CHROMOSOME STUDIES IN SOME SOUTH GEORGIAN BRYOPHYTES

By MARTHA E. NEWTON

ABSTRACT. Chromosome numbers are reported for 16 bryophytes from South Georgia, 15 of which are mosses and one a liverwort. Counts for *Psilopilum antarcticum* (C. Muell.) Par., *Dendroligotrichum squamosum* (Hook. f. et Wils.) Broth., *Dicranella* cf. *hookeri* (C. Muell.) Card., *Distichium* cf. *austro-georgicum* C. Muell., *Tortula robusta* Hook. et Grev., *T. serrata* Dix., *Racomitrium* cf. *crispulum* (Hook. f. et Wils.) Hook. f. et Wils., *Bartramia patens* Brid., *Breutelia integrifolia* (Tayl.) Jaeg., *Brachythecium austro-salebrosum* (C. Muell.) Par. and *Schistochila aberrans* Steph. are reported for the first time, whereas those for *Polytrichum alpestre* Hoppe, *P. piliferum* Schreb. ex Hedw., *Pohlia cruda* (Hedw.) Lindb., *P. nutans* (Hedw.) Lindb. and *Drepanocladus uncinatus* (Hedw.) Warnst., although new for South Georgia, complement counts for these species from other parts of the world.

CHROMOSOME numbers of only three Antarctic bryophytes have been reported (Tatuno, 1963), the cytology of Southern Hemisphere bryophytes being considerably less well known than that of Northern Hemisphere bryophytes. Steere (1954) counted 56 mosses from high northern latitudes in Alaska, and found that the incidence of polyploidy was not generally greater than at lower latitudes. As Tatuno's (1963) report of $n = 20$ in *Bryum argenteum* Hedw. from Ongul Island and Langhovde (lat. 69°01′S.) is diploid, compared with a gametophytic number of $n = 10$ for the same species from various parts of its range, for example from northern Alaska (Steere, 1954), northern India (Chopra, 1957) and Japan (Yano, 1957*a*), cytological investigations of other Antarctic bryophytes would be of interest to see whether a similar difference is of general occurrence.

The present paper records the chromosome numbers of 15 mosses and one liverwort from the sub-Antarctic island of South Georgia (lat. 54°30′S.), and compares them with reports from elsewhere. Conclusions are based on counts from Eastern Europe, Finland, Great Britain, India, Ireland, Japan and North America, which were referred to by Smith and Newton (1966, 1967, 1968), as well as more recent reports for India (Chopra and Kumar, 1967), the Ukraine (Visotska, 1967), Great Britain (Ramsay, 1969) and Estonia (Fetisova and Visotzkaya, 1970).

METHODS AND MATERIALS

Fruiting mosses, gathered during the Antarctic summer, were brought from South Georgia in a cold room at 2–5° C and placed in cold frames or a north-west-facing greenhouse during May. Except in very hot weather, as shading was incomplete, meiosis was found to proceed normally under north temperate conditions. Chromosome preparations of this material were obtained from unfixed sporophytes as they matured over the next few months, using the aceto-carmine squash technique described by Smith and Newton (1966).

A Feulgen technique, outlined by Darlington and La Cour (1962), was used for the mitotic preparations of gametophytes, having been found to give satisfactory results with British mosses and liverworts (Newton, 1971). Its main advantage over the acetic stains lies in the fact that its DNA specificity can produce good contrast consistently, and this is particularly helpful if few dividing cells are present. It is important to note, however, that there is an associated reduction in the size of the chromosomes, as pointed out by Lewis (1957), for example in mitotic chromosomes of *Mnium undulatum* Hedw., where the reduction was found to be approximately 10 per cent of their length in acetic squash preparations (the author's unpublished work).

All slides were made permanent by the CO_2 freezing technique of Conger and Fairchild (1953) followed by mounting in Euparal.

Vouchers of the specimens counted, the collecting details of which are given in the Appendix, have been deposited in the herbarium of the British Antarctic Survey, at present housed in the Department of Botany, University of Birmingham.

POLYTRICHACEAE

Psilopilum antarcticum (C. Muell.) Par. $n = 7$. (Fig. 1a)

The seven bivalents were more or less uniform in size, and closely resembled those reported by various authors for Northern Hemisphere material of *Polytrichum*, *Pogonatum* and *Oligotrichum*. The spore mother cells were, however, relatively larger than is usual in most species of those genera.

The only chromosome number previously reported for this genus is for *Psilopilum cavifolium* (Wils.) Hag., in which Steere (1954) found a wide range of size amongst the seven bivalents in material from Alaska.

Polytrichum alpestre Hoppe $n = 7$. (Fig. 1b)

This report of seven large bivalents in South Georgian material is in close agreement with all previous reports from Alaska, Denmark and Great Britain.

Polytrichum piliferum Schreb. ex Hedw. $n = 7$. (Fig. 1c)

The present report is in close agreement with the first record by Heitz (1928) from Central Europe, as well as subsequent counts from the Canadian Rocky Mountains, Finland, Great Britain and Japan. In addition, Jachimsky (1935) implied that $n = 7$ was found in Central European material.

Dendroligotrichum squamosum (Hook. f. et Wils.) Broth. $n = 7$. (Fig. 1d)

There was a wide range of size throughout the complement and four of the chromosomes were metacentric or sub-metacentric. The centromeres of two chromosomes were about the border line of an acrocentric and sub-metacentric position, and would thus be classed as J-chromosomes by Yano. South Georgian *D. squamosum* coincided with the chromosome formula, $V(H)+3V+2J+m$, described by Yano (1957*b*) for *Polytrichum* and *Pogonatum*, with which Ramsay (1969) was in agreement. The chromosome formula of Patagonian *Dendroligotrichum dendroides* (Hedw.) Broth., however, has been described by Ono (1971) as $V(H)+V(H)+V+I+2J+m(h)$. It should be noted that the m-chromosome recognized by Yano was more than half the size of the next larger chromosome, and was thus greater than the criteria given below under *Schistochila aberrans* would allow.

DICRANACEAE

Dicranella cf. *hookeri* (C. Muell.) Card. $n = 26$. (Fig. 1e)

The small generally rounded-quadrate bivalents stained intensely and could easily be spread apart widely. With the exception of one of the smaller bivalents that divided precociously meiosis was quite normal. The spore mother cells were very large. Aneuploidy, rather than polyploidy, appears to have been generally associated with speciation in *Dicranella*, all previous records being within the range $n = 10$–16. South Georgian *D.* cf. *hookeri* is the first species known to include a complement that is diploid with respect to these reports.

Distichium cf. *austro-georgicum* C. Muell. $n = 14 + 1m$. (Fig. 1f)

Several of the larger bivalents became considerably attenuated during early anaphase–I, although the first to divide was invariably one with median centromeres which did not attenuate. Precocious disjunction of the m-bivalent was not seen.

The morphology of the bivalents, which stained intensely and spread apart readily, was similar to some other species of *Distichium*, such as *D. capillaceum* (Hedw.) B.S.G. and *D. inclinatum* (Hedw.) B.S.G. A haploid number of $n = 14 + 1m$ has not, however, been previously discovered in the genus, other reports being of $n = 14$ and 28 in *D. capillaceum*, $n = 13$ in *D. inclinatum* and $n = 42$ in *D. hageni* Ryan. This last number is probably triploid and together with $n = 14$ in *D. capillaceum* is of particular interest in the present context since both have been observed in Arctic material.

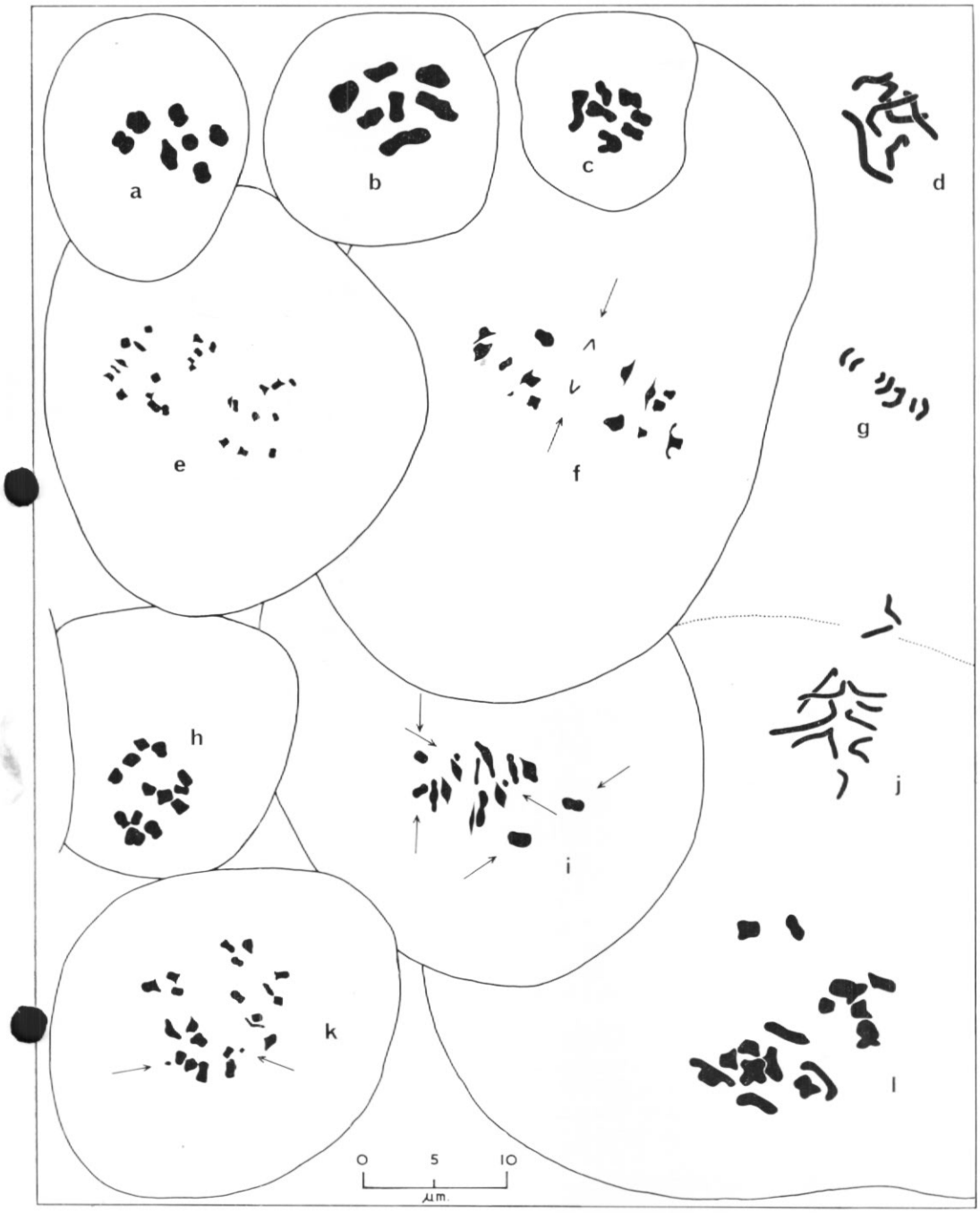

Fig. 1. Meiotic and mitotic chromosome configurations.
a. *Psilopilum antarcticum*, $n = 7$; b. *Polytrichum alpestre*, $n = 7$; c. *Polytrichum piliferum*, $n = 7$; d. *Dendroligotrichum squamosum*, $n = 7$; e. *Dicranella* cf. *hookeri*, $n = 26$; f. *Distichium* cf. *austro-georgicum*, $n = 14 + 1m$; g. *Tortula robusta*, $n = 7$; h. *Tortula serrata*, $n = 13$; i. *Racomitrium crispulum*, $n = 13$; j. *Pohlia cruda*, $n = 11$; k. *Pohlia nutans*, $n = 22$; l. *Bartramia patens*, $n = 16$.
The spore mother cells are shown in outline, part of *Bartramia patens* being dotted. Half-bivalents are indicated by arrows. d, g and j are mitotic configurations.

Pottiaceae

Tortula robusta Hook. et Grev. $n = 7$. (Fig. 1g)

There was a wide range of size throughout the complement and mitotic metaphase configurations suggested that the seven chromosomes were all metacentric or sub-metacentric. However, anaphase chromosomes were invariably rod-shaped and aligned along the spindle, which suggests that their centromeres were terminal or sub-terminal.

Ramsay (1967) has reported $n = 6 + 1$m in Australian material of *T. papillosa* Wils., which is of particular interest since it is the only other record of a low chromosome number in the Pottieae, a sub-family characterized by very high numbers. Moreover, both species belong to the section Syntrichia of the genus *Tortula*. In the present material, none of the chromosomes was small enough to be classed as an m-chromosome.

Tortula serrata Dix. $n = 13$. (Fig. 1h)

The 13 bivalents were typical of the genus in being rounded-quadrate at metaphase-I, and the number is not unusual in this section. The association of spore mother cells in small groups at approximately the same stage of development is characteristic of *Tortula* and was observed in the present material.

Grimmiaceae

Racomitrium cf. *crispulum* (Hook. f. et Wils.) Hook. f. et Wils. $n = 13$. (Fig. 1i)

In common with previous reports of the chromosomes of this genus, there was a wide range of size throughout the complement and the largest bivalent was dimorphic and divided precociously. Meiotic irregularities, resulting in the production of micro-nuclei, were frequent, but their cause is obscure since the material was taken from cold frames when extremes of temperature were not prevalent. This report differs numerically from a previous record of $n = 12$ in Tasmanian material (Ramsay, 1967), but the absence of description and illustration precludes morphological comparison.

Bryaceae

Pohlia cruda (Hedw.) Lindb. $n = 11$. (Fig. 1j)

The number of cells undergoing mitotic metaphase in shoot apices of plants kept in uncovered trays at 10° C was extremely meagre, but very well spread configurations were obtained from this material. The chromosome number observed was identical with a report by Smith and Newton (1968), who also found $n = 22$ in British material. Other counts for this species have revealed $n = 10+$ in Alaskan material, $n = 10 + 4$m and $n = 40$ in Canadian material and $n = 22$ in Ukrainian material.

This is the first account of the mitotic chromosomes of *P. cruda* and it would appear that the karyotype is similar to that of *P. drummondii* (C. Muell.) Andrews, in which Ramsay (1969) suggested that most of the chromosomes were metacentric. However, unlike that species in which only one chromosome was considered to have a sub-terminal centromere, at least two chromosomes of the South Georgian *P. cruda* were acrocentric, an observation which is in agreement with Yano's (1956) report of two large and four or five small acrocentric chromosomes in Japanese species of *Pohlia*.

Pohlia nutans (Hedw.) Lindb. $n = 22$. (Fig. 1k)

The two smallest bivalents stained lightly and divided early, one before the other. This, and the wide range of size amongst the bivalents, is in agreement with previous reports of $n = 22$ from Estonia, Great Britain, Ireland, Japan, North America and the Ukraine. In addition, counts of $n = 21$ in Alaska, $n = 33$ in Great Britain and $n = 11$ in Estonia have been made.

BARTRAMIACEAE

Bartramia patens Brid. $n = 16$. (Fig. 1 l)

This is the first report of $n = 16$ within the genus, although Steere (1954) published that number for Alaskan material of *Conostomum tetragonum* (Brid.) Lindb. (as *C. boreale* Sw.). The bivalents in the South Georgian specimens were large and of varied morphology but were seen very infrequently. The majority of spore mother cells undergoing meiosis contained 32 univalents, or were in anaphase or telophase-I, the chromosome number being confirmed in these two latter stages, both of which appeared to be perfectly normal. Unlike most mosses examined, the spore mother cells were more or less spherical and it is suggested that this may account for the unusually high frequency of cells seeming to contain univalents during metaphase-I. It is possible that such cells were in early anaphase-I and were observed from one of the poles.

A review of the literature led Mehra and Khanna (1961) to conclude that two polyploid series occur in the Bartramiaceae based on $x = 6$ and $x = 8$. The present report establishes the existence of the second of these series in *Bartramia*, previously known chromosome numbers being $n = 6$ (Khanna, 1967), 8, 8 + 1m and 12. Moreover, it is of interest that *B. patens* is included in the section Vaginella of the genus, a group in which only *B. papillata* Hook. f. et Wils. has been found with $n = 8$, whereas reports of $n = 12$ and $n = 6$ in *Bartramia* are restricted to this section.

Breutelia integrifolia (Tayl.) Jaeg. $n = 6$. (Fig. 2a)

The six metacentric or sub-metacentric chromosomes observed in two gatherings of South Georgian material were in keeping with all previous reports in this genus, the Bartramiaceae being a cytologically uniform family. The chromosome number of *B. integrifolia* was hitherto unknown, but Müller (1849) quoted Wilson's opinion that *B. integrifolia* is scarcely distinct from *B. pendula* (Sm.) Mitt., a species for which Ramsay (1967) has reported an identical number in material from New South Wales. Moreover, $n = 6$ has also been counted (Ramsay, 1967) in Australian specimens of *B. affinis* (Hook.) Mitt. which, according to Sainsbury (1955), differs in few respects from *B. pendula*.

HYPNACEAE

Drepanocladus uncinatus (Hedw.) Warnst. $n = 11$. (Fig. 2b)

The 11 bivalents of one of the two specimens examined were of varied morphology. In common with a report of $n = 10$ in British material (Smith and Newton, 1967), two bivalents

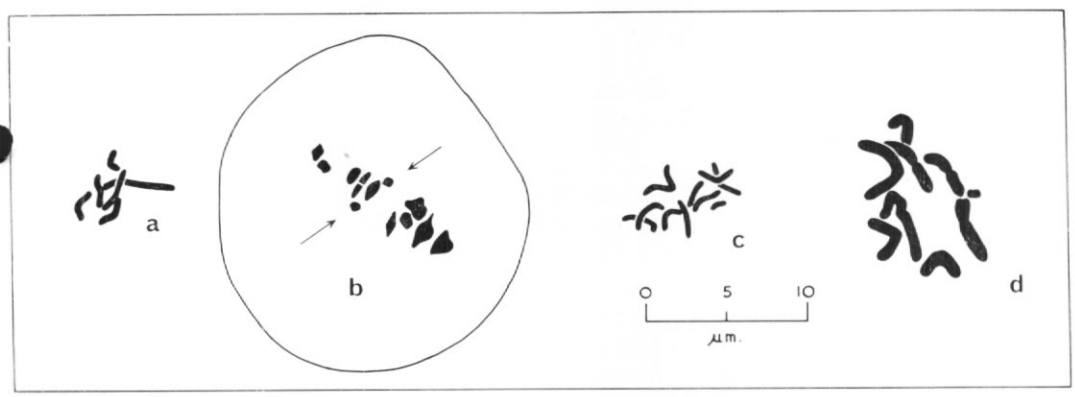

Fig. 2. Meiotic and mitotic chromosome configurations.
a. *Breutelia integrifolia*, $n = 6$; b. *Drepanocladus uncinatus*, $n = 11$; c. *Brachythecium austro-salebrosum*, $n = 10$; d. *Schistochila aberrans*, $n = 8 + 1$m.
The spore mother cell is shown in outline, the half-bivalents being indicated by arrows. a, c and d are mitotic configurations.

divided precociously, but South Georgian material differed in that lagging chromosomes were not seen. A metacentric bivalent was the first to disjoin, and it invariably became ring-shaped prior to separation of the half-bivalents.

Meiosis in the second gathering coincided with a period of hot weather, which it is considered may have had a deleterious effect on bivalent formation and subsequent cell division. Normal spore mother cell development up to and including meiotic prophase had been observed prior to the excessive heat, and then metaphase-I was precipitated. Up to 22 univalents resulted, and the report of $n = 11$ is based on a number of counts from each of three capsules.

The complement showed a wide range of size, one bivalent being very small. It was not, however, small enough to be regarded as an m-bivalent. As well as irregular bivalent formation, karyokinesis and cytokinesis were extremely abnormal. Spore mother cells containing two to four unequal spores were seen, as were spore mother cells in which one to four nuclei were included within a single undivided protoplast.

The present count is in agreement with Yano's (1967) report for Japanese material but differs from all others. Thus, $n = 12$ has been recorded from Alaska, Canada, Estonia, Finland and the United States of America. A haploid number of $n = 20$ has also been reported in Canadian and Estonian material and $n = 10$ has been counted in British material, which lacked a very small chromosome.

Brachythecium austro-salebrosum (C. Muell.) Par. $n = 10$. (Fig. 2c)

The mitotic chromosomes of shoot apices were very small but showed a wide range of size, the length of the smallest being approximately one-quarter that of the longest. At least one chromosome was acrocentric.

Schistochilaceae

Schistochila aberrans Steph. $n = 8 + 1$m. (Fig. 2d)

All the chromosomes, including the m-chromosome, had median or sub-median centromeres. They were amongst the largest of hepatic chromosomes and were particularly large for a leafy liverwort.

The smallest chromosome could be designated an m-chromosome in the sense implied, for example, by Lorbeer (1934), Proskauer (1958) and Berrie (1963). It was a very small chromosome and by analogy with dioecious liverworts, in which both sexes are known cytologically, it might be considered a sex-chromosome or, in monoecious species, homologous with a sex-chromosome. Such usage, however, is not comparable with the application of the term to mosses, where sex-determination or homology with sex-chromosomes is usually not implied. In the absence of direct evidence of homology of chromosomes between genera (Schuster, 1966), the term is applied to *S. aberrans* in the same sense as it has been used for the South Georgian mosses.

The only previous chromosome counts in this family are for Japanese *S. nuda* Horikawa and Malayan and Taiwan *S. sciura* (Nees) Schiffn., in which Tatuno (1941) and Inoue (1968), respectively, reported $n = 8 + 1$m. Tatuno described two J-chromosomes in the former, but it is clear from his diagrams that the centromeres were sub-median, and that the complements of *S. aberrans* and *S. nuda* were structurally similar, although the chromosomes of *S. aberrans* were larger. However, Inoue reported three J-chromosomes in *S. sciura*.

Discussion

Although the highest chromosome numbers yet reported in species of *Bartramia* and *Dicranella* have been discovered in South Georgian material, the numbers of the other specimens examined show close agreement with those of related species in other parts of the world. It may be concluded tentatively that, in common with Arctic species, the incidence of polyploidy in Southern Hemisphere bryophytes does not increase with latitude. However, more studies, particularly from farther south, are necessary to confirm this view.

Meiotic material became available during the summer in which mosses were brought from South Georgia, which is noteworthy in view of the fact that maturity was thus attained out of

phase in relation to the original environment. For example, Clarke and Greene (1970) have shown that sporophytes of *Pohlia nutans* normally over-winter in the early calyptra intact stage, the stage at which the material was transferred to northern latitudes. The early operculum intact stage, when meiosis usually occurs, would not normally have been produced until the following December, but was observed in August. However, this represented a delay in comparison with British material, and was probably paralleled by the other species examined. It would be of interest to investigate this in view of the evidence produced by Hughes (1962), which suggests that sporophyte development in *Pogonatum aloides* is delayed by long-day treatment. Thus, material brought from decreasing day-length on South Georgia was subjected to increasing day-length for more than a month on return to Great Britain, and it might be suggested that this could account for the observed delay. In other species, for example *Polytrichum piliferum*, it is possible that the low temperatures to which plants were subjected during the journey north were sufficient to break any winter dormancy of the immature sporophytes, such as that envisaged by Hughes (1962).

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APPENDIX

DETAILS OF SOUTH GEORGIAN SPECIMENS EXAMINED

MUSCI

Bartramia patens Brid. Near wooden dam above Grytviken football pitch, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 36.

Brachythecium austro-salebrosum (C. Muell.) Par. Near Grytviken, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 33.

Breutelia integrifolia (Tayl.) Jaeg. Inland from small cove to south of Shallop Cove, Queen Maud Bay, GR 075 125, leg. R. I. L. Smith, 30.xii.1970, BAS MISC. 18.

Breutelia integrifolia (Tayl.) Jaeg. Near Gull Lake, GR 130 120, leg. R. E. Longton, 1964, BAS MISC. 19.

Dendroligotrichum squamosum (Hook. f. et Wils.) Broth. Inland from small cove to south of Shallop Cove, Queen Maud Bay, GR 075 125, leg. R. I. L. Smith, 30.xii.1970, BAS MISC. 12.

Dicranella cf. *hookeri* (C. Muell.) Card. Half-way between Grytviken and head of Bore Valley, GR 130 125, leg. N. J. Collins, 11.iv.1969, BAS MISC. 13.

Distichium cf. *austro-georgicum* C. Muell. Lower slopes of Mount Duse, at *c.* 8 m. above track between King Edward Point and Grytviken whaling station, GR 130 120, leg. R. I. L. Smith, 14.iv.1971, BAS MISC. 14.

Drepanocladus uncinatus (Hedw.) Warnst. Near Grytviken, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 38.

Drepanocladus uncinatus (Hedw.) Warnst. Above football pitch behind Grytviken whaling station, GR 130 120, leg. R. I. L. Smith, iii.1970, BAS MISC. 32.

Pohlia cruda (Hedw.) Lindb. Above track from King Edward Point to Grytviken, GR 130 120, leg. G. C. S. Clarke, 1967–68, BAS MISC. 34.

Pohlia nutans (Hedw.) Lindb. Outside manager's house, Grytviken whaling station, GR 130 120, leg. G. C. S. Clarke, 1967–68, BAS MISC. 35.

Polytrichum alpestre Hoppe. Below Gull Lake, GR 130 120, leg. R. I. L. Smith, 1970–71, BAS MISC. 10.

Polytrichum piliferum Schreb. ex Hedw. Near wooden dam above Grytviken football pitch, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 11.

Psilopilum antarcticum (C. Muell.) Par. Below Gull Lake dam, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 9.

Racomitrium cf. *crispulum* (Hook. f. et Wils.) Hook. f. et Wils. Valley north of Grytviken, GR 130 125, leg. R. I. L. Smith, 1969–70, BAS MISC. 17.

Tortula robusta Hook. et Grev. Bank to east of Gull Lake, GR 130 120, leg. R. I. L. Smith, 1969–70, BAS MISC. 15.

Tortula serrata Dix. North side of King Edward Cove, GR 130 120, leg. R. I. L. Smith, 8.iv.1971, BAS MISC. 16.

HEPATICAE

Schistochila aberrans Steph. Below Gull Lake dam, GR 130 120, leg. N. J. Collins, 11.iv.1969, BAS MISC. 37.

Specimens which have been retained as permanent records have been incorporated into the British Antarctic Survey herbarium, at present housed in the Department of Botany, University of Birmingham, as part of the BAS MISC. series as indicated.