

## Re-appearance of the rare intergeneric hybrid fern *×Asplenophyllitis jacksonii* Alston (Aspleniaceae) in the flora of Cornwall

C. N. PAGE

*Gillywood Cottage, Trebost Lane, Stithians, Truro, Cornwall TR3 7DW*

### ABSTRACT

The extremely rare fern *×Asplenophyllitis jacksonii*, the natural hybrid between *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium*, has been found in the wild in Cornwall after an absence of records of it in mainland Britain as a whole for nearly one and a half centuries. Here, the occurrence, field-appearance, habitat, origins and onward progress of the plant are described and discussed in relation to the habitat and ecology of this striking intergeneric hybrid fern.

### INTRODUCTION

A single plant of the extremely rare fern *×Asplenophyllitis jacksonii*, the natural intergeneric hybrid between *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium*, has been found by the author in the wild in West Cornwall (v.-c. 1), after an absence of native records of it in mainland Britain as a whole for nearly one-and-a-half centuries.

In the British flora in Victorian times, this hybrid was reportedly known in the wild from widely scattered stations in the Channel Islands (Guernsey in 1856, Jersey 1863), Cornwall (c. 1860) and Devon (1872) (McClintock 1975; Ivimey-Cook 1984; Le Sueur 1984; French *et al.* 1999). According to Alston (1940) and Lovis (1975), no further wild sightings of this plant had up to then been made anywhere on the British mainland or in the Channel Islands since 1872. More recently, F. J. Rumsey (pers. comm., 2004) reports the discovery of a small plant demonstrated to be this hybrid in Guernsey in 1996, but that this plant could not be refound. Apart from this, the only other known record for this hybrid anywhere in the intervening century has been that of a single plant also found in the 1990s in western France (Brittany - Prelli 1996).

Details of the reputed earlier Cornish locality are given as a 'dot' for the District of Penwith, west Cornwall in Jermy *et al.* (1978), but no further locality details are known locally (French *et al.* 1999; R. J. Murphy pers. comm. 2004). Furthermore, F. J. Rumsey (pers. comm. 2004) states that the only previous Cornish record of *×Asplenophyllitis jacksonii* backed by a specimen is incorrect, the specimen being *×Asplenophyllitis microdon*, and that it is therefore likely that this present find constitutes the first record of the hybrid from Cornwall – certainly the first unequivocal one.

### OCCURRENCE AND INITIAL RECOGNITION OF THIS HYBRID

A single plant of this hybrid was found by the author in September 2002, and, since its first encounter, its subsequent progress has been carefully and continuously monitored.

The plant grows in the old mortar of a west-south-west facing wall of a dilapidated farmstead outbuilding. This locality is within the extensive former mine-working region of west Cornwall between Truro and Redruth at an altitude of c. 75 m. The plant occurs at the side of a rough farm track used mainly by farm tractors and agricultural machinery, and is an inland but nevertheless somewhat maritime-influenced Cornish site.

First impression of the plant was of a fern of unusual appearance, resembling in size and colour, but not in form, a small and rather pointed-fronded polypody of non-colonial habit and hence

worthy of further investigation. On closer approach, it appeared to have coarsely-lobed and rather fleshy fronds, in texture and colour more like *Asplenium marinum*. But the fronds were more spreading away from the wall and with longer, darker stipes to each frond than this species, and the blades, although fleshy, were each wider at the base and the whole of each blade more undulate. It thus became rapidly clear that this was an even more unusual plant - an  $\times$ *Asplenophyllitis* - the intergeneric hybrid between *Asplenium* (the Spleenworts) and *Phyllitis scolopendrium* (Hart's Tongue Fern). The occurrence of any fern of intergeneric origins is rare in any combination.

But this plant was not the very local  $\times$ *Asplenophyllitis microdon* that I had previously seen in Guernsey (which has the parents *Asplenium obovatum* (=billotii)  $\times$  *Phyllitis scolopendrium* - silhouetted in Hegi 1984 and Page 1997). For  $\times$ A. *microdon* has somewhat slender, tapering, less triangular and more ovate-outlined fronds, although its fronds can also be undulate (see photo in Page 1988). However, in this Cornish plant, the parental involvement of a different *Asplenium* seemed indicated; the wide and spreading basal pinnae and overall triangular outline of each of the fronds in the hybrid suggested that this parent was *Asplenium adiantum-nigrum*. This new mainland Cornish fern find is thus of  $\times$ *Asplenophyllitis jacksonii* ('Jackson's Fern'). This diagnosis is further supported by the presence of the two parent species *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium* on the same wall (and only these two members of the Aspleniaceae in the locality). Both the latter are also much more abundant on adjacent hedgebanks (built of stone faces with an earth infill and turf capping - see Page 1988, 2005) in the general vicinity.

#### STRUCTURAL DETAILS OF THIS HYBRID

The following structural details of the fern are mainly as recorded directly from this plant in the field at the time of first finding. The plant has six main intact or semi-intact fronds c. 9.5–15.5 cm long (including stipes) with blades c. 7.5–11.0 long and 3.5–5.8 cm broad across the basal pinnae. The fronds spread away variously from the wall as they adopt more-or-less horizontal to slightly ascending orientations. The stipes are somewhat thicker and shorter than those of comparably-sized *A. adiantum-nigrum*, while the overall plant has fronds considerably larger than those of *A. adiantum-nigrum* in the same site. Compared with this parent, pinnae throughout all fronds of the hybrid are clearly much more entire and congested, slightly overlapping in the lower half of the blade, becoming more so and progressively more confluent in the upper half of the blade. The widest pinnae are the lowest in nearly all fronds, giving the blades a notably triangular outline, and individual pinnae are also each broadest at the base and typically taper rapidly to bluntly-rounded tips. The lowermost 3–5 pinnae bear conspicuous small acroscopic or basiscopic lobes (often both), the basiscopic of which is especially developed on the lowermost one or two pinna-pairs on most fronds, reflecting the shape of the largely auricled cordate base of the *Phyllitis* parent. The lower pinnae are also in life somewhat forwardly-inclined and themselves waved slightly along their length, giving the whole blade the slightly undulate surface so apparent in the field.

On the underside, all fronds (at first finding and also those subsequently appearing) bear copious long sori, which include a mixture of ones of 'single' (i.e. *Asplenium*-like) and 'twinned' structure (opening towards each other, i.e. *Phyllitis*-like) in approximately equal numbers. The latter character in particular, together with the unusually bright green colour of the upper surface of each blade, confirm the involvement of *Phyllitis scolopendrium* in its parentage.

To authenticate and affirm the scientific record in case the plant failed to survive, the plant was photographed and, at the end of the growing-season of 2002, when a blade was starting to discolour naturally, this single frond was collected by careful removal with fine scissors from the stipe base without disturbance to the rest of the plant. Pressed to form a voucher specimen (see silhouette, Fig. 1), this has been temporarily retained for collective study by local botanists in order to calibrate memories in case of independent location of further specimens. It will in due course be deposited at the **BM**.



FIGURE 1. ×*Asplenophyllitis jacksonii*. Single typical frond from the new Cornish site. Natural size.

#### HABITAT AND KNOWN HABITAT HISTORY

The hybrid grows on a west-south-west facing wall of a somewhat dilapidated farmstead outbuilding, which otherwise (at the time of finding) carries mainly only scattered ivy and *Cymbalaria muralis* plants. The short length of wall is typical of local rural construction: built a few centuries ago of a small number of large squared granite 'quoins' (cornerstones) with smaller pieces of more irregularly shaped 'killas' rocks (partly-metamorphosed shaly-mudstones of Upper Devonian/Lower Carboniferous age) forming the main 'run' of the wall, among which are also further smaller scattered granite inclusions. The hybrid fern itself lies at a point in the wall forming a junction of granite quoin and killas stone beneath. The original mortar is probably based on local granite sand with added lime, and the wall itself, with the rest of the farmstead, is believed to date originally from the 1700s with some rebuilding work in the 1800s. Most of the stonework appears to have received little structural attention since.

The killas rocks are almost certainly native to the immediately surrounding area, which was formerly heavily mined for metal ores. Only the granite quoins would have been brought in, probably from quarries a few miles away. The presence of numerous nearby old mineworkings suggests that the majority of the killas rocks were those outcast from these sources, and which themselves could be variably metalliferously influenced (here with copper, tin and arsenic). In this light, it seems significant that, unlike the nearby lanebanks, the immediate wall is scarcely rich in ferns: there are merely two stunted plants of *Phyllitis scolopendrium*, also on the immediate wall-face, less than a metre from the hybrid and a single specimen of rather stunted *A. adiantum-nigrum* more than a metre in the opposite direction, with further specimens of *Phyllitis* more abundantly round an adjacent corner. Apart from scattered buildings, the remainder of the farm track is defined largely by traditional (and probably old) Cornish 'hedges' of earth-and-stone construction, carrying populations especially of *Polypodium interjectum*, *Polystichum setiferum*, *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium*. Close searching both in the immediate vicinity and in other similar habitats nearby have, however, so far failed to reveal any further specimens of ×*A. jacksonii*.

Following initial finding of this hybrid (Page 2003), the plant has continued to be monitored by the author. It continues to thrive now nearly three years on. Throughout 2003 the hybrid fern

persisted successfully even through a relatively prolonged late summer drought (when it was monitored frequently, but without interference). During this time it appeared to suffer less from temporary flagging of the fronds than did adjacent specimens of either parent in the same habitat. The plant now has a considerably increased number of fronds (twelve produced by the end of 2003 – all of which are soriferous and continue to follow the soral structural patterns described above). It has become noteworthy that the hybrid appears to remain much larger on the immediate wall than are either of the parent species, suggesting an innate vigour to this particular hybrid plant.

I am told by the owner of the site that this particular wall was cleared of much ivy growth about six years prior to my finding this fern. The hybrid fern appeared clearly at least several years old when initially found. However, the subsequent observations showing it to continue to increase in size and frond number indicate that the plant was not fully-grown when originally found, and this suggests that its origin might well date from immediately after the time of clearance of the ivy mantle. If so, its formation may indeed have been stimulated by the surface disturbance of the mortar-courses during the process of this removal event.

#### COMPARISONS WITH THE ORIGINAL GUERNSEY MATERIAL AND WITH THE RECENT FRENCH (BRETON) MATERIAL

The first known record of this plant recorded anywhere was in Guernsey, Channel Islands, where it was originally found by C. Jackson in June 1856 (McClintock 1975). In comparison with the actual fronds from the plant recorded in Guernsey, almost all of the details seen in this new Cornish plant are virtually identical, though the Cornish plant is still of a slightly smaller maximum frond size (15.5 cm compared with 10–16 cm but up to 20 cm long for the original Guernsey material). However, the overall variation in size and form between the fronds of this plant and those of the total of seven fronds I have seen preserved from Guernsey is remarkably similar. No exact habitat details of the Guernsey plant are known to me, although it was probably originally from a lanebank. Literature suggests that it was dug up and thereafter seems to have been successfully maintained in cultivation for over the next half a century, becoming propagated and listed by at least four fern nurseries between 1865 and 1928 (McClintock 1975). This does seem to suggest that, like the present Cornish plant, that from Guernsey may too have had a reasonable degree of individual vigour.

The recent record for this hybrid found in Brittany in September 1994 was regarded by Prelli (1996) also as 'extremely rare'. This plant possessed 5 small fronds, measuring 6–11 cm long, with only a few sori, and a further three 15–20+ cm in length, which were more fertile. Cytological analysis confirmed the plant to be triploid, with  $n = c. 108$  chromosomes, thus according with its ascribed parentage. Nearly all of the morphological details of the fronds described and illustrated by Prelli compare closely with those of the present plant, the exception being that about half of the sori of the present plant are 'twinned' in a *Phyllitis*-like fashion. In terms of habitat, however, the French one is, as with this Cornish one, associated with the ferns *Polystichum setiferum*, *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium*, within a sub-coastal wood, but rooted into the ground at the edge of a small footpath where 'the earth has been disturbed'.

#### EVIDENCE OF THE INTERGENERIC STATUS OF $\times$ ASPLENOPHYLLITIS

The occurrence of this and other hybrids involving *Phyllitis scolopendrium* as one parent, and a species of *Asplenium* as the other, immediately begs the question of whether we are dealing here with a pteridophyte hybrid which is truly intergeneric in origin, or whether it is the result of a cross between species of the same genus which happen to look very different.

My reasons for maintaining generic distinction of *Phyllitis* from *Asplenium*, and thus for regarding this present plant as of intergeneric status include:

- differences in vegetative morphology [with the blade of *Phyllitis* not just entire, but also having a distinctively auricled, cordate base],
- differences in reproductive structure [in which the sori of *Phyllitis* are consistently large, long and run along almost the entire length of the available veins of the lamina, and are always 'twinned'],

- the known experimental difficulty in artificial synthesis of ×*Asplenophyllitis* hybridity (Lovis & Vida, 1969) [which contrasts with the far larger number and frequency of hybrids occurring naturally in the wild between many but not all species of typical *Asplenium* (in Europe see for example Lovis & Reichstein 1981; Jalas & Suominen 1972; Hegi 1984; Vogel *et al.* 1996, and in North America, Wagner 1954)],
- distinctiveness of chromosomal morphology [in which the whole chromosome set of *Phyllitis scolopendrium* is consistently larger than are those of typical *Asplenium* (Vida 1963; Lovis 1973), which has been interpreted as a fundamental distinction of *Phyllitis* (Vida 1970; Lovis 1975; Wagner & Hagenah 1989)],
- recent molecular comparisons [which either identify *Phyllitis* as basal within the whole family Aspleniaceae forming a clade which is the sister-group of true *Asplenium* (Murakami *et al.* 1999) or identify *Phyllitis* as sister-group to *Ceterach*, the two together forming a single clade (Pinter *et al.* 2002)].

Some of the above lines of evidence for considering *Phyllitis* generically distinct, when taken separately are indeed not unique in the family: for entire fronds (though not necessarily with cordate auricled bases) have probably evolved several times in the family, as have, I presume, twinned sori. Yet it is the consistency of these in *Phyllitis* that remains notable, while it is also the constant combination of these with the other characters (and especially the distinctiveness of chromosomal morphology) which, in the author's view, continues to justify generic recognition of *Phyllitis* in a global fern taxonomy\*.

#### DISCUSSION

##### BIOGEOGRAPHIC AND ECOLOGICAL IMPLICATIONS OF THIS FIND

In Britain (as also in the Channel Islands and in north-western France), both parent fern species, *Asplenium adiantum-nigrum* and *Phyllitis scolopendrium*, are common and widespread, especially on old earth-and-stone 'hedges', as well as on a wide variety of old mortared walls. In such hedges within Cornwall, *A. adiantum-nigrum* shows a particularly wide variation in frond form with locality, and sometimes within individual hedges, and a similar picture emerges in Devon. Such hedges in south-west England have themselves been cited as important habitats both for preservation of ancient fern diversity and for presenting sites in which new fern diversity can actively arise (Page 2005). *Phyllitis scolopendrium* is present throughout essentially the same range of habitat types, but when growing in the widespread man-made earth-and-stone hedges of the region becomes abundant, successful and luxuriant (with fronds to 60–85 cm or more in length). No doubt it is the particularly moist climate of this region (with a rainfall of c. 40+ inches (c. 100+ cm) per annum in the area of the hybrid) and frequent high humidity as well as the long (nearly year-round) growing season, that is particularly conducive to the success of both of these parental evergreen ferns, and clearly too of their hybrid, when formed.

Under these conditions it might well be expected that opportunities for hybridisation between the parental frequently-occurring ferns ought to be very high. In this light, the scarcity and clear infrequency of records of the hybrid is probably realistic, considering the degree of close botanical attention which the region has always enjoyed (e.g. Davey 1909; Thurston & Vigurs 1922; McClintock 1975; Margetts & David 1980; Le Sueur 1984; Ivimey-Cook 1984; Jee 1994; French, Murphy & Atkinson 1999) and the interest which the occurrence of natural hybrids in our flora has always aroused (e.g. Manton 1950; Stace 1975 *et seq.*). Were this hybrid to be of genuinely wider occurrence, it might thus well be expected that it would have been recorded before now. One can

\*The concept of *Phyllitis* as an independent genus has been widely accepted, especially where the plant is most frequent, both locally (e.g. Girard & Lovis 1968; Lovis 1973, 1975; McClintock 1975; Hyde & Wade 1978; Le Sueur 1984; Ivimey-Cook 1984; Jee 1994; Page 1988, 1997; Stace 1997; French *et al.* 1999; Preston *et al.* 2002), and within its national and disjunct international range (e.g. Pichi-Sermolli 1953, 1977; Vida 1963; Emmott 1964; Jalas & Suominen 1972; Lovis 1975; Lovis & Reichstein 1981; Hegi 1984; Lellinger 1985; Hulten & Fries 1986; Mickel & Beitel 1988; Wagner & Hagenah 1989; Bir 1998; Cody & Britton 1989; Gureyeva, 2001). Encompassing its whole range, Mickel & Beitel (1988) recognise *Phyllitis* as a genus of 3–5 species of Europe, Asia, North America and some of the neotropics of southern Mexico and Hispaniola.

only conclude that reasons for the scarcity of this hybrid are a natural consequence of the parents being not generally successful at crossing with one another. Certainly, even *×Asplenophyllitis microdon* (the hybrid between *Asplenium obovatum* and *Phyllitis scolopendrium*) is only modestly more widely known in the wild, with a particular focus of occurrence on the island of Guernsey (Page 1991; Jee 1994).

It is interesting that this plant of *×Asplenophyllitis jacksonii* may have originated in its wall-mortar site following a surface disturbance event when the former ivy mantle was removed. In comparison, the account of Prelli (1996) describes the Breton site, though by a path, as being, significantly, where the earth had been disturbed. In Guernsey, it is suggested that statutory obligations on landowners to regularly cut back lanebank vegetation may promote the occurrence of appropriately disturbed sites (A. C. Jermy, pers. comm., April 2004) as new nuclei for fern and potentially hybrid occurrence. Indeed, the possible role of disturbance in enabling prothalli to grow synchronously in close enough proximity to cross would certainly accord with the view I have put forward separately that disturbance processes across a whole range of scales are vitally important in promotion of the re-establishment process of many (and possibly all) pteridophytes via prothalli, and are particularly vital in permitting unusual but successful hybrid formation (Page 2002).

#### CONSERVATIONAL IMPLICATIONS OF THIS FIND

The presence of this fern, as a single individual plant, and so far as is known, the only plant of its kind extant anywhere in the British Isles, immediately raises some conservational issues. Its site is one which is already clearly actively used in a practical sense by the workers on the particular farm. Yet it may well be some elements of this active use that have created the habitat which has brought this plant into being in the first place and which has clearly promoted it to survive thus far. If there are any conservation generalisations to be drawn from this, it is perhaps that there needs to be a plea for non-remortaring of old walls wherever possible or at least not without prior botanical survey, and for continued botanical surveying to include ones such as this which appear, at least at first, to be pteridologically unpromising.

I estimate that in this case the natural persistence of this hybrid fern does not appear to be unduly threatened, unless interfered with, or unless the plant comes into accidental physical conflict with passing agricultural machinery. However, because such a single plant could be far more vulnerable to wanton destruction, its exact locality has not been revealed other than to the landowner, who has been asked to ensure that the particular wall is not deliberately destroyed, cleared or re-mortared. The habitat details provided above are thus purely for the scientific record. Being on private land in daily use well away from public access, its location seems reasonably well protected. With the owner's continuing permission (a requirement of which is that I do not reveal the exact location to anyone), its further progress and survival seem likely, and are being carefully onwardly recorded by the author.

#### CONCLUSIONS

This find of *×Asplenophyllitis jacksonii* from west Cornwall, that from Brittany by Prelli (1996) and that reported from Guernsey by Rumsey clearly achieve a matching trio of records of similar rare crosses, appearing initially probably within the same decade and perhaps even closer in time than this. The occurrence at all, anywhere, of this particular cross is clearly extremely rare and infrequent. Yet there would seem to have been apparent geographic and temporal clusters of its occurrence in our Atlantic periphery around the middle of the 19th century, and again over much the same geographic area around the mid 1990s. I think I can largely rule out lack of vigilance amongst botanists in observing their occurrence, for such plants have the recording-advantage of being distinctive. Hence I am tempted to ask, after such a long period of absence of records, has the last decade of the 20th century itself produced any special circumstances by which the re-occurrence of this rare hybrid could have been similarly stimulated at these discrete Channel-separated but highly Atlantic-influenced sites? Further, are there any similarities of climatic patterns to those occurring in the mid-1800s? Clearly Brittany, the Channel Islands and Cornwall have much in common climatically as well as geologically. The past decade has also been one of unusual winter mildness, coupled also with some exceptionally hot summers, and also

characterised by significant (and sometimes unseasonal) periods of enhanced storm conditions. Could the greater number of occurrences of this hybrid, together with other ×*Asplenophyllitis* hybrids, as well as other unusual pteridophyte hybrids occurring recently (as has already been found with *Equisetum* – Duckett & Page 1975; Page & Barker 1985; Page 1988, 1997 and subsequent observations) correspond with the occurrence of certain specific climatic combinations, coupled with perhaps increased surface-disturbance of sites, by which unusual hybrid combinations in pteridophytes have been especially stimulated to form and succeed?

Finally, evidence at least from this Cornish plant would clearly suggest that the resulting hybrid can be vigorous, and to have every potential to ecologically persist, once successfully formed. The occurrence of such unusual hybrid ferns, whether they may prove to be evolutionary dead-ends or the very beginnings of new lines, are always of interest. For, besides being potentially valuable environmental indicators, they are also especially important in practically illustrating, under field conditions, how details of micro-evolutionary processes in pteridophytes can take place and under what circumstances these may be achieved. I thus echo the comments recently made by Chater (2003) about the importance of including information on infraspecific taxa (to which I also add here hybrid taxa) within floras, if we are going to be able to best understand more exact details of cause-and-effect between ecological stimuli and our constantly-changing micro-evolutionary floristic dynamics, as illustrated particularly well by those of Pteridophyta.

## ACKNOWLEDGMENTS

I am grateful to the landowner for access to the site of ×*Asplenophyllitis jacksonii*, for information on the known history of this site and for permission to return to monitor the continuing progress of this fern. I am further indebted to Miss Rose Murphy, Dr Colin French, Clive Jermy and Ian Benallick for valuable local discussion of the find, and to Dr Fred Rumsey for helpful comments on the resulting manuscript.

## REFERENCES

- ALSTON, A. H. G. (1940). Notes on the supposed hybrids in the genus *Asplenium* found in Britain. *Proc. Linn. Soc. Lond.* **152**: 132–144.
- CHATER, A. O. (2003). The treatment of infraspecific taxa in local Floras. *Watsonia* **24**: 281–286.
- CODY, W. J. & BRITTON, D. M. (1989). *Ferns and Fern Allies of Canada*. Agriculture Canada Research Branch, Ottawa.
- DAVEY, F.H. (1909). *Flora of Cornwall*. Penryn.
- DUCKETT, J. G. & PAGE, C. N. (1975). *Equisetum*, in STACE, C. A. (ed.) *Hybridisation and the Flora of the British Isles*, pp 99–103. Academic Press, London
- EMMOTT, J. I. (1964). A cytogenetic investigation in a *Phyllitis-Asplenium* complex. *New Phytologist* **63**: 306–318.
- FRENCH, C., MURPHY, R. & ATKINSON, M. (1999). *Flora of Cornwall. Atlas of the Flowering Plants and Ferns of Cornwall*. Wheal Seton Press, Camborne.
- GIRARD, P. J. & LOVIS, J. D. (1968). The rediscovery of ×*Asplenophyllitis microdon*, with a report on its cytogenetics. *British Fern Gazette* **10**: 1–8.
- GUREYEVA, I. I. (2001). Homosporous Ferns of South Siberia: Taxonomy, Origin, Biomorphology, Population Biology. Tomsk State University Publishers, Tomsk. (In Russian).
- HEGI, G. (1984). *Illustrierte Flora von Mittel-europa. Band I. Pteridophyta*. Paul Parey, Berlin & Hamburg.
- HULTEN, E. & FRIES, M. (1986). *Atlas of North European Vascular Plants North of the Tropic of Cancer. I.* : Koeltz Scientific Books, Königstein.
- HYDE, H. A. & WADE, A. E. (1978). *Welsh Ferns*. Sixth edition, revised by S.G. Harrison. National Museum of Wales, Cardiff.
- IVIMEY-COOK, R. B. (1984). *Atlas of the Devon Flora*. The Devonshire Association, Exeter.
- JALAS, J. & SUOMINEN, J. (1972). *Atlas Florae Europaeae. Vol. I. Pteridophyta*. The Committee for Mapping the Flora of Europe, Helsinki.
- JEE, N. (1994). The Guernsey Fern, ×*Asplenophyllitis microdon*. *Report and Transactions, La Société Guernesiaise* **23**: 724–749.
- JERMY, A. C., ARNOLD, H. R., FARRELL, L. & PERRING, F. H. (1978). *Atlas of Ferns of the British Isles*. Botanical Society of the British Isles and British Pteridological Society, London

- LELLINGER, D. B. (1985). *A Field Manual of the Ferns and Fern-Allies of the United States and Canada*. Smithsonian Institution Press, Washington DC.
- LE SUEUR, F. (1984). *Flora of Jersey*. Société Jersiaise, Jersey, C.I.
- LOVIS, J. D. (1973). A biosystematic approach to phylogenetic problems and its application to the Aspleniaceae, in JERMY, A. C., CRABBE, J. A. & THOMAS, B. A. (eds.), *The Phylogeny and Classification of the Ferns*, pp. 211–227. Linnean Society of London, London.
- LOVIS, J. D. (1975). *Asplenium* L.  $\times$  *Phyllitis* Hill =  $\times$ *Asplenophyllitis* Alston, in STACE, C. A. (ed). *Hybridisation and the Flora of the British Isles*. Academic Press, London.
- LOVIS, J. D. (1977). Evolutionary patterns and processes in ferns. *Advances in Botanical Research* **4**: 229–415.
- LOVIS, J. & REICHSTEIN, T. (1981). Hybrids in European Aspleniaceae (Pteridophyta). *Bot. Helv.* **91**: 89–139.
- LOVIS, J. D. & VIDA, G. (1969). The resynthesis and cytogenetic investigation of  $\times$ *Asplenophyllitis microdon* and  $\times$ *Asplenophyllitis jacksonii*. *British Fern Gazette* **10**: 53–67.
- MANTON, I. (1950). *Problems of Cytology and Evolution in Ferns*. Cambridge University Press, Cambridge.
- MARGETTS, L. J. & DAVID, R.W. (1981). *A Review of the Cornish Flora*. Institute of Cornish Studies, Camborne.
- MCCCLINTOCK, D. (1975). *The Wild Flowers of Guernsey*. Collins, London.
- MICKEL, J. T. & BEITEL, J. M. (1988). Pteridophyte Flora of Oaxaca, Mexico. *Memoirs of the New York Botanic Garden* **46**: 1–586.
- MURAKAMI, N., NOGAMI, S., WATANABE, M. & IWATSUKI, K. (1999). Phylogeny of Aspleniaceae inferred from rbcL nucleotide sequences. *American Fern Journal* **89**: 232–243.
- PAGE, C. N. (1988). *Ferns. Their Habitats in the British and Irish Landscape*. Collins New Naturalist series No. 74, London & Glasgow.
- PAGE, C. N. (1991). Past and present possible occurrence of the rare fern  $\times$ *Asplenophyllitis microdon* (T. Moore) Alston in Cornish hedgebanks. *Botanical Cornwall* **5**: 31–32.
- PAGE, C. N. (1997). *The Ferns of Britain and Ireland*. Second edition. Cambridge University Press, Cambridge.
- PAGE, C. N. (2002). The role of natural disturbance regimes in pteridophyte conservation management. *Fern Gazette* **16**: 284–289.
- PAGE, C. N. (2003). The intergeneric hybrid fern  $\times$ *Asplenophyllitis jacksonii* in West Cornwall. *Botanical Cornwall* **12**: 42–46.
- PAGE, C. N. (2005). Celtic Hedges as refuges for fern diversity in predominantly agriculturalised landscapes, in LEACH S. J., PAGE, C. N., PEYTOURAU, Y. & SANFORD, M. N. (Eds.) *Botanical Links in the Atlantic Arc*. Botanical Society of the British Isles, London (in press).
- PAGE, C. N. & BARKER, M. A. (1985). Ecology and geography of hybridisation in British and Irish horsetails. *Proceedings of the Royal Society of Edinburgh* **86B**: 265–272.
- PICHI-SERMOLLI, R. E. G. (1953). The nomenclature of some fern genera. *Webbia* **9**: 387–454.
- PICHI-SERMOLLI, R. E. G. (1977). Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. *Webbia* **31**: 313–512.
- PINTER, I., BAKKER, F., BARRETT, J., COX, C., GIBBY, M., HENDERSON, S., MORGAN-RICHARDS, M., RUMSEY, F., RUSSELL, S., TREWICK, S., SCHNEIDER, H. & VOGEL, J. (2002). Phylogenetic and biosystematic relationships in four highly disjunct polyploid complexes in the subgenera *Ceterach* and *Phyllitis* in *Asplenium* (Aspleniaceae). *Organic Diversity and Evolution* **2**: 299–311.
- PRELLI, R. (1996). *Asplenium*  $\times$  *jacksonii* rediscovered in the wild (Aspleniaceae: Pteridophyta). *Fern Gazette* **15**: 83–86.
- PRESTON, C. D., PEARMAN, D. A. & DINES, T. D. (2002). *New Atlas of the British and Irish Flora*. Oxford University Press, Oxford.
- STACE, C. A. (1975). *Hybridisation and the Flora of the British Isles*. Academic Press, London & New York.
- STACE, C. A. (1997). *New Flora of the British Isles* (2nd edn). Cambridge University Press, Cambridge.
- THURSTON, E. & VIGURS, C. C. (1922). *A Supplement to F. Hamilton Davey's Flora of Cornwall*. Truro.
- VIDA, G. (1963). A new *Asplenium* (Sectio *Ceterach*) species and the problem of the origin of *Phyllitis hybrida* (Milde) Christ. *Acta Biol. Hung.* **9**: 197–215.
- VIDA, G. (1970). The nature of polyploidy in *Asplenium ruta-muraria* L. and *A. lepidum* C. Presl. *Caryologia* **23**: 525–547.
- VOGEL, J. C., RUSSELL, S. J., BARRETT, J. A., & GIBBY, M. (1996). A non-coding region of chloroplast DNA as a tool to investigate reticulate evolution in European *Asplenium*, in CAMUS, J. M., GIBBY, M., JOHNS, R. J. (eds.), *Pteridology in Perspective*, pp. 313–327. Royal Botanic Gardens, Kew.
- WAGNER, W. H. (1954). Reticulate evolution in the Appalachian *Asplenium*s. *Evolution* **8**: 103–118.
- WAGNER, W. H. & HAGENAH, E. (1989). A synthetic trigenic hybrid  $\times$ *Asplenosorus pinnatifidus*  $\times$  *Phyllitis scolopendrium* var *americana*. *American Fern Journal* **19**: 1–6.

(Accepted April 2005)