

HISTORICAL REVIEW OF THE UNCERTAIN TAXONOMIC STATUS OF *CYSTOPTERIS DICKIEANA* R.SIM (DICKIE'S BLADDER FERN)

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Cystopteris dickieana R.Sim is a rare fern protected in Britain under the 1981 Wildlife and Countryside Act. Most current floras treat it as a distinct species but ever since it was first discovered in Scotland in the 1830s, there has been considerable debate about its taxonomic status within the *C. fragilis* complex. This debate centres on the relative importance of two characters, the architecture of the fronds and the surface sculpturing of the spores, in delimiting *C. dickieana* from other taxa in the *C. fragilis* complex. The type specimens of *C. dickieana* have distinctive fronds. Plants with similar frond architecture have, to date, been recorded growing naturally only at the site in Scotland from which the type specimens were collected and at one other site nearby. The type specimens of *C. dickieana* also have mature spores with surface sculpturing often described as 'rugose'. These are distinctive and unusual in the genus *Cystopteris*, in which most taxa have 'echinate' spores. However, rugose-spored plants have been recorded not only at, and near, the type locality in Scotland but also at many other sites in the northern hemisphere in populations of plants defined largely on the basis of frond architecture as *C. fragilis* or *C. baenitzii*. This indicates that spore sculpturing should not be used alone to delimit *C. dickieana* from other taxa within the *C. fragilis* complex but, despite this, the literature on '*C. dickieana*' contains many reports of studies on material identified as *C. dickieana* solely on the basis of spore sculpturing. This, combined with the fact that most comparative studies have also failed to include material known to have come from the type locality, has resulted in considerable and continuing uncertainty over the taxonomic status and distribution of *C. dickieana*.

Keywords. *Cystopteris baenitzii*, *Cystopteris dentata*, *Cystopteris fragilis*, frond architecture, spore sculpturing.

INTRODUCTION

Cystopteris dickieana R.Sim is, at present, a fern species protected in Britain under the 1981 Wildlife and Countryside Act on the basis that it is endemic to Scotland and extremely rare. However, ever since it was first discovered in the 1830s, there has been considerable debate about its taxonomic status within the *Cystopteris fragilis* complex. Opinions have ranged from acceptance of *C. dickieana* as a distinct species endemic to Scotland to: acceptance of *C. dickieana* as a distinct species but not endemic to Scotland to: acceptance that the same taxon is no more than a variety of the widespread and polymorphic species *C. fragilis*. It has even been suggested

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(though not yet in Britain) that some '*C. dickieana*' should, in fact, be recognized as *C. baenitzii*.

The complexities of the long-running, and continually evolving, debate on *C. dickieana* are presented here in the form of an historical review so that the results of a new investigation on Scottish *Cystopteris*, recently undertaken at The Royal Botanic Garden Edinburgh, can be more easily placed in context (see Parks *et al.*, 2000).

HISTORICAL REVIEW

It [i.e. Cystopteris fragilis] is a plant so polymorphous in character that the species which botanists have from time to time endeavoured to separate from it, though sometimes assuming a distinct-looking aspect, appear in other cases to become united by intermediate forms, and are then with difficulty defined even as varieties. Cystopteris fragilis must indeed be considered as being, like the still more polymorphous Athyrium filix-foemina and Lastrea dilatata a botanical ignis fatuus, alluring the incautious novelty-seeker among the quagmires of species-making, in which, at length when his mental vision becomes cleared by more extended observations, he finds himself hopelessly floundering.' Moore (1859; 258).

'Cystopteris is dominated by the widespread and polymorphic C. fragilis complex, which constitutes perhaps the most formidable biosystematic problem in the ferns.' Lovis (1977: 356).

More than a century after Moore's comment in 1859, and despite the advent of biochemical and molecular techniques (Haufler *et al.*, 1990; Haufler & Windham, 1991), the genus *Cystopteris* as a whole, and *C. fragilis* in particular, continues to present difficult problems to fern taxonomists. Of special interest in Scotland is the status within the *C. fragilis* complex of the fern widely known as *Cystopteris dickieana* (locally known as 'Dickie's bladder fern'), which is one of Scotland's rarest taxa and, in the form which characterizes all plants at the type locality (see below), apparently unique to Scotland.

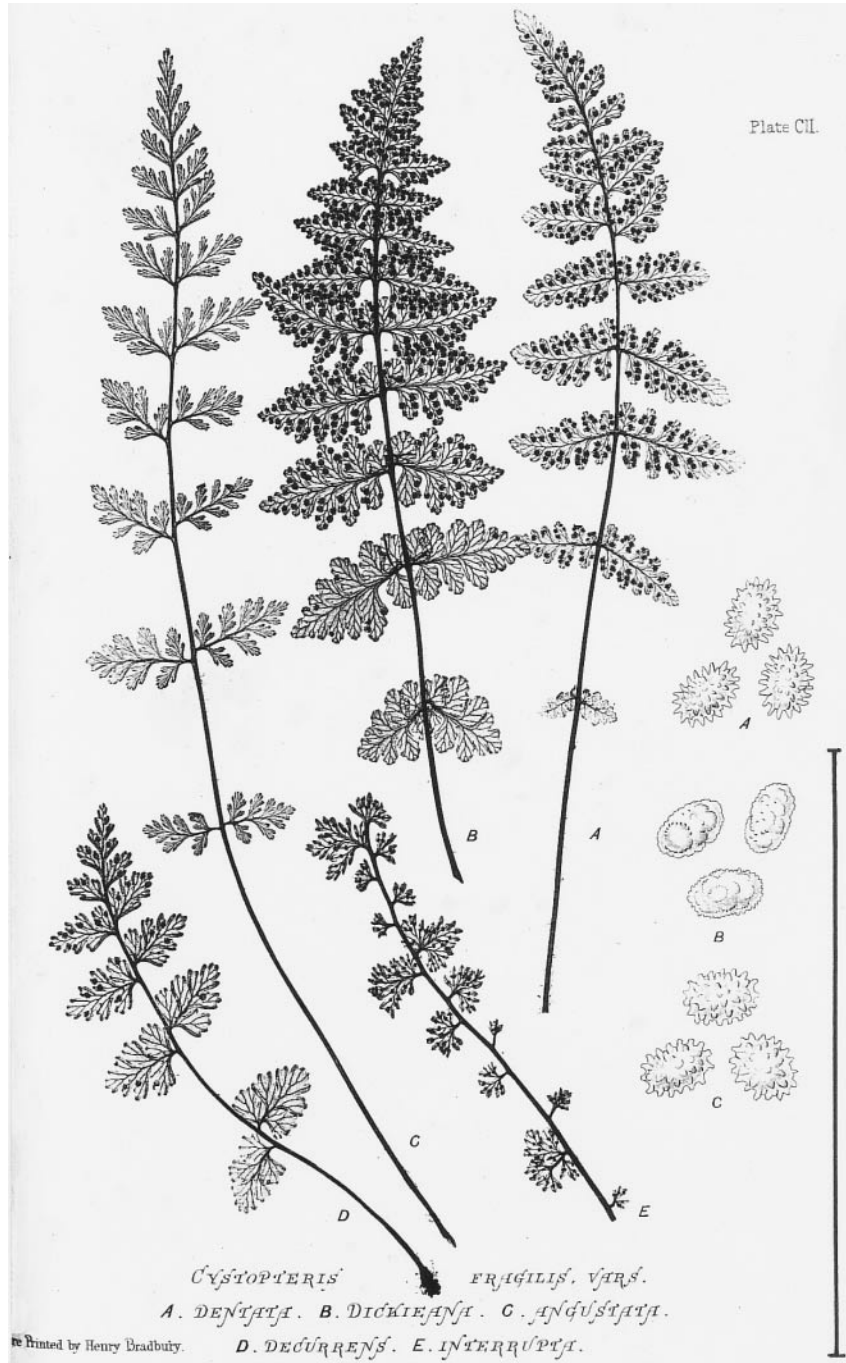
Cystopteris fragilis (L.) Bernh. is a cosmopolitan polyploid taxon, (Crabbe & Jermy, 1993; Haufler *et al.*, 1993), which is thought to be of ancient origin because of the lack of diploids and the worldwide distribution (Lovis, 1977) and because it acts as a diploid at many of its enzyme loci (Haufler & Windham, 1991). Chromosome studies reveal that most plants are tetraploid or hexaploid and the considerable morphological and allozymal variation indicates that there is evolutionary divergence in these polyploids.

Cystopteris dickieana R. Sim is a taxon which has long been recognized within the *C. fragilis* complex (Marren, 1984). It was discovered in the 1830s by William Knight (Dickie, 1860). The earliest published reference to it was under the name *C. fragilis* (Dickie, 1838) but the description of its habitat makes it clear that Dickie was

referring to what is now the type material of *C. dickieana*. The type specimens were collected from a sea cave at Cove, a few miles south of Aberdeen, Scotland, in 1842 by George Dickie and are now in the herbaria of the Natural History Museum London (BM) and the Royal Botanic Gardens Kew (K). The type locality has been described in detail by Marren (1984). Living material was sent to several people including Robert Sim, a nurseryman in Kent, England, who wrote the first published description of the plant (Sim, 1848). He placed it in a new taxon, *Cystopteris Dickieana*, adding that ‘If any of the recorded species [i.e. the taxa recognized within the *C. fragilis* complex in Britain at that time] apart from *C. fragilis* have a claim to rank as such, so also must *C. Dickieana*’. The first published illustration, this time as *C. fragilis* var. *Dickieana*, appeared a year later (Moore, 1849a) and a more detailed description appeared the same year (Moore, 1849b). An early and important illustration appeared in 1859 (Moore, 1859). It was produced by Henry Bradbury’s Nature Printing method whereby each print was taken from a copper replica of an impression made by an actual specimen on a polished lead sheet. No drawing or engraving was involved, so the print is completely accurate in all details (Fig. 1). Moore first cultivated plants from the cave in 1846 and, having proved very easy to grow, it has been in cultivation ever since. It was collected in quantity by nurserymen for resale in the early 1850s. James Backhouse from Yorkshire visited the site in August 1852 (Backhouse, 1852) and collected herbarium specimens (Fig. 2) and live plants.

In the 150 years since it was formally described, there has been a continuing debate about the proper taxonomic status of ‘*Cystopteris dickieana*’ but there has been no recent review of the history of this debate. Johnson and Sowerby (1855) called the type material *C. Dickieana* but referred to it as a variety. Moore published it as a variety of *C. fragilis* but, according to Sowerby and Johnson, remarked that ‘I am inclined to think *C. dentata* [one of the taxa then recognized within the *C. fragilis* complex in Britain; see Fig. 1] to be sufficiently distinct to take rank as a species, and to look upon *C. Dickieana* as an extreme form of it’. Newman included it as a species, *C. Dickieana* Sim, in the 1854 edition of his book, *A History of British Ferns* (Newman, 1854), but stated ‘My own judgement, improved but by no means matured, by the observations of sixteen years, regards *dentata* as a nonentity, *angustata* as a synonyme of that nonentity, and *Dickieana* as a *possible*, but by no means *established*, species.’ He based his doubts about its specific status on ‘first, the present restriction of the species to a single locality, and that a very peculiar one; and, secondly, the absence of any obvious character whereby it may be distinguished from *C. fragilis*.’ Most later 19th-century authors favoured varietal or subspecific status for material from the type locality but it has been accorded species rank in most of the more recent British floras, field guides and other publications (e.g. Manton, 1950; Clapham *et al.*, 1952; Page, 1988; Jermy & Camus, 1991; Hutchinson & Thomas, 1996; Page, 1997; Stace, 1997), though frequently accompanied by an indication of the uncertainty regarding its status. Lovis (1977), obviously referring to the type material, stated: ‘Modern European taxonomic practice accepts *Cystopteris dickie-*

Plate CIL



CYSTOPTERIS FRAGILIS, VAR. *FRAGILIS*.
 A. *DENSATA*. B. *DICKIEANA*. C. *ANGUSTATA*.
 D. *DECURRENS*. E. *INTERRUPTA*.

Printed by Henry Bradbury.

ana, which possesses distinctive morphological features other than its highly characteristic spores, as a valid species related to but distinct from *C. fragilis*.’ It is apparently the combination of unique frond architecture and distinctively sculptured spores that encourages this recognition as a separate species but it is worth noting that other equally extreme frond architectures exist within the *C. fragilis* complex. Although many of these have, at some point in the past, also been recognized as distinct taxa, only two are occasionally recognized in Britain today and then only as varieties of *C. fragilis*: *C. fragilis* (L.) Bernh. var. *alpina* Hook., and *C. fragilis* (L.) Bernh. var. *dentata* Hook., (Tennant, 1995).

As indicated in Sim’s original description and illustrated by Moore (see drawings in Fig. 1), typical *C. dickieana* has rugose and minutely verrucate spores (also described in the literature as rugose, rugate, verrucose, verrucate, or tuberculate, and here subsequently referred to as ‘rugose’), which is a distinctive feature within *Cystopteris*. Most *Cystopteris* taxa, including most variants of *C. fragilis*, have echinate spores (also described in the literature as spiny, spinulose, or spinose and here subsequently referred to as ‘echinate’), (Blasdell, 1963; Pearman, 1976; Tryon & Lugardon, 1991). However, as early as 1855, Johnson and Sowerby recognized that other variants of ‘*C. dentata*’ (considered by them as a species but now included in *C. fragilis*) also had non-echinate spores. In 1891, *C. baenitzii* Dörf., reported from Scandinavia to Siberia but said to be rare in Western Europe, was described from Norwegian type material as a species distinct from *C. fragilis* solely on account of its non-echinate spores (Manton, 1950). Hagenah (1961) observed plants with ‘non-spiny’ spores that otherwise fitted the description of *C. fragilis* var. *fragilis* in North America. Pearman (1976) reported spores with modified spines or no spines in four species, including some identified as *C. fragilis*. Tennant (1995) described somewhat intermediate, ‘tuberculate’, spores in *C. fragilis* var. *alpina* from Teesdale, England. Non-echinate spores are thus not unique to the type material of *C. dickieana* and occur elsewhere within the *C. fragilis* complex as well as in other species. Rich & Jermy (1998) concluded that the rugose surface of the spores of *C. dickieana* is a character ‘of little taxonomic significance’. Nevertheless, the delimitation of *C. dickieana* from *C. fragilis* has sometimes been reduced to the one character: the presence of rugose spores (e.g. Blasdell, 1963; Profumo, 1965, 1969; Vida, 1974; Pearman, 1976; Wang, 1983; Prada, 1986; Roa *et al.*, 1988; Fraser-Jenkins, 1997). This has resulted in reports of *C. dickieana* from elsewhere in Britain (Tennant, 1996; Jermy & Harper, 1971) as well as from a wide area of Europe, and from North Africa,

FIG. 1. Plate CII from Moore (1859) including one of the earliest published illustrations of *C. dickieana* (here referred to as *C. fragilis* var. *dickieana*). The illustration is a Nature Print taken from an actual specimen. Scale bar=10cm. Note that the taxa referred to as var. *angustata*, var. *decurrens* and var. *interrupta* are not recognised in any modern taxonomic treatment of the *C. fragilis* complex.



FIG. 2. Photocopy of a herbarium specimen (at E) of *C. dickiana* collected at the type locality by James Backhouse Senior in August 1852. Scale bar = 10cm.

India, Pakistan, China, Greenland and North America (e.g. Profumo, 1965, 1969; Nardi, 1974; Pearman, 1976; Vida & Mohay, 1980; Wang, 1983; Prada, 1986; Labatut, 1988; Roa *et al.*, 1988; Haufler & Windham, 1991; Berg, 1992; Nakaike &

Malik, 1992, 1993; Crabbe & Jermy, 1993; Øllgaard & Tind, 1993; Fraser-Jenkins, 1997).

As emphasized by Lovis (1977), the plants used to typify *C. dickieana* have a suite of morphological characters that, along with rugose spores, are distinctive (Newman, 1854; Page, 1997). Above a short stipe, the pinnae are oblique to the plane of the leaf. They are less finely dissected than in *C. fragilis*, with broad, bluntly rounded ultimate segments, and crowded on the rachis so that they overlap, and they have crisped margins. A review of the literature reveals that when those who have recognized *C. dickieana* on the basis of rugose spores alone have also provided descriptions of frond architecture (e.g. Nardi, 1974; Haufler & Windham, 1991; Berg, 1992; Øllgaard & Tind, 1993; Tennant, 1996; Fraser-Jenkins, 1997), the plants they identified as *C. dickieana* were often unlike the type material of that species and fell within the wide range of variation found within *C. fragilis* and its varieties. So-called '*C. dickieana*', indistinguishable from *C. fragilis* apart from the spores, can even be found growing together in the same populations as plants that have echinate spores (Haufler & Windham, 1991; Berg, 1992; Øllgaard & Tind, 1993). Hagenah (1961) described eight instances where, in a survey of herbarium collections of North American specimens, he had found some individuals with echinate spores and some with rugose spores among plants identified as *C. fragilis* with the same collection number and presumably therefore from the same population. Where plants producing either echinate or rugose spores occur close together, plants producing intermediate spore types have been reported (Øllgaard & Tind, 1993).

Nardi (1974) and Labatut (1988) divided '*C. dickieana* s.l.' with rugose spores into '*C. dickieana* s.str.' and a group related to *C. baenitzii* Dörfl on the basis of a number of spore and frond characters. However, *C. dickieana* s.str. as defined by them still includes plants from Spain, Sicily, and Sardinia that are otherwise more similar to *C. fragilis* than to the type material of *C. dickieana*. Øllgaard and Tind (1993) expressed concern over the application of the name *C. dickieana* to Scandinavian plants with rugose spores but *fragilis*-like fronds and suggested that it might be more appropriate to call these *C. baenitzii*. Crabbe and Jermy (1993) included *C. baenitzii* as a synonym of *C. dickieana*, with the Scottish type material of *C. dickieana* as an extreme variant of the species. Prada (pers. comm.) also treated *C. baenitzii* as a synonym of *C. dickieana* for plants with rugose spores resembling *C. fragilis* in frond architecture. Page (1997) has suggested that these plants might be the product of introgression between the typical *C. dickieana* and typical *C. fragilis*. Fraser-Jenkins (1997) included all these plants within *C. fragilis* subsp. *dickieana* but uniquely considered that the plants fitting the type description for *C. dickieana* and now in garden-cultivation should be treated as a cultivar, *C. fragilis* (L.) Bernh. subsp. *dickieana* (R.Sim) Hyl. 'Dickie' Fraser-Jenk.

The widespread use of the broader definition of *C. dickieana*, based solely on spore sculpturing while ignoring the overlap with *C. fragilis* in frond architecture, has led to further confusion. Thus, it does not necessarily follow that statements by various authors about *C. dickieana* are valid for material from the type locality which may not even have been included in their investigations.

Statements about the distribution of *C. dickieana*, as recognized by spore sculpturing, hide the fact that, with the possible exception of a plant from Arran, Ireland, mentioned but not described in detail by Moore (1859), plants with frond architecture fitting the type description of *C. dickieana* have been found only at, and close to, the type locality. There are no substantiated reports of such plants at any other locality within or outside Britain. In a study of the North American distribution of *Cystopteris* with 'non-spiny' spores, based on light-microscopy, Hagenah (1961) argued against the recognition of either *C. dickieana* or *C. baenitzii* as distinct from *C. fragilis* var. *fragilis*, and concluded that 'the recognition of species on the grounds of spore sculpturing alone does not seem justifiable at this time'. Blasdel (1963), in a monograph considered to be an inadequate treatment by Lovis (1977), concluded that *C. dickieana* was 'worthy only of designation as a spore form within *C. fragilis*' and included it, with *C. baenitzii*, under *C. fragilis* var. *fragilis*. However, again it appears that no British material was included in the survey. By contrast, in a later electron microscopy study of spore morphology, Pearman (1976) recognized *C. fragilis* var. *dickieana* but once more the decision was taken without examining the type material or more recent collections from the type locality.

C. dickieana in the form which characterizes the type locality is tetraploid (Manton, 1950). However, Manton & Reichstein (1965) and Vida & Mohay (1980) reported hexaploid plants with non-echinate spores from USA, Greenland and the Swiss Alps and concluded that *C. dickieana* includes at least two cytotypes. Roa *et al.* (1988) and Profumo (1969) stated that there were no significant differences in gametophyte morphology between *C. dickieana* and *C. fragilis* but examined gametophytes raised from plants of *C. dickieana* identified solely on the basis of spore sculpturing and only from Spain and Italy respectively; they did not include material from the type locality. Comparisons of isozyme banding patterns (Haufler & Windham, 1991) that contributed to the conclusion that *C. dickieana* was not distinct from *C. fragilis* were based entirely on North American material in which only the spore sculpturing consistently separated the two groups. Manton and Reichstein (1965) reported that a plant that they presumed to be a hybrid between tetraploid *C. fragilis* and tetraploid *C. dickieana* was sterile, reinforcing their decision to attribute them to different species or at least subspecies, but the plants were from Norway (so it was presumably *C. dickieana* s. l., with *fragilis* frond architecture and rugose spores) and again material from the type locality was not studied. By contrast, Vida (1974) used only material from the type locality of *C. dickieana* in a genome analysis of *C. dickieana* and examined a synthetic hybrid between this and *C. fragilis* of Polish origin. He did not comment directly on the spore sculpturing of the parent plants but presumably they were rugose and echinate respectively. He concluded that these two tetraploids were genomically distinct allopolyploids with only one genome in common (i.e. YYZZ and XXYY). However, an observed excess of bivalents over the 42 expected in the hybrid XYYZ if only the Y genomes paired suggests that genomes X and Z are also related, even in these two widely separated populations. Vida did not study the relationship of the type *C. dickieana* with *C. fragilis* from

Britain, which may be more closely related to the type than is the Polish material. Lovis (1977) reviewed Vida's cytological evidence and concluded that *C. dickieana* was probably a segmental allopolyploid (i.e. YYY'Y').

As a generalization, over the last 50 years or so, most of those who have conferred specific status upon *C. dickieana* have included type material or material known to have come from the type locality in their investigations. Most of those who favour synonymy of *C. dickieana* with *C. fragilis*, either unnamed (e.g. Blasdell, 1963), or as a variety [*C. fragilis* (L.) Bernh. var. *dickieana* (Sim.) Lindberg., *Medd. Soc. Fauna et Flora Fennica* 32: 21–24. (1905)] or a subspecies [*C. fragilis* subsp. *dickieana* (Sim) Hylander, *Uppsala Univ. Arsskr.* 1945 (7): 59. (1945)] have not included type material or material known to have come from the type locality in their investigations. Thus, most of the current fern floras and field guides covering Scotland (Stace, 1997; Page, 1997; Crabbe & Jermy 1993; Jermy & Camus, 1991) refer to *C. dickieana* as a distinct species, albeit with some reservations.

In conclusion, the taxonomic status of *C. dickieana* within the *C. fragilis* complex remains uncertain and controversial. Indeed, 140 years after Moore's reference to the 'quagmires of species making', the two basic taxonomic questions regarding *C. dickieana* still remain: 1, are all the members of the *C. fragilis* complex that have rugose spores members of the same taxon as the type material of *C. dickieana*?; and 2, is the type material of *C. dickieana* a distinct species or a variety/subspecies of *C. fragilis*?

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