Cystopteris diaphana (Bory) Blasdell (Woodsiaceae) – an overlooked native new to the British Isles?

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ABSTRACT

Cystopteris diaphana (Bory) Blasdell (Diaphanous Bladder-fern) is reported for the first time in the British Isles. This predominantly Macaronesian fern is locally abundant and appears native along nearly 1 km of the R. Camel, Cornwall (v.c. 2), where it was discovered in February 2000, after being initially misidentified as *C. fragilis* (L.) Bernh. An ongoing critical reassessment of other Bladder-fern records from S. W. England indicates that the species is also present on a Cornish hedgebank by a lane at Penjerrick, Mawnan Smith (v.c. 1), from where it has been considered to be an escape from cultivation, and in a railway cutting near Tavistock, S. Devon (v.c. 3), where its status is uncertain. Historical reports of *Cystopteris* from similar habitats in the South-west suggest that the species may have been and possibly still could be more widely distributed.

KEYWORDS: Diaphanous Bladder-fern, identification, ecology, Macaronesia, native or alien status, conservation, Cornwall.

INTRODUCTION

In February 2000, Matt Stribley found a small number of plants of the bladder-fern *Cystopteris* in rocky recesses on a damp woodland bank at Polbrock Bridge, E. Cornwall (SX06). These were initially identified as the widespread *C. fragilis* (L.) Bernh. and, as this is regionally very uncommon, its discovery stimulated further visits by various members of the local recording community. During the course of these it became clear that the plant was present in much greater quantity and luxuriance close by, on the almost vertical, heavily shaded banks of the River Camel. Here dense stands clothe the steep, c. 2 m soil slopes, beneath an overhanging fringe of *Hedera*, *Rubus*, etc. In this locality the fern is obviously periodically inundated, many of the plants being covered with deposited silt. The underlying geology of this area is of Staddon grit, a rather base-poor substrate unlike the limestone usually favoured by *C. fragilis*. This, and closer scrutiny of finer morphological characters, led the first author to question the initial identification. Discussion with Christopher Fraser-Jenkins, then working in the Natural History Museum, led to the suggestion that the plants may belong to the Macaronesian – Atlantic species *C. diaphana* (Bory) Blasdell (syn. *C. viridula* (Desv.) Desv.), a suggestion that was confirmed when specimens were sent to CFJ and FJR for determination.

Subsequent examination of other Cornish gatherings of *Cystopteris* revealed that some specimens recently collected by RJM from beside the lane bisecting the garden at Penjerrick, Mawnan Smith (v.c. 1, Grid ref. SW72) were *C. diaphana*. Plants of the genus were first noticed in this locality by Len Margetts in 1961 (Margetts & David 1981). Perhaps significantly when considering the status of the species in this locality, Christopher Fraser-Jenkins has identified both *C. diaphana* and *C. fragilis* among specimens from this site.

Knowledge of these finds and identifications spread and as a result a further British site for *C. diaphana* has come to light. Material collected by R. Hutchins from beside a disused railway line in the Tavistock area, S. Devon (v.c. 3) (SX47), was brought to the B.S.B.I. exhibition meeting in November 2003 and confirmed by FJR as this species. *Cystopteris* was first recorded in the vicinity of the recent collection as long ago as 1934 (Keble-Martin & Fraser 1939) but voucher specimens, to ascertain whether this earlier record also relates to *C. diaphana*, have not been located.

Cystopteris diaphana has long been confused with *C. fragilis*, included in *C. fragilis*, or treated at infraspecific level. Blasdell (1963) commented on their great superficial similarity of overall frond shape but placed *C. diaphana* within a separate section of the genus (section Emarginatae) from *C. fragilis* (section Cystopteris), on the basis of the venation and of cell shape characters of the adaxial epidermis and indusium. He believed that where these species occurred sympatrically these distinctions were less clear-cut and he suggested large-scale gene exchange between them was responsible. Detailed cytological or molecular examination has yet to substantiate this claim and hybridity, evidenced by spore abortion, has yet to be observed.

NOMENCLATURE

Nomenclaturally the use of the epiphet *diaphana* has been contentious, with some authors, e.g. Castroviejo *et al.* (1986) questioning the conspecificity of Macaronesian material with that from the type locality, given the wide disjunction; the basionym *Polypodium diaphanum* Bory is based on material from the remote Indian Ocean island of Réunion. The description and illustration in Tardieu-Blot (1958), under *C. fragilis*, clearly indicate that the plant from the Comoros and Réunion has the vein and spore characters of *C. diaphana sensu lato* and Prelli & Boudrie (1992) state that it is hexaploid, as are all Macaronesian and European plants counted (Dostál 1984). Prior to this confirmation the species was frequently referred to *C. viridula* (Desv.) Desv. and it is under this name that it appears in many European texts (e.g. Amaral Franco & Rocha Afonso 1982, Castroviejo *et al.* 1986, Salvo Tierra 1990).

THE WORLD DISTRIBUTION OF *C. DIAPHANA*

Cystopteris diaphana sensu lato is believed to be widely distributed in the warm temperate and tropical regions of the Old and New World. Pearman (1976) suggested that there were clear differences in spore morphology between Central and Southern American plants and those from Macaronesia; both, however, possessed what he termed spiny-lacunar perispore ornamentation which very clearly differed from the simple spines of *C. fragilis sensu stricto*. Examination of a wider range of material, however, indicates that the perceived differences among spiny-lacunar types are less clear cut than Pearman believed and we feel it is not possible to discriminate between Old and New World material on the basis of spore morphology. (cf. Fig. 2 and his Fig. 5).

In Central and Southern America *C. diaphana sensu lato* would appear effectively to replace *C. fragilis* except at the highest altitudes (see Smith 1981): it does not apparently extend as far north as North America (Haufler *et al.* 1993). In Macaronesia it is the sole species in the Azores (Schäfer 2002) and Madeira (Press & Short 1994) but in the Canaries it is replaced by *C. dickieana* at high altitude (Rumsey unpubl.). The species is also reported from North Africa (Morocco and Algeria) (Greuter *et. al.* 1984). In Europe the species is widespread in Portugal and western Spain (Castroviejo *et al.* 1986), with scattered outlying populations further east in Navarra in the Pyrenees and in the mountains of Granada in the south (Salvo Tierra 1990). It is, somewhat surprisingly, apparently absent from the area inland of Algeciras, southernmost Spain, where the majority of the Macaronesian pteridophytes and gametophytes disjunct to Europe occur (Rumsey & Vogel 1998). In France the species has been included in the national red-list (Olivier *et al.* 1995). It is restricted to a dozen sites in Corsica (on the west coast and the Tenda massif) where it is said to be under no immediate threat. On mainland France it is restricted now to a few sites in the Pyrénées-Atlantiques, where it is declining. Populations discovered in the 19th century from much further north on the Ile de Ré and in Cher in central France, where the species was present in wells (mirroring the situation of *Trichomanes speciosum* in Brittany), have apparently long since disappeared (Prelli 2001).

Pignatti (1982) largely follows Fiori (1943) in recognising, with some doubt, the occurrence of this species in Sicily, Corsica and the mountains of the Abruzzi. He gives its distinguishing characteristic as possessing a glandular indusium but does not mention venation or spore morphology. The illustrations in Fiori (1943) are unclear and the characters upon which he discriminates *diaphana* as a forma of *fragilis*, "folia bipinnatisecta", including it in the group which have "dentes plurimi lobulosum non emarginatae; nervi plurimi dorsum dentium intrantes, ad apicem desinentes" strongly suggests his concept of this taxon was in error. Prelli (2001) states that the species has been recently discovered in Lombardy.

IDENTIFICATION

The five British species of *Cystopteris* can be differentiated using all of the characters given in the key below, but microscopy is essential for confirmation. Field identification of similar species is difficult. However, although *C. fragilis* might be found in the vicinity of *C. diaphana*, within the British Isles other taxa are highly unlikely to be present to cause confusion. Therefore, *C. diaphana* and *C. fragilis* can be separated with reasonable confidence in the field using the clearest non-microscopical character that discriminates between just those two, that of the venation as used by Blasdell (1963). The majority of veins in the frond of *C. diaphana* do not end in the apices of the pinnule teeth, as in *C. fragilis*, but between them, often in emarginated notches (Fig. 1). This character is also shown to a very limited degree by *C. dickieana* but is best developed in the arctic-alpine *C. alpina* (Lam.) Desv. (syn. *C. regia* Desv.), another overlooked British native last seen in Upper Teesdale in July 1911 (Rumsey 2003, Tennant 1995). This montane taxon is distinguished by its more finely dissected fronds and by the characters outlined in the key below; it is unlikely to be naturally sympatric with *C. diaphana*.

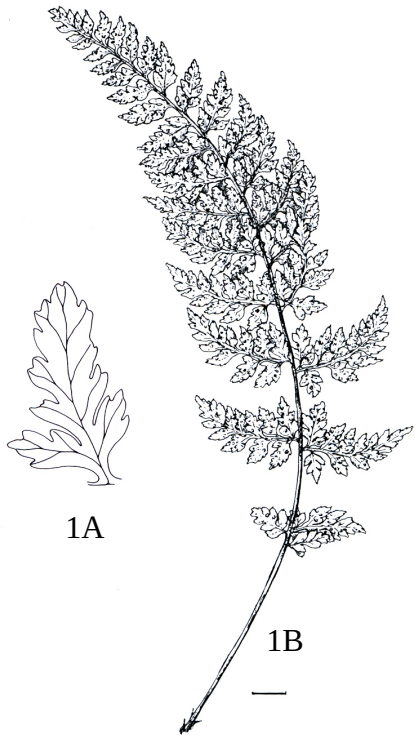

FIGURE 1. *Cystopteris diaphana* (Bory) Blasdell.
A. Detail of pinnule showing characteristic vein endings. B. Typical frond

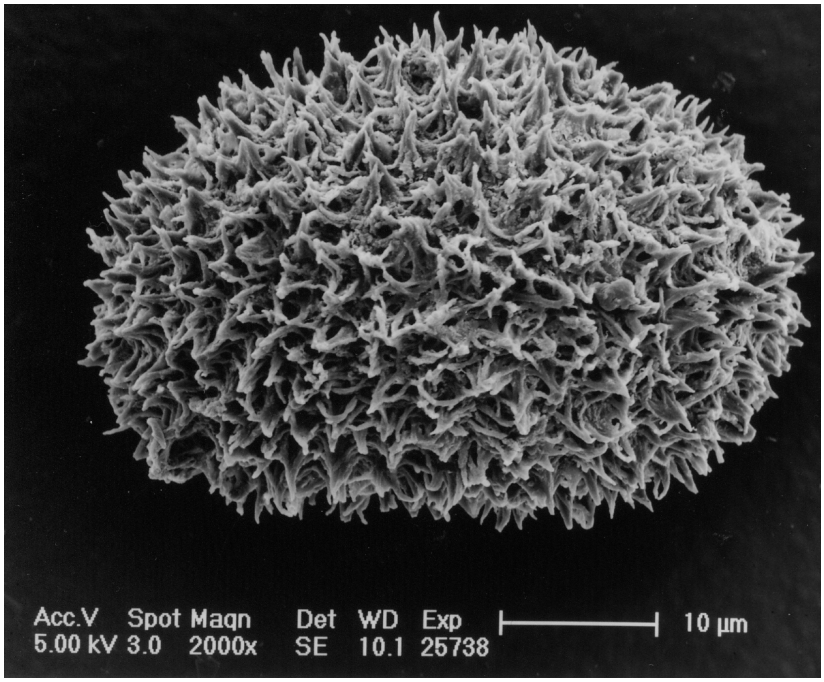

FIGURE 2A. *Cystopteris diaphana*. Bagaçinha, Terceira, Azores (*AMP98/31*).

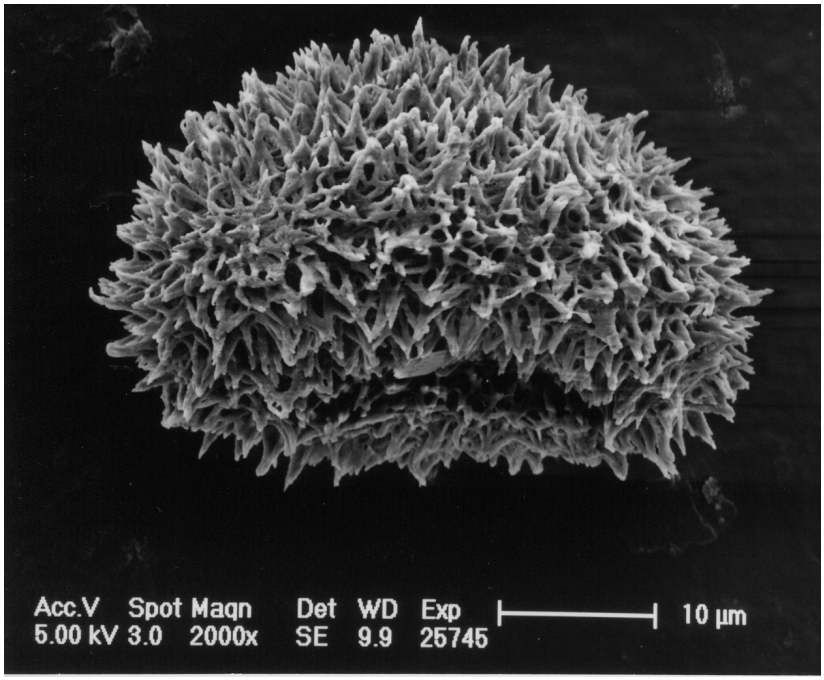

FIGURE 2B. *C. diaphana*. Polbrock Bridge, Cornwall. (*FJR 03-09-01*)

FIGURE 2. Perispore ornamentation showing typical spiny-lacunar (*C. diaphana*) as opposed to spiny (*C. fragilis*) morphology.
All specimens **BM**

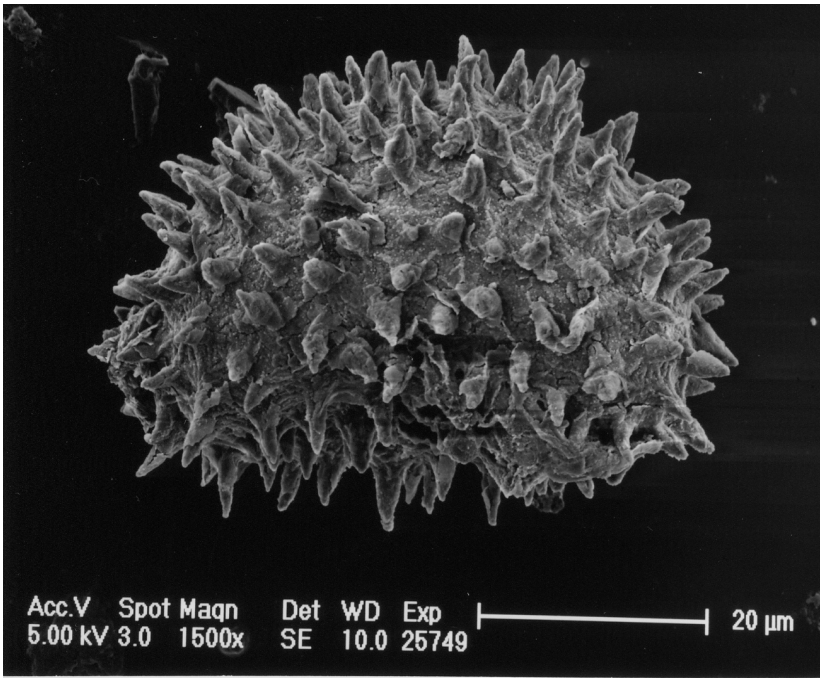

FIGURE 2C. *C. fragilis*. v.c. 64. ex herb. W. C. Barton, s.n.

In addition to the pinnule venation, *C. diaphana* can best be discriminated from the frequent and variable *C. fragilis* by examination of the ornamentation of the perispore. Both taxa have spores which appear spiny under lower magnification but, as Pearman (1976) demonstrated using electron microscopy, the spines of *C. diaphana* are composite structures made up of slender, often haphazardly arrayed units, more densely arranged than the simple stout spines of *C. fragilis* (Fig. 2). Under the light microscope the effect is such that for *C. diaphana* each "spine" appears broader at its base than the distance to the adjacent spines and the spore is more densely spinose in appearance than that of *C. fragilis*. Density and shape of the spination is, however, somewhat variable. To what extent the differences in the spiny-lacunar spore types might reflect a difference in ploidy is uncertain, Jermy & Harper (1971) having reported an increase in spine density with increasing ploidy in *C. fragilis*.

As with other species complexes within the genus *Cystopteris*, *C. diaphana* has been reported to exist at several ploidy levels, from diploid (n = 42), tetraploid (n = 84), to hexaploid (n = 126). All counts of material from Macaronesia and the European mainland to date are hexaploid (Dostál, 1984). The ploidy level of Cornish material has yet to be determined, but on spore size it appears highly likely that our material is also hexaploid.

KEY TO BRITISH *CYSTOPTERIS* SPECIES.

1 Fronds triangular, arising singly from long creeping rhizome ..... *C. montana*
1 Fronds ovate-lanceolate to lanceolate, tufted from erect to shortly creeping rhizome 2
2 Spores echinate* 3
2 Spores rugose ..... *C. dickieana*
3 ±All veins ending in apices of pinnule teeth ..... *C. fragilis*
3 Most, or all, veins ending in notches between teeth apices 4
4 Fronds deciduous, with narrow ± parallel-sided pinnules (at least below) ..... *C. alpina*
4 Fronds wintergreen, pinnules not parallel-sided ..... *C. diaphana*

* Be careful to look at mature spores. Immature spores and abortive spores from intra- and interspecific hybrids may lack characteristic surface features.

In its first detected Cornish site the species exists as an often dense population extending almost continuously for over 700 m along the vertical, deeply-shaded, north-to east-facing banks of the River Camel, close to Polbrock Bridge (SX06). The fern extends downstream as far as the upper limit of tidal influence. A few small, scattered patches occur on the west-facing bank of the river where suitably sheltered and shaded. Some small plants also occur in damp rocky recesses on a steep woodland bank above an adjoining path up-slope of the main riverbank population. It is most likely that the small, scattered individuals on this bank, which are the most obvious to the casual visitor, derive from spores blown from the main riverbank population less than 20 m distant. The associated species are for the most part unremarkable; the most interesting, certainly from a phytogeographic viewpoint, is *Trichomanes speciosum*, which occurs in an old adit close to Polbrock Bridge, around which small plants of the *Cystopteris* are found.

The near-vertical soil and gritstone riverbanks are from c. 1·5 to 3 m tall and are shaded by a dense canopy of deciduous trees, including *Acer pseudoplatanus* L., *Alnus glutinosa* (L.) Gaertn. and *Corylus avellana* L. with a sparse understorey of scrub and herbaceous vegetation, some of which, e.g. *Hedera helix* L. subsp. *hibernica* (G. Kirchn.) D. C. McClint. and *Rubus fruticosus* L. agg., hang down over the vertical bank face. The banks themselves are largely dominated by cryptogamic species, including *Athyrium filix-femina* (L.) Roth and a range of common woodland and aquatic bryophytes, including locally extensive mats of the thallose hepatics *Conocephalum conicum* (L.) Dumort. and *Lunularia cruciata*. (L.) Dumort. ex Lindb. Herbaceous species on the bank include *Oenanthe crocata* L. and the established alien *Tolmeia menziesii* (Pursh.) Torr. & A. Gray. The *Cystopteris* forms an at times dense stand over much of the height of the bank but is sparser in the lowest third, i.e. nearest the water level, where small juvenile plants predominate. Presumably the river flow more actively dislodges plants and substratum at this level. Each individual plant produces few fronds at any one time, often only one or two, and these may be produced throughout the year from an upright, very shortly creeping rhizome. Fronds over-winter, unlike the other British species of *Cystopteris*. Most fronds are fertile to some degree once plants reach a certain size. The vast majority of spores are released from late summer through to early winter.

The presence of a fine silt encrusting the majority of the older fronds would indicate that water levels fluctuate quite markedly during the year and that the plants are forced to cope with these fluctuations and the damage to the banks that ensues. The riverbank is obviously an unstable and dynamic system but the *Cystopteris* produces copious spores and recruitment of new sporophytes is very apparent throughout the site.

At Penjerrick the species is present at the base of a Cornish hedgebank at the lowest level of a lane which bisects this impressive garden, created in the 19th Century. The area is shaded, sheltered and kept humid by a nearby flush that becomes a small stream on the other side of the hedgebank. Here it is associated with many of the same common bryophytes present by the River Camel but also with the established alien *Selaginella kraussiana* (Kunze) A. Braun, with which it naturally co-occurs in the western Azores. A *Cystopteris* species is known to occur as a garden plant in a nearby grotto section of the garden but its specific identity has yet to be determined.

The Devon locality is on the vertical wall of a steep cutting of the now disused railway line in Tavistock, which is very damp and heavily shaded. The railway runs adjacent to and crosses the River Tavy nearby.

Throughout its European and Macaronesian range characteristic habitats of *C. diaphana* are sheltered, with deep shade and high humidity, often by running water. In the westernmost Azores it may be found widely on damp rock faces and is often frequent in deep roadside drainage culverts. Farther eastwards in the archipelago it becomes scarcer as general humidity and precipitation levels fall. On Faial, in the central Azores, Schäfer (2001) reported it as “rare in crevices of wet rocks in very shady ravines, usually above 600 m altitude; restricted to the most humid habitats of the island”, whereas on Sao Miguel in the drier eastern group Wilmanns & Rasbach (1973) concluded it was “one of the most hygrophilous of ferns”, finding it in fissures of lava rock in gorges with dripping water.

In the Canary Islands the species is often associated with *Trichomanes speciosum* on damp shaded streamside rocks in deep gulleys under evergreen forest. The few remaining sites in the French Pyrenees (Valon du Laxia, Vallée du Bastan) have also long been noted for the presence of *Trichomanes speciosum*, *Dumortiera hirsuta*, etc. (Jovet 1933). Little information exists as to the precise habitat and associates of *C. diaphana* in the many sites reported in western Iberia, or those from North Africa and Corsica.

DISCUSSION

The British localities are by some distance the most northerly world occurrence of this species, but we suggest that this distribution is not so unremarkable as to rule out a native status. Furthermore, historical records in central France do narrow the current gap. Several frequent cryptogamic associates of *C. diaphana* in Macaronesia and the Iberian peninsula, many of them bryophytes, show similar distributions, with scattered northernmost localities in the South-west of Britain, or rarely further north up the climatically ameliorated Atlantic coast, eg. *Fissidens serrulatus* Brid., *F. polyphyllus* Wilson ex B., S & G., *Dumortiera hirsuta* (Sw.) Nees and the fern *Trichomanes speciosum*.

Against this scenario must be put the knowledge that this fern was in cultivation in Britain by the mid 19th century, although probably not widely grown. Spores from these plants rather than longer distance spore dispersal from native sites elsewhere in Europe could be responsible for the apparently native R. Camel population. Germane to this is the second site for the species, which came to light as a result of the checking of herbarium material from other south-western sites. Material from this Penjerrick site Fraser-Jenkins (*in litt.*) felt differed somewhat from that by the River Camel and he considered was possibly the form cultivated in Victorian times as "sempervirens". It seems most likely that both *Cystopteris* species are escapes from cultivation at the Penjerrick site but we cannot rule out the possibility that *C. diaphana* was naturally present in the area, as much suitable habitat exists. The Devon station is also in an artificial habitat but suitable natural sites (not yet extensively searched) and a major river are adjacent to the site. The association of the plant here with a disused railway line and the proximity of the Polbrock Bridge site to another disused line (now the Camel trail) pose additional questions as to modes of dispersal and status. Plants of the genus *Cystopteris* have however been present in, or close to, the present Tavistock site since at least as far back as 1934 (Keble Martin & Fraser 1939).

Is there compelling evidence that this species has historically been present in the British Isles, thus raising the probability of its native status? All past records of *C. fragilis* from Cornwall need to be reconsidered and must be treated with a degree of doubt. Strongly calcareous rocks are absent from the county and the records, where habitats are stated, appear not to be on walls where they might benefit from mortar, but on damp rocks. The majority of the historic records are from squares adjacent to the Polbrock Bridge *C. diaphana* site (Crackrattle Moor, Denzell downs SW86, Bosnieves SW96, Davey 1909), from elsewhere on the R. Camel (SX18, Margetts & David 1981), or by rivers in damp sheltered coastal valleys e.g. by the Tamar at Landulph (Thurston 1935) and those of the Tintagel area (SX08, Margetts & David 1981). These valleys are known to support other Macaronesian/Atlantic species, e.g. *Trichomanes speciosum* Willd. and *Dumortiera hirsuta* (Sw.) Nees. The location and examination of voucher specimens for these records is clearly desirable.

Similarly, in Devon, old records may require close scrutiny, as again many are by rivers, e.g. the Exe, Taw, Bray, Tavy and Plym and in damp, sheltered, non-calcareous areas. Interestingly, as long ago as the 1850s, it is possible that this species had been detected but even then its status was questioned. Keys (1871), citing the Rev. T. F. Ravenshaw, stated "*C. viridis*, a foreign species, hitherto unrecorded as British, was found a few years since near Ilfracombe, by Rev. J. M. Chanter, who has plants of it now in his garden. He sent specimens to Mr. Moore, who named it. The station no longer exists, someone having removed the whole of the plants." The record is repeated almost verbatim in Ravenshaw (1877). Thomas Fitzarthur Ravenshaw was curate of Ilfracombe where John Chanter was vicar. Chanter's wife Charlotte, the sister of the author Charles Kingsley, was obviously interested in pteridophytes, publishing a small work called Ferny

Coombes (Chanter 1856). Moore (1860) under *sempervirens* states "reputed to have been found both in Devonshire and Kent….There are some doubts as to the English origin of this plant…. The reputed British plant has been found at Tunbridge Wells, and is in cultivation from this source, but there are rumours of it having been planted there; it is further stated to have been found in Devonshire, but this is also open to suspicion, the garden whence it has been distributed having been enriched by importations from Madeira."

Climatically the other region in which the species might be expected to occur but from which it is currently unreported is the south and west of Ireland. Scully (1916) regarded *C. fragilis* as rather common on damp cliffs in the mountains of Co. Kerry but also as very rare at low levels on lowland walls and rocks. It is these latter cases which are more likely to represent *C. diaphana*. Any *Cystopteris* found growing at low altitudes and particularly those in river bank habitats should be critically examined.

CONCLUSIONS

On balance we see no reason why *C. diaphana* should not be a British native but we cannot disprove the possibility that it is an escape from cultivation. The case for its native status would be greatly strengthened by examination of supporting specimens from the 19th century if they could be found.

Further search of river systems and sheltered glens in the south-west of England (and Ireland) may yet reveal the species to be more widespread.

Many ferns have suffered in the past from collection. The species is currently restricted as a probable native to one easily accessible linear population and so the conservation implications for this species must be considered. Application of the I.U.C.N. threat categories and selection criteria (I.U.C.N. 1994) suggests that on the basis of the very restricted British range (criterion D_2) this species, like *C. dickieana*, should be considered Vulnerable (VU) and would qualify for inclusion in the British Red Data listing when next revised. *Cystopteris diaphana* is present in such quantity and reproducing so freely that, if visitors to the site behave responsibly, we feel it is unlikely to be threatened by anything other than major changes to the area. The greatest risk to its continuing survival would undoubtedly be if the woodland fringing the river in this section were opened by felling. It is also highly vulnerable to any major pollution event occurring upstream. To guard against such catastrophic loss, spore gatherings should be made and the plant thus introduced to botanic gardens and the horticultural community for *ex situ* conservation.

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