

CHROMOSOME STUDIES IN SOME ANTARCTIC AND SUB-ANTARCTIC BRYOPHYTES

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ABSTRACT. Illustrated cytological records of 13 mosses and six liverworts from Signy Island, South Orkney Islands, and the sub-Antarctic island of South Georgia support the view that the incidence of polyploidy does not increase with latitude in the Southern Hemisphere. Intra-specific variation in chromosome number is not unusually extensive but identifies *Bartramia patens* Brid., *Brachythecium austro-salebrosum* (C. Muell.) Kindb., *Pohlia cruda* (Hedw.) Lindb., *Tortula robusta* Hook. et Grev. and *Riccardia georgiensis* (Steph.) Hässel as species justifying further cyto-taxonomic investigation.

CYTOLOGICAL studies in Antarctic (Tatuno, 1963; Inoue, S., 1976) and sub-Antarctic bryophytes (Newton, 1972, 1979) form part of a worldwide interest in chromosome numbers which has yet to prove as helpful in bryophyte taxonomy as have similar studies in higher plants (e.g. Crundwell, 1970; Stotler, 1976). This is due not to fundamental differences in the reproductive behaviour and evolutionary responses of bryophytes, although they may exist, but to practical considerations (Newton, 1975, 1977a, in press). In particular, numerically uniform complements are widespread in many genera, families and even in some orders, while intra-specific variation is frequent in others (cf. Fritsch, 1972).

The meaning of these observations is unknown but it is on a proper understanding of them that further advances in bryophyte cyto-taxonomy will depend. For instance, constancy of chromosome number between taxa may not necessarily reflect unchanged and unchanging karyotypes. It could result from structural re-arrangement rather than numerical alteration. Moreover, in attaching taxonomic weight to cytological data, it is essential to be able to distinguish changes within the basic complement from those attributable to the presence of supernumerary B-chromosomes.

Until recently, solutions to these problems were seriously hindered because bryophyte chromosomes could rarely be recognized individually (e.g. Schuster, 1966; Wigh, 1972; Newton, 1977a) but, with the development of modern light microscope techniques, it is now possible to make the necessary shift in emphasis towards structural studies (Newton, in press). However, as a means of identifying promising taxa for work of this kind, there remains a need for further chromosome counts, particularly from bryologically less well-known regions such as Antarctica and the sub-Antarctic islands. Cytological data for 14 species from South Georgia and six from Signy Island, South Orkney Islands, are therefore provided in this paper.

MATERIALS AND METHODS

Culture techniques and cytological procedures were identical to those used previously for South Georgian bryophytes (Newton, 1972). Mitotic squash preparations of gametophytic apices were stained according to the Feulgen schedule detailed elsewhere (Newton, 1971) and aceto-carmin was employed for meiotic cells as described by Smith and Newton (1966).

Chromosome numbers have been determined and, wherever possible, attention has been drawn to centromere position. Meiotic features such as bivalent attenuation, precocious anaphase division and univalent formation have also been noted. In defining karyotypes, whether mitotic or meiotic, the term m-chromosome has been applied to the smallest member of a complement when it was less than half the size of the shortest of the remainder. The value of such a distinction has been discussed previously (Newton, 1971, 1975), the main drawback being that discontinuity of variation elsewhere in the karyotype might be equally significant and yet be ignored. Bearing this possibility in mind, such situations have been identified specifically in the text.

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Advantage has been taken of a list of bryophyte chromosome numbers compiled by Fritsch (1972) as a convenient means of referring to a large body of literature. Apart from papers not included by Fritsch, original sources are quoted only where they refer to Antarctic or sub-Antarctic material, or where a point of particular interest has been raised. Classification follows Crosby and Magill (1977) for mosses and Schuster (1966) for liverworts.

Voucher specimens, details of which are provided in the Appendix, have been preserved and incorporated in the herbarium of the British Antarctic Survey as part of the BAS Misc. series. The bryophyte section of the herbarium is presently housed in the Institute of Terrestrial Ecology, Bush Research Station, Penicuik, Midlothian, Scotland EH26 0QB.

ANDREAEACEAE

Andreaea australis F. Muell. ex Mitt. $n = 10$ (Fig. 1a), South Georgia.

Overall chromosome size was too small to allow the determination of centromere position. However, the count, the first for the species, is consistent with previous records of $n = 10$ and 11 in other members of the genus (cf. Fritsch, 1972).

DICRANACEAE

Dicranoweisia antarctica (C. Muell.) Kindb. $n = 13$ (Fig. 1b), Signy Island.

D. antarctica was hitherto unknown cytologically but $n = 13$ has been reported for the genus in British *D. cirrata* (Hedw.) Lindb. in Mild. (Smith and Newton, 1967). In that species, it was associated with irregular bivalent disjunction, which was not, however, a feature of *D. antarctica*. A haploid chromosome number of 13 is only one of several already known in *Dicranoweisia* (cf. Fritsch, 1972; Bryan, 1973; Kumar and Verma, 1975) but slight attenuation of bivalents, as seen in this gathering from Signy Island, is characteristic of many of the Dicranaceae *sensu lato* (Smith and Newton, 1968).

POTTIACEAE

Tortula robusta Hook. et Grev. $n = 12$ (Fig. 1c), South Georgia.

An example of intra-specific cytological variation was revealed by the present discovery of $n = 12$, there being an earlier report of $n = 7$ in South Georgian *T. robusta* (Newton, 1972). The relationship of the two cytotypes is unknown because centromere position and other structural details of the chromosomes have not yet been determined.

GRIMMIACEAE

Grimmia cf. *asperitricha* Dix. et Sainsb. $n = 13$ (Fig. 1d), South Georgia.

Although those spore mother cells which contained 13 bivalents underwent perfectly normal meiosis, the most striking feature of this specimen was its extensive meiotic irregularity. Various numbers of univalents up to 22 were frequently excluded from the first metaphase plate and abnormal first and second anaphases were abundant. These involved incomplete cyto-kinesis as well as the formation of micro-nuclei. For example, in a random sample of 63 spore mother cells at first telophase and 129 at second telophase, about 50% and 79%, respectively, were abnormal.

Grimmia syntrichiacea C. Muell. in Neum. $n = 13$ (Fig. 1e), South Georgia.

There are no previous cytological records for this species in which, unlike *G. cf. asperitricha*, meiosis was quite undisturbed. Bivalents tended to become more attenuated in *G. syntrichiacea* but the observation is unlikely to be of taxonomic significance in this genus (Smith and Newton, 1967).



Fig. 1. Meiotic (within outlined spore mother cells) and gametophytic mitotic metaphase configurations. a. *Andreaea australis*, $n = 10$; b. *Dicranoweisia antarctica*, $n = 13$; c. *Tortula robusta*, $n = 12$; d. *Grimmia* cf. *asperitricha*, $n = 13$; e. *Grimmia syntrichiacea*, $n = 13$; f. *Bryum algens*, $n = 20$; g. *Pohlia cruda* var. *imbricata*, $n = 11$; h. *Bartramia patens*, $n = 11 + 1$ m; i. *Bartramia patens*, $n = 16$. Arrows indicate half-bivalents.

BRYACEAE

Bryum algens Card. $n = 20$ (Fig. 1f), Signy Island.

The present chromosome count is in agreement with two previous reports of $n = 20$ in *B. algens*, both of them based on collections from the Ongul Islands (Tatuno, 1963; Inoue, S., 1976).

Pohlia cruda (Hedw.) Lindb. var. *imbricata* (Card.) Bartr. $n = 11$ (Fig. 1g), Signy Island.

Centromere position could not be established with certainty but appeared to be median or slightly sub-median in five chromosomes. Four were acrocentric and two telocentric. The gametophytic chromosomes covered a very wide range of size and confirmed an earlier mitotic count of $n = 11$ in a South Georgian specimen of the type variety (Newton, 1972). All other chromosome counts for this species refer to Northern Hemisphere material and include $n = 10, 10+4 m, 11, 22$ and 40 (cf. Fritsch, 1972).

BARTRAMIACEAE

Bartramia patens Brid. $n = 11+1 m$ (Fig. 1h), Signy Island; $n = 16$ (Fig. 1i), South Georgia.

The discovery of $n = 16$ during gametophytic mitosis confirmed an earlier meiotic count in South Georgian material (Newton, 1972) but $n = 11+1m$ was hitherto unknown in this species. Cytological heterogeneity is not, however, surprising in view of the great morphological variation associated with *B. patens* (Newton, 1973, 1974) and haploid complements of 12 are known elsewhere in the genus (cf. Fritsch, 1972). What is of interest is the fact that the smallest bivalent was less than half the size of the next larger and, hence, was an m-bivalent. Nevertheless, the bivalent which invariably divided early was not the smallest but a metacentric one of medium size.

Conostomum pentastichum (Brid.) Lindb. $n = 8$ (Fig. 2a), South Georgia.

Determination of structural details was precluded by the small size of the chromosomes. However, their number was consistent with counts of $n = 8$ and 16 in other species of *Conostomum* (cf. Fritsch, 1972; Inoue, S., 1974).

AMBLYSTEGIACEAE

Campylium polygamum (B.S.G.) C. Jens. $n = 11$ (Fig. 2b), Signy Island.

There was a wide range of size among the chromosomes and, although all were less than $2 \mu m$ long, none was relatively small enough to be classed as an m-chromosome. Previous counts for this species are of $n = 11$ and 20 from Britain (cf. Fritsch, 1972) and $n = 11$ from Lithuania (Daniliv, 1976).

BRACHYTHECIACEAE

Brachythecium austro-salebrosum (C. Muell.) Kindb. $n = 11$ (Fig. 2c), Signy Island.

Size variation between chromosomes was considerable. At least seven of the 11 chromosomes were metacentric or sub-metacentric but centromere position in the two smallest members of the complement and two of medium size could not be decided. It is impossible, therefore, to suggest what relationship exists between this cyto-type and those of South Georgian *B. austro-salebrosum* with $n = 10$ and 13 (Newton, 1972, 1979).

POLYTRICHACEAE

Polytrichum alpinum L. ex Hedw. $n = 7$ (Fig. 2d), South Georgia.

The seven large, unattenuated bivalents coincided with previous counts based on Asian, European and North American material (Sharma, 1960; Ono, 1970; cf. Fritsch, 1972; Kumar and Garg, 1974), although there are also records of $n = 14$ in the var. *arcticum* (Schrad.)



Fig. 2. Meiotic (within outlined spore mother cell) and gametophytic mitotic metaphase configurations. a. *Conostomum pentastichum*, $n = 8$; b. *Campylium polygamum*, $n = 11$; c. *Brachythecium austrosalebrosum*, $n = 11$; d. *Polytrichum alpinum*, $n = 7$; e. *Psilopilum trichodon*, $n = 7$; f. *Roivainenia jacquinotii*, $n = 9$; g. *Blepharidophyllum densifolium*, $n = 8+1$ m; h. *Leptoscyphus expansus*, $n = 8+1$ m; i. *Lophocolea willii*, $n = 8+1$ m; j. *Cephaloziella varians*, $n = 16+2$ m; k. *Riccardia georgiensis*, $n = 10$; l. *Riccardia georgiensis*, $n = 20$.

Wahlenb. and the var. *brevifolium* (R. Brown) C. Muell. from North America (Khanna, 1964; cf. Fritsch, 1972).

Psilopilum trichodon (Hook. f. et Wils.) Mitt. $n = 7$ (Fig. 2e), South Georgia.

Despite the generally large size of the chromosomes, centromere positions were uncertain. However, it was possible to confirm in gametophytic cells of this specimen an earlier meiotic count of $n = 7$, which was also based on South Georgian material (Newton, 1972).

LOPHOZIACEAE

Roivainenia jacquinotii (Mont.) Grolle $n = 9$ (Fig. 2f), South Georgia.

The smallest chromosome was relatively too large to be classed as an m-chromosome, although both it and the next larger were distinctly smaller than the remaining seven chromosomes. Median or sub-median centromeres occurred in at least three chromosomes, whereas a fourth was sub-terminal. There are no other cytological accounts of this species.

SCAPANIACEAE

Blepharidophyllum densifolium (Hook.) Angstr. ex Mass. $n = 8+1$ m (Fig. 2g), South Georgia.

This is the first cytological record for *B. densifolium*, in which at least six of the nine chromosomes were found to be metacentric or sub-metacentric. The specimen examined was remarkable for extreme chromosome condensation at metaphase of mitosis and also for a great abundance of heterochromatin *sensu lato* (cf. Newton, 1977a, b, in press).

LOPHOCOLEACEAE

Leptoscyphus expansus (Lehm.) Grolle $n = 8+1$ m (Fig. 2h), South Georgia.

In this material of a species hitherto unknown cytologically, the smallest member of the complement of generally very large chromosomes was only just within the limits defined for m-chromosomes. A notable feature of the karyotype was the high degree of symmetry, whereby all seven of the chromosomes in which centromere position could be determined were metacentric or sub-metacentric.

Lophocolea willii Grolle $n = 8+1$ m (Fig. 2i), South Georgia.

Five chromosomes, including the m-chromosome, were metacentric or sub-metacentric. Two were acrocentric but centromere position could not be recognized in the remaining two. As far as it is possible to tell from work so far, *L. willii* is not atypical of the genus, there being numerous records of haploid complements of nine (Segawa, 1971; cf. Fritsch, 1972; Inoue, H., 1974; Newton, 1975; Steel, 1978), several of which include an m-chromosome.

CEPHALOZIACEAE

Cephaloziella varians (Gottsche) Steph. $n = 16+2$ m (Fig. 2j), South Georgia.

Among the nine pairs of chromosomes, the smallest was unique in being composed of two unequal m-chromosomes, which were clearly a pair on the basis of the order of size. The only previous count for the genus (Inoue, H., 1976) is haploid by comparison.

ANEURACEAE

Riccardia georgiensis (Steph.) Hässel $n = 10$ and 20 (Fig. 2k and l), South Georgia.

Individual chromosomes of the haploid specimen were rather larger than those of the diploid, but detailed structural comparison was impracticable because determination of centromere position in the genus *Riccardia* requires well-spread anaphase configurations (Newton, 1977a) and none was available. However, both the diploid complement of ten pairs of chromosomes and that of the haploid covered a similar range of size, neither including an

m-chromosome. *R. georgiensis* was hitherto unknown cytologically, but $n = 10$ and 20 are well known in other species (Hewson, 1970; Newton, 1971, 1975, 1977a; Proskauer, 1971; Segawa, 1971; cf. Fritsch, 1972; Inoue, H., 1977).

DISCUSSION

By analogy with higher plants, in which a positive correlation between chromosome number and latitude may exist (Löve and Löve, 1949), it has been thought that the same may be true of bryophytes (Mehra and Khanna, 1961). Steere (1954) and H. Inoue (1976), however, have discounted the idea as far as their Northern Hemisphere data are concerned and, in a paper based exclusively on South Georgian bryophytes (Newton, 1972), it was suggested tentatively that chromosome number does not increase with latitude in the Southern Hemisphere. Supporting evidence was cited from Australian and a few Antarctic records (cf. Fritsch, 1972). While it is still too early to draw definite conclusions, the present observations tend to confirm such a view. Indeed, the six records from Signy Island, at a latitude of $60^{\circ}40'S$, include one of $n = 11+1$ m for *Bartramia patens*, whereas only $n = 16$ has been found in the species on South Georgia (lat. $54-55^{\circ}S$).

Intra-specific variation in chromosome number has also been discovered in *Tortula robusta*, *Pohlia cruda*, *Brachythecium austro-salebrosum* and *Riccardia georgiensis* and, although one would hesitate to claim any special geographical significance, its existence does deserve consideration in that context. The search for satisfactory explanations of extensively heterogeneous chromosome numbers is one of the greatest outstanding difficulties of bryophyte cytotaxonomy but it is particularly so in austral regions, where bryology is still in an exploratory phase (Richards, 1978). In such an area, there must be an attempt to resolve not only the problem of infra-specific recognition of cytotypes but also the question as to whether or not the concept of a particular species, perhaps based on inadequate material, is acceptable.

Several authors (e.g. Smith and Hill, 1975; Steel, 1978; Szweykowski, 1978) have taken the view that, if intensive study fails to correlate morphological distinctions with cytological variation, then it is expedient, at least temporarily, to recognize a single cytologically heterogeneous species. The problems raised by such a treatment would be slight if, as Wigh (1973) has proposed for members of the Brachytheciaceae, the variation depended on the presence or absence of supernumerary B-chromosomes, but conclusive evidence of B-chromosomes in bryophytes is still wanting. That they are unlikely to account for the difference between $n = 11+1$ m and $n = 16$ in *Bartramia patens*, for example, is suggested by the fact that the two cytotypes have been observed to undergo what appears to be perfectly normal meiosis. *B. patens* is thus one of several species which is in need of further cytotaxonomic study. Should it, for instance, be regarded as an aggregate of incipient or inconspicuously distinct species, as has been suggested for *Tortula muralis* Hedw. (Newton, 1968), or is it a well-defined species which includes two interbreeding cytotypes?

Meiotic irregularities of the type observed in *Grimmia* cf. *asperitricha* have similarly far-reaching evolutionary implications and, moreover, are not of isolated occurrence. In view of the successful establishment of 13 bivalents in some spore mother cells, the high frequency of univalents in others cannot be attributed to a lack of homology but two possibilities, environmental and genetical, exist. Of the latter, the controlled frequency of chiasmata and/or univalent formation either in the complement as a whole (cf. Riley and Law, 1965) or in specific pairs of homologues (e.g. Parker and others, 1976) is particularly relevant. However, whichever interpretation applies, the phenomenon may result in a reduced rate of re-combination and, hence, in limited genetical variation with a concomitant effect on evolutionary strategy.

Cytological survey work such as that reported here undoubtedly indicates unlimited scope for further research which, it has been predicted elsewhere (Vaarama, 1976; Newton, in press), will rely heavily on the comparison of heterochromatin both within and between chromosomes.

It is of considerable interest, therefore, that exceptionally large quantities were found in *Blepharidophyllum densifolium*.

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REFERENCES

- BRYAN, V. S. 1973. Chromosome studies on mosses from Austria, Czechoslovakia and other parts of Central Europe. *Öst. bot. Z.*, **121**, Ht. 3-4, 187-226.
- CROSBY, M. R. and R. E. MAGILL. 1977. *A dictionary of mosses*. St. Louis, Missouri Botanical Garden.
- CRUNDWELL, A. C. 1970. Intraspecific categories in Bryophyta. *Biol. J. Linnean Soc. Lond.*, **2**, No. 3, 221-24.
- DANILKIV, I. S. 1976. New data on chromosome numbers of mosses from Lithuania. *Ukr. bot. Zh.*, **33**, No. 5, 507-10.
- FRITSCH, R. 1972. Chromosomenzahlen der Bryophyten, eine Übersicht und Diskussion ihres Aussagewertes für das System. *Wiss. Z. Friedrich Schiller-Univ. Jena*, **21**, Ht. 5/6, 839-944.
- HEWSON, H. J. 1970. The family Aneuraceae in Australia and New Guinea: I. The genus *Aneura*. *Proc. Linn. Soc. N.S.W.*, **94**, Pt. 2, 173-93.
- INOUE, H. 1974. Chromosome numbers of some Japanese Hepaticae, I. *J. Jap. Bot.*, **49**, No. 11, 337-41.
- . 1976. Chromosome studies in some Arctic hepatics. *Bull. natn. Sci. Mus., Tokyo*, Ser. B, **2**, No. 2, 39-46.
- . 1977. Chromosome numbers of some Japanese Hepaticae (2). *Bull. natn. Sci. Mus., Tokyo*, Ser. B, **3**, No. 2, 55-61.
- INOUE, S. 1974. Chromosome studies in some Alaskan mosses. *Miscnea bryol. lichen., Nichinan*, **6**, No. 10, 177-79.
- . 1976. Chromosome studies on five species of Antarctic mosses. *Kumamoto J. Sci.*, Ser. B, Sect. 2, **13**, No. 1, 1-5.
- KHANNA, K. R. 1964. Cytology of some mosses from the Adirondack Mountains. *Bryologist*, **67**, No. 3, 343-50.
- KUMAR, S. S. and R. G. GARG. 1974. Cytological studies on some west Himalayan mosses. *Miscnea bryol. lichen., Nichinan*, **6**, No. 9, 153-56.
- and S. K. VERMA. 1975. Cytological observations on some west Himalayan mosses. *Miscnea bryol. lichen., Nichinan*, **7**, No. 2, 33-38.
- LÖVE, A. and D. LÖVE. 1949. The geobotanical significance of polyploidy, I. Polyploidy and latitude. *Port. Acta biol.*, Ser. A, R.B. Goldschmidt Volume, 273-352.
- MEHRA, P. N. and K. R. KHANNA. 1961. Recent cytological investigations in mosses. *Res. Bull. Panjab Univ. Sci.*, **12**, No. 1, 1-29.
- NEWTON, M. E. 1968. Cyto-taxonomy of *Tortula muralis* Hedw. in Britain. *Trans. Br. bryol. Soc.*, **5**, Pt. 3, 523-35.
- . 1971. Chromosome studies in some British and Irish bryophytes. *Trans. Br. bryol. Soc.*, **6**, Pt. 2, 244-57.
- . 1972. Chromosome studies in some South Georgian bryophytes. *British Antarctic Survey Bulletin*, No. 30, 41-49.
- . 1973. A taxonomic assessment of *Bartramia*, *Breutelia* and *Exodokidium* on South Georgia. *British Antarctic Survey Bulletin*, No. 32, 1-14.
- . 1974. A synoptic flora of South Georgian mosses: IV. *Bartramia* and *Breutelia*. *British Antarctic Survey Bulletin*, No. 38, 59-71.
- . 1975. Chromosome studies in some British bryophytes. *J. Bryol.*, **8**, Pt. 3, 365-82.
- . 1977a. Heterochromatin as a cyto-taxonomic character in liverworts: *Pellia*, *Riccardia* and *Cryptothallus*. *J. Bryol.*, **9**, Pt. 3, 327-42.
- . 1977b. Chromosomal relationships of heterochromatin bodies in a moss, *Dicranum tauricum* Sapehin. *J. Bryol.*, **9**, Pt. 4, 557-64.
- . 1979. A taxonomic assessment of *Brachythecium* on South Georgia. *British Antarctic Survey Bulletin*, No. 48, 119-32.
- . In press. Chromosome morphology and bryophyte systematics. (In CLARKE, G. C. S. and J. G. DUCKETT, ed. *Bryophyte systematics*. London, Academic Press.)
- ONO, K. 1970. Karyological studies on Mniaceae and Polytrichaceae, with special reference to the structural sex-chromosomes. III. *J. Sci. Hiroshima Univ.*, Ser. B, Div. 2, **13**, No. 1, 167-221.

- PARKER, J. S., JONES, G. H., TEASE, C. and R. W. PALMER. 1976. Chromosome-specific control of chiasma formation in *Hypochoeris* and *Crepis*. (In JONES, K. and P. E. BRANDHAM, ed. *Current chromosome research*. Amsterdam, New York, Oxford, North-Holland, 133-42.)
- PROSKAUER, J. 1971. Notes on Hepaticae, V. *Bryologist*, **74**, No. 1, 1-9.
- RICHARDS, P. W. 1978. The taxonomy of bryophytes. (In STREET, H. E., ed. *Essays in plant taxonomy*. London, New York, San Francisco, Academic Press, 177-209.)
- RILEY, R. and C. N. LAW. 1965. Genetic variation in chromosome pairing. *Adv. Genet.*, **13**, 57-114.
- SCHUSTER, R. M. 1966. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. I.* New York, London, Columbia University Press.
- SEGAWA, M. 1971. Cytological studies on some liverworts. *Hikobia*, **6**, Nos. 1-2, 3-8.
- SHARMA, P. D. 1960. Chromosome number of some Himalayan Polytrichaceae. *Curr. Sci.*, **29**, No. 6, 231.
- SMITH, A. J. E. and M. O. HILL. 1975. A taxonomic investigation of *Ulota bruchii* Hornsch. ex Brid., *U. crispata* (Hedw.) Brid. and *U. crispata* Brid. I. European material. *J. Bryol.*, **8**, Pt. 4, 423-33.
- and M. E. NEWTON. 1966. Chromosome studies on some British and Irish mosses. I. *Trans. Br. bryol. Soc.*, **5**, Pt. 1, 117-30.
- and ———. 1967. Chromosome studies on some British and Irish mosses. II. *Trans. Br. bryol. Soc.*, **5**, Pt. 2, 245-70.
- and ———. 1968. Chromosome studies on some British and Irish mosses. III. *Trans. Br. bryol. Soc.*, **5**, Pt. 3, 463-522.
- STEEL, D. T. 1978. The taxonomy of *Lophocolea bidentata* (L.) Dum. and *L. cuspidata* (Nees) Limpr. *J. Bryol.*, **10**, Pt. 1, 49-59.
- STEERE, W. C. 1954. Chromosome number and behavior in Arctic mosses. *Bot. Gaz.*, **116**, No. 2, 93-133.
- TOTLER, R. E. 1976. The biosystematic approach in the study of the Hepaticae. *J. Hattori bot. Lab.*, No. 41, 37-46.
- SZWEYKOWSKI, J. 1978. Modern taxonomic methods: perspectives of their application in hepaticology. *Bryophytorum Bibliotheca*, **13**, 435-42.
- TATUNO, S. 1963. Zytologische Untersuchungen über die Laubmoose von Antarktis. *Hikobia*, **3**, No. 4, 268-74.
- VAARAMA, A. 1976. A cytotaxonomic approach to the study of bryophytes. *J. Hattori bot. Lab.*, No. 41, 7-12.
- WIGH, K. 1972. Cytotaxonomical and modification studies in some Scandinavian mosses. *Lindbergia*, **1**, Nos. 3-4, 130-52.
- . 1973. Accessory chromosomes in some mosses. *Hereditas*, **74**, No. 2, 211-23.

APPENDIX

DETAILS OF SPECIMENS EXAMINED

MUSCI

South Georgia

- Andreaea australis* F. Muell. ex Mitt. Wet flush, leg. C. J. Barrow, 1972-73, BAS Misc. 109.
- Bartramia patens* Brid. Wet flush, leg. J. R. Tallowin, 1972-73, BAS Misc. 110.
- Conostomum pentastichum* (Brid.) Lindb. North side of King Edward Cove, alt. c. 8 m, GR 133 125, leg. R. I. L. Smith, c. 25.iii.1971, BAS Misc. 90.
- Grimmia* cf. *asperitricha* Dix. et Sainsb. Leg. R. I. L. Smith, 1969-70, BAS Misc. 124.
- Grimmia syntrichiacea* C. Muell. Leg. R. I. L. Smith, 1969-70, BAS Misc. 123.
- Polytrichum alpinum* Hedw. King Edward Point, leg. E. P. Wright, 16.xi.1968, transferred to Signy Island, xii.1968, transferred to United Kingdom, iii-iv.1970, BAS Misc. 74.
- Silopilum trichodon* (Hook. f. et Wils.) Mitt. Wet flush, leg. C. J. Barrow, 1972-73, BAS Misc. 103.
- Tortula robusta* Hook. et Grev. Wet flush, leg. J. R. Tallowin, 1972-73, BAS Misc. 97.

Signy Island

- Bartramia patens* Brid. Observation Bluff, alt. c. 61 m, leg. R. Webb, 18.iii.1972, BAS Misc. 83.
- Brachythecium austro-salebrosum* (C. Muell.) Kindb. East shore of Lake 5, alt. c. 24 m, leg. R. Webb, 18.iii.1972, BAS Misc. 79.
- Brachythecium austro-salebrosum* (C. Muell.) Kindb. East shore of Lake 5, alt. c. 24 m, leg. R. Webb, 18.iii.1972, BAS Misc. 80.
- Bryum algens* Card. Marble ridge to south of Foca Point hut, Thulla Point, alt. c. 30 m, leg. R. Webb, 8.iii.1972, BAS Misc. 81.
- Campylium polygamum* (B.S.G.) C. Jens. North shore of Lake 6 in Three Lakes Valley, alt. c. 30 m, leg. R. Webb, 18.iii.1972, BAS Misc. 78.
- Dicranoweisia antarctica* (C. Muell.) Kindb. Between Lakes 3 and 4, across the outflow from Lake 4, leg. R. Webb, 15.iii.1972, BAS Misc. 82.
- Pohlia cruda* var. *imbricata* (Card.) Bartr. Marble ridge to south of Foca Point hut, Thulla Point, alt. c. 30 m, leg. R. Webb, 8.iii.1972, BAS Misc. 84.

HEPATICAE

South Georgia

- Blepharidophyllum densifolium* (Hook.) Angstr. ex Mass. Wet flush, leg. J. R. Tallwin, 1972-73, BAS Misc. 102.
Cephaloziella varians (Gottsche) Steph. Wet flush, leg. C. J. Barrow, 1972-73, BAS Misc. 106.
Cephaloziella varians (Gottsche) Steph. Wet flush, leg. C. J. Barrow, 1972-73, BAS Misc. 108.
Leptoscyphus expansus (Lehm.) Grolle. Wet flush, leg. J. R. Tallwin, 1972-73, BAS Misc. 98.
Lophocolea willii Grolle. Wet flush, leg. C. J. Barrow, 1972-73, BAS Misc. 107.
Riccardia georgiensis (Steph.) Hässel. Wet flush, leg. J. R. Tallwin, 1972-73, BAS Misc. 99. ($n = 10$)
Riccardia georgiensis (Steph.) Hässel. Wet flush, leg. J. R. Tallwin, 1972-73, BAS Misc. 104. ($n = 20$)
Roivainenia jacquinotii (Mont.) Grolle. North side of King Edward Cove, alt. c. 8 m, GR 130 125, leg. R. I. L. Smith, c. 25.iii.1971, BAS Misc. 91.