A. G. Kenneth & E. M. Bullard*, 13 July 1967 (**BM**)*; Ben Hope, 29/4749, *A. G. Kenneth*, 18 July 1966 (**BM**)*.

V.C. 109 CAITHNESS: Summit of Morven, 39/0028, *F. J. Hanbury*, 18 July 1887 (**BM**)*.

V.C. 110 OUTER HEBRIDES: South Uist, 08/71 to 74, *A. Somerville*, July 1888 (**BM**)*; near Loch Maddy, North Uist, 08/9367, *W. A. Shoolbred*, 12 July 1894 (**BM, CGE, NMW**); Cleisham, Harris, 19/1507, *W. S. Duncan*, August 1889 (**BM**)*; north rocks, Sgaoth Ard, North Harris, 19/1603, *J. W. Campbell*, 1 Aug. 1939 (**BM**)*.

V.C. 111 ORKNEY: Hoy: Enegass, SE side of meadow of the Kame, N30/1904, *H. H. Johnston 4733* (**E**)*; Mainland: hill between Sowa Dee and Stany Knowe, Sandwick, 310 ft., N30/2214, *H. H. Johnston 2594* (**E, K**)*; Naversdale, Orphir, N30/3304, *J. T. Boswell*, Aug. 1875 (**BM, CGE, E, NMW**), *H. H. Johnston*, 7 Sept. 1878 (**E**); quarries E of Loch of Stenness, N30/3304, *J. T. Boswell*, Aug. 1875 (**BM, E**); Russa Dale, Stenness, 300 ft., N30/3309, *E. M. Bullard*, 24 Aug. 1966 (**BM**).

V.C. 112 ZETLAND: Bressay, N41/4940, *R. Tate*, 26 June 1865 (**CGE**)*.

Hybrids

Triploid hybrids have been detected in populations where *D. assimilis* and *D. dilatata* grow together in S. Aberdeen, v.-c. 92, Easterness, v.-c. 96, Argyll, v.-c. 98 and West Ross, v.-c. 105 (all coll. S. Walker); and in Kintyre, v.-c. 101 (coll. A. G. Kenneth). They are intermediate between the parents, having the dark-centred scales and dissection of *D. dilatata* and the flatness of lamina and erectness of *D. assimilis*; the sporangia are mostly abortive. Cytological investigation shows that chromosome pairing at meiosis in these hybrids agreed with that of synthesised hybrids (Walker 1955), giving approximately equal numbers of bivalents and univalents. Wild hybrids between these species have been reported and cytologically examined previously from Bavaria (Walker 1955) and Switzerland (Döpp & Gätzi 1964). No wild hybrids between *D. assimilis* and *D. carthusiana* have been recorded for Britain at the time of writing. Other plants with abortive spores which on morphological grounds have some features characteristic of *D. aemula* (Ait.) O. Kuntze (see Jermy 1968) may turn out to be hybrids between that species and *D. assimilis* or *D. dilatata*; such hybrids have to be proved cytologically and must remain dubious until they are further studied.

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APPENDIX: A NOTE ON THE PREPARATION OF MATERIAL FOR THE SCANNING ELECTRON MICROSCOPE

By A. C. JERMY and B. S. MARTIN*

**British Museum (Nat. Hist.) Electron Microscope Unit*

MOUNTING MATERIAL

Whenever possible, large quantities of spores were shaken on to a clean sheet of tracing, greaseproof, or similar high glazed paper and the aluminium stub, covered with the appropriate mountant, was inverted and pressed gently on to the spore-mass. Where spore material was scarce, a sorus was moistened with water to which had been added a drop of 0·1 per cent solution of 'Alcopol 0' wetting agent and the selected undehisced sporangium lifted to the prepared stub. On drying, dehiscence was provoked with the tip of a needle. Latterly the mountant used was double-sided Sellotape because, (i) it is easy to apply; (ii) it remains sticky for a considerable time; and (iii) tape plus coated specimens can be removed from stub at the end of the investigation and stored for future reference. One disadvantage is that, on drying, the Sellotape latex may crack and form a distracting background to the specimen. There is also evidence to indicate that double-sided Sellotape increases the amount of contamination in the

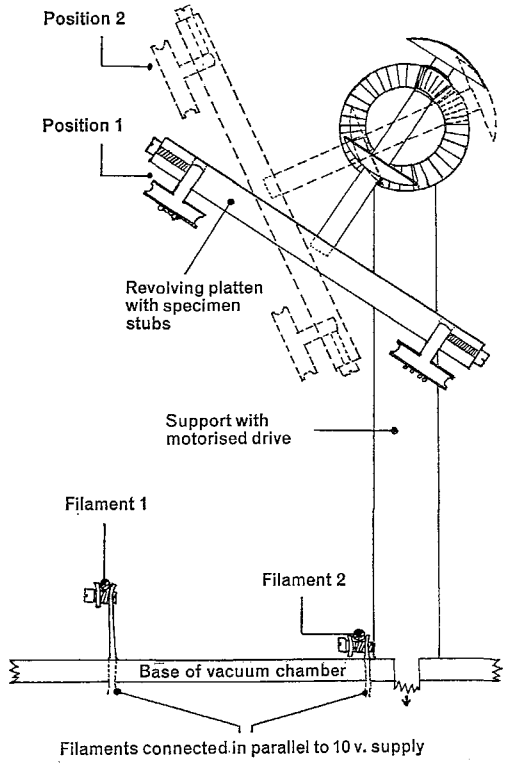

FIGURE 2. Sectional diagram showing the positions of filaments and specimen holders in the coating unit vacuum chamber.

microscope column. Other mountants, e.g. 'Turtox' clear mountant (water soluble), 'Durofix' nitrocellulose cement (benzene soluble) and 'Araldite' epoxy resin were used with equally good effect but did not have all the advantages mentioned above.

COATING THE SPECIMEN

The stubs were coated with gold-palladium or gold metal alone; this latter has become the standard for botanical material investigated at the British Museum. The metal wire was evaporated in a vacuum of 10^{-4} Torr in an Edwards 12E6 coating unit. Approximately 4cm of 36 SWG gold wire were wound around the V-notch of each of two filaments (consisting of approximately 5cm of 25 SWG tungsten wire); these were simultaneously gently heated, sufficient to melt the gold and then the current was increased to *c* 35 amps for evaporation. (The filaments were connected, in parallel, to a

10 volt supply). At all times both the filaments and the gold wire were handled with 'Velin' tissue to prevent grease contamination. The stubs were fixed to a platen which revolved about 5 revolutions per second at such distances and angles from the filament as to allow even deposition of metal (see Fig. 2). A second evaporation of a similar amount of gold was then carried out, the angle of incidence of the specimen platen to the filaments having been altered to position 2 (see Fig. 2).

It is essential that a continuous metal coat covers both stub and spores, and to this end an improved platen has been designed which gives the stubs an additional planetary rotation during coating. It is estimated that the total thickness of metal deposited may be as much as 30 nm from the four filaments. It was found best to coat speciments the same day as observations were being made and specimens studied over a period of six months were re-coated as many as three or four times with no obscuring of detail at the magnifications used (up to × 10,000).

The scanning microscope used was the Cambridge Scientific Instruments Limited 'Stereoscan' using an accelerator voltage of 20KV. Photographs were made on Ilford HP3 film developed in Microdol-X.

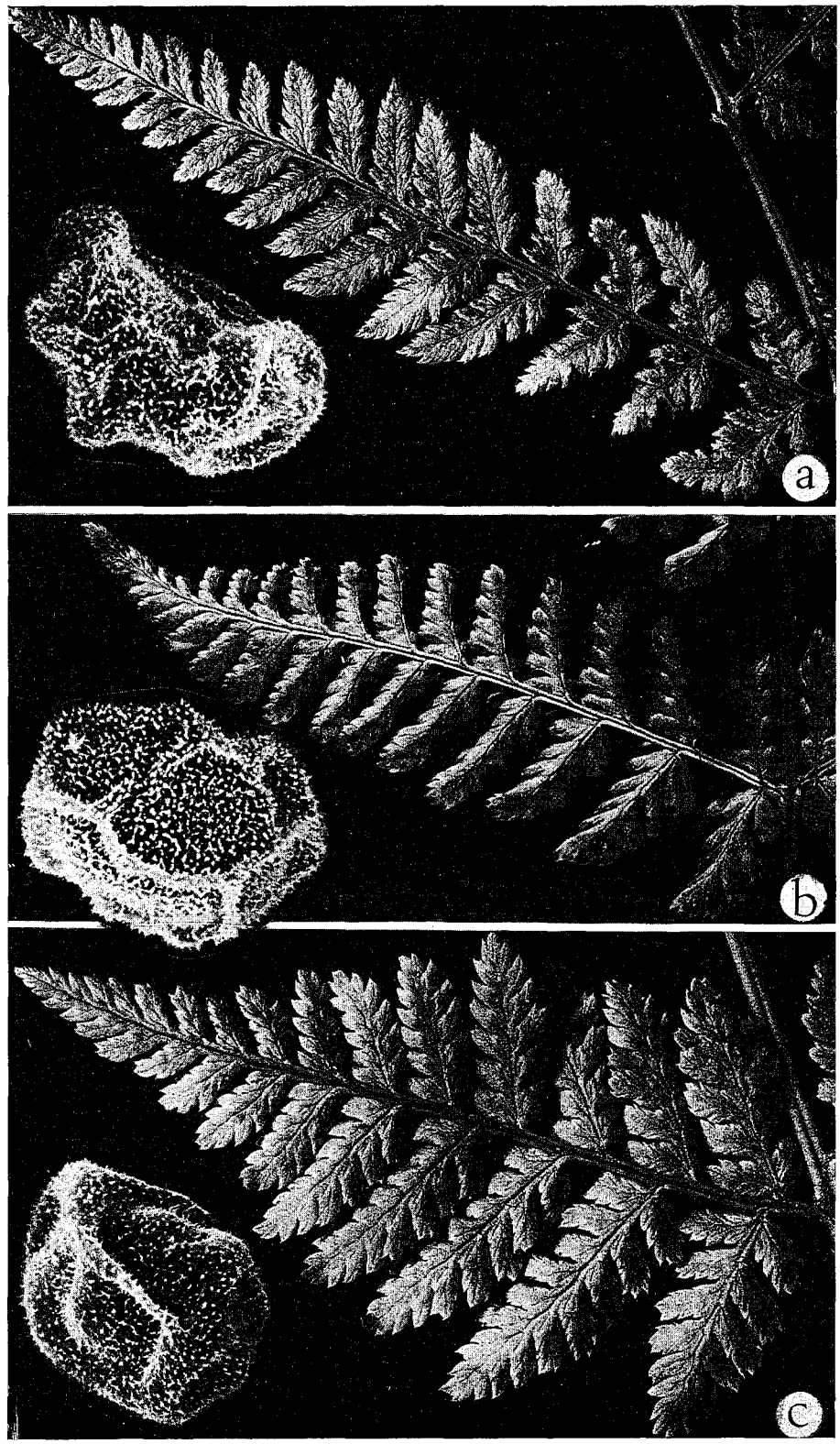

PLATE 2. Spores and median pinnae of species of the *Dryopteris dilatata* complex. (a) *D. carthusiana*; (b) *D. dilatata sensu stricto*; (c) *D. assimilis*.

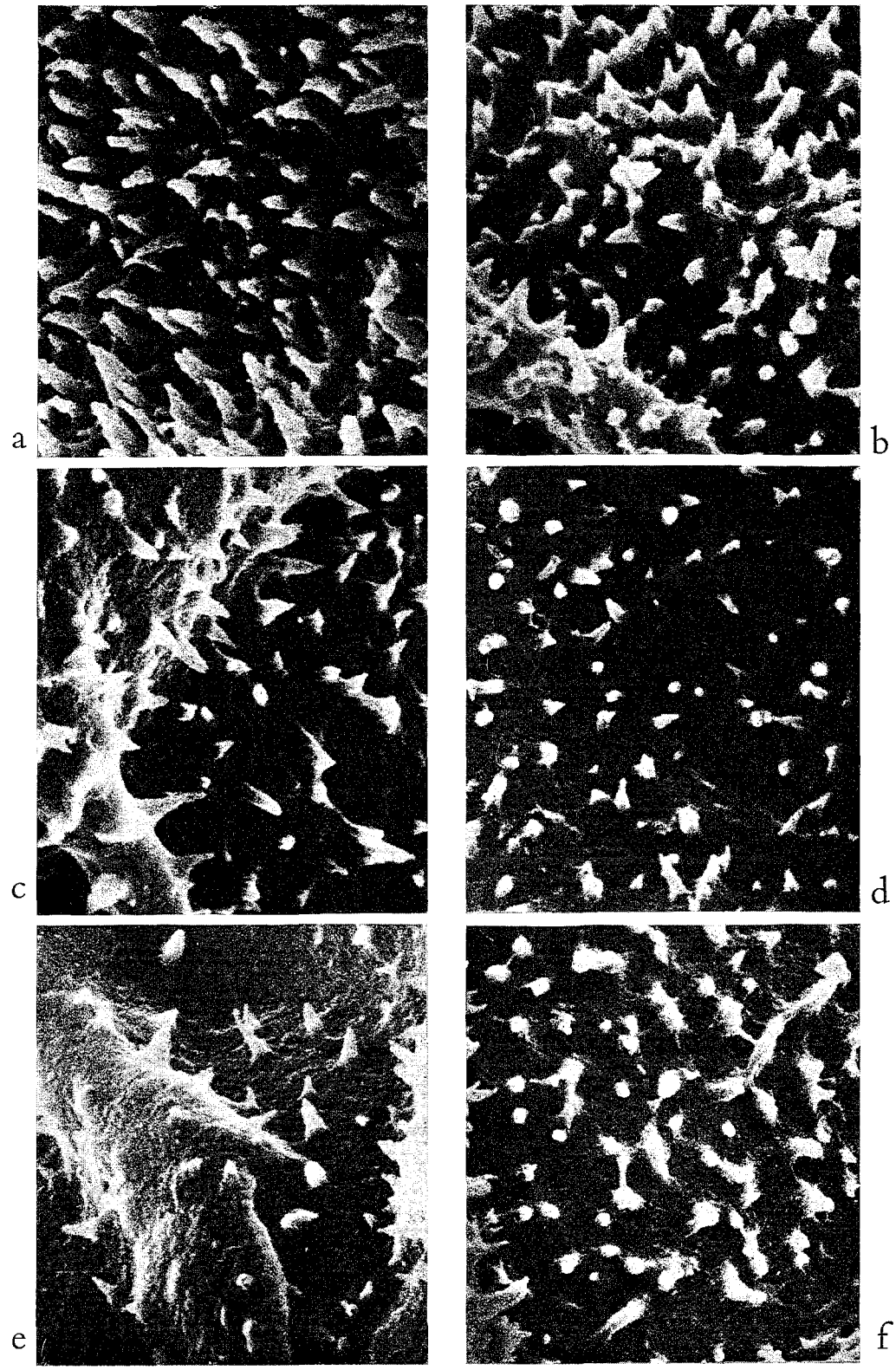

PLATE 1. Perispore surface in the *Dryopteris dilatata* complex (all × 6000). (a) *D. dilatata* [*Corley*, Argyll]; (b) *D. carthusiana* [*Crabbe & Jermy 11790*, Sussex]; (c) *D. assimilis* [*Jermy 6173*, Argyll]; (d) *D. assimilis* [*Corley*, Strome Ferry, W. Ross]; (e) *D. assimilis* [*Jackson*, Borrowdale, Cumberland]; (f) *D. assimilis* [*Dyce*, Cullen, Banffshire].