A NEW TYPE OF APOGAMY IN FERNS

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Summary

Studies on apogamous members of the *Asplenium aethiopicum* complex in Africa have shown a marked departure of cytological behaviour from that previously known in apogamous ferns. The sporangial development is characterized by all sporangia producing sixteen spore mother cells each showing complete asynapsis at diakinesis with either 288 or 330–357 chromosomes. The first meiotic division ends in a restitution nucleus which then divides regularly to produce diads of diplospores. This abbreviated meiosis is compared with the cytological phenomena accompanying apogamy in other ferns and with a similar division process known from apomictic Angiosperms. Evidence is presented from the literature which indicates that a similar abbreviated meiosis may accompany apogamy in the Hymenophyllaceae. Little new evidence on either the causal aspect of apogamy or the possible origin of the apogamous forms within the *A. aethiopicum* complex can be adduced at present.

Introduction

The known cytological phenomena accompanying apogamy in ferns were documented by Döpp (1932) and Manton (1950). Further studies (Manton and Sledge, 1954; Mehra and Bir, 1960; Manton, 1961) revealed almost identical phenomena in all cases and it seemed likely that apogamy in ferns would always be accompanied by a similar sporangial development. Recent work on apogamous forms of *Asplenium aethiopicum* (Burm) Bech. from Africa however, has revealed a marked departure from the cytological behaviour previously known. This new type of apogamous development is the subject of the present paper.

Material and methods

Within the *Asplenium aethiopicum* complex, apogamous reproduction was first detected in a plant from East Africa (first on Table 1), already in cultivation at Leeds when the investigation began. Further live material was obtained as a result of personal field work in South Africa between July 1960 and June 1961. Collectors in southern Africa supplied other plants whilst the author was in South Africa, and one plant (Mitchell 88) was already in cultivation in the National Botanical Garden at Kirstenbosch. Two plants, one of which is still too young to provide cytological data, have been raised from spores taken from herbarium sheets in the national herbaria in London. The details of source and locality of the eleven plants available for study are given in Table 1.

The cytological and photographic methods employed are now standard and may be found in Manton (1950). Spores were mounted in gum chloral and samples of fifty were measured using a calibrated micrometer eyepiece and a $\times 40$ objective.

RESULTS

Prothallial culture and development

The methods of culture used were outlined by Walker (1955). For most reliable germination the pots were kept in a closed frame at a temperature of 55–65° F, and under these conditions spores usually germinated in 15–20 days from sowing. Subsequent growth of the prothalli was slow and apogamous outgrowths producing the first leaves were not usually evident until $4\frac{1}{2}$–$5\frac{1}{2}$ months had elapsed from the date of sowing. The first leaves were smaller but of a morphologically more advanced character than those of the sexual sporelings, a feature noted for many apogamous ferns.

Table 1. *Details of source, locality and cytological data for the live material of apogamous* A. aethiopicum

Collector	Locality	Chromosome No.	Ploidy	Sectioned
Curle & Schelpe 1 (live plant)	Dessie Rd., Nr. Addis Ababa, Ethiopia	2n = *c.* 288	8×	+
Nash 183 (spores)	Musitu, Abercon Dist., N. Rhodesia	2n = *c.* 288	8×	+
Mitchell 88 (live plant)	Dombashawa, Nr. Salisbury, S. Rhodesia	2n = 288	8×	–
Mitchell 479 (spores)	Chinamora Reserve, Nr. Salisbury, S. Rhodesia			
Williams U.M.T. 1A (live plant)	Murakwa's Hill, Umtali, S. Rhodesia	2n = 288	8×	–
Williams U.M.T. 1B (live plant)	Murakwa's Hill, Umtali, S. Rhodesia	2n = *c.* 288	8×	–
Braithwaite 222 (live plant)	Pilgrims Rest, Transvaal, S. Africa.	2n = *c.* 288	8×	+
Braithwaite 228 (live plant)	Pilgrims Rest, Transvaal, S. Africa	2n = 288	8×	+
Nat. Herb. Pretoria 'Garst C' (live plant)	Garstfontein, Pretoria, S. Africa	2n = 288	8×	–
Braithwaite 103A (live plant)	Nr. Conway, Cape, S. Africa	2n = *c.* 330–357	10×	+
Braithwaite 103B (live plant)	Nr. Conway, Cape, S. Africa	2n = *c.* 346	10×	–

The prothalli cultured so far have shown very poor antheridial production at $2\frac{1}{2}$–3 months after sowing. On immersing these prothalli in water to obtain swimming spermatozoids for hybridization experiments, only occasional very sluggish spermatozoids have been observed. This behaviour contrasts strongly with the situation in other apogamous ferns where prothalli produce abundant antheridia which readily yield swimming spermatozoids (Manton, 1950; Walker, 1958). Although the paucity of antheridia in my material may be caused by unsuitable horticultural procedures, it could also be an inherent characteristic of the prothalli. The lack of active spermatozoids has made it impossible to incorporate any of the apogamous plants into hybrid combinations with sexual members of the group.

In common with other apogamous ferns, the prothalli often show a few archegonial structures near, or on the site of, the developing apogamous bud; however, it is doubtful whether these can ever be functional. The bud usually appears on the underside of the prothallial cushion but may arise sometimes from the apical region. The development of the bud is often preceded by the appearance, on the site, of small scales similar to those covering the rhizome of the mature plant.

The sporelings grow slowly and may require as long as 2 years before fronds bear sporangia. A population has been raised from the prothallial culture of Nash 183 and the

mature plants show the expected morphological uniformity following an apogamous mode of reproduction, although the majority of these plants have not been cytologically examined.

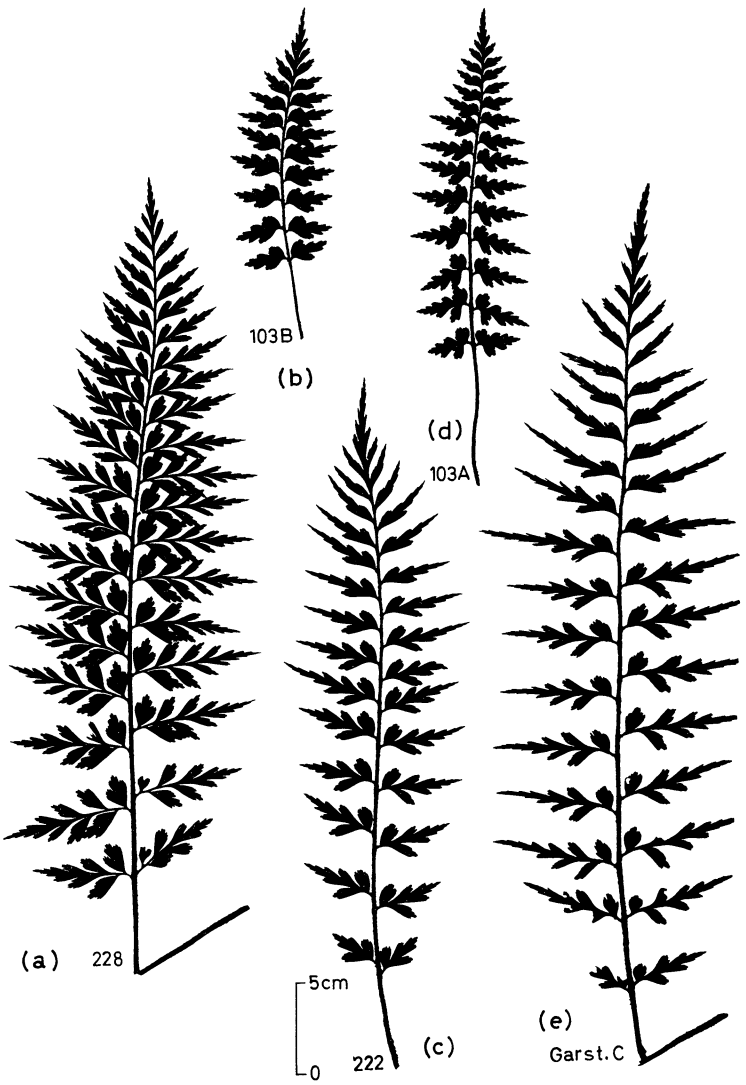

Fig. 1. Forms of apogamous *Asplenium aethiopicum* from South Africa. Silhouettes of fresh fronds taken from plants of comparable ages in cultivation. For explanation of the collector's numbers accompanying each silhouette see Table 1, $\times\frac{1}{4}$.

Morphology of the plants

The sexual and apogamous members of the group exhibit a complicated pattern of variation which has proved difficult to treat taxonomically and the practice of including the whole range under *Asplenium aethiopicum* (Burm) Bech. is being followed here with one exception. A detailed morphological survey of even the apogamous forms would be an unnecessary encumbrance in a primarily cytological paper. It is, therefore, intended

to deal with morphology only to the extent of differentiating the apogamous from the sexual representatives of this group and then to illustrate the range of variation within the apogamous forms.

Examples of fronds from apogamous plants are assembled in Figs. 1 and 2. Frond characters alone are, however, insufficient to distinguish apogamous from sexual individuals. This can be more effectively done by utilizing spore characters such as size,

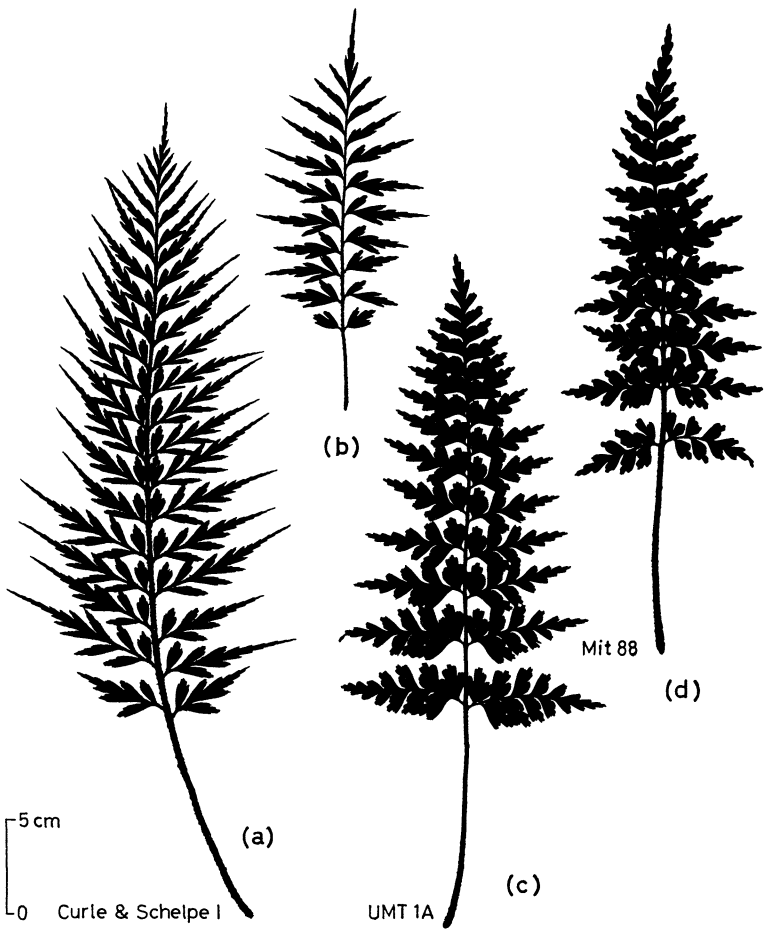

Fig. 2. Forms of apogamous *Asplenium aethiopicum* from Ethiopia (a and b) and Southern Rhodesia (c and d): (a) and (b) are fronds from the same plant. Silhouettes of fresh fronds taken from plants of comparable ages in cultivation. For explanation of the collector's numbers accompanying each silhouette see Table 1, $\times\frac{1}{4}$.

shape, ornamentation and number per sporangium. The most useful of these characters is that of spore shape, the spores of apogamous plants being more spherical than the plano-convex spores of the sexual plants. With a low power microscope the difference is usually apparent at a glance (Plate 20, Nos. 15 and 16) and it also emerges clearly if the character is expressed as a simple length–breadth ratio of the spore. The spores are large and usually possess a more heavily winged perispore than their sexual counterparts. A scatter diagram is shown in Fig. 3 utilizing spore size and shape to separate sexual and

apogamous material from S. Africa. Only occasionally is it necessary to resort to the counting of spores in sporangia to determine the mode of reproduction.

The exceptional plant referred to above (Table 1, Curle and Schelpe 1) is the only one for which an alternative name exists in the literature. This plant (Figs. 2a and 2b) agrees closely with the type specimen of *A. filare* (Forsk.) Alston in its spores, in the long attenuated pinnae and in their degree of dissection. Forskal's specimen came from Arabia and is in the British Museum (Natural History). The chief features which may be used to distinguish *A. filare* from *A. aethiopicum* are the long filiform apices of the

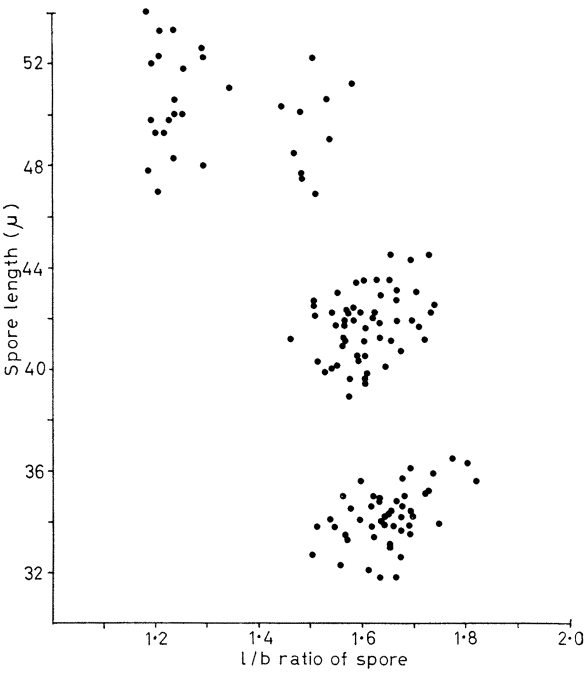

Fig. 3. Scatter diagram compiled from herbarium material of *Asplenium aethiopicum* from South Africa. Each dot represents one herbarium specimen. The group showing the lowest l/b ratio (top left) are the apogamous forms, the three remaining groups corresponding to the sexual tetraploid, octoploid and dodecaploid cytotypes. The l/b ratio was calculated from the means of the length and breadth of fifty spores for each specimen.

pinnae and sharply decrescent apex of the frond. These characters are, however, shown to a lesser extent by some of the South African apogamous plants (Figs. 1c and 1e) although the latter have never been included in *A. filare*. The usefulness of retaining *A. filare* as a specific concept will not be discussed here but it is perhaps important to mention it since this is the only specific name so far encountered other than *A. aethiopicum* which could be applied to any of the live apogamous material.

Distribution and ecology

The apogamous forms of *A. aethiopicum* in Africa are scattered over a large part of the continent covering approximately the same geographical area as sexual members of the group. The distribution is illustrated in Fig. 4. The localities of herbarium specimens show a range in altitude from just over 4000 ft in South Africa to 7000–8000 ft in East

Africa, so that the distribution pattern is partially determined by the relief features of the continent.

In southern Africa the apogamous plants are not generally so closely associated with the forest areas as are some of the sexual plants, but tend to occupy slightly drier areas, usually on the central plateau. A good illustration of this feature is seen in the Transvaal of South Africa where the apogamous plants show a spread on to the plateau from the rim of the forested escarpment formed by the northern extension of the Drakensberg. Here they are found on rocky outcrops and in small wooded *kloofs* or ravines of the *high*

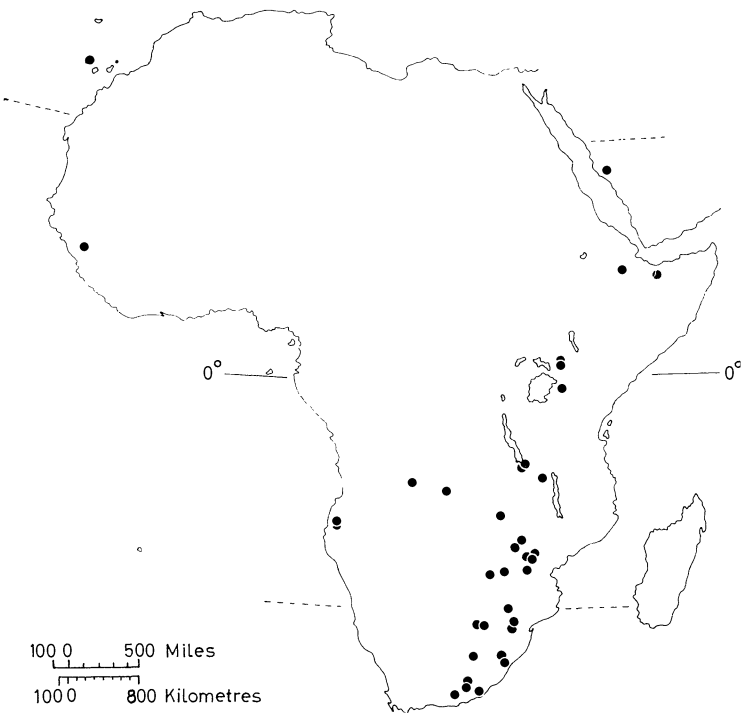

Fig. 4. Distribution map of apogamous forms of *Asplenium aethiopicum* in Africa compiled from herbarium material and fieldwork.

veldt. Although at times locally frequent, the apogamous material was never seen in large quantities and sometimes a population consisted of only a few solitary individuals.

The collections from the northern half of Africa and Angola are rather sparse, particularly from the more remote and inaccessible regions, so that data available for these areas are probably far from complete.

Chromosome numbers

Cytological examination of the plant described above as *A. filare* revealed complete failure of pairing at meiosis, squash preparations showing approximately 288 univalents at diakinesis or first meiotic metaphase. The frond from which these preparations were obtained went on to produce good, viable spores. Further preparations from subsequent fronds again gave cells with only univalents. Similar behaviour was demonstrated for all the apogamous plants examined (see Table 1) and this complete failure of chromosome pairing coupled with good spore production were clearly inherent features of these ferns.

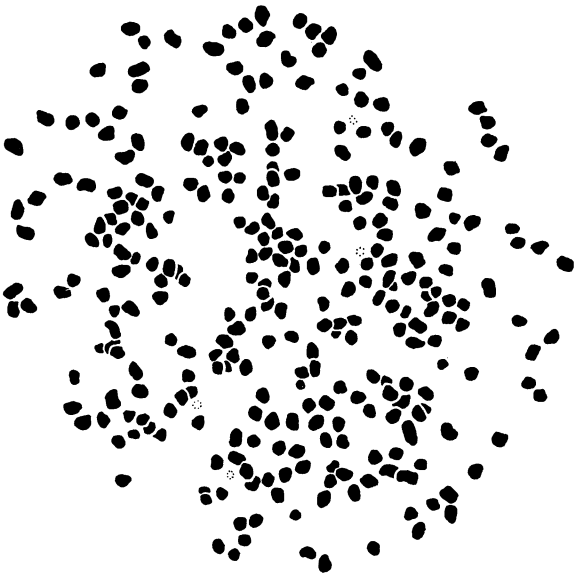

Fig. 5. Explanatory diagram for Plate 20, No. 11, showing 288 univalents, ×1500.

Fig. 6. A diagram for a cell at diakinesis from Braithwaite 228, not otherwise illustrated, showing 288 univalents, ×1500.

The chromosome number and grade of ploidy of each plant listed, are included in Table 1 except for the one specimen (Mitchell 479) which is still too young for cytological analysis. Cells from Mitchell 88 and Braithwaite 103A are shown in Plate 20, Nos. 11 and 12, respectively. An explanatory diagram for No. 11 is reproduced in Fig. 5 and a diagram for a cell, not otherwise illustrated, from Braithwaite 228 is reproduced in Fig. 6. From these it will perhaps be clear that in spite of very high numbers the absence of pairs permits counts to be made to a high degree of accuracy in most cases. Slight uncertainty caused by the overlapping of a few individual chromosomes does not prevent effective establishment of ploidy, but where a recognized element of uncertainty exists, although in no case greater than ±eight chromosomes, an approximation sign (*c.*) is put before the count in the table.

Chromosome numbers already established for sexual members of the group in Africa and Ceylon (Manton and Sledge, 1954; Manton, 1959) have shown that they fall into a high polyploid series based on n = 72. Since the monoploid chromosome number in *Asplenium* is thirty-six (Manton, 1950) the numbers actually represented by *A. aethiopicum* in Africa are tetraploid (n = 72), octoploid (n = 144) and dodecaploid (n = 216). From this it seems probable that the majority of plants listed in Table 1 will have had exactly 288 somatic chromosomes (i.e. the normal octoploid number). Slight deviations would however be difficult to detect and cannot be entirely discounted although they are certainly not great. Two plants from one locality in South Africa (Braithwaite 103A and 103B) gave considerably higher chromosome counts and have been provisionally designated as decaploid.

Sporangial development

In a large number of squash preparations of sporangia involving all the adult plants listed in Table 1, spore mother cells at diakinesis were invariably characterized by lack of any pairing of the chromosomes. The inevitable conclusion that these mother cells must be producing good spores raised the interesting problem of how this could be achieved, regular meiosis in such cells being impossible. Another notable feature of the squash preparations was the almost complete absence of tetrads, either good or abortive; nevertheless, good spores were being produced, which often appeared to be in diads. To confirm the diad condition of the spores and to resolve the problem of their formation, sporangia were sectioned.

The sequence of stages in the sporangia was reconstructed by combining the information from sections with that from squash preparations. Not all the plants have been sectioned but the agreement between the five specimens examined in this way is so close that further sectioning seemed unnecessary.

The sections showed immediately that all sporangia contained sixteen spore mother cells. The mother cells arise in the usual way following four successive mitotic cleavages of the archesporium. Each mother cell then enlarges and rounds up, while the inner tapetal layer becomes plasmodial, flowing into the interstices between the mother cells. During these processes the sporangium as a whole enlarges considerably.

The onset of meiosis is marked by the nuclear changes normally associated with meiotic prophase (Plate 18, No. 1). These lead to a very characteristic diakinesis (Plate 18, No. 2; Plate 19, No. 7) in which, however, only univalents are present (Plate 20, Nos. 11 and 12). The nuclear membrane then breaks down and the spindle for the first meiotic division appears. The univalents, now highly contracted, begin to congregate in the equatorial region of the spindle but many cells show a considerable scatter of

univalents throughout the spindle area (Plate 18, No. 3; Plate 19, No. 8). This imparts an exceedingly irregular appearance to these metaphase figures, which may be best interpreted as being due to the slow movement of the scattered univalents towards the equator rather than to irregular movements of the univalents towards the poles, since eventually all the univalents come to lie on the equatorial region of the spindle (Plate 19, No. 9). The chromosomes then lose their identity and restitution nuclei are formed (Plate 18, No. 4; Plate 19, No. 10).

The restitution nuclei take their shape from the preceding division figure and form a flat plate in the equatorial plane of the spindle. In side view they are very distinctive, appearing as elongated nuclei, often somewhat curved or lobed, lying across the centre of each mother cell (Plate 19, No. 10). The formation of these nuclei is precise, the omission of any chromosome material being rare.

After a period of rest of unknown duration the restitution nuclei undergo what at first sight could be mistaken for a simple mitotic division. Except for the presence of only one spindle the chromosome behaviour is however that of a typical second meiotic division. The metaphase chromosomes are longer and different in shape from those at the first meiotic division being manifestly double (Plate 20, Nos. 13 and 13a). They form a very regular metaphase plate (Plate 18, No. 5) and at anaphase the constituent chromatids move to opposite poles of the spindle, forming two nuclei at telophase. The cytoplasm finally cleaves to produce diads (Plate 18, No. 6; Plate 20, No. 14).

Every sporangium is therefore capable of producing thirty-two spores, each containing the same number of chromosomes as appeared in the spore mother cell at diakinesis. Thus the inherent requirement of apogamous ferns for an unreduced chromosome complement in the spore, to compensate for the absence of sexual reproduction in the prothallus is satisfied.

Counts of spores in sporangia indicate that the theoretical maximum of thirty-two spores in each is not always attained, 'good' sporangia yielding anything from twenty-three to thirty-two spores and occasionally less. This may be explained by a residual tendency for the mother cells to cleave into triads or tetrads at the end of the division. When these cytoplasmic activities interfere with one or both of the telophase nuclei the resulting spores will be abortive. Often these abnormal cleavages result in a diad with two small portions of cytoplasm cut off on either side without nuclear material. The latter probably do not seriously affect the viability or appearance of the mature spores.

A proportion of sporangia abort completely in both wild and cultivated plants. The number of such sporangia is usually low but can rise considerably from time to time, particularly in cultivated plants. The extreme case of complete abortion of almost all the sporangia has been observed once in a plant which in a previous year had produced an abundance of good spores. Similar differences from frond to frond have been noted in herbarium specimens of wild gatherings. Much of this variation is probably attributable to the metabolic state of the plants at the time the different fronds are unfolding since in cultivation the abortion tends to increase when the plants are growing unsatisfactorily during our long summer days or when they are pot bound. The complete abortion of sporangia may occur at any stage during the meiotic process but is most evident in the later stages. In sections it is manifest by apparent degeneration of the mother cells or diads combined in some cases with the perpetuation of first division univalents. The abbreviated meiosis presumably requires a delicate metabolic balance within the sporangium which may be impossible to maintain for all sporangia particularly under unfavourable conditions.

DISCUSSION

There is evidence in the literature to suggest that cytological phenomena similar to those in *Asplenium aethiopicum* may be present in other apogamous ferns.

Complete absence of chromosome pairing at meiosis was reported by Manton and Sledge (1954) in two separate wild collections of *Hymenophyllum javanicum* Sprengel from Ceylon, both subsequently brought into cultivation at Kew. It could not be determined at that time whether the asynapsis was due to metabolic failure of pairing or whether this was an apogamous fern which did not show eight-celled sporangia at the time of fixation. The further possibility now exists that this fern was apogamous and had a meiotic process similar to that of *Asplenium aethiopicum*. Later, Mehra and Singh (1957) working with squash preparations of *Trichomanes insigne* v.d.B. forma β from the Darjeeling Himalayas, found complete asynapsis at diakinesis and they described how these asynaptic mother cells divided by an abbreviated meiosis to form diads. Spore counts from sporangia showed twenty-eight to thirty apparently good spores in each, but these authors were unable to record anything regarding germination. The chromosome number compared with that of the morphologically similar *T. insigne* v.d.B. forma α, possessing normal meiosis with thirty-six chromosome pairs, led them to suggest that forma β was an asynaptic triploid. The possibility that it was also apogamous was not considered. Bell (1960) working on *T. proliferum* Bl. from Gunong Poe, Sarawak, saw an asynaptic diakinesis with 108 univalents and again the sporangia contained thirty-two apparently well-filled spores. Because of the small amount of material available no further division stages were seen but it seemed likely that meiosis would have been similar to that in *T. insigne* v.d.B. forma β. Since the cytological behaviour of these two *Trichomanes* species would lead to an unreduced chromosome complement in the spores, Bell suggested that they could be apogamous, a mode of reproduction which would be necessary if the chromosome number were to remain stable. The evidence is, therefore, strongly indicative of cytological behaviour occurring in the Hymenophyllaceae similar to that accompanying apogamy in *Asplenium aethiopicum*.

Although perhaps uncommon among ferns, an abbreviated meiosis similar to that in *A. aethiopicum* has been known in apomictic flowering plants for a considerable time (Gustafsson, 1946, 1947). It has been observed in both the *Taraxacum* and *Antennaria* types of diplosporous embryo sac formation and in male meiosis of *Hieracium boreale* amongst others. Gustafsson refers to this type of meiosis as a 'restitution nucleus together with a pseudohomeotypic division' and it is usually preceded by complete asynapsis. In some of these examples meiosis may be further shortened to a pseudohomeotypic division when, instead of forming restitution nuclei, the univalents gather on the spindle and the constituent chromatids then separate, resulting in diads. The occurrence together of these division processes in the same plant probably shows a close interrelation of the two, which may be governed by growth disturbances causing differential delay of the division process. Although in apogamous *Asplenium aethiopicum* restitution nuclei have been seen in all material sectioned, this would not exclude completely the possibility that in some instances the division may proceed in a pseudohomeotypic manner without prior formation of restitution nuclei.

A more recent example was observed in the genus *Geum* (Gajewski, 1957) among artificial hybrids between sexual plants. In cells undergoing meiosis with some pairing of the chromosomes, restitution nuclei were formed as a result of retarded segregation of the univalents at the first division. This led to the production of diads and the percentage of cells behaving in this way was sometimes as high as 2%.

An interesting feature arising from a comparison of the abbreviated meiosis in the flowering plants and *Asplenium aethiopicum* is the different orientation of the restitution nucleus in relation to the spindle. In *Geum* it lies parallel to the polar axis whereas in the fern it is parallel to the equator. The orientation in *Geum* (where some chromosome pairing is present) is clearly controlled by the divided bivalents being at the poles at the time of restitution, and that in *Asplenium aethiopicum* by the fact that the polar regions are devoid of chromosomes, all the univalents eventually lying in the equatorial plane of the spindle. The diplosporous apomictic Angiosperms however, in spite of the absence of bivalents in most cases, show restitution nuclei orientated as in *Geum*. The difference in orientation, therefore, cannot be completely correlated with the presence or absence of bivalents.

There is no known case among ferns in which apogamy has been synthesized artificially by an act of hybridization between two sexual individuals although there is a good deal of indirect evidence for such an origin in many examples of apogamy of the usual type (cf. Manton, 1950, 1961). The situation is however different for the particular manifestations of apogamy described here. Complete asynapsis, so characteristic of the present case, is virtually unknown among a large number of hybrids both wild and artificially synthesized which have been studied among sexual members of the *Asplenium aethiopicum* complex. Such hybrids are often sterile showing the usual meiotic disturbances caused by irregular pairing, but pairing is never wholly absent no matter how many univalents may be present. This fact makes it somewhat improbable that the univalents in the apogamous specimens are unpaired solely on account of lack of homologous partners. It seems far more likely that pairing has been prevented by genetical factors suppressing the effects of chromosome homology. Genetically imposed asynapsis of this type could have arisen either directly by mutation or by a combination of genes through hybridization. A hybrid origin, as seems likely for other apogamous ferns, would therefore be possible for the *A. aethiopicum* apomicts although the evidence available at present regarding the most probable of the two alternative origins for asynapsis is inconclusive.

In two types of sporangial development now known in apogamous ferns the doubling of chromosomes required for the formation of a diplospore is achieved in both cases by means of restitution nuclei either before, or during, the meiotic process. These produce two very different types of meiotic appearance. On the one hand (Manton, 1950), meiosis is normal resulting in tetrads of diplospores. This occurs in a sporangium with eight mother cells following a restitution nucleus at the premeiotic mitosis of the archesporium, e.g. *Pteris cretica*, *Asplenium monanthes*, etc. On the other hand, a restitution nucleus affecting the first meiotic division in a sporangium with sixteen mother cells, results in an abbreviated meiotic process ending in diads as described above for *A. aethiopicum*. In both cases there are thirty-two spores per sporangium.

The uniform behaviour of each sporangium before meiosis in *A. aethiopicum*, where sixteen spore mother cells are always formed, contrasts strongly with the rather complex situation in apogamous ferns hitherto known. In the latter, three principal types of sporangia arise with four, eight and sixteen spore mother cells respectively. Only the eight-celled sporangia produce diplospores. Traces of cytoplasmic activity during the abortive telophase of the last archesporial division sometimes results in a fourth type of sporangium exhibiting partial or complete amitotic cleavages of the mother cells. These correspond in a general way with the abnormal cleavages sometimes encountered in *A. aethiopicum* as described on page 301. A tendency towards amitosis following a restitution

nucleus is thus present in both types of apogamy although it is manifested at correspondingly different places in the spore production process.

The nature of the other factors involved in the establishment of an apogamous life cycle are almost wholly obscure. On the one hand there is the apparently obligate sequence of diplospores and apogamously reproducing prothalli about which this study has provided no new causal evidence; on the other hand, there is the problem of the addition of a restitution nucleus to a developmental sequence normally without such a stage. The *A. aethiopicum* condition is perhaps the easier one in which to bring this about given the prerequisite condition of total asynapsis, since prolonged delay on the equator by chromosomes unable to move to the poles is often followed by reversion to the so-called resting condition, even when produced artificially as with colchicine treatment. The relative scarcity of this type of sporangial development among apogamous ferns in general may, therefore, be attributed more perhaps to the infrequency of genetically imposed asynapsis than to any intrinsic peculiarity of the processes described here.

It is of interest to note that both types of sporangial development now known to accompany apogamy in ferns are present in the genus *Asplenium*.

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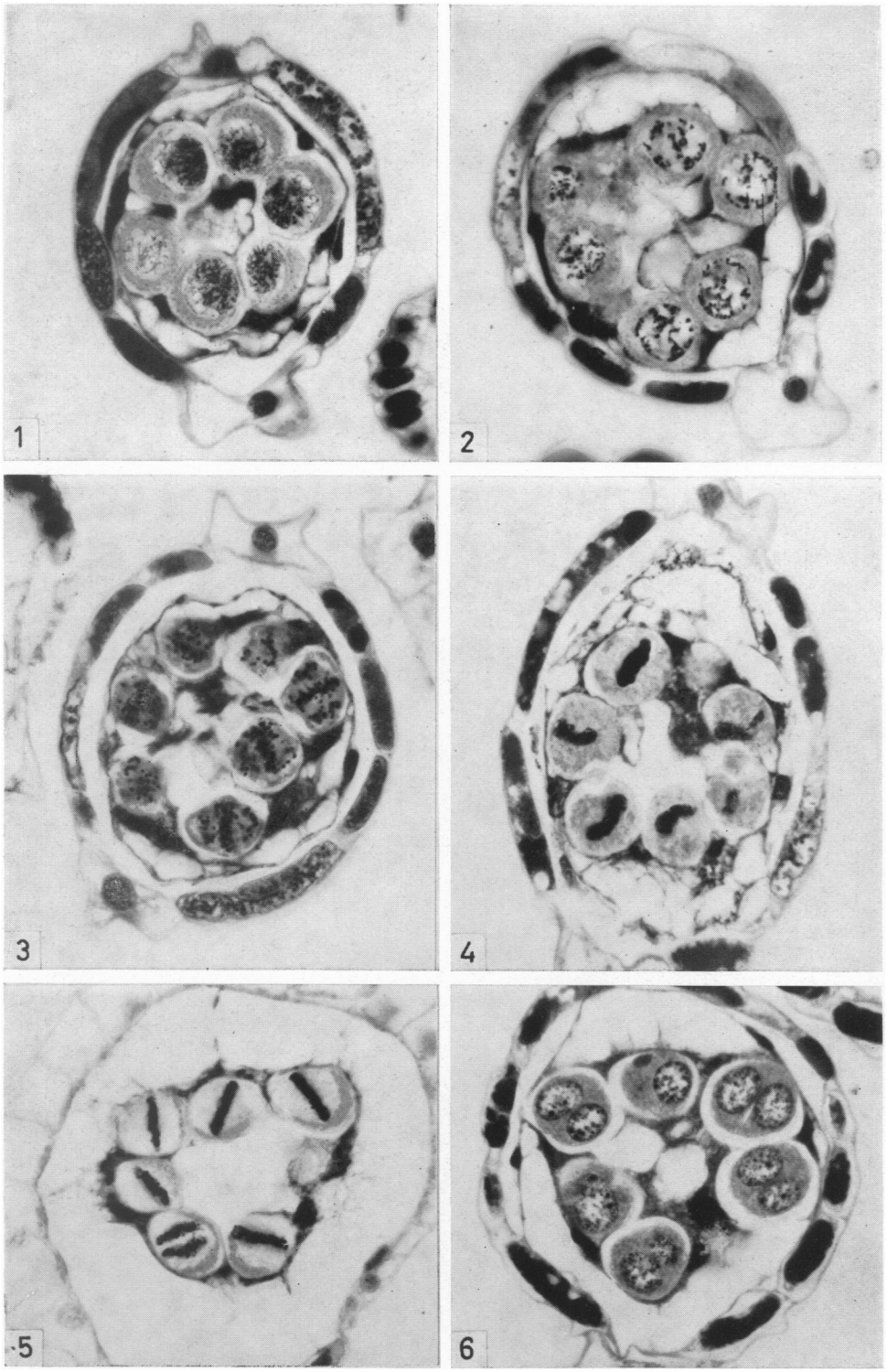
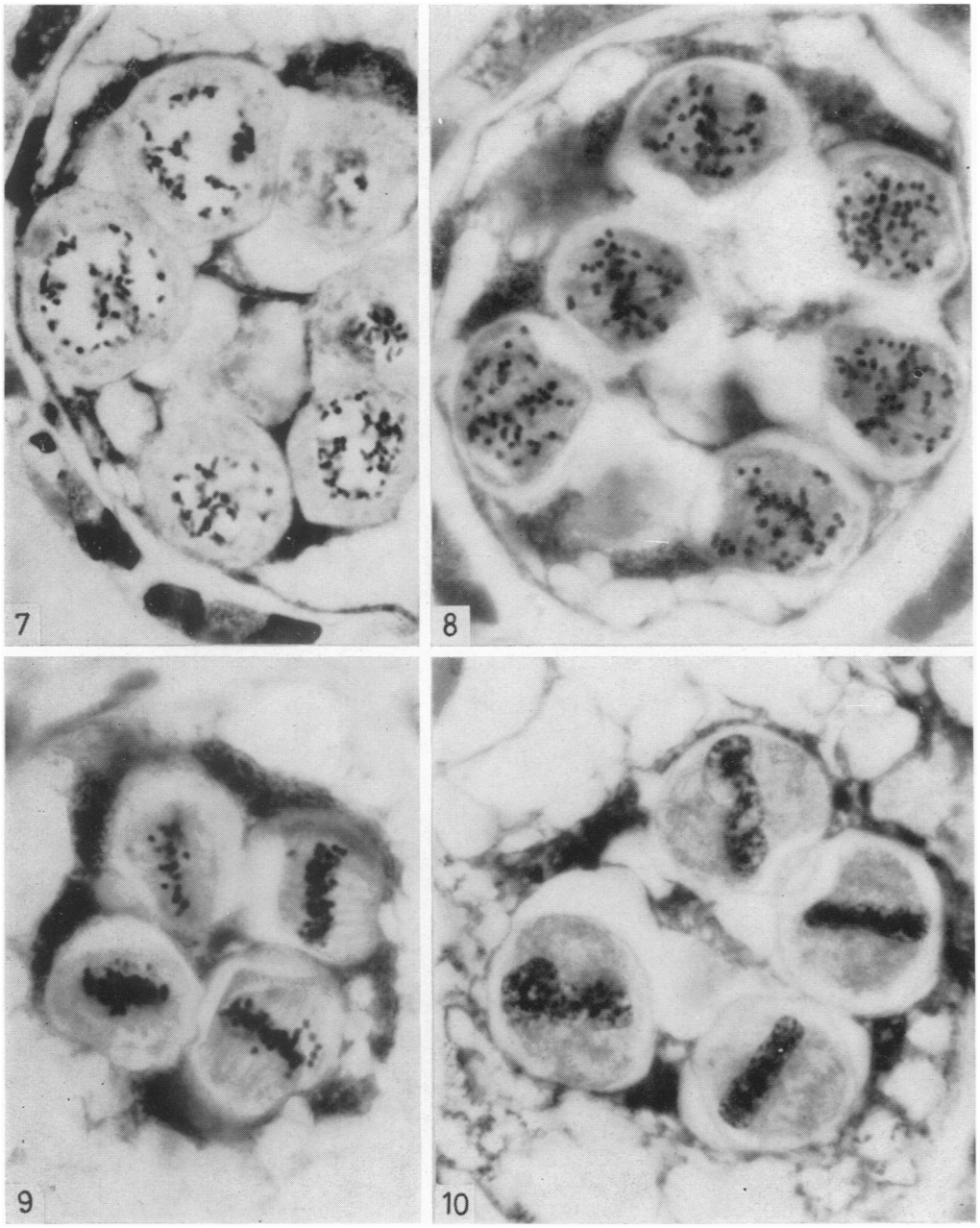
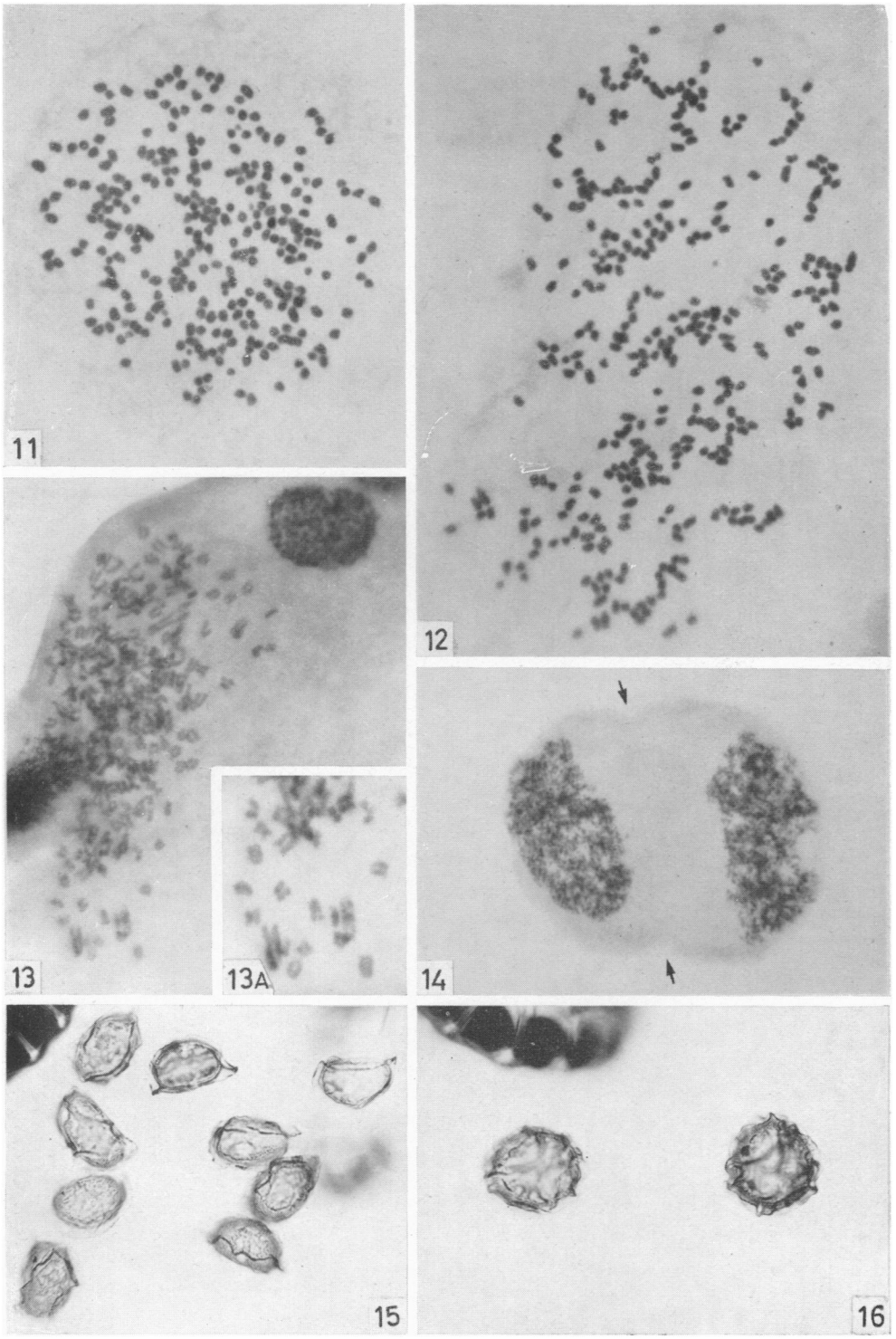


A. F. BRAITHWAITE—*A NEW TYPE OF APOGAMY IN FERNS*



A. F. BRAITHWAITE—*A NEW TYPE OF APOGAMY IN FERNS*



A. F. BRAITHWAITE—*A NEW TYPE OF APOGAMY IN FERNS* (*facing page* 305)

EXPLANATION OF PLATES

PLATE 18

Meiosis in apogamous *Asplenium aethiopicum*. Sections of sporangia from Braithwaite 228, Nos. 1–4 and 6, and Nash 183, No. 5. All preparations stained in Heidenhain's haematoxylin and photographed at a magnification of ×500.

No. 1. Prophase.
No. 2. Diakinesis.
No. 3. The first meiotic division. Note the exceedingly irregular appearance.
No. 4. Restitution nuclei representing interphase.
No. 5. The second meiotic division with only one spindle.
No. 6. Diads.

PLATE 19

Meiosis in apogamous *Asplenium aethiopicum*. Sections of sporangia from Braithwaite 228. All preparations stained in Heidenhain's haematoxylin and photographed at a magnification of ×1000.

No. 7. Diakinesis showing univalents from the same sporangia as Plate 18, No. 2.
No. 8. The first irregular metaphase showing highly contracted univalents scattered over the spindle area. The same section as Plate 18, No. 3.
No. 9. Cells showing nearly all the univalents lying in the equatorial region of the spindle.
No. 10. Detail of restitution nuclei from the same sporangium as Plate 18, No. 4. Traces of a former spindle may be sometimes observed as in the mother cell to the lower right.

PLATE 20

Acetocarmine squash preparations of meiosis in apogamous *Asplenium aethiopicum*.

No. 11. Metaphase from Mitchell 88 showing 288 univalents. For an explanatory diagram see Fig. 5, ×1000.
No. 12. A cell from Braithwaite 103A with approximately 357 chromosomes, ×1000.
No. 13. The second meiotic metaphase from Nash 183 showing the univalents to be conspicuously double, ×1000.
No. 13A. (Inset) shows detail of the split univalents more clearly, in the same cell as No. 13 but photographed at a slightly different focal level, ×1500.
No. 14. A diad from Braithwaite 228; arrows point to the cleavage plane, ×1000.
Nos. 15 and 16. Spores of *A. aethiopicum* from a sexual octoploid from Kenya and an apogamous plant (Curle & Schelpe 1) from Ethiopia respectively. Photographed at a magnification of ×250.