A TAXONOMIC ASSESSMENT OF *Brachythecium* ON SOUTH GEORGIA

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ABSTRACT. A combination of statistical and qualitative discriminatory techniques has demonstrated the presence of six species of *Brachythecium* on the sub-Antarctic island of South Georgia. Their taxonomic limits have been defined and considered in relation to type and historical specimens. Earlier records of *B. subpilosum* (Hook. f. et Wils.) Jaeg. and *B. subplicatum* (Hamp.) Jaeg. have been confirmed, whereas *B. austro-glareosum* (C. Muell.) Kindb., *B. austro-salebrosum* (C. Muell.) Kindb., *B. glaciale* B.S.G. and *B. majusculum* M. E. Newton are new to the island. *B. georgico-glareosum* (C. Muell.) Kindb. and *B. skottsbergii* Card., previously reported from South Georgia, have been reduced to synonymy with *B. austro-salebrosum*. Cytological information for five of these species, *B. austro-glareosum* ($n = 13$), *B. austro-salebrosum* ($n = 10, 13$), *B. glaciale* ($n = 8$), *B. subpilosum* ($n = 13$) and *B. subplicatum* ($n = 13$), has been provided.

DESPITE the well-known vegetative variability of species of the genus *Brachythecium*, taxonomic emphasis must be placed almost exclusively on gametophytic characters because many species rarely complete their life cycles. Moreover, numerous species have been described as new without the benefit of the large samples that are required to assess such variation and this has led to a considerable amount of confusion, particularly in less well-known floras such as those of the Antarctic and sub-Antarctic. For instance, Clifford (1953), van Zanten (1971) and Robinson (1972) drew attention to inadequately defined austral species which had been described on the basis of very few specimens.

Steere (1961*b*) and Greene (1973) listed four species, *B. georgico-glareosum* (C. Muell.) Kindb., *B. skottsbergii* Card., *B. subpilosum* (Hook. f. et Wils.) Jaeg. and *B. subplicatum* (Hamp.) Jaeg., that had been reported from South Georgia. In addition to *B. antarcticum* Card. and its variety *cavifolium* Card., *B. austro-glareosum* (C. Muell.) Kindb., *B. austro-glareosum* var. *diffusum* Card., *B. georgico-glareosum*, *B. skottsbergii*, *B. subpilosum* and *B. turquetii* Card. have been reported from Antarctica (Steere, 1961*a*) but *B. subplicatum* is still unknown in the Antarctic botanical zone. As South Georgian and Antarctic taxa of *Brachythecium* show affinities with those of southern South America and Iles Kerguelen, the present study was carried out in an attempt to find satisfactory taxonomic limits for the island's taxa and, following examination of type material, to determine which species are present.

MATERIALS AND METHODS

A total of 509 South Georgian specimens of *Brachythecium* from the bryophyte herbarium of the British Antarctic Survey (at present on permanent loan to the Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland) was examined and found to be readily divisible into two groups, designated groups I and II, on the basis of leaf characters. At least in the decurrent parts of the leaves of group I, the cells are not arranged in distinct rows, being of variable shape and sometimes inflated. However, this type of cell is not always uniform throughout the alar region and in some specimens it merges above into a region of quadrate or rectangular cells that are regularly arranged in longitudinal rows. Conversely, the alar cells of group II are seriate, even within the leaf auricles when the latter are present, and they are uniformly quadrate or rectangular throughout. Plane leaf margins, rarely slightly revolute at the extreme base, are also typical of group I, whereas conspicuous recurvature of at least the basal part of the leaf margin is invariably associated with group II.

A random sample of 32 specimens from group I and 69 from group II was used initially for detailed measurement but, on the basis of evidence of a single unique specimen, a further 11 were selected for comparison within the larger sample. It is well known that stem and branch leaves of many species of *Brachythecium* differ widely and, therefore, in order to establish the

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smallest sample size consistent with statistical confidence, measurements were confined to stem leaves. The dimensions and ratios chosen to give an indication of leaf shape (Table I) were recorded for five leaves from each of five stems per specimen and were found to provide an adequate sample within 10 per cent confidence limits. Cell length was similarly recorded for 25 cells but, in this instance, taking five measurements from one leaf from each of five stems. Leaf-cell breadth was sampled only once in each of the above five leaves, since it was found to be less variable.

TABLE I. STEM LEAF CHARACTERS ASSESSED FOR THE SOUTH GEORGIAN SPECIES OF *Brachythecium*

Total leaf length (*a*)
Length from leaf insertion to widest point (*b*)
Leaf breadth at widest point (*c*)
Leaf length/breadth ratio (*a*/*c*)
Ratio of leaf length to position of widest point (*a*/*b*)
Nerve length (*d*)
Nerve length/leaf length ratio (*d*/*a*)
Leaf-cell length
Leaf-cell breadth
Leaf-cell length/breadth ratio

Most of the living material used for cytological investigation was collected during the Antarctic summer and stored deep-frozen without previous air drying. At intervals during the following year, it was thawed slowly in polythene bags and kept at low temperatures between about 0° and 5° C until regeneration occurred, which was usually within a fortnight. Although representatives of all the four available species survived this treatment, the overall failure rate was as high as *c.* 50 per cent. A small amount of material brought from South Georgia at 4° C produced more reliable regeneration and was also studied cytologically. Mitotic material was prepared for chromosome counting by the Feulgen staining technique described elsewhere (Newton, 1971) and used satisfactorily for other South Georgian bryophytes (Newton, 1972). Voucher specimens, detailed in the Appendix, have been preserved and incorporated in the bryophyte herbarium of the British Antarctic Survey as part of the BAS Misc. series.

The references to herbaria cited with the type specimens follow those recommended by Holmgren and Keuken (1974). Descriptions of the taxa recognized and an account of their distribution on South Georgia will be found in Newton (1979).

MORPHOLOGICAL VARIATION IN *Brachythecium* GROUP I

A scatter diagram of leaf and cell dimensions (Fig. 1) suggests a single normal distribution of variation within this group but, when qualitative characters of apex and auricles are added, two sub-groups can be distinguished. Amongst the plants with proportionately broader leaves, a small sub-group can be recognized with rounded leaf auricles and suddenly constricted leaf apices (sub-group Ia). Rounded leaf auricles are absent from the remaining specimens, in which the leaf tapers more gradually to a fine acumen, and these may be designated sub-group Ib. Discontinuity of variation was detected in none of the leaf dimensions assessed, although members of sub-group Ia are characterized by narrower laminar cells than those of sub-group Ib with similar leaf dimensions. The gross morphology of specimens belonging to the two sub-groups is also distinct, sub-group Ia consisting of strongly turgid plants with non-plicate leaves, whereas specimens belonging to sub-group Ib, although more variable, have leaves which are generally more or less spreading when wet and deeply plicate. It would appear, therefore, that two taxa of specific rank can be distinguished by a combination of gross morphological and microscopical characters.

MORPHOLOGICAL VARIATION IN *Brachythecium* GROUP II

It is evident from Figs. 2 and 3 that the distribution of variation in group II is not the normal bivariate type expected of a single taxon. Leaf length and breadth show strong positive corre-

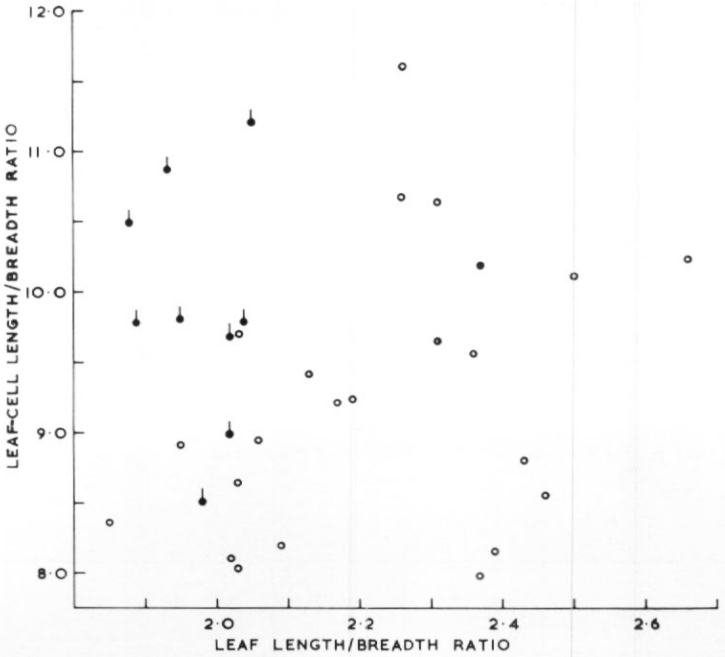

Fig. 1. Scatter diagram of suddenly constricted leaf apex (|), the presence of rounded auricles (●) or their total absence (○), in relation to variation in leaf-cell length/breadth ratio and leaf length/breadth ratio in South Georgian specimens of *Brachythecium* group I.

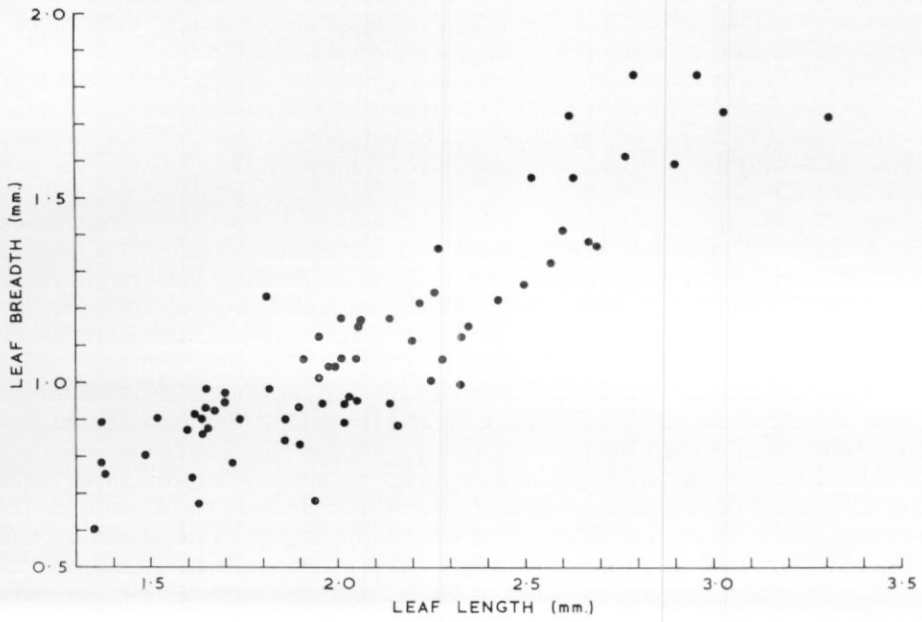

Fig. 2. Scatter diagram of variation in leaf breadth and leaf length in South Georgian specimens of *Brachythecium* group II.

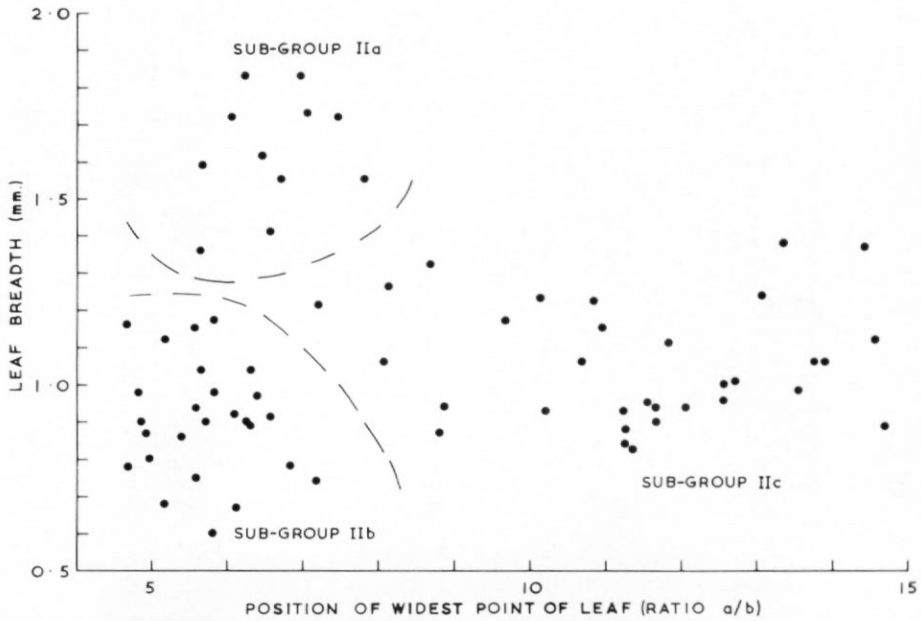

Fig. 3. Scatter diagram of variation in leaf breadth and the ratio of leaf length to the position of the widest point of the leaf (ratio *a*/*b*) in South Georgian specimens of *Brachythecium* group II.

lation and, although marked discontinuity does not occur, the asymmetrical concentration of variation towards the lower limits (Fig. 2) requires consideration. Either the variation was not unimodal or there was an unsuspected bias towards specimens with smaller leaves in what was believed to be a random sample. By introducing a ratio (Table I) to indicate the position of the widest point of the leaf (ratio *a*/*b*) for comparison with leaf breadth, three linear characters could be considered simultaneously. As shown in Fig. 3, 11 of the specimens (sub-group IIa) with low *a*/*b* ratios are clearly excluded from a tight cluster of points representing sub-group IIb, in which the *a*/*b* ratio is similar. However, unambiguous sub-division of the remaining specimens, those with more or less triangular leaves (sub-group IIc), is impossible using the dimensions studied.

A number of qualitative leaf characters was examined and two which display considerable diversity in the group as a whole firmly establish the existence of three discrete taxa (Fig. 4). Decurrent leaf auricles are, with a single exception, long and broad in sub-groups IIa and IIb whereas leaves of sub-group IIc are scarcely if at all decurrent. Sub-group IIa differs from IIb by the more or less sudden constriction of the leaf to form a sub-piliferous point, a character which is, however, shared by some members of sub-group IIc. The negative correlation between leaf-cell length and leaf-cell breadth in sub-group IIc (Fig. 5), contrasting with the positive correlation of these characters in sub-groups IIa and IIb, affords further confirmation of the separate identity of sub-group IIc.

As mentioned above, a single specimen occupies an anomalous position in the scatter displayed in Fig. 4. Not only does its slightly to non-decurrent leaf preclude it from inclusion in sub-groups IIa or IIb but leaf shape and growth form suggest a lack of affinity with sub-group IIc. In sub-group IIc, intricate mats are produced with only the lateral branches ascending, whereas both the stems and branches of the excluded specimen are erect or ascending. Leaves of this gathering are narrower than those of sub-group IIc, being ovate-lanceolate rather than triangular or ovate-cordate, and they are also atypical by virtue of the gradually as-

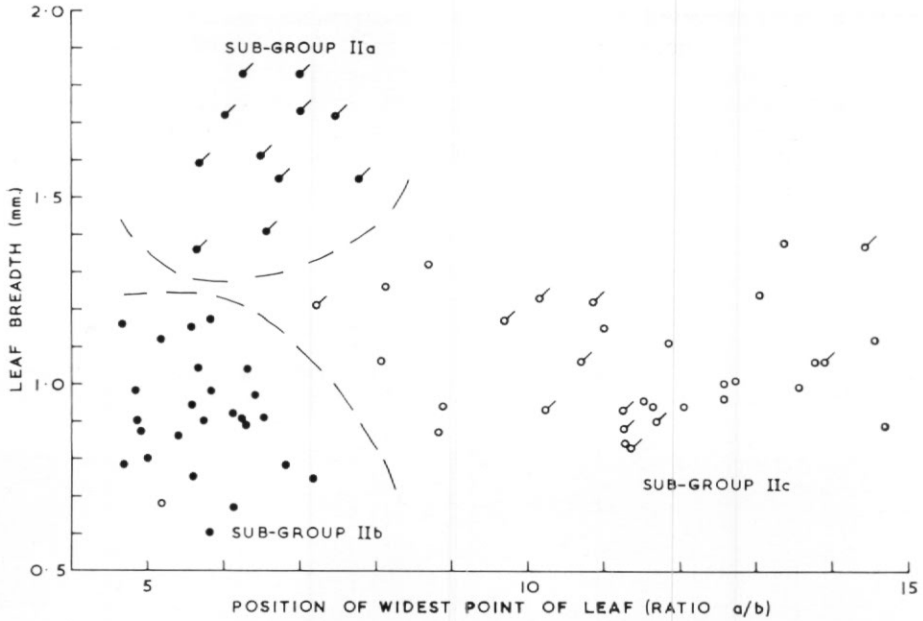

Fig. 4. Scatter diagram of decurrent leaves (●), non-decurrent leaves (○) and obtuse leaf apex with acumen (/) in relation to variation in leaf breadth and the ratio of leaf length to the position of the widest point of the leaf (ratio *a*/*b*) in South Georgian specimens of *Brachythecium* group II.

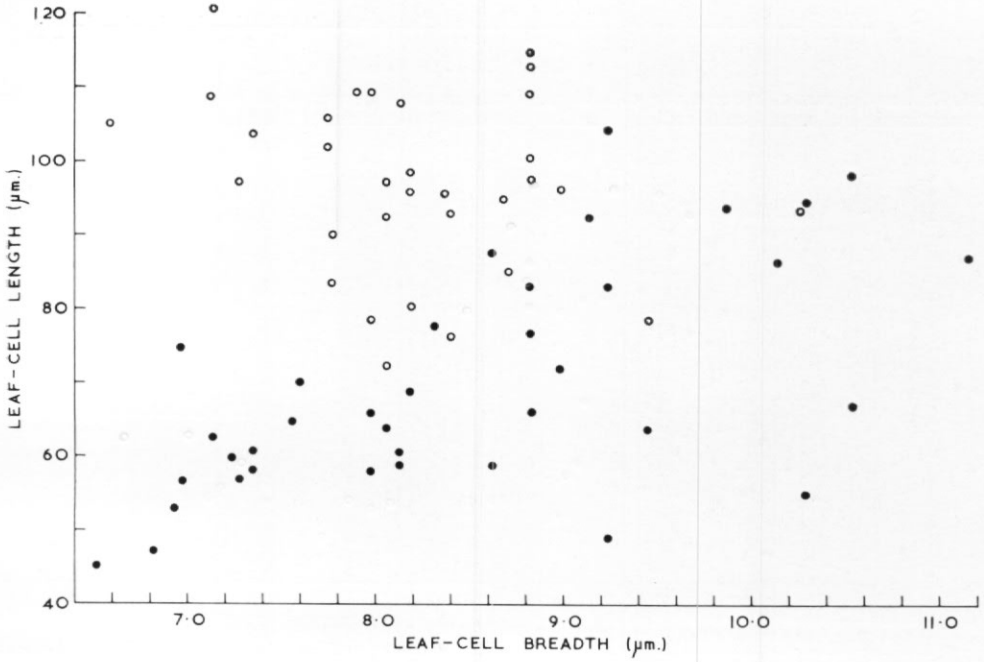

Fig. 5. Scatter diagram of variation in leaf-cell length and leaf-cell breadth in South Georgian specimens of *Brachythecium* sub-groups IIa and IIb (●) and sub-group IIc (○).

opposed to suddenly narrowed leaf bases. On further examination, the leaves were found to be revolute above the widest point and thus unique amongst the 101 specimens studied numerically, the remaining material available yielding 11 other specimens with this character. Although more were subsequently discovered in collections that became available later, the statistical comparison of these 11 specimens with randomly chosen material is considered to have been justified by the objective inclusion of all representatives known at that time. Their leaf dimensions (Figs. 6 and 7) are regarded as evidence of the uniformity and morphological isolation

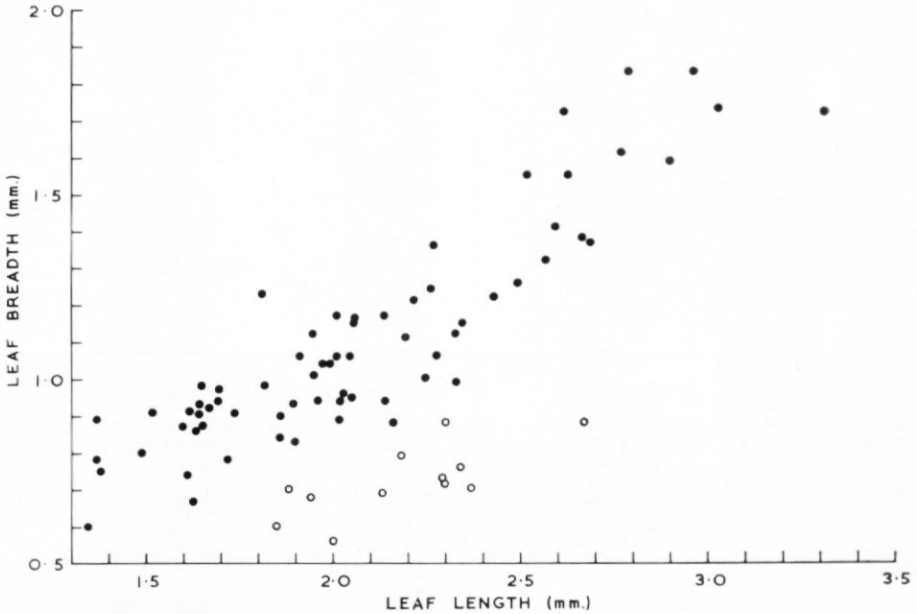

Fig. 6. Scatter diagram of recurvature, of lower leaf margin only (●) and of entire margin (○), in relation to variation in leaf breadth and leaf length in South Georgian specimens of *Brachythecium* group II.

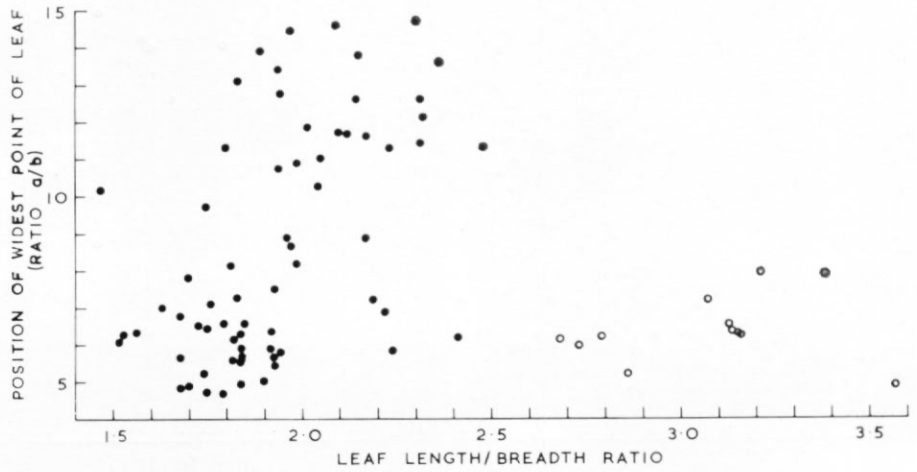

Fig. 7. Scatter diagram of recurvature, of lower leaf margin only (●) and of entire margin (○), in relation to variation in the ratio of leaf length to the position of the widest point of the leaf (ratio *a*/*b*) and leaf length/breadth ratio in South Georgian specimens of *Brachythecium* group II.

of this small group of plants with revolute leaf margins (sub-group IId). Insufficient collections are available to provide absolute proof of complete discontinuity in leaf-breadth variation between sub-groups IIc and IId (Fig. 6) and of complete disjunction of the ovate-lanceolate leaf shape in sub-group IId from extreme forms of sub-group IIb (Fig. 7) but, in view of the absence of specimens with equivocal leaf margins, it is considered that specific rank is warranted for each of these three taxa, as well as for sub-group IIa.

Cytology

Cytological information, although not exhaustive, has been obtained from five of the six morphologically defined groups of *Brachythecium* (Fig. 8) and tends to confirm some of the

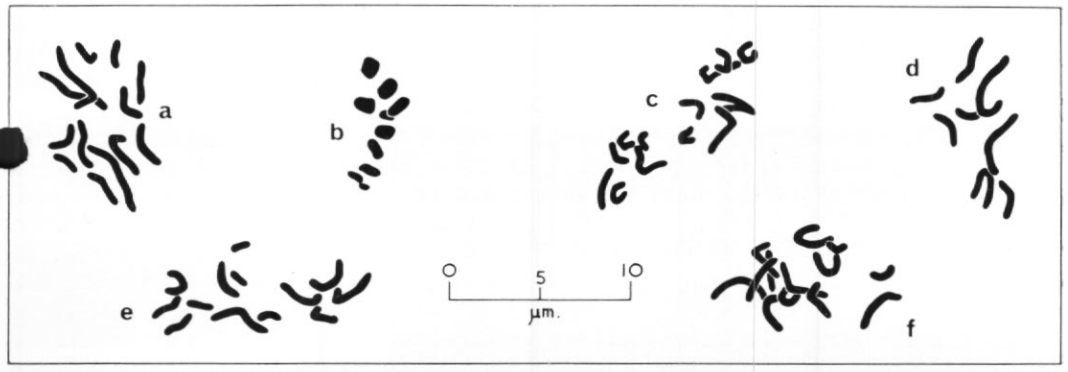

Fig. 8. Mitotic chromosome configurations.
a. *Brachythecium subplicatum* (sub-group Ia), $n = 13$; b. *B. austro-salebrosum* (sub-group Ib), $n = 10$; c. *B. austro-salebrosum* (sub-group Ib), $n = 13$; d. *B. glaciale* (sub-group IIb), $n = 8$; e. *B. subpilosum* (sub-group IIc), $n = 13$; f. *B. austro-glareosum* (sub-group IId), $n = 13$.

conclusions reached on morphological grounds. A chromosome count was obtained for only a single specimen of sub-group Ia, as $n = 13$ (Fig. 8a). Sub-group Ib is cytologically heterogeneous, one specimen with a gametophytic chromosome number of $n = 10$ (Fig. 8b) having been studied while three had $n = 13$ (Fig. 8c). Cytological evidence thus presents no additional means of discriminating between the two taxa within group I. However, evidence is available to support the treatment of sub-groups IIb and IIc as separate taxa, the haploid chromosome number of $n = 8$ being known in eight gatherings of the former (Fig. 8d) compared with $n = 13$ in two representatives of the latter group (Fig. 8e). Therefore, the available cytological data coincide with morphological characters in suggesting that sub-groups IIb and IIc are each more uniform than the variable sub-group Ib. The only available living specimen of sub-group IId was found to have $n = 13$ (Fig. 8f).

Identity and Synonymy of South Georgian Taxa

The present study has indicated the presence of six taxa of *Brachythecium* on South Georgia and, since each is characterized by a combination of two or more characters, it is proposed that each taxon should be awarded specific rank. All, except the species represented by sub-group Ib, have been defined within narrow limits by the characters examined. In sub-group Ib, the gametophyte shows a wide range of continuous morphological variation and it might be possible to subdivide the taxon further, for example by the use of sporophytic characters. Unfortunately, however, only one out of the 152 South Georgian specimens assigned to it was fruiting and, since capsules were also sparse amongst the South American and Antarctic herbarium material examined, it is necessary to recognize it as a very variable species. Detailed

illustrated descriptions of this and the remaining five more uniform species, together with habitat and distribution data and keys for their identification, will be given elsewhere (Newton, 1979) but their nomenclature and history are considered below.

Sub-group Ia. *B. subplicatum* (Hamp.) Jaeg.

As far as it has been possible to examine type material, specimens within this sub-group are indistinguishable from *Brachythecium subplicatum* (Hamp.) Jaeg., a species described by Hampe (*in* Müller, 1851, p. 363) as *Hypnum subplicatum* from material collected by Hooker (J. D. Hooker, BM, Falkland Islands, Antarct. Exp. 1839–1843, ex herb. Hampe) which was originally described by Wilson and Hooker (1847) as *Hypnum rutabulum* Dill. Linn. var. 5. Unfortunately, the type specimen is too small to justify its dissection for verification of the dioecious state reported by Hampe (*in* Müller, 1851, p. 363) and this remains the only point of difference from the autoecious South Georgian material. However, it is considered that this does not preclude its recognition as *B. subplicatum*, a species previously reported from the island by Cardot (1906, 1908). Neither the description by Wilson and Hooker (1847) nor the one by Hampe (*in* Müller, 1851, p. 363) drew attention to the leaf auricles as a diagnostic character although their presence in the type specimen has been confirmed. It would appear that this omission led Hébrard (1970) to describe a gathering of the present species as a new taxon in the genus *Calliergon*, a genus in which the leaf nerve, unlike that of *Brachythecium*, is typically percurrent. Examination of the holotype (J. P. Hébrard, PC, Crozet, 23.ii.1969) revealed no significant differences from *B. subplicatum*, and *C. joveti-asti* J. P. Hébrard is therefore reduced to synonymy.

Failure to recognize leaf auricles would also appear to account for other points of confusion associated with *B. subplicatum* in both the literature and herbarium specimens. For instance, Cardot (1906, 1908) drew a comparison with *B. skottsbergii*, a species lacking auricles and one which Dixon (1932) considered was probably a form of *B. subplicatum*. However, Dixon (*in scheda*) used the name *B. skottsbergii* to identify a South Georgian specimen (T. Tröim 77, BM, Grytviken, South Georgia, 4.iv.1933) that is identical to *B. subplicatum*. Conversely, although it is reasonable to assume that Dusén had observed the presence of auricles in specimens he referred to by the unpublished manuscript name of *B. alari-decurrens*, an examination of the material (P. Dusén 255, H, Fuegia austr., Rio Azopardo in paludosis, *c.* 600 m.s.m., 9.iii.1896, 2 specimens (1 s.n.) ex herb. V. F. Brotherus) indicated that he had failed to appreciate its identity with *B. subplicatum*.

In his description of *B. turgens* Dus., Dusén (1905) compared it with *B. cuspidarioides* Dus. but not with *B. subplicatum*. Cardot (1908) subsequently reduced *B. cuspidarioides* to synonymy with *B. subplicatum* and the type material of *B. cuspidarioides* (P. Dusén, S-PA, Patagonia occ. in valle fluminis Aysen in terra, 5.i.1897, 3 specimens ex herb. HJ. Möller) clearly supports such a view, although it is noteworthy that a specimen which might be considered a putative isotype (P. Dusén 389, BM, Patagonia occ. in valle fluminis Aysen in terra, 5.i.1897) does not belong to this species. After seeing type material of *B. turgens* (P. Dusén, S-PA, Tierra del Fuego, Rio Grande, 23.i.1896; P. Dusén 153, H, Fuegia australis prope Rio Grande in paludosis, 23.i.1896, 2 specimens ex herb. V. F. Brotherus), it is clear that *B. turgens* is synonymous with *B. subplicatum*, as recently proposed by Seki (1974).

Sub-group Ib. *B. austro-salebrosum* (C. Muell.) Kindb.

Examination of two specimens *ex museo botanico Berolinensi* (Naumann, BM, Kerguelens land, 1874; Naumann, S-PA, Kerguelensl., Betsys Cove, 1874, ex herb. P. Dusén), together with another that was seen by Müller (Fr. Naumann, BM, Kerguelen, xii.1874, ex herb. Müller) from the *locus classicus* of *Brachythecium austro-salebrosum*, a species first described by Müller (1884) as *Hypnum austro-salebrosum* from Iles Kerguelen, has shown that South

Georgian specimens belonging to sub-group Ib are similar, although the leaf dimensions and cell size of the Iles Kerguelen material approach the upper limits of the South Georgian specimens. The type specimen of *B. austro-salebrosum* (Ins. Kerguelen, *sine loco natali*, 12.i.75) has not yet been traced but there seems no doubt that this is the most appropriate name for the South Georgian material. The compression of the stems suggested by Müller (1889) has not been confirmed and it is clear that his reference to intermittent recurvature of the lower leaf margin of *B. austro-salebrosum* is also misleading, since it is not substantiated by authentic material and the extreme base shows a slight tendency to be revolute in only a few South Georgian specimens. It should be mentioned in this context that Müller's (1889) description of the alar cells as "solum majoribus magis quadratis nonnullis reticulata" has been interpreted to mean those referred to group I in the present paper.

Distinctions between *B. austro-salebrosum* and *B. euryodictyon* (C. Muell.) Kindb., which was also first described from Iles Kerguelen as a species of *Hypnum* (Müller, 1884), were based solely on gametophytic characters. The aquatic habit and denuded lower parts of the stems were considered to be diagnostic of *B. euryodictyon* but isotypes (Naumann, BM, S-PA, Kerguelensland, Betsys Cove, xii.1874, ex herb. P. Dusén) and three probable duplicates (BM, S-PA) are indistinguishable from aquatic forms of the South Georgian species, sub-group Ib, the slightly serrate leaf being perfectly acceptable within the present concept of *B. austro-salebrosum*. The two are, therefore, synonymous. Although *Hypnum euryodictyon* and *H. austro-salebrosum* were published simultaneously (Müller, 1884), the latter name is preferable since the former appears to refer to habitat variation. *B. euryodictyon* is therefore reduced to synonymy with *B. austro-salebrosum*.

Isotypes of *B. georgico-glareosum*, (Will, HBG, Quelle auf dem Hochplateau, Süd-Georgien, 14.vii.1883; Will, HBG, Landzunge, nicht Häufig, Süd-Georgien, 14.i.1883), a species first described as *Hypnum georgico-glareosum* C. Muell. from South Georgia by Müller (1890), can also undoubtedly be included with the specimens comprising sub-group Ib of the present study. Müller's only comparison of this species was with *B. austro-glareosum* and was probably suggested by his recognition of a revolute leaf margin in *B. georgico-glareosum*, although the specimens quoted above fail to substantiate his opinion. *B. georgico-glareosum* is here reduced to synonymy with *B. austro-salebrosum*.

Failure to appreciate the wide variation displayed by *B. austro-salebrosum* has led to a profusion of species based on extremes of this range. For instance, Cardot (1900, 1901) was unsure of taxonomic limits in Antarctic and sub-Antarctic specimens when he described *B. antarcticum* as distinct from South Georgian *B. georgico-glareosum* on the basis of larger, less imbricate leaves with plane margins and laxer areolation but duplicates of one of the syntypes (Racovitza 232a, BR, Canal de la Belgica: XI ème débarquement, sur les corniches de la falaise, 1.ii.1898; Racovitza 232a, H, Canal de Gerlache: XI ème débarquement, falaises, 1.ii.1898; Racovitza 232a, S-PA, Detroit de Gerlache: XI ème débarquement, 1.ii.1898) fail to endorse all these points. Although falling within the variation of South Georgian material of *B. austro-salebrosum*, the leaves of *B. antarcticum* are shorter and narrower than in the majority of the island's plants and are also smaller than those of the type specimens of *B. georgico-glareosum*. It is considered that *B. antarcticum* represents part of the range of *B. austro-salebrosum*, in which lax leaf areolation is often associated with shorter leaves, and is therefore reduced to synonymy, thereby confirming the opinion expressed tentatively by Cardot (1908). Similarly, type material of *B. antarcticum* var. *cavifolium* described by Cardot (1900, 1901) (Racovitza 215a, BR, H, Canal de la Belgica: I èr débarquement, á la surface de l'argile mêlée de guano, 26.i.1898; Racovitza 151a, BR, Canal de la Belgica: IX ème débarquement, sur les rochers humides, 29.i.1898; Racovitza 205d, BR, Canal de la Belgica: IX ème débarquement, sur les petites, terranes humides de la falaise, 29.i.1898; Racovitza 232a′, BR, Canal de la Belgica, XI ème débarquement, sur les corniches de la falaise, 1.ii.1898) is unexceptional in the context of South Georgian *B. austro-salebrosum* and is also regarded as synonymous.

A further species, *B. skottsbergii*, described from South Georgian material by Cardot (1906, 1908) was apparently considered to be intermediate between *B. antarcticum* and *B. georgico-glareosum* with regard to leaf shape and length, although leaf breadth is close to the upper limit shown by *B. austro-salebrosum* on the island. Since other characters displayed by two syntypes (C. Skottsberg 405, H, S-PA, South Georgia, Cumberland Bay, May Harbour, 2.v.1902; C. Skottsberg 407, S-PA, South Georgia, Cumberland Bay, Pot Harbour, 21.v.1902) conform with those of *B. austro-salebrosum*, *B. skottsbergii* is also reduced to synonymy with that taxon, a treatment which is in accord with Dixon's (1920) opinion of its taxonomic proximity to *B. antarcticum* var. *cavifolium*.

Sub-group IIa. *B. majusculum* M. E. Newton

The name *B. majusculum* has already been adopted and published (Newton, 1974) for the species delimited by sub-group IIa. Dusén (1903) was the first to use the epithet, though as a *nomen nudum* when naming specimens from southern South America but, because his specimens represent extremes of the species' variation as currently understood, a South Georgian holotype was selected.

Sub-group IIb. *B. glaciale* B.S.G.

As it was impossible to refer the specimens of this sub-group to any taxon known from the Southern Hemisphere, attention was turned to boreal members of the section *Reflexa* Broth. A syntype of *B. glaciale* (BM, Zwischen dem fauthorn in dem Wildgerst, ex herb. Schimper), first described by Bruch and others (1853), was found to have smaller than average leaves but to agree in all essential points with the specimens of sub-group IIb. It is therefore considered that the South Georgian specimens should be referred to this species, an opinion confirmed by Mr. A. C. Crundwell (personal communication).

B. glaciale is a clearly defined species presenting a narrow range of variation on South Georgia but it is regarded as highly variable in Europe (Mårtensson, 1956; Crundwell, 1959; Nyholm, 1965) and only separated with difficulty from a number of other species including *B. reflexum* (Stark.) B.S.G., *B. starkei* (Brid.) B.S.G. and *B. collinum* (C. Muell.) B.S.G. Of these, *B. starkei*, as recognized by Bruch and others (1853) and subsequent authors, is also consistent with the South Georgian species. However, Crundwell (1959) pointed out that the stem leaves are not or very slightly decurrent and the basal leaf margin is scarcely revolute, characters which were confirmed by the type material (Starke, BM, Silvia, 1808) and are unknown in sub-Antarctic material of sub-group IIb.

Although this taxon is a common constituent of the South Georgian flora, and is now known to occur in South America (A.D.L. Hoppe 52, AAS, Head of Strindberg/Frankei Glacier, Patagonia, 21.i.1973), it may be suggested that it has been overlooked in the Southern Hemisphere because of its resemblance to certain forms of plants belonging to sub-group IIc and to *B. majusculum*. These three species have been shown to be quite distinct, although critical in some respects, but it is evident that these differences were not apparent in the past. For example, it is surprising that Dixon, who was familiar with *B. glaciale* in Europe, identified a South Georgian specimen (O. Olstad 24, BM, Hystadhullet, South Georgia, 20.ii.1928, ex herb. H. N. Dixon) as *B. skottsbergii*, a very different species which has been reduced to synonymy with *B. austro-salebrosum* during the present study.

Sub-group IIc. *B. subpilosum* (Hook. f. et Wils.) Jaeg.

The specimens included in sub-group IIc were found to agree closely with the type specimen of *B. subpilosum*, a species described by Hooker and Wilson (1844) as *Hypnum subpilosum* (J. D. Hooker 165, BM, Hermite Island, Cape Horn, Antarct. Exp. 1839–1843, ex herb. Hooker), as well as with some probable duplicates (BM, Cap Horn, Ant. Exp., ex herb. R. J.

Shuttleworth; Wilson 165, BM, Hermite Isld., Cape Horn; J. D. Hooker, BM, Hermite Island, Cape Horn, Antarct. Exp. 1839–1843, ex herb. Hampe). Although the erect growth form implied by the method of pressing and sticking the Hermite Island specimens on herbarium sheets is not a feature of the South Georgian specimens, their leaf and leaf-cell dimensions, including proportions, are well within the established range of variation of South Georgian plants, the cell size lying within but close to the lower limits. Thus, it is possible to recognize sub-group IIc as *B. subpilosum*, a species previously reported from South Georgia by Cardot (1906, 1908) and Dixon (1920).

Although *B. subpilosum* clearly belongs to group II, as defined above, its history has been confused with species included here in group I. Mitten (1869), for example, regarded *B. subpilosum* and *B. subplicatum* as synonymous and, although Cardot (1905) recognized their separate identities, Brotherus (1925) classified the former with species that are reduced to synonymy with *B. austro-salebrosum* in this paper. However, a robust specimen of *B. subpilosum* (Hamilton 543, BM, South Georgia, 1919, ex herb. W. Lillie) was correctly determined by Dixon (1920), although later (*in scheda*) he gave it the manuscript name of *B. serribracteatum* Dixon with the intention, which was never carried out, of describing a new species. His notes on a herbarium specimen indicate that he intended to use as the holotype (Tonelli 13, BM, Dawson I., Fuegia, v.1910) a specimen which closely resembles two isotypes of *B. trachychaete* Dus. (P. Dusén A9, S-PA, Patagonia occident, Rio Aysen, 16.ii.1897), a species which Dusén (1905) separated from *B. subpilosum* on the basis of the former being slender. Although Dusén confused *B. subpilosum* with *B. subplicatum*, for example in a specimen labelled *B. subpilosum* (P. Dusén 105, BM, Chile australis ad Corral portum in rupibus litoreis, 6.vi. 1896, 2 specimens) which is *B. subplicatum*, there is some similarity between *B. trachychaete* and *B. subpilosum*. However, the more flaccid habit and prostrate growth form as well as very pronounced leaf serration are all characters which isolate *B. trachychaete* from *B. subpilosum* as known on South Georgia.

Sub-group IId. *B. austro-glareosum* (C. Muell.) Kindb.

The South Georgian specimens of this sub-group agree closely with *B. austro-glareosum*, a species first described as *Hypnum austro-glareosum* by Müller (1884) from material from Iles Kerguelen, a more complete description being provided later (Müller, 1889). An isotype (Naumann, S-PA, Kerguelensl., Betsys Cove, 1874, ex *museo botanico Berolinensi*) and probable duplicates (BM, H) all fall within the scatter of variation shown by specimens assigned to sub-group IId, which is noteworthy since the only comparisons made by Müller were with *B. glareosum* (Spruc.) B.S.G., *B. austro-salebrosum* and *B. albicans* (Hedw.) B.S.G. However, distinction from *B. austro-salebrosum* is emphasized by the fact that revolute leaf margins of plants on South Georgia and in the type specimens are invariably associated with an absence of irregularly shaped non-seriate alar cells, as well as by the independent distributions of variation displayed in Fig. 9.

As far as it is known on South Georgia, *B. austro-glareosum* is a uniform species varying only within narrow limits. While the leaf margin is usually almost entire, serrate specimens also occur and in some, for example Greene 2340, serration is more pronounced than it is in the type specimen. This is of particular interest since Cardot (1916) distinguished *B. gramontii* Card. from *B. austro-glareosum* by the former species' pronounced serration in the upper third of the leaf. Since it was found on examination that the type specimen of *B. gramontii* (Rallier du Baty, BM, Kerguelen) not only resembles *B. austro-glareosum* in this respect but also in other important respects including the presence of revolute leaf margins, *B. gramontii* is here included in the synonymy of *B. austro-glareosum*.

B. austro-glareosum var. *diffusum* Card., distinguished from the type variety by its looser growth form and more widely spaced leaves (Cardot, 1911), is not recognized in the present

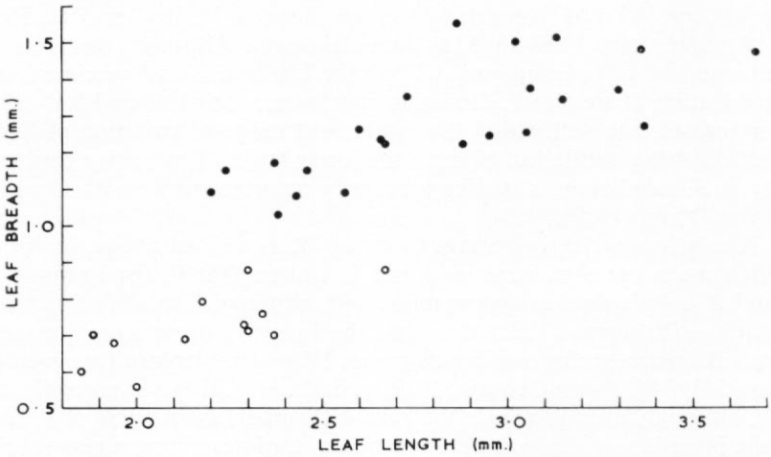

Fig. 9. Scatter diagram of variation in leaf breadth and leaf length in South Georgian specimens of sub-group Ib (●) and sub-group IId (*B. austro-glareosum*) (○).

treatment. Type material (Gain 249, H, Baie Marguerite, île Jenny, dans une grotte humide; BM, Baie Marguerite: île Jenny, dans une petite grotte humide, alt. 80 m., 30.xii.1909) does not warrant varietal status since it is indistinguishable in all its dimensions, although the growth form of the Helsinki specimen was found to be rather lax.

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APPENDIX

DETAILS OF SOUTH GEORGIAN SPECIMENS EXAMINED CYTOLOGICALLY

Brachythecium austro-glareosum (C. Muell.) Kindb. South Georgia, leg. J. Tallowin, 1972–73, BAS Misc. 64.
Brachythecium austro-salebrosum (C. Muell.) Kindb. Behind Shackleton House, King Edward Point, GR 133 124, leg. B. G. Bell, 27.ii.1972, BAS Misc. 50.

Brachythecium austro-salebrosum (C. Muell.) Kindb. Behind dam, King Edward Point, GR 133 124, leg. B. G. Bell, 27.ii.1972, BAS Misc. 60.

Brachythecium austro-salebrosum (C. Muell.) Kindb. Behind Grytviken whaling station, GR 132 124, leg. B. G. Bell, 28.ii.1972, BAS Misc 61.

Brachythecium austro-salebrosum (C. Muell.) Kindb. South Georgia, leg. J. Tallowin, 1972–73, BAS Misc. 63.

Brachythecium glaciale B.S.G. Echo Pass, GR 129 123, leg. B. G. Bell, 15.iii.1972, BAS Misc. 53.

Brachythecium glaciale B.S.G. By main stream on floor of Bore Valley, GR 132 125, leg. B. G. Bell, 28.ii.1972, BAS Misc. 54.

Brachythecium glaciale B.S.G. Behind Grytviken whaling station, GR 132 124, leg. B. G. Bell, 28.ii.1972, BAS Misc. 55.

Brachythecium glaciale B.S.G. Lower slopes of Brown Mountain, near Gull Lake, GR 131 123, leg. B. G. Bell, 1.iii.1972, BAS Misc. 56.

Brachythecium glaciale B.S.G. Junction Valley, south of Brown Mountain, GR 131 122, leg. B. G. Bell, 6.iii.1972, BAS Misc. 57.

Brachythecium glaciale B.S.G. Echo Pass, GR 123 130, leg. B. G. Bell, 15.iii.1972, BAS Misc. 58.

Brachythecium glaciale B.S.G. North side of Echo Pass, GR 125 123, leg. B. G. Bell, 15.iii.1972, BAS Misc. 59.

Brachythecium glaciale B.S.G. Echo Pass, GR 129 128, leg. B. G. Bell, 15.iii.1972, BAS Misc. 62.

Brachythecium subpilosum (Hook. f. et Wils.) Jaeg. Behind gully north of Aniline Island, Dartmouth Point, GR 136 120, leg. B. G. Bell, 28.iii.1972, BAS Misc. 49.

Brachythecium subpilosum (Hook. f. et Wils.) Jaeg. Behind gully north-east of Aniline Island, Dartmouth Point, GR 136 120, leg. B. G. Bell, 28.iii.1972, BAS Misc. 52.

Brachythecium subplicatum (Hamp.) Jaeg. Southern end of Bore Valley above Grytviken, GR 132 125, leg. B. G. Bell, 28.ii.1972, BAS Misc. 51.