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# A revision of some of the taxonomic characters of *Polypodium australe* Fée

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ABSTRACT

In addition to the presence of paraphyses three other characters have been emphasized for identifying *Polypodium australe*. These are the number of indurated annulus cells, the length of the rhizome scales and frond shape. A reassessment of these characters from cytologically determined plants shows that the variation in all of them is greater than has been supposed, and the overlap with *P. interjectum* Shivas is such as to reduce their taxonomic value considerably. It is also evident that most of the plants formerly thought to be morphologically intermediate between *P. australe* and *P. interjectum*, and consequently regarded as hybrids, fall within the ambit of *P. australe*. The shape of the rhizome scales as an accessory taxonomic character is discussed, and support is given to the view that the large, morphologically distinct paraphyses of *P. australe* are its best single distinguishing character.

## INTRODUCTION

The existence of three distinct taxa in Europe within the aggregate species *Polypodium vulgare* L. was first recognized by Rothmaler (1929). He ranked them as subspecies, namely subsp. *vulgare*, subsp. *prionodes* Rothm. and subsp. *serratum** (Willd.) Christ. Cytological support for this view was provided some eighteen years later by Manton (1947, 1950), who showed that three cytotypes occurred within the European aggregate. It is well to recall, however, that the form shown by Manton (1950) to be diploid had been recognised as a distinct entity as long ago as 1810 by Willdenow, who had named it *P. vulgare* L. var. *serratum*. On several occasions subsequently specific rank has been proposed for it, for example by Futo (1905). As a result of cytogenetic and biometric studies Shivas (1961) raised the three cytotypes to specific rank, the diploid becoming *P. australe* Fée (= *P. vulgare* L. subsp. *serratum* (Willd.) Christ), the tetraploid *P. vulgare* L. *sensu stricto* and the hexaploid *P. interjectum* Shivas (= *P. vulgare* L. subsp. *prionodes* Rothm.). She also described their morphological characters and most Flora descriptions published since have been based largely on her work, e.g. Warburg (1962) and Valentine (1964).

Nevertheless, during the examination of a large number of specimens, the writer encountered considerable difficulties. These were particularly apparent in the case of the diploid, *P. australe* Fée, whose published descriptions seemed to contain some serious errors, especially with regard to the number of indurated annulus cells and frond shape (Roberts 1966). Two characters had been relied upon to identify the specimens on which my observations were based. The first was the presence of paraphyses among the sporangia; the second was the

* The correct name for this taxon at the subspecific level is actually subsp. *serrulatum* Arcangeli.

contracted appearance of the flattened annulus in *P. australe* compared with *P. interjectum* Shivas. These annulus differences have been studied by Benoit (1966), who gives excellent figures of them, and by Roberts (1966). However, paraphyses were reported among the sporangia of *P. interjectum* in the Netherlands (Meinders-Groeneveld & Segal 1967), and in those of both *P. interjectum* and *P. vulgare* in Germany (Lenski 1962, 1964). The presence of paraphyses could thus no longer be regarded as an absolute diagnostic character of *P. australe*, as I had assumed in 1966. The possibility arose that some of the specimens on which my observations had been made might have been referable to *P. interjectum*. It was clear that the solution could be found only by the reappraisal of these characters in plants which had been determined cytologically.

## MATERIALS AND METHODS

Several of the plants used in my previous study had been kept in cultivation. Further collections of living plants were made subsequently, making a total of twenty-eight plants from ten localities. Fixations of young sporangia from all of them were made in 1:3 acetic-alcohol and examined as soon as possible afterwards by squashing two or three sori in aceto-carmine. Suitable preparations were preserved for a few hours by ringing the cover-slip with paraffin wax. A few were made permanent in Euparal. Spore mother cells showing well-spread chromosomes were drawn under an oil-immersion objective and counts made from the drawings.

Meiosis was found to be perfectly normal in all of these twenty-eight plants. There was no evidence of lagging chromosomes or any other irregularities found during meiosis in hybrids. Moreover, they all showed 37 bivalents, as

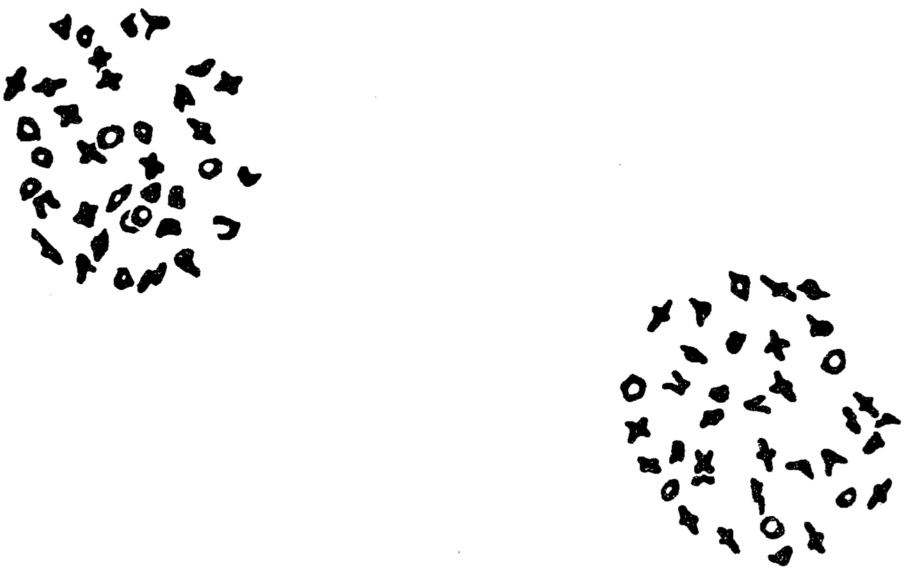

FIGURE 1. Diagram of the photomicrograph of meiosis, Plate 1a.

can be seen in the photomicrograph of meiosis in one of them (Plate 1a and Fig. 1).

Twenty plants each of *P. interjectum* and *P. vulgare* were also determined cytologically and used for comparison with the diploid plants.

## SPORANGIUM CHARACTERS

The number of annulus cells* in each of the diploid plants was counted in fairly large, random samples of sporangia when these had dehisced later in the season. The results are given in Table 1. They differ widely from those given by

TABLE 1. THE NUMBER OF INDURATED ANNULUS CELLS IN TWENTY-EIGHT PLANTS OF *P. AUSTRALE*, ALL WITH A CHROMOSOME NUMBER OF $n = 37$

| Locality | Range | Mode | No. of sporangia examined |
|---|---|---|---|
| Caernarvonshire, v.c. 49 | | | |
| Conway No. 1 | 3–13 | 6 | 300 |
| Conway No. 2 | 4–14 | 7 | 330 |
| Conway No. 3 | 3–9 | 5 | 450 |
| Conway No. 4 | 3–10 | 6 | 370 |
| Conway No. 5 | 3–8 | 5 | 220 |
| Criccieth No. 1 | 3–10 | 6 | 200 |
| Criccieth No. 2 | 5–14 | 9 | 360 |
| Criccieth No. 3 | 5–15 | 9 | 250 |
| Criccieth No. 4 | 4–12 | 8 | 200 |
| Glanwydden No. 1 | 3–10 | 6 | 300 |
| Glanwydden No. 2 | 3–11 | 7 | 450 |
| Great Orme | 4–10 | 6 | 300 |
| Little Orme No. 1 | 2–8 | 5 | 500 |
| Little Orme No. 2 | 4–12 | 8 | 540 |
| Little Orme No. 3 | 4–16 | 9 | 530 |
| Little Orme No. 4 | 3–13 | 8 | 610 |
| Penrhynside No. 1 | 3–10 | 6 | 200 |
| Penrhynside No. 2 | 3–13 | 7 | 450 |
| Anglesey, v.c. 52 | | | |
| Lligwy Wood No. 1 | 4–13 | 7 | 770 |
| Lligwy Wood No. 2 | 5–10 | 7 | 220 |
| Lligwy Wood No. 3 | 3–10 | 6 | 250 |
| Lligwy Wood No. 4 | 4–8 | 6 | 200 |
| Pentraeth No. 1 | 3–11 | 6 | 350 |
| Pentraeth No. 2 | 3–10 | 6 | 450 |
| Pentraeth No. 3 | 4–14 | 9 | 250 |
| Pentraeth No. 4 | 6–18 | 10 | 350 |
| Denbighshire, v.c. 50 | | | |
| Llanddulas | 5–14 | 9 | 260 |
| North Somerset, v.c. 6 | | | |
| Cheddar | 3–9 | 6 | 240 |

* To avoid tiresome repetition 'indurated annulus cells' are referred to in most of this paper as 'annulus cells'

Futo (1905), Manton (1950), Shivas (1961) and Rothmaler & Schneider (1962), who give the following values respectively: 6, (4–)5(–6), (3–)6(–8), and (4–) 6(–9). On the other hand they agree remarkably well with the counts of annulus cells in paraphyses-bearing plants given by Martens (1950) and Fernandes (1968).

From these results it is clear that the range of this character in *P. australe* completely overlaps the range in *P. interjectum*, as may be seen from the histograms of the number of annulus cells in the three taxa (Fig. 2). The modal class in many of the diploid plants is as high as that found in those of the hexaploid, and in one instance higher. Indeed, in some hexaploid plants the average number of cells in the annulus is as low as 7, as was also found by Shivas (1961).

It is noteworthy, too, that large differences in the number of annulus cells are found between plants of *P. australe* in the same locality and clearly belonging to the same breeding population. For instance, the four plants from the Little Orme, Caernarvonshire, included in Table 1, were all found growing on the limestone outcrop within 120 yards of each other. The distributions of the number of annulus cells in three of the Little Orme plants are shown in Fig. 3. That of the fourth plant from this locality is nearly identical with one of them and is therefore omitted. A similar distribution of this character was found in most of the plants included in Table 1; in only four of them was the skewness

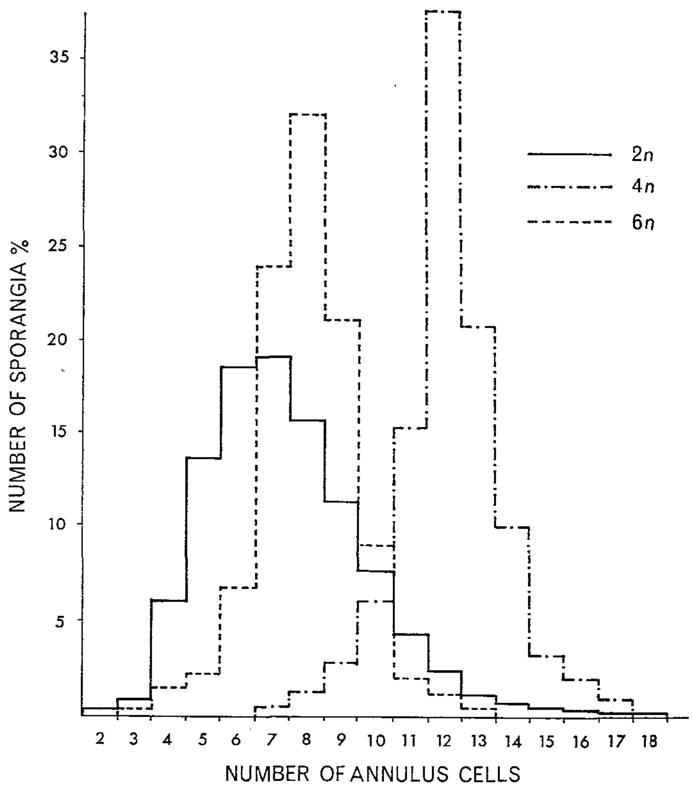


FIGURE 2. Histograms of the number of annulus cells in the three species of *Polypodium*. (Based on 9,900 sporangia of *P. australe* and 1,000 sporangia each of *P. vulgare* and *P. interjectum*).

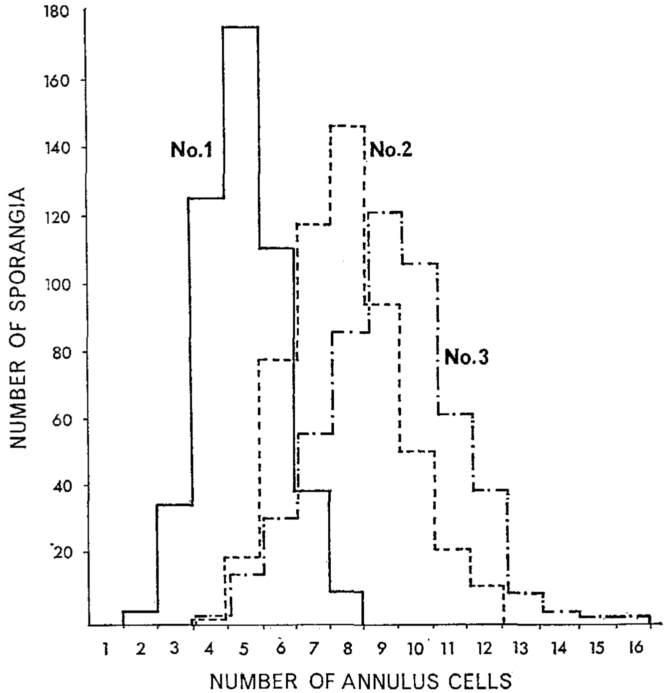


FIGURE 3. Histograms of the number of indurated cells of the annulus in three of the plants of *P. australe* from the Little Orme, Caerns. Numbers as in Table 1.

more markedly positive. The annulus cells in some of the Conway plants had been counted when they were first gathered several years ago. When these counts were repeated in 1968 they showed no significant differences from the previous ones, although the length of the fronds had increased in cultivation from around 12 cm to 28 cm or more.

Other sporangium characters, however, have proved to be of considerable taxonomic value. Lenski (1964) found a constant difference between the tetraploid and the other two species in the number and size of the 'basal cells.' According to her, both the diploid and the hexaploid have usually from two to four large cells separating the sporangium stalk from the annulus; the tetraploid has none or one (rarely two), which, when present, is smaller. Counts made from the material used in the present study (Fig. 4) agree well with those of Lenski. *P. vulgare* has almost invariably only one small basal cell, which is usually as wide as, or very little wider than the annulus. *P. interjectum* has mostly 2 or 3 and *P. australe* 3 or 4, and in both of these the basal cells are much wider than the annulus, as can be seen from the photomicrographs of dehisced sporangia (Plate 1b and e). This character is thus absolutely diagnostic for *P. vulgare*, but is only occasionally of use to distinguish between *P. australe* and *P. interjectum*. The figures of sporangia given by Rothmaler & Schneider (1962) are incorrect regarding this detail.

The difference between the diploid and hexaploid in the appearance of the

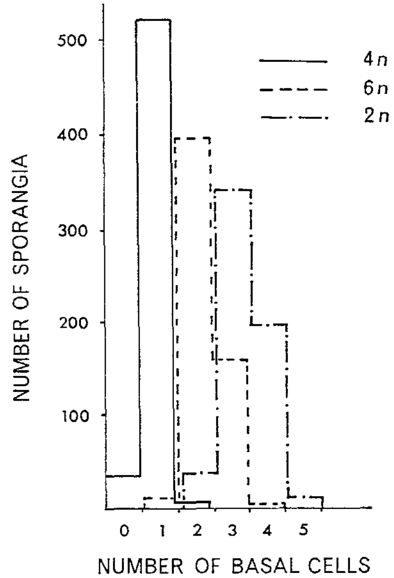


FIGURE 4. Histograms of the number of basal cells of the sporangium in the three species of *Polypodium*.

flattened annulus has already been mentioned. This can only be observed when completely dehisced sporangia are subjected to moderate finger pressure between two glass slides. Many of the annuli will then be flattened, i.e. spread out to their full length. The indurated cells of *P. australe* are shorter (mean from ten annuli 21–26$\mu$m) and broader (mean of five annuli 81–100$\mu$m), thus giving the annulus a distinctive, contracted appearance compared with that of *P. interjectum*. In the latter the indurated cells are longer (mean from ten annuli 28–35$\mu$m) and the annulus narrower (mean of five annuli 76–86$\mu$m) (Benoit 1966, Roberts 1966). This difference can be appreciated by a glance at the photomicrographs of the flattened annuli (Plate 1b and e).

Lastly, the three species differ in the colour of the annulus, a character to which Benoit (1966) first drew attention as the best non-microscopic character for separating *P. vulgare* ('red-brown') from *P. interjectum* ('pale golden brown'). In *P. australe* the colour of the annulus, seen under the microscope, is usually bright yellow and shows little variation. In *P. interjectum*, on the other hand, it varies considerably, not only from one plant to another, but even among the sporangia on the same plant. Usually a pale buff or golden brown (when it hardly differs in colour from the rest of the sporangium), it varies to pale or bright yellow, and occasionally to a deeper orange-yellow. This variability is perhaps the most striking feature of annulus colour in the hexaploid and is in itself often a useful diagnostic character. Thus, despite its variability in the hexaploid, annulus colour can be of great value in separating the diploid from the hexaploid. In *P. vulgare*, as Benoit (1966) has indicated, the annulus is a dark reddish-brown, which contrasts so sharply with the rest of the sporangium that it can be seen clearly as a dark line even with a $\times 10$ lens.

## PARAPHYSES

Martens (1950) first drew attention to the value of the branched paraphyses as a diagnostic character of *P. australe*. Shivas (1961) also found paraphyses of the type illustrated by Martens in all the plants which she determined cytologically as diploid. Lenski (1962, 1964), however, stated that paraphyses were present in 35 out of 50 hexaploid plants and even in 10 out of 67 tetraploid plants examined by her. Meinders-Groeneveld & Segal (1967) have also reported paraphyses in the hexaploid in the Netherlands, but failed to find them in the tetraploid.

In view of these conflicting reports, a careful search was made among the sporangia of the cytologically attested plants of *P. interjectum*. These were supplemented by a further eighty plants not determined cytologically, making a total of one hundred. No paraphyses similar to those of *P. australe* were found in any of them. In many instances (38 of the 100 plants) the minute, glandular hairs which occur scattered on the lower surface of the frond in all the European species of *Polypodium*, were found either among the sporangia or close to the base of the sorus. In rare instances they were even found attached to the base of the sporangium stalk. A search of the sori of 100 plants of *P. vulgare* gave a similar result. However, these organs are quite distinct from the paraphyses of *P. australe*. They are much smaller—usually only 3 or 4 cells long—with their glandular, inflated, terminal cells mostly coloured a dark reddish-brown, and as long as the other cells: from 45 to 80$\mu$m. They are, in fact, identical with the illustrations of the 'paraphyses' of *P. interjectum* given by Lenski (1964). In the paraphyses of *P. australe* the terminal cells are invariably much shorter than those at the base, which are mostly from 100$\mu$m to 240$\mu$m long. In their illustrations of the paraphyses of *P. interjectum*, Meinders-Groeneveld & Segal (1967) appear to show both kinds: a few (Fig. 5a-c) are somewhat similar to those of *P. australe*; the others (Fig. 5d-i) are exactly like the small, glandular hairs described above. It is not clear what criterion was used by these

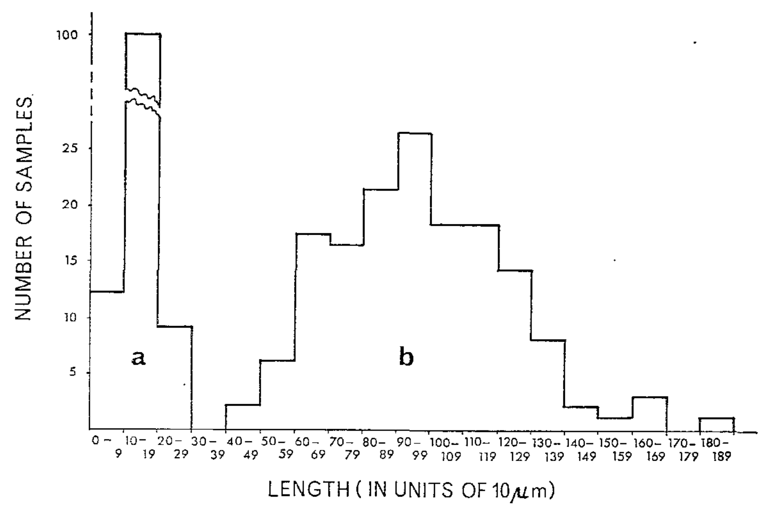


FIGURE 5. Histograms, in 10$\mu$m units, of the length of (a) the glandular hairs of *P. interjectum*, and (b) the paraphyses of *P. australe*.

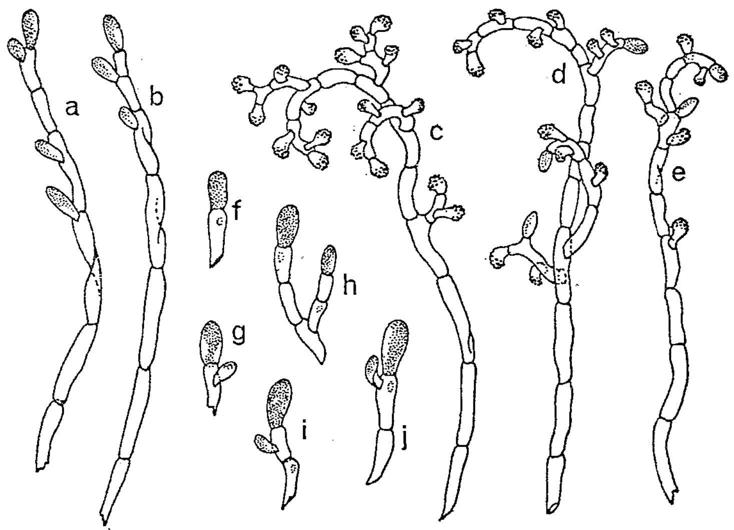


FIGURE 6. Paraphyses of the hybrid *P. australe* × *interjectum* (a—b); of *P. australe* (c—e); the glandular hairs ('paraphyses') of *P. interjectum* (f—j). All to the same scale.

authors to identify the plants in which they found the larger, branched paraphyses. If they relied solely on the number of annulus cells, it would now appear desirable that these plants should be examined cytologically.

The large difference in length between the glandular hairs of *P. interjectum* and the paraphyses of *P. australe* is shown in the histograms (Fig. 5), and the difference in their morphology in the figures (Fig. 6) drawn to the same scale. The mean length of the paraphyses of *P. australe* (970 $\mu$m) is nearly seven times that of the glandular hairs of *P. interjectum* (140 $\mu$m). Because of their large size and very distinctive morphology, together with the relative ease with which they can be found, the paraphyses of *P. australe* remain its best single diagnostic character, as was originally claimed by Martens (1950).

## FROND SHAPE

The shape of the frond in *P. australe* is described as ovate to triangular-ovate, with narrow, acute and usually dentate pinnae. Shivas (1961) states that the longest pair of pinnae is the second or third from the base.

However, both the diploid and hexaploid are extremely variable in frond shape. The ratio of length to breadth of the blade varies from 1·2 to 2·4 (mean 1·6) in the diploid plants, and from 1·5 to 3·2 (mean 2·1) in the hexaploid plants. The ratio of length to breadth of the longest pinna on each frond was found to vary from 3·0 to 5·9 in the diploid, and from 2·3 to 4·3 in the hexaploid. In both these characters there is thus a large overlap between these two species. The variation in the ratio of length to breadth of the blade seems to be partly genetic and partly environmental. Poorly grown specimens generally have lower values of this ratio in both species. Thus this character is of least help with the plants most likely to be confused.

Pinna serrations in the diploid plants also vary widely, as Shivas (1961) has already observed. They are entirely lacking in two of the twenty-eight plants in Table 1, and so slight as to be scarcely noticeable in another three of them. The well-marked serrations usually shown in illustrations of *P. australe* (e.g. Hyde & Wade 1962) occur in only eight of these plants.

A frond character of the diploid which is often very striking in the field is the tendency for the lowest pair or several pairs of pinnae to be inflexed (Manton 1950), often with the lowest pair crossing. But even this is entirely lacking in some plants. This characteristic remains constant in cultivation, suggesting that it is genetically controlled and not the result of environmental factors.

The silhouettes of fronds (Fig. 7), taken from six of the diploid plants, illustrate the range of variation in almost every detail of frond shape which occurs in this species.

The number of bifurcations of the secondary veins has been stated to be

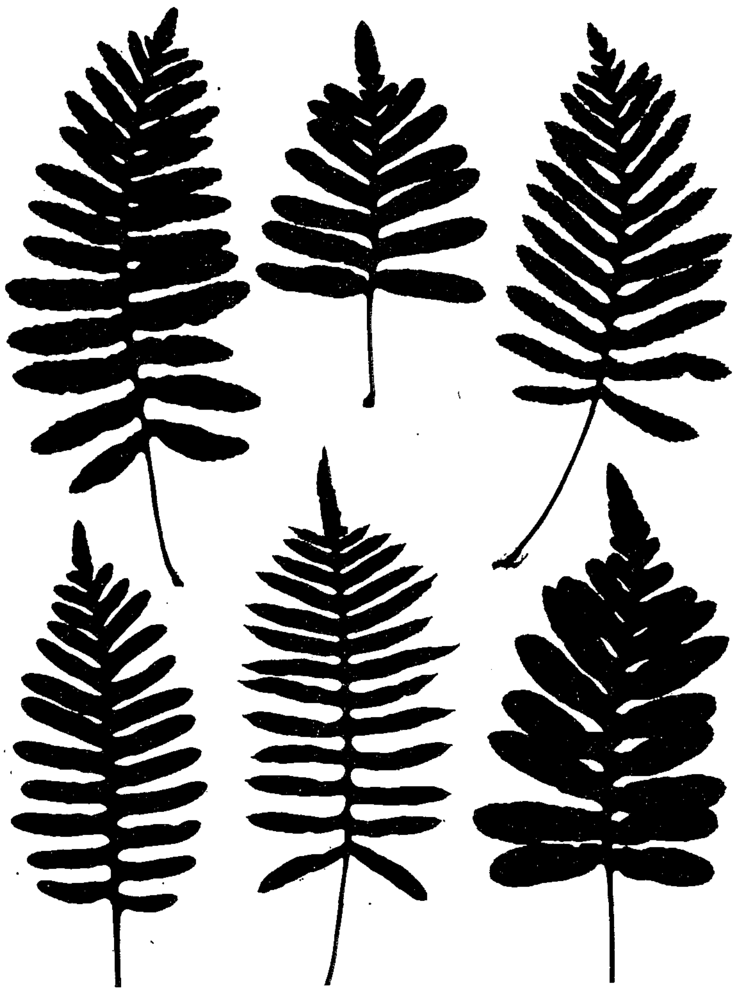

FIGURE 7. Silhouettes of fronds from six of the plants of *P. australe* listed in Table 1.

taxonomically useful, for example, by Rothmaler & Schneider (1962). But the variation in this character in both the diploid and the hexaploid plants is so great that it is evidently of very little use for separating these two species.

## THE RHIZOME SCALES

The length and shape of the rhizome scales have been studied by Rothmaler & Schneider (1962). According to them the scales are 3–7mm long in *P. vulgare*, 3–6mm long in *P. interjectum*, and 5–11mm long in *P. australe*. Valentine (1964) cites this as a key character with only slight modification: 3–6mm in both *P. vulgare* and *P. interjectum*, and 5–11mm in *P. australe*.

Measurements of rhizome scales were made from the twenty plants of *P. interjectum* determined cytologically and from the plants of *P. australe* listed in Table 1. All measurements were made under the microscope, the width being taken from the widest part of the scale near its base. The results are shown in the scatter diagram (Fig. 8), but for convenience the measurements of scales less than 4·5 mm long have been omitted. The ranges of scale length found were: 3·5–11 mm for *P. interjectum*, 5–16 mm for *P. australe*. Only twenty-five scales of *P. vulgare* were measured. In these the length was 3–6 mm, which agrees with the values given by the other authors; but the ranges found for *P. interjectum* and *P. australe* differ a good deal from their results, especially in the case of the hexaploid. The overlap is so much greater than they have indicated that the taxonomic value of scale length on its own is considerably reduced.

On the other hand the shape of the rhizome scales appears to provide a useful accessory diagnostic character, although it is not as absolute as the illustration given by Rothmaler & Schneider (1962) indicates. In *P. australe* the scales are mostly linear-lanceolate. In *P. interjectum* they are often rather abruptly narrowed just above the dilated and relatively broader base, as can be seen in Plate 2. The difference between the two species in the ratio of the length to the width of the scales is evident from Fig. 8.

Two other differences between the rhizome scales of the diploid and hexaploid were noticed. Those of *P. australe* are thinner and have appreciably shorter cells than those of *P. interjectum*. The means of the lengths of ten cells (measured near the middle of the scale) vary from 165$\mu$m to 200$\mu$m in *P. australe*, from 230$\mu$m to 320$\mu$m in *P. interjectum*. These results suggest that it may be possible to separate the two species on this character alone, but further observations are needed to verify this.

## HYBRIDS

Wild hybrids of *P. australe* with both *P. vulgare* and *P. interjectum* have been reported by Manton (1950, 1961) and Shivas (1961), and confirmed cytologically. Perring & Sell (1967) state that these hybrids have also been recognized on morphological grounds. On several occasions during the present study plants have been collected which on frond characters were suspected to be hybrids of *P. australe* with one of the other species. However, cytological examination has shown them to be only *P. australe*. Three of them are among those listed in Table 1.

So far only one plant has been found which appears to be a hybrid involving *P. australe*. This is very conspicuous in the field because it forms a large, leafy mass in a locality (Lligwy Wood, Anglesey) where both *P. australe* and *P. interjectum* occur in abundance. Its robust growth, vigorous vegetative spread and large fronds (many of them over 60 cm long) suggest hybrid vigour. In frond shape it more closely resembles *P. interjectum*, but the blade is thinner and its colour lighter than is usual in the hexaploid. Microscopic examination showed its spores to be highly sterile, and the few (usually 3 or 4) fully-developed spores present in some sporangia are uneven in shape and size. The mean number of annulus cells is 7 with a total range of 4–9. Paraphyses as long as those of *P. australe* are present (Fig. 6), but are not so branched nor as abundant as in the diploid. This is contrary to the view expressed by Shivas (1961) that paraphyses are absent from hybrids of *P. australe*.

Meiosis in this plant was examined on several occasions. It was found to be highly irregular, but only approximate counts were obtained. These showed about 32–36 bivalents and around 70 univalents. They agree fairly closely with the counts of 37 bivalents and 74 univalents found during meiosis in the tetraploid hybrid by Shivas (1961). Although further cytological examination of this plant is desirable, the evidence certainly suggests that its parentage is that inferred from its morphology.

## DISCUSSION

The suggestion first made by Futo (1905) that *P. australe* (as *P. vulgare* var. *serratum* Willd.) could be identified by the small number of annulus cells (mostly 6) was reaffirmed by Manton (1950) and by Shivas (1961). Martens (1950), however, found much higher numbers of annulus cells—from 4 to 20—in plants which he identified as var. *serratum* by the large, branched paraphyses among their sporangia; and similar values were obtained by Roberts (1966). Three plants determined as diploid from root-tip counts by Lenski (1964) were found to have correspondingly high numbers of annulus cells: from 4 to 17; and a study of herbarium material by Fernandes (1968) has given equally high counts.

Probably because both Manton (1950) and Shivas (1961) had made their observations on cytologically determined material, most recent Flora writers have accepted their evaluation of this character. For example, Hyde & Wade (1962), Valentine (1964) and Warburg (1962) all cite a range of 4–7 annulus cells for *P. australe*. Perring & Sell (1968) have also used this character for separating the three European taxa. Furthermore, these authors state that specimens with an 'intermediate' number of annulus cells were also found to have a number of aborted and empty spores. In view of the results presented here, it is clear that most of the 'intermediates' referred to by Perring & Sell (1967, 1968) are not hybrids involving *P. australe*, as these authors seem to have assumed. Some degree of lowered spore fertility can often be observed in plants of all three species of *Polypodium*, and is due to factors other than hybridity—probably environmental conditions during the early stages of spore formation. However, such plants usually have some of their sporangia with a full complement of good spores. The symptoms of spore sterility in hybrids have been clearly described by both Manton (1961) and Shivas (1961). Not only are the great majority of the spores aborted, but the few full spores produced are highly irregular in shape and size.

In view of the frequent occurrence of the pentaploid hybrid, *P. vulgare* ×

*interjectum*, the apparent rarity of hybrids involving *P. australe* is rather unexpected. Yet such appears to be the case. The diploid species reaches the northern limit of its distribution in the British Isles, where it has been recorded as far north as Westmorland (near Lowood, J. Sidebotham, July, 1846, **MANCH**), Cringlebarrow in Lancashire (**LANC**) and on Ingleborough in Yorkshire (Manton 1950). In Wales it occurs in small, isolated patches, most of which grow on mortared walls, limestone, or other rocks with a high base content. Only in rare instances has it been found on an apparently base-deficient substratum or as an epiphyte on trees. This is in agreement with Manton's observations on its occurrence in limestone habitats in northern Europe. Its sporadic distribution in Wales is in marked contrast to that of the other two species, both of which are widely distributed and often abundant. For the survival of such small populations of *P. australe* the formation of hybrids will, presumably, be disadvantageous. They will tend to compete with the diploid parent in a habitat which is already severely restricted. Under such conditions any genetic barrier to hybridization would tend to be strengthened.

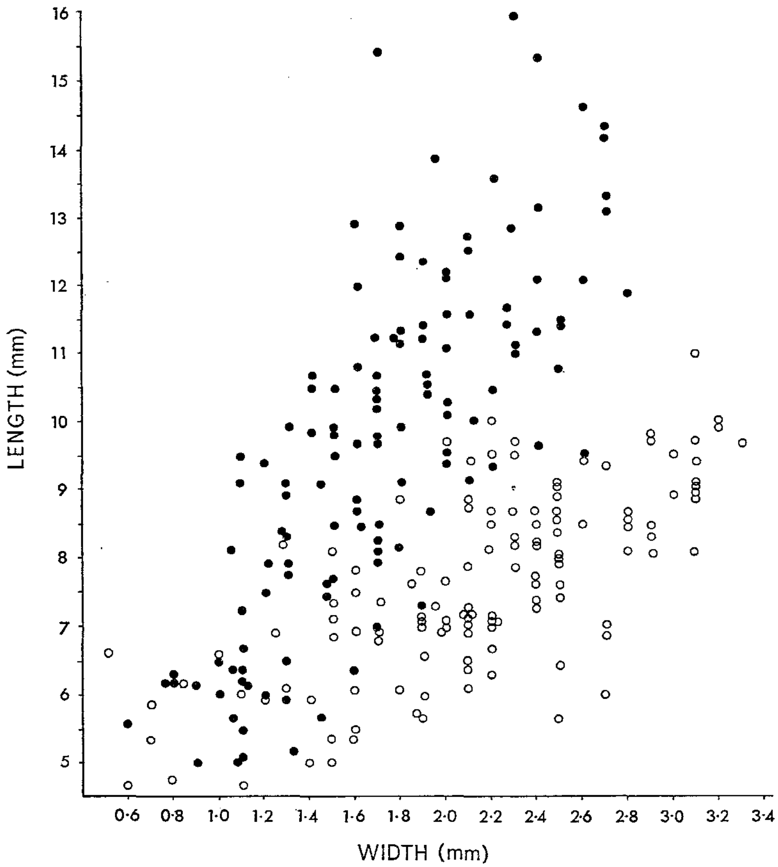


FIGURE 8. Scatter diagram of the length and width of the rhizome scales of *P. australe* (solid dots) and of *P. interjectum* (open dots).

Perring & Sell (1967) have reduced the three cytotypes to the rank of subspecies on the grounds that the presence of hybrids between them makes field identification impossible. If ease of identification in the field is accepted as the criterion of a good species, then this view is to a great extent justified, for the large overlap between *P. australe* and *P. interjectum* makes it impossible in many instances to separate them on frond characters. Nevertheless there are several microscopic characters which enable *P. australe* to be identified with certainty. From *P. interjectum* it can be separated by the large, distinctive paraphyses, as well as by the colour and appearance of the flattened annulus, and the overall difference in the shape of the rhizome scales. From *P. vulgare* it can always be separated by the number of basal cells of the sporangium; but confusion with this species is seldom likely in any case.

In spite of the much greater overlap between *P. australe* and *P. interjectum* in some of the characters hitherto used to separate them, Shivas's taxonomic conclusions regarding the diploid are, in my opinion, not affected. The fact remains that *P. australe* also differs from the other European taxa in chromosome number, in its ecological requirements and in its geographical range. Moreover, Shivas (1961) has shown that it is not closely related to *P. vulgare* sensu stricto. To place it as a subspecies of *P. vulgare* is to ignore the cytogenetic evidence. While, therefore, there is no sound biological reason why the diploid should be reduced to the rank of subspecies, this must remain, like the species concept itself, a matter of opinion.

## ACKNOWLEDGMENTS

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PLATE 2. Rhizome scales of (a) *P. australe* from the Little Orme, Caerns.; (b) *P. interjectum* from Beaumaris, Anglesey. Both at the same magnification.

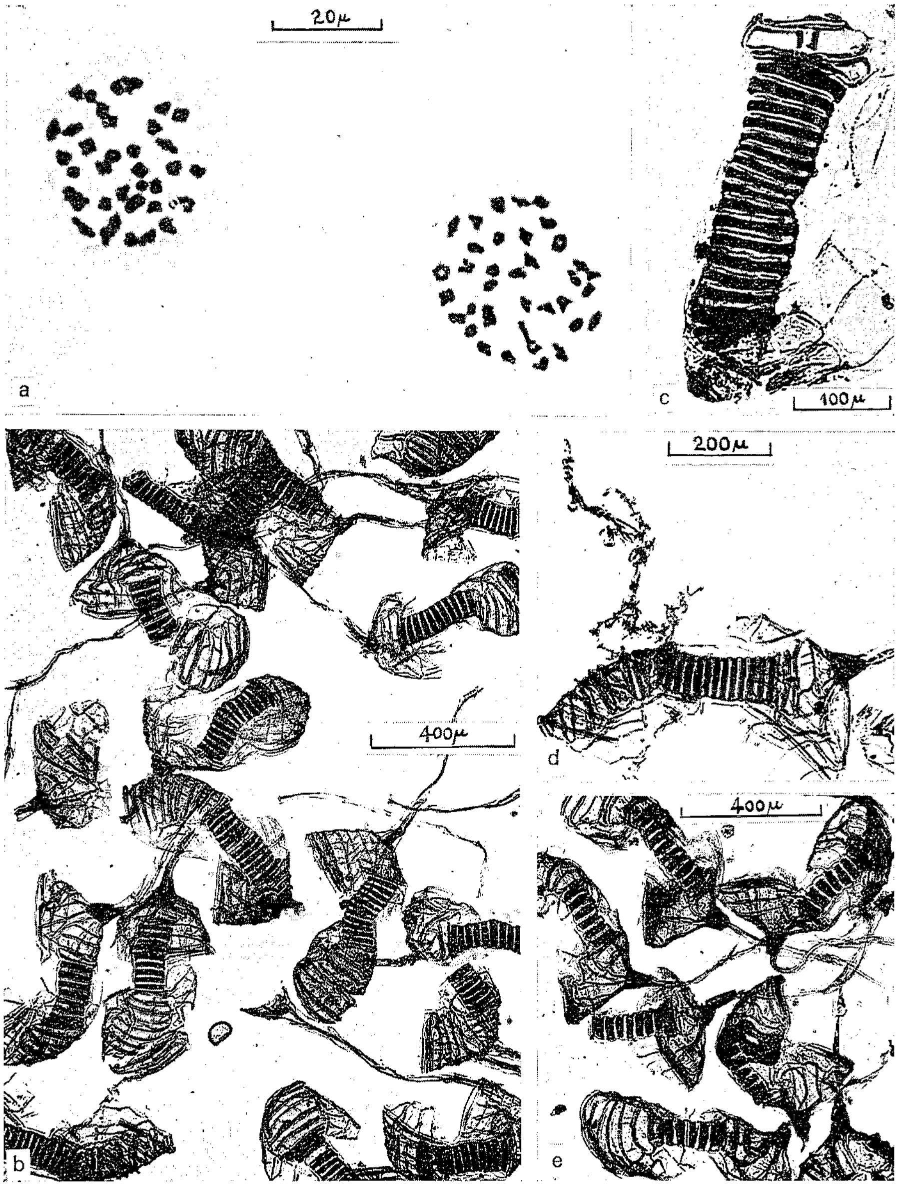


PLATE 1. (a) Meiotic chromosomes in two spore-mother-cells of *P. australe* from Llanddulas, Denbs., showing 37 bivalents. (b) Flattened annuli from the same plant as (a), with 6-12 indurated cells (appearing dark). (c) Flattened annulus of *P. australe* from the Little Orme, Caerns., with 16 indurated cells. (d) A single annulus from the same sample as (b), with 12 indurated cells and showing one of the characteristic paraphyses. (e) Flattened annuli of *P. interjectum* from Anglesey, shown at the same magnification as (b), for comparison.