PART II. THE TERRESTRIAL BOTANY OF THE TRISTAN DA CUNHA ISLANDS

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[Plates 35 to 42]

CONTENTS

1. Introduction

The islands of Tristan da Cunha, Inaccessible, Nightingale and Gough are alike in their climate and physiography, and also in their plant and animal life. They form a single biogeographical province, and the botany of all four islands will be dealt with here.

The biotas of remote islands have long been considered of unusual interest, especially since the classical studies of Darwin in the Galapagos group. To the earlier explorers, their biological productions were matters only of curiosity and some speculation, but since the publication of Darwin's *Origin of species* and Alfred Russel Wallace's *Island life*, it has been realized that insular biotas present features of outstanding biological, evolutionary and geographic interest. A very great deal of attention has therefore been concentrated upon studies of the plant life of many oceanic islands, especially in Hawaii (Hillebrand, 1888; Campbell 1933; Skottsberg 1940), Islas Juan Fernandez (Skottsberg 1953–56) and other 'high' islands in the Pacific (references in Merrill 1947); in the Macaronesian islands, Bermuda and St Helena (Wallace 1895; Hemsley 1885; and later references in Turrill 1953, 1959); and in the scattered islands of the Southern Ocean (references in Wace 1960). Although the Tristan–Gough islands share many of the classical features of island life (such as endemism, ecological disharmony, species poverty and radiation) with the better known tropical and sub-tropical archipelagoes, they have hitherto escaped the concentrated attention that has been given to many of the islands listed above. Because of their extreme remoteness, their inhospitable climate, and their rugged terrain, they have been little exploited by man, although Tristan has supported a resident human population since 1810. Their native biotas have so far escaped the widespread disturbance and devastation which has been visited upon St Helena, Hawaii, and many other islands as a result of human activities. Gough Island, the most remote of the group, is probably unique among the oceanic islands of the temperate zones in having a plant and animal life almost untouched by man. Nightingale and Inaccessible have also escaped major damage. This virtual absence of human interference in three of the four islands adds greatly to the biogeographic interest of the group.

2. History of botanical investigations

All the visits of botanists to the islands, or periods during which other substantial botanical collections have been made there by residents, are listed chronologically in table 1, which also notes the principal publications dealing with the vascular plants and the vegetation. Publications describing collections of lower cryptogams are listed under their phyla in table 2.

Dupetit Thouars was the first botanist to visit any of the islands, when he collected on Tristan in 1793. Between this date and 1937 there was a considerable amount of piecemeal collecting, but no botanists were in the islands for long enough to make anything approaching a comprehensive survey of the flora, although Hemsley (1885), Phillips (1913) and Christophersen (1934, 1937) all summarize the known floras of the islands they dealt with until the dates of their publications. Since 1937, two prolonged investigations of the flora and vegetation have been made—by the Norwegian Scientific Expedition of 1937–38, and by the Gough Island Scientific Survey of 1955–56. Between them, these expeditions covered all the islands of the Tristan–Gough group, in which they stayed for 4 and 7 months, respectively. The accounts of the island floras which follow, and the systematic lists of plants given in the Appendix A (p. 336) are based largely upon the papers resulting from these two expeditions, with the addition of some recent collections and observations made in the Tristan group by Dickson during the Royal Society Expedition of 1962.

The vegetation of Tristan main island has been described by Wace & Holdgate (1958), and of Gough Island by Wace (1961); but the only accounts of the vegetation on Nightingale and Inaccessible Islands, by Moseley (1875) and Hafsten (1951), are very superficial because Moseley was only on the islands for very brief periods and the description by Hafsten relies on secondhand knowledge of the observations made by members of the Norwegian Expedition. Summaries of the vegetation types on Tristan and Gough, taken from the above papers, will be given here for comparative purposes and to serve as a basis for Dickson's account of the effects of the recent Tristan eruption on the plant communities (Part IV). So little is known of the vegetation of Nightingale and Inaccessible

TABLE 1. THE PRINCIPAL VASCULAR PLANT COLLECTIONS MADE IN THE TRISTAN–GOUGH GROUP, WITH A LIST OF THE PUBLICATIONS DESCRIBING THEM OR THE VEGETATION OF THE ISLANDS

				islands on which collections were made (+), or for which plant lists or vegetation accounts have been published (*)			
number	date of visit	ship, or occasion of visit, collector and/or author	date of publication	Tristan	Inaccessible	Nightingale	Gough
1	1793 (Jan.)	A. Dupetit Thouars	1811	+*	—	—	—
2	1816–17 (Nov.–May)	*British Garrison* D. Carmichael	1819	+*	—	—	—
3	1852 (Nov.)	*H.M.S. Herald* J. MacGillivray and M. G. Milne	—	+	—	—	—
4	1873 (Oct.)	*H.M.S. Challenger*					
(a)		H. N. Moseley	1875, 1892	+*	+*	+*	—
(b)		W. B. Hemsley	1885	*	*	*	—
5	1904 (April)	*S.Y. Scotia* (Scottish National Antarctic Expedition) R. N. Rudmose Brown	1905, 1912	—	—	—	+*
6	1908–09	*Fishing and farming venture*					
(a)		P. C. Keytel	—	+	—	—	—
(b)		E. P. Phillips	1913	*	—	—	—
7	1922 (June)	*R.Y.S. Quest* (Shackleton–Rowett Expedition) G. H. Wilkins	1925	—	+	+	+*
8	1924–26	*Residents on Tristan* Rev. R. A. Rogers and D. Glass	1926	+*	+*	+*	—
9	1927 (June)	*William Scoresby* (Discovery Expedition) E. R. Gunther	1928	—	—	—	+*
10	1933 (Feb.)	*M.S. Thorshavn* (whaler)					
(a)		L. Christensen	—	—	—	—	+
(b)		E. Christophersen	1934	—	—	—	*
11	1934 (Nov.)	*M.S. Thorshammer* (whaler)					
(a)		E. Siggeson	—	+	—	—	—
(b)		E. Christophersen	1937	*	—	—	—
12	1937 (Mar.)	*H.M.S. Carlisle* R. A. Dyer	1939	+*	—	—	—
13	1937–38 (Dec.–Mar.)	*Norwegian Scientific Expedition*					
(a)		E. Christophersen	1939	+*	+*	+*	—
(b)		C. Christensen	1940	*	*	*	—
(c)		E. Christophersen	1940*a*, *b*	+*	—	—	—
(d)		E. Christophersen	1944	+*	+*	+*	—
(e)		U. Hafsten	1951	*	*	*	—
14	1955–56 (Oct.–May)	*Gough Island Scientific Survey*					
(a)		N. M. Wace and M. W. Holdgate	1958	+*	—	—	—
(b)		U. Hafsten	1960*a*, *b*	*	—	—	*
(c)		N. M. Wace	1961 (and in prep.)	—	—	—	+*
15	1956–58	*South African Weather Station* J. J. van der Merwe	—	—	—	—	+
16	1962 (Feb.–Mar.)	*Royal Society Expedition* J. H. Dickson	—	+	+	+	—
17	1963 (April–Dec.)	*Tristan Administration* H. G. Stableford	—	+	—	—	—

TABLE 2. PUBLICATIONS LISTING OR DESCRIBING NON-VASCULAR CRYPTOGAMS FROM THE ISLANDS OF THE TRISTAN–GOUGH GROUP

occasion of collection (table 1)	author, and date of publication	islands for which plant lists included			
		Tristan	Inaccessible	Nightingale	Gough
	BRYOPHYTA				
Musci					
1	Dupetit Thouars 1811	+	—	—	—
1, 3	Mitten 1875	+	—	—	—
4†	Hemsley 1885	+	+	+	—
5	Wright 1905	—	—	—	+
1, 3	Geheeb & Herzog 1910	+	—	—	—
5	Cardot 1912	—	—	—	+
7	Wilkins 1925	—	—	—	+
10†	Christophersen 1934	—	—	—	+
11†	Christophersen 1937	+	—	—	—
12	Dyer 1939	+	—	—	—
13†	Dixon 1960	+	+	+	—
14	Dalby (ined.*)	—	—	—	+
15	Bartram 1959	—	—	—	+
Hepaticae					
1	Dupetit Thouars 1811	+	—	—	—
1, 3	Mitten 1875	+	—	—	—
4†	Hemsley 1885	+	+	+	—
5	Wright 1905, 1912	—	—	—	+
7	Wilkins 1925	—	—	—	+
10†	Christophersen 1934	—	—	—	+
11†	Christophersen 1937	+	—	—	—
13, 14	Arnell 1958	+	+	+	—
14	Arnell (ined.*)	—	—	—	+
	ALGAE (almost entirely marine species)				
1	Dupetit Thouars 1811	+	—	—	—
4	Dickie 1874 Hemsley 1885 } same list	+	+	+	—
11†	Christophersen 1937	+	—	—	—
12	Dyer 1939	+	—	—	—
13†	Baardseth 1941	+	+	+	—
14	Chamberlain (1965)	—	—	—	+
13	Cleve-Euler 1949	+	+	+	—
13	Lindstet 1962	+	+	+	—
	LICHENS				
1	Dupetit Thouars 1811	+	—	—	—
4	Hemsley 1885	+	+	+	—
5	Darbishire 1905, 1912	—	—	—	+
7	Wilkins 1925	—	—	+	+
10†	Christophersen 1934	—	—	—	+
11†	Christophersen 1937	+	—	—	—
12	Dyer 1939	+	—	—	—
13	Mackenzie Lamb 1940 (*Placopsis*)	+	+	—	—
	des Abbayes 1940 (*Cladonia*)	+	+	+	—
14	James (ined.*)	+	—	—	+
	FUNGI				
1	Dupetit Thouars 1811	+	—	—	—
4	Hemsley 1885	+	+	+	—
5	Rudmose Brown 1905	—	—	—	+
10	Christophersen 1934	—	—	—	+
11	Christophersen 1937	+	—	—	—
12	Dyer 1939	+	—	—	—
13	Jørstad 1947	+	+	+	—
	Dennis 1955	+	+	+	—
	Reid 1955	+	+	+	—
	Singer 1955	+	—	—	—
14	Balfour-Browne (ined.*)	—	—	—	+

* Some identifications published in Wace (1961); all from Gough Island to be included in *The Plants of Gough Island.* Ed. Wace (in preparation).

† Summarized all previous lists.

Islands, that it has been thought worthwhile to include an account of the plant communities on Nightingale, based on a stay of 3 days (28 February to 2 March 1962) by Dickson; his two visits to Inaccessible Island were so short that little can be added to the accounts noted above, except for a list of the alien species (also incorporated in the appendix). Very few botanical photographs of Nightingale and Inaccessible Islands have been published previously: figures 18, plate 36; 27, plate 40; and 28, plate 41 show some of the principal plant communities on Nightingale Island, and figures 30, 31, plate 42 those of the West Point area of Inaccessible Island. Some studies have been made on the recent history of the vegetation in the islands: the collection of peat samples by the Norwegian Expedition and the Gough Island Survey have led to papers by Hafsten (1951, 1960*a*, *b*), who has produced pollen diagrams from Tristan (two sites), Nightingale and Gough Islands.

It is clear from the foregoing paragraphs and tables 1 and 2 that there is a considerable amount of published information on the plant life of the Tristan–Gough group. However, it has not hitherto been possible to synthesize this into a comprehensive account embracing all four islands and making comparisons between them. This paper attempts to summarize the present state of knowledge of the terrestrial plant life in all the islands, by workers who have between them covered the entire group. The data are here presented to emphasize the fields in which future work is especially needed. There are still many gaps in our knowledge of their native floras, and much critical taxonomic work on all groups is necessary. The following section will discuss the composition of the island floras, and seek to point out where these gaps lie. Enough is now known to enable contrasts to be drawn between the islands, and to discuss the origin, age and relationships of their flora and vegetation. The discussion of these topics will occupy the major part of the later sections.

3. The flora

The numbers of species of plants that have been recorded from the different islands of the Tristan–Gough group are set out in table 3. The figures have been derived from all the published accounts and certain unpublished herbarium collections, but especially from the descriptions of the collections made in the Tristan group by the Norwegian Expedition, and from those of the Gough Island Scientific Survey. Doubt about the taxonomic validity and native status of various species accounts for the lack of precise figures in some phyla, and it is obvious that the unevenness of collecting has given rise to many apparent differences between the size of the known floras in the several islands, especially amongst the lower cryptogams. These deficiencies in botanical knowledge will be discussed in the parts which follow. Systematic lists of the known terrestrial floras of all the islands are included in the appendix.

3·1. *Angiospermae*

There is no recent list of the flowering plants in the Tristan group, but a list of the Gough Island species is included in Wace (1961). Full accounts of the flowering plants of both the Tristan group (Christophersen) and Gough Island (Wace) are in preparation. The figures in table 4, which have therefore been derived from the work of a number of different authors over a considerable period of time, suffer from being based on a more uneven taxonomic treatment than those of the pteridophytes and bryophytes. Almost all botanists who have visited the islands have collected flowering plants, so that their total angiosperm flora is probably known fairly adequately (or at least represented in the existing collections, even if these have not been worked out taxonomically). But the lowland vegetation of the islands is extremely dense, and much of the terrain very rugged and almost inaccessible. It is therefore quite possible that such species as *Peperomia tristanensis*, or even small trees the size of *Sophora macnabiana* (which are known only from single valleys on Inaccessible and Gough Islands, respectively), may have a wider range in the islands than is at present known, and that other species of flowering plants may yet remain to be discovered. This observation applies with greater force to the less conspicuous cryptogams.

TABLE 3. THE NUMBERS OF SPECIES OF TERRESTRIAL PLANTS RECORDED FROM THE TRISTAN–GOUGH GROUP, WITH SOME MAJOR PHYSICAL CHARACTERISTICS OF THE ISLANDS

Figures for the number of species in the angiosperms are only approximate, due to taxonomic uncertainties. The numbers recorded for the lower cryptogams give no indication of the importance of these groups in the islands, since all are seriously under-collected. For a discussion of the state of the collections and the systematics of the different groups in the islands, see text, pages 277 to 286.

	whole group	Tristan	Inaccessible	Nightingale	Gough
area (sq. km.)	159	86	12	4	57
altitude (m)	—	2060 (6760 ft.)	*ca.* 777 (*ca.* 2000 ft.)	*ca.* 300 (*ca.* 1000 ft.)	910 (2986 ft.)
estimated age (millions of years)	—	1	6	18	6
angiosperms	124	114	45	22	43
native species	41	32	26	17	31
introduced species	*ca.* 83	*ca.* 82	19	5	12
pteridophytes	33	29	27	14	26
bryophytes	309	230	109	42	146
musci	149	121	31	19	66
hepaticae	160	109	70	23	80
lichens	49	31	4	9	24
fungi	*ca.* 92	*ca.* 60	*ca.* 20	*ca.* 12	*ca.* 20
total known terrestrial flora in the islands	*ca.* 600	*ca.* 450	*ca.* 205	*ca.* 100	*ca.* 250

Although most of the native flowering plants of the islands are in need of systematic study, the instability of nomenclature suggests that the monocotyledons are in general in a more confused state than the dicotyledons. This is confirmed by field experience. In particular, the genera *Scirpus* and *Agrostis* in the islands have had a considerable number of names applied to them. Some of these names have been described as endemic species, while the status of some of the plants in the islands is in doubt, and it is possible that hybridization between introduced and native species has occurred in *Agrostis*. Both genera are important in the insular vegetation, and are notably polymorphic. The flowering heads of *Scirpus* proliferate, and it is quite possible that it is reproducing subsexually, leading to a pattern of variation which it is difficult for orthodox systematic methods to encompass. In addition to *Agrostis*, several other grasses in the islands are in need of systematic work. Undescribed species of *Deschampsia* and *Glyceria* have been found in the collections from Gough Island (J. Lewis and A. Melderis, personal communication to N. M. W.), and these are probably present in the Tristan group also. It is not certain whether any species of *Festuca* is native to the group (the plant from Tristan that has been named *Festuca erecta* was sterile), and certain names used by Thouars (*Phalaris caespitosa* and *P. mollis*) and Carmichael (*Polypogon intermedius*) have not been used for any later collections or linked very statisfactorily to modern taxa.

Among the dicotyledons, the relationships of many island species to others elsewhere remains uncertain (see below), but the numbers of species in the islands appears to be more accurately known. The genera *Acaena*, *Nertera* and *Cotula*, each of which has several native species in the islands, are probably in need of close taxonomic study, and the number of species of *Callitriche* in the islands is problematical.

The status of a few flowering plants in the islands is doubtful. Although Dupetit Thouars made the first collections on Tristan before permanent human settlement there, all the islands had been visited and possibly lived on by sealing parties beforehand, and certain species may have been introduced by man which are here accepted as native. Conversely, a few species which are here regarded as introduced may have arrived independently of man. These species of doubtful status are:

probably native	probably introduced
Atriplex plebeia	*Centella asiatica*
Polypogon intermedius	*Calystegia sepium*[†]
	C. soldanella
	Scirpus cernuus
	Agrostis simulans

As yet, pollen analyses of the peat deposits (§4·7) have thrown no light on the true status of these species. Although the distribution of the species within the islands, and especially the absence of records of any of them (except *Calystegia sepium* and *Centella asiatica*) from the three smaller islands, suggests that they may all have been introduced by man on Tristan, it is best to regard their origin in the islands as uncertain at present. Several of the species are of doubtful taxonomic standing, and *Atriplex plebeia* and *Polypogon intermedius* are both names which were first used by Carmichael which have not been taken up by any later authors (except to be repeated in the check-list of Christophersen (1937)).

There are no endemic genera of flowering plants in the islands. About two-thirds of the native species have been described as 'endemic', either to several islands or the whole group ('group endemics') or else to single islands ('exclusive endemics'), but the true level of endemism is difficult to estimate due to the confused state of taxonomy of many of the native flowering plants. Many plants which Thouars described as new species due to lack of comparative material from other southern lands at the time, have simply been accepted as endemic by later workers, although they are often similar (if not identical) to widespread southern hemisphere temperate or South American species.

In cases of doubt, it is very much easier to describe any new-found plant from the islands as a new species, and *ipso facto* as 'endemic' to the islands (especially when remote islands are places where endemic species may be expected to be found), than it is to carry out laborious comparisons with collections from other southern lands whose floras may be inadequately represented in herbaria.

[†] Material of *Calystegia sepium* collected by Dickson from Inaccessible and by Keytel from Tristan has been identified recently as subspecies *americana* (Sims) Brummitt ined. by Dr R. K. Brummitt. The sub-species is a coastal plant widely distributed on the Atlantic coasts of temperate North and South America and occurs in the Azores and on the Cape Peninsula of South Africa. Perhaps the plant is best regarded as probably native.

The process of describing newly discovered species from the islands as endemic has continued with later workers, and it illustrates the need for a wider geographical view of all the insular floras of the Southern Ocean to assess their true relationships and the degree of divergence of their plants from those of the continents (Wace 1965).

The following species have at one time or another been described as 'endemic' to the islands. Many of them are listed alongside closely related species, which are known from elsewhere, and in which in some cases they have been included:

Tristan–Gough species described as endemic	similar species with a distribution outside the islands
Ranunculus caroli Christophersen	*R. biternatus* Sm.
Cardamine propinqua Carmichael	*C. glacialis* Forst.
Acaena sarmentosa (Thouars) Carmichael	*A. anserinifolia* (Forst. & Forst. f.) Druce
A. stangii Christophersen	
Callitriche christensenii Christophersen	*C. antarctica* Engelm.
Pelargonium acugnaticum Thouars	*P. grossularioides* (L.) Ait.
Hydrocotyle capitata Thouars	*H. leucocephala* Cham. & Schlecht.
Apium goughensis Wilkins	*A. australe* Thouars
Nertera assurgens Thouars	
N. holmboei Christophersen	
Cotula goughensis Rudmose Brown	
C. moseleyi Hemsley	
Gnaphalium pyramidale Thouars	
Chenopodium tomentosum Thouars	*C. ambrosioides* L.
Rumex frutescens Thouars	*R. cuneifolius* Campd.
Peperomia tristanensis Christophersen	*P. berteroana* Miq.
Rostkovia tristanensis Christophersen	*R. magellanica* (Lam.) Hook f.
Carex insularis Carmichael	
C. thouarsii Carmichael	
Uncinia brevicaulis Thouars	
U. gracilis Thouars	*U. compacta* R. Br.
Scirpus sulcatus Thouars	
S. thouarsianus Schult	
Agrostis media Carmichael	
A. carmichaelii J. A. & J. H. Schult	

We accept the species printed in bold type as endemics.

While it is undoubtedly true that the trend has been towards the abolition of many of the 'endemics' recognized by the earliest collectors, and this may perhaps be expected to continue with more collecting in southern lands, later workers (especially Christophersen) have recognized new endemic species. It is difficult for the non-specialist in the taxonomy of the different genera to make any valid estimate of the true incidence of endemism until much more critical taxonomic work has been done on the island floras by systematists who are familiar with the plants on the ground as well as in the herbarium. Under the conditions of relaxed competition in the species-poor insular ecosystems, it is possible that the native species have a higher ecological amplitude and are more polymorphic than their continental relatives. Taxonomic judgements based on small collections from the islands may therefore be of even less use in assessing relationships than they are in continental regions.

TABLE 4. THE ANGIOSPERMS OF THE ISLANDS

The figures indicate the numbers of families, genera and species recorded from the different islands, and from the Tristan–Gough group as a whole. The figures for the numbers of endemic species, which are given in brackets after the totals, are only approximate due to the uncertain taxonomic status of many species (see text, p. 279).

	whole group	Tristan	Inaccessible	Nightingale	Gough
Native plants					
number of families	18	15	13	10	16
genera per family	1·72	1·67	1·54	1·30	1·56
number of genera	31	25	20	13	25
species per genus	1·39	1·28	1·30	1·38	1·24
number of species	41 (15)	32 (12)	26 (10)	17 (9)	31 (11)
species on several islands	30 (12)	28 (11)	25 (9)	16 (8)	26 (10)
species on only one island	11 (3)	4 (?1)	1 (1)	1 (1)	5 (1)
Introduced plants					
number of species	*ca.* 83	*ca.* 82	19	5	12
total number of species of flowering plants recorded from the islands	124	114	45	22	43

Out of a total native angiosperm flora of about forty species, the twenty-five listed above have at one time or another been called 'endemic' to the islands. Between the view that would accept them all as endemic at the specific level, and the view that would accept only the twelve species which have not been compared to (or included in) others occurring outside the islands, it will be impossible to judge until the matter is resolved by taxonomic study often involving wholesale revisions of southern genera. Estimates of the incidence of endemism in the flowering plants may thus be said to range from thirty to sixty percent of the known native flora. The selection of the fifteen species of 'good' endemics, as noted in the appendix and included in heavier type in the list above, is based on our acquaintance with the plants and their relatives both in the islands and in the herbarium; but this estimate (36 % of the known native angiosperm flora) must remain tentative for the reasons already stated. This difficulty of estimating the degree of endemism is only a particular case of the general need for critical revisions to be made in almost all the southern circumpolar insular flowering plants (Greene & Greene 1963; Wace 1965).

3·2. *Pteridophyta*

A full account of the pteridophytes of the Tristan group, which was based on the Norwegian Expedition collections, but also included previous records from the three northern islands, was published by Christensen (1940). This list, together with the collections made up to 1956 on Gough Island (Wace 1961), forms the basis of the list of pteridophytes in the appendix and the figures in table 5. Although further species may remain to be discovered in the islands, the pteridophytes are probably the most completely known and best understood taxonomically of the major plant groups. However, considerable doubt exists about the status of various species. For instance, *Adiatum poiretii* is considered as endemic tentatively by Christensen (1940) and with confidence by Pichi-Sermoli (1957). The matter is thought by Tryon (1964) to be unresolved. All species present on the islands are considered to be native there, although *Azolla* on Inaccessible Island is possibly a recent arrival (Christensen 1940), and has not yet been found on any of the other islands.

The proportion of endemic species is probably similar in the pteridophytes (42%) to that in the flowering plants (*ca.* 36%) in so far as any reliance can be placed upon the estimate for the flowering plants in their present taxonomic state.

TABLE 5. THE PTERIDOPHYTES OF THE ISLANDS

The figures indicate the numbers of species recorded from the islands. The numbers of endemic species, as recognized by Christensen (1940), are given in brackets after the totals.

	whole group	Tristan	Inaccessible	Nightingale	Gough
Lycopodiales	3 (2)	3	2	1	3
Ophioglossales	1 (0)	1	—	—	1
Salviniales	1 (0)	—	1	—	—
Filicales	28 (12)	25	24	13	22
total numbers of species of pteridophytes recorded from the islands	33 (14)	29 (14)	27 (13)	14 (8)	26 (12)
on several islands	27 (13)	27 (13)	25 (13)	14 (8)	24 (12)
on only one island	6 (1)	2 (1)	2 (0)	0 (0)	2 (0)

3·3. *Bryophyta*

The considerable number of bryophytes is one of the striking features of the Tristan–Gough flora. In all, *ca.* 300 species have been recorded from the islands (table 6). This figure is based mainly on the accounts of the mosses (Dixon 1960) and the hepatics (Arnell 1958) which were collected by the Norwegian Expedition in the Tristan group, but also includes the unpublished identifications from Wace's collections on Gough Island, and species listed in a paper by Bartram (1959) describing another collection from there. In addition, some collections remain unnamed in herbaria. For example, there are about forty gatherings of mosses made by Wace on Gough Island which have not yet been named.

But despite the large numbers of known species, and even taking the unnamed collections into account, there are undoubtedly many more species to be discovered on the islands, and more collecting by specialists is necessary before a reasonably complete picture of the bryophyte flora is obtained. This situation is only a particular case of the poor state of bryological knowledge of the southern hemisphere islands, which is only now being rectified, and can be illustrated by the following figures. Ridley (1930) gave the numbers of bryophyte species then recorded from various islands, including Juan Fernandez and the Tristan group. The former islands then had 15 known hepatics and 23 mosses, and the latter 20 hepatics and 23 mosses. Today the numbers known are:

	Islas Juan Fernandez	Tristan–Gough Islands
mosses	150 (Bartram 1957)	149 (totals derived from appendix,
hepatics	147 (Skottsberg 1956; Arnell 1959)	160 q.v. for sources)

The material which led to these great increases was collected by botanists who were compelled to give much less attention to bryophytes than the large numbers of species deserved. In the Tristan–Gough group, the Royal Society Expedition of 1962 was the first to include a bryologist, and more field observations by trained bryologists will undoubtedly lead to further discoveries and taxonomic re-assessments which may alter the present figures of numbers of bryophytes very markedly.

TABLE 6. THE BRYOPHYTES OF THE ISLANDS

The figures indicate numbers of species recorded from the islands. The numbers of endemic species are given in brackets after the totals.

	whole group	Tristan	Inaccessible	Nightingale	Gough
MUSCI					
Sphagnales	4	1	1	0	4
Andreaeales	7	6	0	0	3
Bryales	131	108	35	18	56
Polytrichales	7	6	3	1	3
total number of the species in the islands	149 (64)	121 (51)	39 (13)	19 (7)	66 (23)
on several islands	64 (23)	61 (19)	34 (10)	18 (6)	47 (18)
on only one island	85 (41)	60 (32)	5 (3)	1 (1)	19 (5)
HEPATICAE					
Anthocerotales	3	2	1	0	1
Jungermanniales	128	88	58	18	64
Metzgeriales	24	15	8	2	13
Marchantiales	5	4	3	3	2
total number of hepatic species in the islands	160 (22)	109 (18)	70 (8)	23 (1)	80 (7)
on several islands	76 (8)	70 (7)	59 (7)	22 (1)	47 (5)
on only one island	84 (14)	39 (11)	11 (1)	1 (0)	33 (2)
total number of species of bryophytes recorded from the islands	309 (87)	230 (69)	109 (21)	42 (8)	146 (31)

Nevertheless, the present state of knowledge has already revealed several characteristics of the islands' bryophyte flora, and some important differences between that of the various islands in the group. A marked feature of the moss flora is the abundance and ecological importance of *Campylopus*, *Dicranoloma*, *Trematodon*, *Thysanomitrium* (Dicranaceae), *Breutelia* (Bartramiaceae), *Ptychomnion* (Ptychomniaceae) and *Thuidium* (Thuidiaceae). *Rhacomitrium lanuginosum* and *Drepanocladus uncinatus* are very abundant on the Peak of Tristan main island. A feature of the hepatic flora is the large number of leafy species which are epiphytic on the trunks of *Blechnum palmiforme* and *Phylica arborea* in the fern bush vegetation. However, there appear to be no minute bog hepatics associated with sphagna in the ombrogenous bogs. *Lophocolea*, with twenty-nine species known from the group, is the most prolific genus in the islands, and most of its species are epiphytic. *Jamesoniella* is an important genus ecologically in wet heath communities on all the islands, and is one of the principal components of soligenous bogs on Gough Island. Sphagna show a greater taxonomic variety on Gough Island (from where four species are recorded) than in the Tristan group (where only a single species is known): this difference is probably accounted for by the wetter conditions and flatter upland topography on Gough, giving rise to larger areas of bog than on Tristan (see below).

There are no endemic genera of bryophytes on the islands, and estimates of specific endemism of the mosses and the hepatics differ substantially (43 % of mosses, 14 % of hepatics). It is impossible to judge how far this is due to any real differences in the divergence of the two groups from their continental relatives, or how far it is due to a different interpretation of specific criteria by the different systematists. The figure for endemism in the mosses is close to that for the vascular plants.

3·4. *Algae*

A systematic and ecological account of the marine algae of the Tristan group has been given by Baardseth (1941), who was a member of the Norwegian Expedition and the first cryptogam specialist to visit the islands. The littoral diatoms collected by Baardseth were described by Cleve-Euler (1949) and the marine Cyanophyceae by Lindstet (1962). Systematic and ecological accounts of the Gough Island seaweeds await publication (Chamberlain 1965; Chamberlain, Holdgate & Wace, in preparation).

While the seaweeds of the islands are known in outline, and a high proportion of the species present has probably been collected, the terrestrial and freshwater algae are almost wholly unknown. There are no published records of terrestrial or freshwater species, and only a single generic record—*Trentepohlia*, which is conspicuous on Gough Island (Wace 1961). Unpublished generic identifications of Gough Island collections, by Messrs R. Ross and P. James of the British Museum (Natural History) are:

Chlorophyceae:	*Ulothrix*	Cyanophyceae:	*Gleocapsa*	both amongst lichens
Bacillariophyceae:	*Achnanthes*		*Scytonema*	
	Frustulia			
	Pinnularia			

There are apparently no desmids in the Gough Island collections (Ross, personal communication), although some effort was made to collect from bog habitats in which they might be found, because of their absence from Antarctic regions (Fritsch 1935, p. 360).

Algae were found by Dickson to be growing on wet blocks of lava formed by the recent eruption on Tristan (Part IV). The main growth was a species of *Stigeoclonium*, perhaps *S. tenue* Kuetzing. There were twenty species of diatoms amongst the filaments. The following algae were gathered from rocks in the stream which splashes on to the new lava: *Oedogonium* sp., *Spirogyra* sp., *Zygnema* sp. and a species of *Nostoc*, perhaps *N. fuscescens* F. E. Fritsch (all were identified by Mr E. A. George). Mr J. R. Carter has recognized about sixty diatoms from this gathering (Part IV, §7). The only other alga collected by Dickson was the robust blue-green *Schizothrix cuspidata* W. and G. G. West which grew by the side of a waterfall at *ca.* 600 m in Council Gulch on Tristan.

Amongst the marine algae of the Tristan group, Baardseth (1941) recognized three species of Rhodophyceae (*Delesseria minor*, *Gonimocolax corymbosa* and *Neuroglossum multilobum*) so distinct as perhaps to represent new genera. He considered about 40 % of the seaweeds to be endemic species. Although some algae form a very conspicuous element of the islands' vegetation (notably *Macrocystis pyrifera*, *Iridaea* spp. and *Durvillea antarctica* around the coasts), only passing reference will be made to the algae in this account and no list of them is included in the appendix.

3·5. *Lichens*

The lichens are the most neglected group of the conspicuous terrestrial plants in the islands. Systematic accounts of only two genera—*Cladonia* (des Abbayes 1940) and *Placopsis* (Mackenzie Lamb 1940) have been compiled from the collections made in the Tristan group. No lichenologist has ever visited the islands, and the records of other genera which are listed in the appendix are names applied to the gatherings of various expeditions in which no particular effort was directed towards collecting lichens.

TABLE 7. NUMBERS OF SPECIES OF FUNGI RECORDED FROM THE ISLANDS

Only some flowering plant parasites, and forms with conspicuous fruiting bodies in the Ascomycetes and Basidiomycetes have been collected. There are no records of Myxomycetes or Phycomycetes from the islands. The numbers of species quoted give no indication of the size of the fungus flora, or of the importance of the different groups represented. A full list of all recorded species is given in the appendix.

collection (see table 1)	systematic group, and author responsible	whole group	Tristan	Inaccessible	Nightingale	Gough
	ASCOMYCETES					
11	Christophersen 1937	1	1	—	—	—
13	Jørstad 1947	2	1	2	—	—
13	Dennis 1955	24	22	3	1	—
14	Balfour-Brown, ined.	3	—	—	—	3
	totals	30	24	5	1	3
	FUNGI IMPERFECTI					
11	Christophersen 1934	2	—	—	—	2
13	Jørstad 1947	6	2	4	2	—
14	Balfour-Brown, ined.	*ca.* 6	—	—	—	*ca.* 6
	totals	*ca.* 12	2	4	2	*ca.* 8
	USTILAGINALES					
13	Jørstad 1947	3	2	1	1	—
	UREDINALES					
11, 13	Jørstad 1934, 1947	13	10	3	1	4
	APHYLLOPHORALES					
5	Rudmose Brown 1905	1	—	—	—	1
13	Reid 1955	8	7	—	2	—
14	Balfour Brown, ined.	2	—	—	—	2
	totals	11	7	—	2	2
	AGARICALES					
13	Singer 1955	18	(individual islands not specified)			
14	Balfour Brown, ined.	*ca.* 7	—	—	—	*ca.* 7
		ca. 24	+	+	+	*ca.* 7
	GASTEROMYCETALES					
13	Reid 1955	1	1	—	—	—
	total number of species recorded from the islands	*ca.* 92	*ca.* 60	*ca.* 20	*ca.* 12	*ca.* 20

It is certain that a considerable number of new records for the islands could be obtained by an expert examination of existing herbarium collections (about twenty-five gatherings of lichens from Gough Island, and an unknown number made by the Norwegian Expedition in the Tristan group, remain unnamed, for example). No reliable estimate of the size of the lichen flora in the islands can be arrived at until collections are made by specialists there. Because of this situation, no table of the lichen figures listed in table 3 is included here, but all extant records are listed in the appendix. A similar difficulty in assessing the size and taxonomic relationships of the lichen flora of Islas Juan Fernandez has been commented on by Skottsberg (1956), and the whole situation is aggravated by the present world-wide shortage of systematists working on lower plants (Corner *et al.* 1963), especially those with experience of southern hemisphere species.

3·6. *Fungi*

A number of papers have been published by specialists in the systematics of various groups of fungi, describing the collections which have been made in the Tristan group by the Norwegian Expedition. The authors are cited in table 7, against the groups with which they have been concerned. The total number of species has been derived by including the few named gatherings of collections made previous to the Norwegians, in addition to the unpublished identifications of Wace's collections from Gough Island. A list of all the fungi recorded from the islands is set out in the appendix.

Despite the considerably greater attention given to the fungi, as compared to the terrestrial algae or the lichens, the present knowledge obviously gives few indications of the size or the relationships or origins of the fungus flora as a whole. No mycologist has ever collected in the islands. Undoubtedly, a great many species remain to be discovered there.

3·7. *Floras of the different islands*

Out of the total known vascular flora of about seventy-four species native to the group, twenty-eight grow on all four islands:

Phylica arborea
Acaena sarmentosa
Callitriche christensenii
Apium australe
Nertera depressa
Gnaphalium pyramidale
Empetrum rubrum
Chenopodium tomentosum
Carex insularis
C. thouarsii
Uncinia compacta
Scirpus sulcatus
S. thouarsianus
Spartina arundinacea
Lycopodium insulare
Asplenium erectum
A. obtusatum
Blechnum palmiforme
B. penna-marina
Dryopteris aquilina
Elaphoglossum laurifolium
E. succisifolium
Grammitis magellanica
Histiopteris incisa
Hypolepis rugosula
Thelypteris tomentosa
Vittaria vittarioides
Hymenophyllum aeruginosum

A further fourteen vascular plants are absent only from Nightingale Island:

Acaena stangii
Hydrocotyle capitata
Lagenophora nudicaulis
Rumex frutescens
Uncinia brevicaulis
Deschampsia sp.
Lycopodium diaphanum
Hymenophyllum peltatum
Adiantum poirettii
Asplenium alvaradense
Blechnum australe
Elaphoglossum hybridum
Gymnogramma cheilanthoides
Rumohra adianteformis

Further collecting and taxonomic study will probably extend the ranges of many species within the islands, and it is probable that a number of the species listed above as being absent from Nightingale Island will be discovered there. The presence of more than a third of the native vascular plants in all the islands, justifies the inclusion of them all in a single phytogeographic province.

It is notable that so far as is known, the only other species of native vascular plant which occurs on three of the islands only (in addition to the fourteen Nightingale absentees above) is *Nertera assurgens*, which is not known from Gough Island. With this single exception, all the vascular plants which occur throughout the Tristan group, also reach Gough Island. This again emphasizes the essential unity of the island floras.

Seven species of native vascular plants which are known from Tristan and Gough have not yet been found on the two smaller islands. To some extent this may be due to taxonomic uncertainties (e.g. *Agrostis* spp.) and insufficient collecting. However, these are species typical of the montane and heath communities which are poorly represented on Inaccessible, and lacking from Nightingale. They are:

Ranunculus caroli
Cardamine glacialis
Rostkovia tristanensis
Agrostis carmichaelii
Agrostis media
Lycopodium magellanicum
Ophioglossum opacum

Another five species are known from Tristan and Inaccessible Islands only:

Pelargonium grossularioides
Chevreulia sarmentosa
Elaphoglossum obtusatum
Athyrium medium
Trichomanes angustatum

while *Nertera holmboei* has been described as endemic to Inaccessible and Nightingale Islands, and has not been found on Tristan or Gough; and a species of *Glyceria* which was discovered in 1956 on Gough Island is apparently present on Inaccessible, but unknown from the other islands. In all, fourteen native vascular plants are confined to two islands in the group, so far as is known at present.

Seventeen species of native vascular plants are known only from single islands in the group, but the taxonomic status of some of these is in doubt. Gough Island possesses the largest number in this category:

Tristan da Cunha	Inaccessible	Nightingale	Gough
Atriplex plebeia	*Peperomia tristanensis*	*Cotula moseleyi*	*Sophora macnabiana*
Agrostis sp. (cf. *bergiana*)	*Azolla filiculoides*		*Cotula goughensis*
Festuca sp. (cf. *erecta*)	*Asplenium platybasis*		*Tetroncium magellanicum*
Polypogon intermedius			*Agrostis* sp. (cf. *magellanica*)
Asplenium monanthes			*Poa flabellata*
Elaphoglossum insulare			*Dryopteris paleacea*
			Polystichum mohroides

It is notable that some of these are elsewhere sub-tropical to tropical in range (*Peperomia*, *Azolla*), whereas several of the Gough Island species are elsewhere sub-Antarctic in range (*Tetroncium*, *Poa flabellata*, *Polystichum mohroides*—see below). But Gough Island is distinguished from the other islands, not so much because of the size of the sub-Antarctic element in its flora, but because of the ecological importance of *Poa flabellata*, *Agrostis* cf.

magellanica and (to a lesser extent) *Tetroncium magellanicum* in the island vegetation. Judged by the number of species in common, Gough resembles Tristan more closely than Tristan resembles any of the other islands in the group (figure 14).

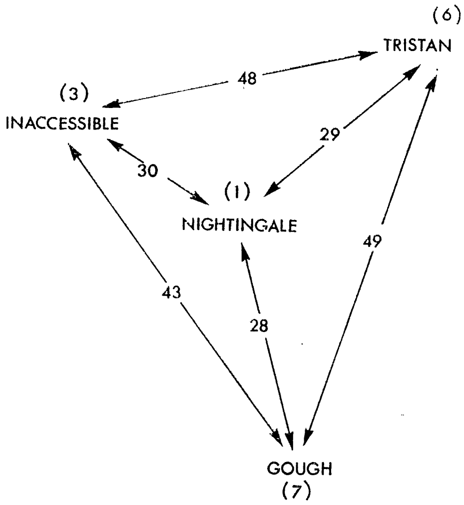

FIGURE 14. Numbers of species of native vascular plants common to the different islands in the Tristan–Gough group. Numbers of species which are only known from single islands are shown in brackets.

Colgan's 'index of floral diversity' (Praeger 1911) is a convenient method of expressing numerically the floral relationships between pairs of islands, irrespective of their different areas. The index for any pair of islands, A and B is

$\frac{a+b}{a+b+x}$, where a = the number of species on A only,
b = the number of species on B only,
x = the number of species common to both the islands.

The indices as calculated for all the native vascular plants between the different islands of the group, arranged in the order of their increasing floral diversity are:

	vascular plants	flowering plants	pteridophytes
Tristan and Inaccessible	0·27	0·34	0·19
Tristan and Gough	0·29	0·375	0·23
Inaccessible and Gough	0·36	0·42	0·29
Inaccessible and Nightingale	0·44	0·40	0·45
Nightingale and Gough	0·53	0·59	0·46
Tristan and Nightingale	0·54	0·56	0·52

The figures show that Nightingale differs somewhat from the other islands, but this is principally due to its small size and the ecological differences already mentioned. The diversity of the different islands in respect of the pteridophytes is lower than in respect of the flowering plants, and this is probably related to the greater ease of pteridophyte dispersal (see below).

Williams (1944, 1947) has shown that it is possible to calculate the numbers of species that might be expected to be found in common to pairs of islands having different areas, assuming that their floras are random samples of the same population. Although the assumption is necessary that the average density of individuals on each island is proportional to its area (and this may not be acceptable for Tristan, with its sparsely vegetated cone as compared to the more uniform cover on the smaller islands); the data are given in figure 15 because they give some indication whether the vascular floras of the individual islands have been derived from a common source. It is seen from the large percentages that most of the vascular flora has probably been recruited from the same areas. The occurrence of some figures over 100 % suggests that much of the individual island floras are derived from other islands, and that the spread of species within the group is at least as important in the build-up of their floras as the independent colonization of the different islands from a distance. A few observations on the movements of marked birds between the islands (Holdgate, Part III; Swales 1965) supports this idea. The higher percentages for the pteridophytes than for the flowering plants may be due to their greater dispersive efficiency either between the islands or from outside, as remarked above. The data given in figure 15 must be regarded as provisional because of the uncertain taxonomy on which they are based, and under-collection on the smaller islands (see above). Because of insufficient data, it is not yet possible to make worthwhile comparisons on a similar basis for the lower plants.

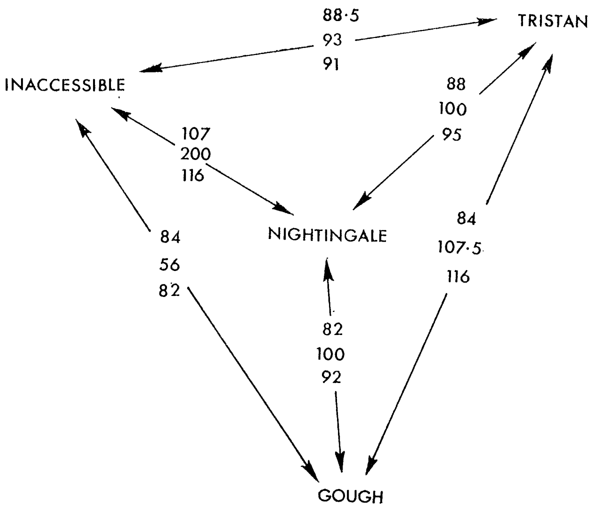

Figure 15. Species of native vascular plants common to different islands within the Tristan–Gough group, as a percentage of those that might be expected to be found in common. The figures are given for the ***observed*** occurrence of (native) flowering plants, pteridophytes, vascular plants, as percentages of those ***expected*** to be found in common between various pairs of islands on the assumption that their floras are random samples of the same population, i.e.

$$\frac{\text{observed numbers of species in common}}{\text{expected numbers of species in common}}\ \% \text{ of } \begin{array}{l}\text{flowering plants}\\ \text{pteridophytes}\\ \text{vascular plants}\end{array}$$

For calculation of expected numbers, see Williams (1947).

Amongst the bryophytes there are considerable differences between the known moss floras of the Tristan group and that of Gough Island. No fewer than thirty moss genera occur in the Tristan group, but have not yet been found on Gough, and although many of these will doubtless be discovered when the existing Gough collections are worked out, and with further collecting there, many are probably absent from the latter island. The genera are:

Ceratodon
Pseudodistichium
Blindia
Dichodontium
Dicranoweisia
Barbula
Didymodon
Gymnostomum
Leptodontium
Tortula
Trichostomum
Funaria
Physcomitrium
Anomobryum
Brachymenium
Schlotheimia
Orthostichopsis
Porotrichum
Distichophyllum
Amblystegium
Calligeron
Campylium
Hygroamblystegium
Meiothecium
Pleuropus
Rigodium
Sematophyllum
Catagonium
Oligotrichum
Psilopilum

Conversely, four moss genera on Gough are unknown in the Tristan group:

Leptotheca
Oncophorus
Rhacocarpus
Thysanomitrium

Rhacocarpus humboldtii and *Thysanomitrium richardii* are such conspicuous plants that they can scarcely have escaped the attention of all the botanists who have collected mosses in the Tristan group. There are also considerable differences between the moss flora of Tristan and those of the two smaller islands of the Tristan group, but these differences probably reflect greater ecological variety and more intensive collecting on Tristan than on Inaccessible and Nightingale Islands. On these smaller and much lower islands, suitable habitats do not exist for eighteen species which are confined to altitudes greater than 1000 m on Tristan main island. Fifteen genera of hepatics have been recorded from the Tristan group, but not from Gough Island:

Acrobolus
Cephalozia
Cololejeunea
Colura
Dumortiera
Fossombronia
Hymenophytum
Lophozia
Marsupidium
Porella
Radula
Reboulia
Solenostoma
Sphenolobus
Tylifmanthus

None of these groups seems to be typical of any particular type of habitat, and as with the mosses, it is probable that further collecting in the islands will reduce the above lists.

Some very marked differences occur in the marine algal flora between the Tristan group and Gough Island. The cold-water species *Durvillea antarctica*, *Iridaea laminarioides* and *Adenocystis utricularis* are all present on Gough (where the first two species are very important in the littoral zone), but apparently absent from Tristan. *Scytosiphon lomentaria* which is included in this category by Knox (1960) is an annual species which may easily have been missed on Tristan, but the other species are unlikely to have escaped the attention of Baardseth (1941) who worked intensively on the Tristan group shores. Because of their geographical position astride the sub-tropical convergence, a comparison of the marine algae of Tristan and Gough is of particular interest (Chamberlain 1965).

It is probable that considerable differences will be found between the lichen and fungal floras of the several islands, but collecting is insufficient for any differences to be clear.

3·8. *Geographical relationships and origins of the flora*

The flora of the islands may be divided into a number of 'elements' according to the areas of the world inhabited by plants which are identical or closely related to the island species. Recognition of the relative sizes and ecological status of such geographical elements is of particular interest in oceanic island floras, because it provides direct evidence of the areas from which the flora may have been recruited. Turrill (1953) has rightly observed that taxa must be precisely defined before their ranges can be mapped, and the present state of knowledge of the native flowering plants in the islands, and in other southern regions, is not sufficient to enable more than about half the angiosperm flora to be allotted to different geographic elements. The pteridophytes and some of the bryophytes can be so assigned, because the relationships of the species have been considered by the taxonomists who have named the collections; but further botanical exploration of the remoter parts of the southern hemisphere will probably reveal that many of the ranges listed below are only a part of the true distributions of the island taxa.

The great majority of the vascular plants and bryophytes in the Tristan–Gough flora are southern circumpolar or South American species, or are closely allied to species with such distributions. Although the islands are closer to South Africa than to South America (Part I, figure 1), the African element in the flora is very small. Christensen (1940), Arnell (1958) and Dixon (1960) all list large numbers of South American cryptogams in the flora. Among the angiosperms, such is the connexion with South America, and especially with Southern Chile, Fuegia and the Falkland Islands, that Skottsberg (1960) considers the flora to be a 'South Atlantic outpost of the Magellanian provinces'.

All the families of flowering plants which are represented in the native flora are very widely distributed throughout the world, and are found on all six continents and many islands (with the single exception of the Empetraceae, which has no African or Australian representatives). There are no representatives in the Tristan–Gough flora of the southern hemisphere, mainly continental families such as Proteaceae and Restionaceae. Of the thirty-one genera of native angiosperms, twenty occur in both hemispheres and many are very widespread (e.g. *Ranunculus*, *Callitriche*, *Chenopodium*, *Carex*); ten are largely or exclusively confined to the southern hemisphere (e.g. *Acaena*, *Rostkovia*, *Sophora* section *Tetrapterae*, *Uncinia*); and the remaining genus *Peperomia* is exceptional in having a pan-tropical range (Good 1953).

The relationships of the native flowering plants are discussed below. Much of the information on distributions is drawn from Skottsberg's (1956) paper on the origins of the Juan Fernandez flora. The term 'sub-Antarctic' is used here in a similar sense to that employed by Wace (1960), as amended by Greene & Greene (1963) from which further distributional data are taken.

Ranunculus caroli is related to *R. biternatus* (Christophersen 1940*b*), which is known from Fuegia and the Falkland Islands (Skottsberg 1913) and from the sub-Antarctic islands (Greene & Greene 1963).

Cardamine glacialis occurs also in the Falkland Islands (Skottsberg 1913) and Fuegia, and may resemble *C. subcarnosa* of Auckland, Campbell and Macquarie Islands (Allan 1961); but further work needs to be done on the relationships of the Tristan–Gough species.

Pelargonium grossularioides is a South African species which may be an introduction in the islands (Christophersen 1939). It resembles *P. australe*, and the Tristan plant was so named by Phillips (1913). This species is recorded from all the southern continents (as *P. acugnaticum* in Good 1953; Allan 1961).

Phylica arborea is known also from Ile Amsterdam in the Indian Ocean, but also occurs on Mauritius (Pillans 1942). The genus is confined to the African continent and its outlying islands (including St Helena), with a great concentration of the 148 species in South Africa (Pillans 1942).

Sophora macnabiana is known only from southern Chile. The late Professor Skottsberg, who named the Gough Island collections, stated that the plants from there cannot be referred either to *tetraptera* (*grandiflora*) or *microphylla* of New Zealand, and that the species on Juan Fernandez (*fernandeziana* and *masafuerae*) and Easter Island (*toromiro*) although closely related to *macnabiana* are more distinct from that species than the Gough Island plant. But more flowering material is needed from Gough Island for comparison with the others.

The section *Tetrapterae* (formerly called *Edwardsia*) to which the Gough Island plant belongs, consists of seventeen closely related species with a curious and mainly insular austral-circumpolar distribution. Skottsberg (1956) lists its species range as: Gough Island (1), Chile (2), Islas Juan Fernandez (2), Easter Island (1), Hawaii (1), Marquesas (1), Rapa (1), Austral Island (1), Lord Howe Island (1), Chatham Island (1), New Zealand (3) and Reunion (1). Details of its range given by Tsoong (quoted in Good 1953) differ somewhat from those of Skottsberg. There is no reason to doubt that *Sophora macnabiana* is native to Gough Island (Wace 1961; cf. Good 1953).

Acaena sarmentosa is one of a group of critical species (Section *Ancistrum* of Bitter 1911) with a distribution centred on South America, but known also from Ile Amsterdam, Australia, New Guinea and New Zealand. *Acaena stangii* belongs to the same group of species as *A. sarmentosa*, but Christophersen (1944) who described the species considered that it was related to Australasian rather than to American forms.

Callitriche christensenii is probably similar to *C. antarctica* Hegelm., which is known from Fuegia and the Falkland Islands (Skottsberg 1913), and from all the sub-Antarctic islands (Greene & Greene 1963). *C. obtusangula* Hegelm., which is a doubtful record for Gough Island, is accepted as a synonym of *C. antarctica* by Greene & Greene (1963). Pollen morphology (Hafsten 1958, 1960*b*) suggests that the Tristan and Gough species resemble *C. antarctica* more than any of the others described from Australia and New Zealand (Moar, in Mason (1959)).

Hydrocotyle capitata is also known from Brazil and other parts of South America (Rudmose Brown 1905, referring to *H. leucocephala* Cham. et Schlecht.). Plants resembling the Tristan–Gough species are represented in the British Museum collections from Paraguay, Ecuador and Chile, but critical taxonomic work is necessary before the relations of the Tristan–Gough species are clear.

Apium australe is known from all the southern continents, and from New Zealand and the islands on the New Zealand shelf (Wace 1960). No species of *Apium* is known from any of the sub-Antarctic islands (Greene & Greene 1963).

Nertera depressa belongs to a complex group of which 'forms said to be conspecific occur in Australia, Tasmania, (New Zealand) and South America' (Allan 1961). Good (1953,

p. 207) considers this to be 'one of the most remarkable of all discontinuous species', and states that it is found in Central and South America, Hawaii, Tristan, Australia, New Zealand, south-east Asia and Malaysia. Skottsberg (1956) noted that the species contains taxonomically distinct forms, and that the Malaysian and Andean forms are different. Until critical taxonomic work is done, it is not clear where the closest relationships of the Tristan–Gough plants lie. *Nertera assurgens* and *N. holmboei*, both described as endemic species, are confined to different islands within the group, and they may be local derivatives of the more widespread species (see below). Critical study is needed.

Chevreulia sarmentosa is known only from Chile, according to Christophersen (1939).

Cotula goughensis and *C. moseleyi* are confined to Gough and Nightingale Islands, respectively, and are there endemic. The subgenus *Leptinella* to which they belong is apparently confined to New Zealand, Australia, Fuegia and the sub-Antarctic islands (Allan 1961, p. 677; Greene & Greene 1963).

Gnaphalium pyramidale belongs to a cosmopolitan genus, and the relationships of the island species (which has been accepted as 'endemic' following Thouars original description) are not known. Two introduced species of *Gnaphalium* are recorded from the islands, and it is possible that the situation is complicated by hybridization between native and introduced species, as in New Zealand (Allan 1961, p. 701).

Lagenophora nudicaulis is known from the Falklands and Fuegia (Skottsberg 1913). Related species occur in the Andes and Juan Fernandez, and the genus is most numerous in New Zealand but reaches Hawaii (Skottsberg 1956).

Empetrum rubrum is known outside the islands only from the Falklands, Fuegia, southern Chile and Argentina, and Masafuera Island in the Juan Fernandez group (Skottsberg 1956). The southern hemisphere plant is very closely related to circumboreal species (Good 1925), and is thus the only known example amongst the native angiosperms of a species with close bipolar relationships (Du Rietz 1940).

Chenopodium tomentosum resembles *C. ambrosioides* L., which is native to Central and South America. Aellen (1960) considers that *C. ambrosioides* is probably not native in Africa (or if so, is a very recent arrival there), and that *C. tomentosum* is a local race of the other species which has its origin and centre of variation in South America.

Rumex frutescens is similar to *R. cuneifolius* Campd. of South America, and the two may be conspecific. Tristan plants in the collections at Kew have been named *R. cuneifolius* by Rechinger in 1952.

Peperomia tristanensis is closely similar to *P. berteroana* Miq. of Juan Fernandez (Skottsberg 1946). The genus is exceptional amongst the native flowering plants in the islands in being tropical in its range elsewhere.

Rostkovia tristanensis is doubtfully distinct from *R. magellanica* (Lam.) Hook. f. (Christophersen 1944) of the Falklands, Fuegia and South Georgia (Skottsberg 1912, 1913; Greene & Greene 1963).

Tetroncium magellanicum is known from the Falklands (Skottsberg 1913) and from Fuegia (Hooker 1847). It is a monotypic genus, and the single species is not known outside southern South America and Gough Island. No male plants of this species have been found on Gough Island, and sex ratios are markedly uneven in Fuegian populations (Holdgate, personal communication to N. M. W.).

Uncinia brevicaulis is known from southern Chile, Juan Fernandez, Fuegia, the Falkland Islands, and Ile St Paul and Ile Amsterdam in the Indian Ocean (Skottsberg 1956).

Uncinia compacta is recorded from Kerguelen (Greene & Greene 1963) and Tasmania (Willis 1962); and related forms occur in New Zealand (Hamlin 1959).

The affinities of the island species of *Carex* and *Scirpus* are unknown. All four have been described as endemic to the group.

Poa flabellata is known from the Falkland Islands and South Georgia, and related species inhabit the southern cool temperate and sub-Antarctic islands (Wace 1960).

Spartina arundinacea is known outside the Tristan–Gough group only in Amsterdam and St Paul Islands in the Indian Ocean (Christophersen 1939). The genus is widespread in temperate regions, but is not native in southern Africa, Australia or New Zealand.

The affinities of the remaining grasses in the islands are not known. Forms similar or identical to *Agrostis magellanica*, *Deschampsia antarctica* (*D. elegantula*—see Skottsberg 1954) and *Festuca erecta* of Fuegia and the sub-Antarctic islands may inhabit the Tristan–Gough group, but the taxonomic status and relationships of these genera in the islands, and of *Glyceria* and *Polypogon*, need investigation.

The geographical relationships of the native angiosperm flora are set out in table 8. Allowing for unevenness of treatment, and the state of taxonomy which makes some of the inclusions in the table debatable, several points are clear concerning the relationships of the flowering plants:

(*a*) The majority of the island plants also occur, or have close relatives, in southern South America.

(*b*) Many of these species or their relatives also inhabit some of the sub-Antarctic islands.

(*c*) A few species occur outside the Tristan–Gough group only in the Mascarene Islands and the Amsterdam–St Paul group in the Indian Ocean. It is of singular interest that both the important dominants of lowland vegetation in the Tristan group (*Phylica arborea* and *Spartina arundinacea*) should have this range; and that both species of similar life form on Gough Island (*Sophora macnabiana* and *Poa flabellata*) should have more distant relatives in the Indian Ocean Islands.

(*d*) There appear to be no native flowering plants in the islands which are otherwise confined to Africa. Most of the insular species have no known relatives there, and those that do (e.g. *Apium australe* and *Pelargonium grossularioides*) have closely related species in other southern lands. *Phylica* is the only genus in the islands centred in Africa.

(*e*) There seem to be no native species with either a northern hemisphere or a cosmopolitan range outside the islands. It is possible that the widespread genera whose relationships remain unknown may yield some species in these categories when their island representatives have been studied. If *Calystegia sepium* or *C. soldanella* are accepted as native in the islands, they are the only indigenous species with a widespread northern hemisphere range; but *Empetrum rubrum*, as noted above, is very similar to circum-boreal plants.

The geographical relationships of the pteridophytes resemble those of the flowering plants in their predominant connexion with America. Of the thirty-three species in the islands, thirty are present (or have close relatives) in America, and nearly half of these are also known from the sub-Antarctic. But unlike the flowering plants, about two-thirds of the pteridophytes (according to Christensen 1940) are also related to African species. How far these predominantly African–American relationships in the pteridophytes are simply part of the circumpolar range is not clear, but Christensen (1940) lists only two species (*Asplenium obtusatum* and *Blechnum penna-marina*) which are present in the islands and in both South America and New Zealand. Table 9 summarizes the geographical relationships of the pteridophytes in the islands. It seems that the ferns in particular show a higher proportion of species with ranges extending into the tropics, and into the northern hemisphere, than do the flowering plants.

TABLE 8. THE GEOGRAPHICAL RELATIONSHIPS OF THE NATIVE ANGIOSPERMS

	closest relatives found in						
Tristan–Gough species	sub-Antarctic islands	South America and Falklands	Australasia	Ile Amsterdam and Ile St Paul	South Africa	other areas	related species
Ranunculus caroli	+	+	+	+	—	—	*Ranunculus biternatus*
Cardamine glacialis	—	+	—	—	—	—	—
Pelargonium grossularioides	—	+	+	—	+	—	*Pelargonium australe*
Phylica arborea	—	—	—	+	—	—	—
Sophora macnabiana	—	+	—	—	—	—	—
Acaena sarmentosa	—	+	+	+	—	—	*Acaena* sect. *Ancistrum*
A. stangii	—	—	?	—	—	—	affinities unknown
Callitriche christensenii	+	—	—	—	—	—	*Callitriche antarctica*
Hydrocotyle capitata	—	?	—	—	—	—	affinities unknown
Apium australe	—	+	+	+	+	—	—
Nertera depressa	—	+	+	—	—	+	—
N. assurgens	—	—	—	—	—	—	affinities unknown
N. holmboei	—	—	—	—	—	—	affinities unknown
Chevreulia sarmentosa	—	+	—	—	—	—	—
Cotula goughensis	+	+	+	—	—	—	*Cotula* subgenus *Leptinella*
C. moseleyi	+	+	+	—	—	—	
Gnaphalium pyramidale	—	—	—	—	—	—	affinities unknown
Lagenophora nudicaulis	—	+	+	—	—	—	—
Empetrum rubrum	—	+	—	—	—	—	—
Chenopodium tomentosum	—	—	—	—	—	—	affinities unknown
Rumex frutescens	—	+	—	—	—	—	*Rumex cuneifolius*
Peperomia tristanensis	—	+	—	—	—	—	*Peperomia berteroana*
Rostkovia tristanensis	+	+	—	—	—	—	*Rostkovia magellanica*
Tetroncium magellanicum	—	+	—	—	—	—	—
Carex insularis	—	—	—	—	—	—	affinities unknown
C. thouarsii	—	—	—	—	—	—	affinities unknown
Uncinia brevicaulis	—	+	—	+	—	—	—
U. compacta	+	?	+	+	—	—	—
Scirpus sulcatus	—	—	—	—	—	—	affinities unknown
S. thouarsianus	—	—	—	—	—	—	affinities unknown
Agrostis media	—	—	—	—	—	—	affinities unknown
A. carmichaelii	—	—	—	—	—	—	affinities unknown
Deschampsia sp.	—	—	—	—	—	—	affinities unknown
Festuca sp.	—	—	—	—	—	—	affinities unknown
Glyceria sp.	—	—	—	—	—	—	affinities unknown
Poa flabellata	+	+	—	—	—	—	—
Polypogon intermedius	—	—	—	?	—	—	affinities unknown
Spartina arundinacea	—	—	—	+	—	—	—
	7	18	9	7	2	1	16 species with unknown affinities

The column totals give an approximate indication of the relationships of the known angiosperm flora. Almost half the flora are insufficiently known to enable their relationships to be tabulated.

As in the flowering plants, there is a particularly close relationship to the pteridophytes of Ile Amsterdam and Ile St Paul, ten species being found in both groups. A notable absentee from the Tristan–Gough flora is *Gleichenia*, which is an important associate of sphagna in bog communities in Tasmania, New Zealand, South America and Ile Amsterdam and in the tropical mountains.

TABLE 9. THE GEOGRAPHICAL RELATIONSHIPS OF THE PTERIDOPHYTES

	closest relatives found in					
Tristan–Gough species	sub-Antarctic islands	South America and nearby islands	Australia and New Zealand	Ile Amsterdam and Ile St Paul	South Africa	other areas
Lycopodium diaphanum	+	+	—	—	+	—
L. insulare	+	+	—	+	+	—
L. magellanicum	+	+	—	—	—	—
Ophioglossum opacum	+	+	—	—	—	—
Azolla filiculoides	—	+	+	—	+	+
Adiantum poiretii	—	+	—	—	+	—
Asplenium alvaradense	—	+	—	—	—	—
A. erectum	—	+	—	—	+	—
A. monanthes	—	+	—	—	+	—
A. obtusatum	+	+	+	+	—	—
A. platybasis	—	—	+	—	+	—
Athryium medium	—	—	—	—	+	—
Blechnum australe	—	+	—	+	+	—
B. palmiforme	—	+	—	—	+	—
B. penna-marina	+	+	+	+	—	—
Dryopteris aquilina	—	+	—	+	—	—
D. paleacea	—	—	—	—	—	?
Elaphoglossum insulare	—	+	—	—	+	—
E. hybridum	—	+	—	—	+	—
E. laurifolium	—	+	—	—	+	—
E. obtusatum	—	+	—	—	+	—
E. succisifolium	—	+	—	+	+	—
Grammitis magellanica	+	+	—	—	—	—
Gymnogramma cheilanthoides	—	+	—	—	—	—
Histiopteris incisa	+	+	+	+	+	+
Hypolepis rugosula	+	+	+	—	+	—
Polystichum mohroides	+	—	—	+	—	—
Rumohra adianteformis	+	+	—	—	+	—
Thelypteris tomentosa	—	+	—	—	+	—
Vittaria vittarioides	—	+	—	—	—	—
Hymenophyllum aeruginosum	+	+	—	+	+	—
H. peltatum	+	+	—	+	+	—
Trichomanes angustatum	—	+	—	—	—	+
	13	29	6	10	21	—

This table has been compiled largely from the details of distribution given by Christensen (1940). Records from the sub-Antarctic islands (Greene & Greene 1963), New Zealand (Allan 1961) and Australia (Willis 1962) have been added. Since Christensen does not define the area that he designates 'sub-Antarctic', and since opinions on the limits of taxa have undoubtedly changed since 1940, the table does not define the geographical relationships precisely, but the column totals give some indication of the directions in which those relationships lie.

The relationships of the bryophytes also resemble those of the vascular plants in the predominance of species common to the islands and to South America, but a small cosmopolitan element is present, and several other bryophytes of narrower range are also known from the northern hemisphere.

Dixon (1960) tabulated the ranges outside the islands of sixty-nine species of mosses known from the Tristan group, but unfortunately he did not consider the relationships of the further fifty-nine species which he described as endemic to the islands. Bartram (1959) noted the ranges of five additional species from Gough Island, but the relationships of most of the Gough Island mosses have not been determined, and many collections from there remain unidentified. A comprehensive view of the geographical relationships of the Tristan–Gough mosses is therefore not possible at present, but some indication of the likely relations may be obtained from Dixon's tabulated list of Tristan group species, in which he refers the sixty-nine species to the following categories:

41 common to Tristan and Fuegia
22 common to Tristan and the Andes
28 common to Tristan and the sub-Antarctic islands
22 common to Tristan and Australasia
13 common to Tristan and South Africa
13 common to Tristan and Mascarene Islands
12 with cosmopolitan distributions.

The American relationship clearly predominates, followed by that to the sub-Antarctic islands. Further bryological exploration of the southern hemisphere will probably reveal that many of the disjunct ranges noted are only part of the true distributions (e.g. the Tristan–New Zealand species are likely to be southern circumpolar). It is notable that all the species common to Tristan and South Africa are also present in Fuegia (except one, which is also known from Australia). Of the thirteen species common to Tristan and the Mascarene Islands (including Madagascar), four are not recorded by Dixon from any other southern continents, and may therefore represent an independent relationship to those islands. Three of the four sphagna which are known from Gough Island, but not from the Tristan group have widespread distributions in the northern hemisphere, and the fourth (*Sphagnum scotiae*) is apparently known only from Gough and Ascension Island (Bartram 1959); but it is probable that these may not represent the entire range of the species. Of the other conspicuous mosses recorded from Gough but apparently absent from the Tristan group, *Oncophorus fuegianus* and *Thysanomitrium richardii* are known from South and Central America and the Islas Juan Fernandez, and *Rhacocarpus humboldtii* is a polymorphic species known from Africa, Central and South America, and Australasia (Skottsberg 1956).

The geographical relationships of the hepatics in the islands have been considered in some detail by Arnell (1958, and unpublished). Of the 124 species that are recorded from the Tristan group, 74 (60%) are also known from South America, or closely related to species found there; twelve species are common to Australasia and Tristan; and thirteen species are included in an 'Antarctic' (?sub-Antarctic) element. Fourteen species from Tristan are also known from South Africa, and five of these are unknown elsewhere, thus providing a tenuous link hardly known in other terrestrial groups. A small group of Atlantic species, with a curious distribution along the length of the Ocean from Ireland to Gough Island forms a parallel to a moss with a similar range (*Cyclodictyon laetevirens*). The Gough Island hepatics show a similar pattern of distribution to those in the Tristan group, but with a more pronounced South American and sub-Antarctic relationship. Of the eighty-three species known from the island (fifty-two of which also occur in the Tristan group), seventy are also known from South America and sub-Antarctic regions; three (also known from Tristan) have an Atlantic range; three are known from New Zealand and Tasmania but have not yet been found in South America, and two species (*Calypogeia bidentula* and *Frullania lindenbergii*) are South African. The remaining species are endemic either to the whole Tristan–Gough group, or to Gough Island alone.

Knowledge of the insular species in the remaining phyla of terrestrial plants is not complete enough to enable any conclusions to be drawn regarding their geographical relations. In contrast to all the other plant groups, the marine algae display a marked South African relationship. Baardseth (1941) considered that the South African element in the marine algae of the Tristan group was the largest, that many species had relationships with southern South America, and some with the North Atlantic coasts, and that other connexions were almost negligible. The Gough Island seaweeds probably differ considerably from those of the Tristan group, and Knox (1960) referring to the sublittoral zone of Gough Island states that 'the general picture is that of an impoverished South American shore'.

Summarizing the foregoing information on distribution, it is possible to recognize four geographical elements amongst the native terrestrial plants in the Tristan–Gough group. But it is clear that much critical taxonomic work will be necessary in many southern taxa before any such system of geographic elements can be regarded as established.

First, there is the sub-Antarctic and southern temperate circumpolar element which consists of plants whose relatives have a circumpolar range, mainly or exclusively outside the tropics in the southern hemisphere:

Ranunculus caroli
Acaena sarmentosa
A. stangii
Callitriche christensenii
Apium australe
Cotula goughensis
C. moseleyi
Rostkovia tristanensis
Uncinia compacta
Poa flabellata
Lycopodium magellanicum
Asplenium obtusatum
Blechnum penna-marina
Grammatis magellanica
Polystichum mohroides

Possibly *Nertera* spp., and the following pteridophytes, which have more tropical relationships, are additions. However, some of them have sub-Antarctic representatives:

Lycopodium diaphanum
L. insulare
Adiantum poiretti
Asplenium erectum
A. monanthes
A. platybasis
Blechnum australe
B. palmiforme
Vittaria vittarioides
Elaphoglossum (5 species)
Histiopteris incisa
Hypolepis rugosula
Rumohra adiantiformis
Thelypteris tomentosa
Hymenophyllum aeruginosum
H. peltatum
Trichomanes angustatum

A few of these pteridophytes extend into the northern hemisphere tropics, but, with the exception of *Hymenophyllum peltatum*, none has its closest relatives extending to the northern temperate zone.

Amongst the bryophytes, the sub-Antarctic and southern temperate circumpolar element is exemplified by:

Polytrichiadelphus magellanicus
Philonotis scabrifolia
Frullania magellanica
Symphogyna hymenophylla

Both Dixon (1960) and Arnell (1958, and unpublished) include 'Antarctic' and 'sub-Antarctic island' groups in the mosses and hepatics of the islands, respectively, but it is impossible to arrive at any reliable figures for the proportion of bryophytes in the islands with these ranges, due to incomplete collecting in some parts of the southern hemisphere (see §3·3).

Most of the flowering plants, and the pteridophytes in the upper list (above) are either coastal or montane species in the islands. The ferns in the lower list are almost all fern-bush species, confined to more sheltered situations below about 400 m altitude. This distribution of the species in the sub-Antarctic and temperate circumpolar element thus follows the geographical range of the structural units of vegetation of which they form a part (§4). Probably about one-third of the flowering plant species, and two-thirds of the pteridophytes native to the islands belong to the sub-Antarctic and southern temperate circumpolar element.

Secondly, there is the South American, mainly Fuegian and Falkland Island, element which comprises those species whose closest relatives are found in South America, including the nearby Falkland and Juan Fernandez groups. This element is only doubtfully distinguished from the southern circumpolar element, since many Tristan–Gough species which extend to South America have identical species or close relatives in other southern continents—especially in New Zealand and its nearby islands, and in Tasmania. The vascular plants belonging to this South American element are:

Cardamine glacialis
Sophora macnabiana
Lagenophora nudicaulis
Empetrum rubrum
Rumex frutescens
Peperomia tristanensis
Tetroncium magellanicum
Uncinia brevicaulis
Asplenium alvaradense
Dryopteris aquilina
Gymnogramma cheilanthoides
and possibly *Ophioglossum opacum*

Arnell (1958, and unpublished) and Dixon (1960) both recognize large numbers of bryophytes in the islands which are otherwise confined to South America. Examples of species with this range are:

Campylopus vesticaulis
Ptychomnion densifolium
Cephalozia tubulata
Clasmatocolea heterostipa

The members of this element do not seem to be typical of any particular vegetation type or habitat in the islands, although a few are montane in their range, and strictly confined to altitudes above the fern-bush and tussock grassland vegetation (*Cardamine glacialis*, *Tetroncium magellanicum*, *Ophioglossum opacum*). Probably about 15% of the vascular plant species which are native to the islands, and possibly more than half the bryophytes belong to the South American element.

Thirdly, there is the South African and Indian Ocean element which consists of those plants whose closest relatives lie to the east of the Tristan–Gough group, in the islands of the Central Indian Ocean (notably Ile Amsterdam and Ile St Paul; and in the Mascarene Islands), and whose more distant relatives are found in southern Africa. Vascular plants belonging to this element are:

Pelargonium grossularioides
Phylica arborea
Spartina arundinacea
Athryium medium

Although about thirteen vascular plant species are found in common between the Tristan–Gough and Amsterdam–St Paul groups (tables 8 and 9), most of these are also widespread on other southern islands, and therefore show no independent relationship between the southern Atlantic and mid-Indian Ocean Islands. *Phylica arborea* and *Spartina arundinacea* are peculiar in that they have no close South American relatives, and their relationships are of particular interest because of their dominance of much of the lowland vegetation in the islands.

According to Arnell (1958) there are five hepatics known only from the Tristan group and South Africa, but no mosses have such a range (Dixon 1960), although five mosses have been recorded only from the Tristan group and Madagascar and its nearby islands (e.g. *Macromitrium fimbriatum*, *Brachymenium megalacrion*, *Sematophyllum crassiusculum*).

The South African and Indian Ocean element in the island flora is small, and accounts for barely 8 % of the vascular plants. The species concerned seem to be characteristic of the lower ground in the islands, and do not grow at altitudes above the fern bush and tussock grassland, nor are they exclusively coastal. But the element is of particular phytogeographic interest, and may represent the remains of an older vegetation in the islands than the more numerous South American and circumpolar plants.

The last is the cosmopolitan element. With the exception of the doubtfully native *Calystegia* spp. (§3·1), no native vascular plants in the islands have been credited with a cosmopolitan range or relationships, but it is likely that some island species of Cyperaceae or Gramineae may show such relations when their affinities have been thoroughly investigated. Such bryophytes as the following may be considered to be cosmopolitan:

Ceratodon purpureus
Hypnum cupressiforme
Polytrichum juniperinum
Rhacomitrium lanuginosum
Marchantia polymorpha
Reboulia hemisphaerica

Even if other species are subsequently added to this list, it seems that the proportion of cosmopolitan species in the island flora will remain small and the group, as so far recognized, does not comprise an ecological unit in the islands.

A few bryophytes, the ranges of which include islands in the Atlantic from Tristan to Britain, may be considered to represent a fifth, Atlantic, element. Arnell (1958) mentions the following hepatics as having such distributions:

Aphanolejeunea microscopica
Lejeunea holtii
Microlejeunea ulicina
Colura calyptrifolia
L. lamacerina
Mylia cuneifolia

The moss, *Cyclodictyon laetevirens* has a similar Atlantic range (Demaret & Poitier de la Varde 1951).

As stated above, this division of the island flora into geographic elements cannot be regarded as established until more taxonomic work, and studies in many southern hemisphere plants have been made. Between one-third and one-half of the flowering plants, and a considerable number of the bryophytes in the islands have relationships which are not known, but it seems clear that the predominance of South American and southern circumpolar relationships will not be altered by future discoveries and taxonomic work. The present relationships of the island flora all point to South America as the area of origin of most of the native plants, and this is in agreement with the present distribution and direction of dispersing agencies (see below).

3·9. *Dispersal mechanism of the native terrestrial flora*

Wallace (1895) defined oceanic islands as 'Islands of volcanic or coralline formation, usually far from the continents and always separated from them by very deep sea...'. The islands of the Tristan–Gough group are all oceanic in this sense, and (as argued elsewhere, § 5·3) have probably never been connected by land either to the surrounding continents or to one another. Following Darwin (1859), Guppy (1906) and Ridley (1930), it has been generally accepted that the only agents of dispersal which can have led to the pre-human stocking of such oceanic islands with plants are air currents, sea currents and animals. Since there are no bats in the Tristan–Gough islands (and no evidence that they have been there in the past), and diaspore transport by sea mammals or invertebrate animals is improbable, the possible methods of pre-human dispersal are only wind, sea and bird carriage. Adaptations to each of these potential vectors amongst the flowering plants will be considered.

The subject of plant dispersal to remote islands has been a topic of much conjecture and some observations, but surprisingly little experiment. Preager (1913) reviewed much of the early experimental work on floatation, and Ridley (1930) considered the whole subject of plant dispersal, which has been reviewed more recently as it affects island floras, by Skottsberg (1956). Ridley (1930, p. 684) noted some conspicuous adaptations to dispersal amongst a few of the Tristan–Gough flowering plants, and the presence of such adaptations in relation to the range of some island species is discussed by Christophersen (1939). The only experiments in floatation, and observations on the weights of seeds and fruits (hereafter collectively referred to as 'diaspores') of the native plants, which were carried out on some Gough Island species, are summarized below (table 10) and will be more fully described elsewhere (Wace, in preparation). Aerobiological studies (Gregory 1961) have an obvious bearing on dispersal to the islands, but until 1962 no attempts had been made to study the aerospora in the Tristan–Gough group. Such studies are relevant to the dispersal of cryptogams: the following remarks will be concerned mainly with the dispersal mechanisms of the following plants.

It is unlikely that any of the native flowering plants is dispersed to any distance by vegetative means, although floatation of branches bearing diaspores, rootstocks, etc., cannot be ruled out entirely (Barber, Dadswell & Ingle 1959). The pteridophytes, *Lycopodium* spp. and *Azolla filiculoides*, may owe their presence in the islands to dispersal of vegetative organs, and this method cannot be excluded for many non-vascular cryptogams. The diaspores of the flowering plants here discussed all arise as a result of sexual (or in some cases such as *Scirpus*, possibly pseudo-sexual) processes.

3·91. *Wind*

The high proportions of cryptogams to angiosperms have been cited by various authors (e.g. Wallace 1895; Ridley 1930) as evidence of the efficiency of wind dispersal, compared to other vectors, in populating oceanic islands with plants. The high cryptogam proportion in the Tristan–Gough flora is discussed below (§5·1), and similar arguments favouring wind dispersal have been applied to the Gough Island flora (Wace 1960, 1961). But Christ (1910) and Copeland (1940) have both denied that ferns are dispersed over long distances by the wind carriage of their spores. Arguments that the larger numbers of pteridophytes in insular floras can be accounted for by the greater antiquity of these plants (Lovis 1959) have no force in relation to the Tristan–Gough group, because the islands are almost certainly no older than mid-Tertiary in age. In the author's opinion it is difficult to see how the relative abundance of cryptogamic species in the native floras of the Tristan–Gough islands can be accounted for other than by admitting the efficiency of long-range windborne dispersal of their spores. Evidence that particles of the same order of size as cryptogam spores have been blown to the islands in the recent past, is provided by the discovery of thirty-three pollen grains of *Nothofagus* and twenty-five of *Ephedra* at various levels in peat deposits from both Tristan and Gough Island (Hafsten 1951, 1960*a*, *b*). It is most unlikely that these genera have ever inhabited the islands, at least during the period in which the peat in question was laid down (or larger numbers of their pollen grains would be present). By means of pollen trapping carried out in North America it has been shown that *Ephedra* pollen can be dispersed for at least 1000 km (Maher 1964). *Nothofagus* is not present in Africa, and the alternative explanation that the pollen was blown from South America across at least 4000 km of ocean, seems most likely.

Experiments on the longevity, and resistance to dessication and to radiation by spores from the island cryptogams would be interesting to ascertain whether they are capable of surviving such a journey. The work of Pettersson (1940) has shown that some bryophyte spores are capable of being blown long distances in the viable state. Working in Finland, he successfully grew thousands of cryptogams, especially mosses, from spores collected in rain-filter traps. That some of the spores must have travelled large distances (at the least from Sweden according to Persson (1944)) is certain because 278 of the mosses cultivated belonged to the genus *Aloina*, which is unknown in Finland. As Persson (1944) has stated, such spore trapping should now be carried out in mid-ocean.

Ridley (1930) and Christophersen (1939) recognized that only *Chevreulia sarmentosa* and *Gnaphalium pyramidale* amongst the native flowering plants have diaspores which are obviously adapted to wind carriage. The other native Compositae (*Cotula* spp., *Lagenophora nudicaulis*) have adhesive fruits without pappi, and there are no orchids, Asclepiadaceae, or other flowering plants with diaspores having obvious adaptations to wind carriage. Van Steenis (1936), Cain (1944) and Good (1953) have all pointed out that light-seeded or plume-seeded flowering plants are no more widely distributed than heavier seeded types. It seems that this form of dispersal has been of only small importance in transporting flowering plants to the islands.

3·92. *Sea*

Ridley (1930) considered that only *Apium australe*, *Calystegia soldanella* (not here accepted as native to the group), *Sophora macnabiana*, and possibly *Rumex frutescens* were sea dispersed to the islands. The following species of native flowering plants in Gough Island are known to have diaspores which are capable of remaining afloat in periodically stirred sea water for 100 days or more (a period sufficient to drift the specimens from South American shores to the islands at a mean rate of travel of about 32 km or 20 miles a day):

Ranunculus caroli *Uncinia brevicaulis*
Sophora macnabiana *Carex insularis*

The fruits of *Ranunculus* and the sedges only float because air is trapped on the carpel walls or within the utricles. In the case of *Sophora*, the unopened lomenta sink within a week, but of eight seeds put in sea water 10 months after they were gathered from the tree, three floated in sea water for 3 years and two of these were successfully germinated (E. J. Godley, personal communication to N. M. W.)—a most spectacular capacity for long-range oceanic dispersal which may explain the curious distribution of the section *Tetrapterae* (*Edwardsia*) of the genus (§3·8). The diaspores of the other three species did not germinate after the floatation period. No floatation tests were carried out on strand plants such as *Chenopodium tomentosum*, and the diaspores of other mainly coastal species such as *Spartina arundinacea* sank within a few minutes, and those of *Cotula goughensis* and *Rumex frutescens* both sank within a week in sea water. The mericarps of *Apium australe* sank within 2 days, contrary to Ridley's (1930) implied expectation of their behaviour. Christophersen (1939) suggests that *Spartina arundinacea* may have been dispersed to the islands by floatation of its woody rootstocks, and *Calystegia soldanella* may owe its presence in the islands (if it is native) to floatation of its seeds (Guppy 1906).

Seeds belonging to the tropical leguminous genera *Mucuna*, *Caesalpinea* and *Dioclea* are washed up frequently enough on the Tristan beaches to be called 'sea beans' by the islanders (Moseley 1875; Christophersen 1939). 'Foreign woods' are also noted as being cast up on the Tristan beaches (Christophersen 1939). Three specimens of driftwood collected from the beaches of Gough Island were examined anatomically by Dr C. R. Metcalfe, who identified them as probably belonging to the genera *Picea*, *Aesculus* and *Salix*—the last being similar to an Argentinean specimen labelled *S. humdoldtiana* at Kew. Barber, Dadswell & Ingle (1959) note that two specimens of driftwood collected on Tristan were identified as *Nothofagus* sp., probably *N. pumilio* from Fuegia.

Notwithstanding the demonstration that sea dispersal of flowering plant diaspores to the islands is possible, and that in a few cases (notably *Sophora macnabiana*) it has very probably occurred; few of the native angiosperms show evidence of efficient adaptation to long distance sea dispersal, and probably not many have arrived by this means.

3·93. *Birds*

Ridley (1930) recognized three types of adaptation to birds disposal of diaspores amongst the islands' native flowering plants:

(*a*) adhesion by special hooked, barbed or toothed appendages (*Acaena*, *Uncinia*, and possibly *Agrostis* spp. and *Spartina*);
(*b*) viscid adhesion of small seeds or fruits (*Cotula*, and possibly *Chenopodium*);
(*c*) berries adapted to internal dispersal (*Empetrum*, *Nertera*, *Phylica*).

This scheme of classification of bird-dispersed diaspores is expanded below, in the light of further observations and a more complete knowledge of the islands' floras.

The fruits of the following five species all have obvious adaptations to external animal adhesion, due to their possession of various appendages:

Acaena sarmentosa
A. stangii
Pelargonium grossularioides
Unicinia brevicaulis
U. compacta

The entire fruiting heads of *Acaena sarmentosa* were seen to be entangled in the feathers or down of at least three species of sea birds (*Diomedea chlororhynchos*, *Pterodroma mollis*, *Catharacta skua*) on several occasions on Gough Island (cf. Falla 1960). Individual fruits of all the species of *Acaena* and *Uncinia* are a nuisance in attaching themselves to clothing when walking through the vegetation (Carmichael 1819; and personal observations).

In addition to these five species with obvious adaptations to external bird dispersal of their fruits, a number of flowering plants have diaspores which are sticky, or become so when wet, and are light enough to enable them readily to adhere to feathers or birds' feet:

Lagenophora nudicaulis
Cotula goughensis
Rostkovia tristanensis

Five further species of native flowering plants have berries, and are therefore presumably adapted to internal bird dispersal:

Phylica arborea
Nertera assurgens
N. depressa
Nertera holmboei
Empetrum rubrum

All but *N. holmboei* have been observed to be eaten by the native land birds of the islands, or the seeds have been found in their stomach contents (Hagen 1952; M. K. Swales, personal communication).

Although the thirteen species mentioned above have more-or-less obvious adaptations to bird carriage of their diaspores, many of the other native species have diaspores which are light enough and small enough to make external bird carriage possible. The native grasses in Gough Island all have their fruits enclosed in more or less scabrid glumes, which could readily enable them to be entangled in feathers or down, and *Spartina arundinacea* also has a long persistent style. Although there are no data known to the authors on diaspore weights from continental areas for comparison with those quoted (table 10), it is likely that the islands have a higher proportion of light seeded plants than similarly diverse continental regions. If this is so, it may reflect the importance of bird dispersal in populating them with plants.

Even the obvious adaptations to bird dispersal amongst the diaspores of the island angiosperms are more numerous than adaptations to airborne or seaborne dispersal. However, it has been pointed out that the sea birds do not eat berries (Christophersen 1939) and only approach land to breed (when individual birds probably always return to the same site), and that the Tristan–Gough group are not on the migration routes of any land birds. Further, the time taken for any bird to reach the islands from the nearest land probably exceeds the period during which diaspores would remain in the gut; thus making

TABLE 10. WEIGHTS OF DIASPORES, AND THE DISPERSAL POTENTIALITIES OF THE NATIVE FLOWERING PLANTS OF GOUGH ISLAND

Diaspores were collected from January to May 1956; and weighed within 6 months of collection. Floatation experiments were carried out in sea water, in tubes which were mounted on a flask shaker and periodically agitated (to simulate wave motion, and prevent floatation due to surface-tension effects). Germination tests were carried out only on the four species whose diaspores floated for two months or more, and of these only *Sophora* germinated (see text, p. 303).

The numbers of diaspores tested for sea floatation was usually the same as the number weighed. Since the sample sizes are small, and all diaspores tested were often taken from a single plant, and seven native species were untested, few generalizations can be made from these results for the present dispersal of the island flora as a whole. The data are presented as by Preager (1913) for ease of comparison. Full details of the observations are included in *The plants of Gough Island* (Wace, in preparation).

number	species tested	diaspore type	no.	mean wt. per diaspore (mg)	diaspores all sunk in sea water, in less than					adaptations to animal dispersal	remarks
					minutes	hours	days	weeks	months		
1	*Ranunculus caroli*	achene	14	1·25					6+	short hooked style	woody carpel
2	*Cardamine glacialis*	seed	30	0·31		7				—	—
3	*Phylica arborea*	berry	4	56·25			8			fleshy berry	hard when dry
		seed	7	8·43	½					—	hard testa
4	*Sophora macnabiana*	lomentum	1	—			6			—	—
		seed	25	73·08					36+	—	see text, p. 303
5	*Acaena sarmentosa*	achene	20	1·87			2			barbed spines	see text, p. 304
6	*A. stangii*	achene	25	0·75			2			spines	
7	*Callitriche christensenii*	—	—	—	—	—	—	—	—	—	no data
8	*Hydrocotyle capitata*	—	—	—	—	—	—	—	—	—	no data
9	*Apium australe*	mericarp	30	1·10			2			—	—
10	*Nertera depressa*	seed	8	3·65	(no data)					fleshy berry	eaten by buntings, etc.
11	*Cotula goughensis*	cypsela	30	0·16				1		papery pericarp	sticky when wet
12	*Gnaphalium pyramidale*	cypsela	4	0·05	½					roughened cypsela with pappus	—
13	*Lagenophora nudicaulis*	—	—	—	—	—	—	—	—	minute sticky cypselas	—
14	*Empetrum rubrum*	berry	—	—	—	—	—	—	—	fleshy berry	eaten by land birds
		seed	25	0·52				2		—	—
15	*Chenopodium tomentosum*	—	—	—	—	—	—	—	—	—	no data
16	*Rumex frutescens*	nut with perianth	10	2·50	(no data)					—	entire margin to perianth
		nut	20	1·75	—	—	—	—	—	—	
17	*Rostokovia tristanensis*	seed	25	0·09				3		slightly sticky testa	—
18	*Tetroncium magellanicum*	—	—	—	—	—	—	—	—	—	no data (p. 293)
19	*Carex insularis*	nut and utricle	86	1·21					2	—	air trapped in utricle
20	*C. thouarsii*	nut and utricle	168	1·05				2		beaked utricle	—
21	*Uncinia brevicaulis*	nut, awn and utricle	30	1·20					4+	hooked awn, hairy utricle	—
22	*U. compacta*		25	0·75				3		hooked awn	eaten by buntings
23	*Scirpus* spp.	nut	100	0·07				1		—	—
24	*Agrostis carmichaelii*	palea, lemma and caryopsis	20	0·10			1			—	no data
25	*A. media*						1			awned lemma	minute caryopsis
26	*Deschampsia* sp.	—	—	—	—	—	—	—	—	barbed awns and hairy rachilla	—
27	*Glyceria* sp.	caryopsis	10	0·65		1				persistent palea, lemma and floral axis	—
28	*Poa flabellata*	—	—	—	—	—	—	—	—	awned hairy lemma	—
29	*Spartina arundinacea*	caryopsis	10	1·45	1					scabrid glumes and persistent style	eaten by buntings

endobiotic dispersal problematical (cf. Skottsberg 1956, discussing a similar problem in relation to the Hawaiian flora).* Nevertheless, the presence of six endemic species of land birds breeding on various islands of the group, and the casual occurrence of seven further species of land birds (Holdgate, Part III this Report), indicates that many land birds have succeeded in reaching the islands in the past, and still continue to do so today. The enormous numbers of breeding marine birds (especially Procellariidae) is one of the most striking features of the islands least affected by man (Nightingale, Gough), and although these are not known to travel between their different breeding grounds they must have done so in the past, and probably still do so to some extent, for no species of sea bird is peculiar to the islands. There is therefore no lack of potential vectors amongst either the land or sea birds visiting the islands.

Hagen (1952) noted that 'four breeding species or subspecies (of sea birds) which have not been found breeding in any other part of the world' are common to the Tristan–Gough group and the Amsterdam–St Paul group in the Indian Ocean. This range is shared by a number of flowering plants (see table 8), notably *Phylica arborea* and *Spartina arundinacea* (Christophersen 1939). Such coincidences of range strongly suggest that bird transport has been effected in some cases, and from all the data presented above it seems that is has been a far more frequently used agent of flowering plant dispersal to the islands than wind or sea carriage.

3·94. *General remarks*

All the information available on the dispersal of plants to the islands is based on subjective estimates of the possibilities of diaspore transport, and correlations between the geographic ranges of certain plants and those of their likely vectors. It must be admitted that there is no firm evidence that any native plant has arrived in the islands by any particular means. The problems of long distance dispersal which confronted Darwin and Hooker over a century ago, are still unresolved here, and elsewhere (Turrill 1953), and will remain so until new techniques are devised for catching marked diaspores in transit.

In seeking to explain the colonization of the Tristan–Gough group by plants in the past, we can consider only the relative probabilities of the different methods of diaspore transport in the present flora. Amongst birds and many invertebrate groups, the widespread occurrence of flightlessness indicates that their capacity for long-range dispersal has altered since their arrival in the islands (Holdgate, Part III this Report). The classical explanation of flightlessness (Darwin 1859) supposes that the condition evolves because a selective premium is put upon sedentary habits once flighted species have reached isolated islands. Difficulties in accounting for the past dispersals of plants to the islands by examining the dispersive capacities of present species may be due to a similar selective process operating on plant diaspores.

Christophersen (1939) adopted the view that 'the agencies of plant dispersal—wind, ocean currents and migratory birds—operating under present conditions cannot alone account for the origin of the flora of Tristan da Cunha'. Guppy (1906) came to a comparable conclusion when he assumed that the dispersal of most land plants to the remote islands of the Pacific could only be explained by bird movements which took place in the

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* See note added in proof on p. 360.

past, and which had now ceased. In the authors' opinion, our knowledge of the present floras of the Tristan–Gough group does not support this idea of greater dispersive efficiency in the past than at present (except in so far as man has destroyed the breeding bird populations of some islands). In our view, no land connexions or lessening of distances between the islands and the surrounding continents (either by drift or chains of islands) are necessary to account for the present native flora of the Tristan–Gough group. Christophersen's (1939) statement that the agents of dispersal 'have been more efficient at an earlier period of shorter oversea distances' lacks any geophysical support, for the period during which the islands have existed in a habitable form. The evidence at present available suggests that external transport by birds has been the most important agency by which terrestrial plants have arrived in the islands, that sea floatation has been of some importance, and that air floatation has only been of importance in the dispersal of cryptogams.

4. The vegetation

Five structurally distinct vegetation types are native to the group, and are variously represented in the different islands:

- tussock grassland
- fern-bush
- wet heath
- feldmark and montane rock communities
- mires

In addition, several induced types of vegetation are important on Tristan main island, and owe their existence to the effects of man and the animals and plants that he has introduced. The soils of the islands have been given only a passing mention in the published accounts of the vegetation. But there are few mineral soils anywhere, except for immature types in exposed upland areas, and on some of the small lowland plains and raised beaches. Peat accumulation at the surface dominates pedogenesis in most communities (see below).

4·1. *Tussock grassland*

The large grasses *Poa flabellata* (on Gough Island) and *Spartina arundinacea* (throughout the group) dominate extensive areas in some of the islands. Both species form stools up to about 1 m in height, from the top of which the leaves and culms may reach to over 2 m above the ground, arching over the channels which wind between the tussock stools. In closed tussock communities, there may be no associated vascular plants, although *Asplenium obtusatum* and *Scirpus* spp. often colonize the moribund stools, and small herbs and weeds such as *Callitriche* sp., *Poa annua* and *Stellaria media* grow between the tussocks where the shade is not too dense.

The tussock grassland formation in the islands, as in the sub-Antarctic regions, is primarily a submaritime and biotic climax. *Spartina* tussock is most luxuriantly developed where the ground is heavily dunged by penguins or other birds, and the importance of the formation on Nightingale Island may be related to the enormous quantities of guano deposited there by the breeding *Puffinus gravis* (Hagen 1952, p. 209). The *Poa flabellata* tussock on Gough Island covers the most extensive areas on the exposed western cliff-slopes of the island, but its distribution is in places clearly related to the extent of the penguin rookeries (as in the Glen and Sophora Glen, where tussock-dominated rookeries with both *Poa flabellata* and *Spartina arundinacea* are surrounded by fern-bush communities).

Tussock grassland is extremely vulnerable to human activities, especially to burning and to grazing of imported mammals. It is probable that *Spartina* tussock was formerly much more extensive than it is now on Tristan main island, and possible that *Poa flabellata* once dominated tussock communities in the Tristan group as it does now on Gough Island (see below).

4·2. *Fern-bush*

The small heath-like semi-procumbent evergreen tree *Phylica arborea* and various ferns (notably *Histiopteris incisa* and *Blechnum palmiforme*, a species with the habit of a dwarf tree-fern) dominate dense communities in the lower parts of many of the islands. Mature fern-bush comprises three principal communities, usually dominated by the above species.

Phylica forms tangled thickets up to 5 m in height, each tree sending up numerous suckers from its roots and prostrate stems which are generally buried in the peat. An understory of terrestrial ferns sometimes grows beneath the trees, the branches of which are covered in a heavy growth of cryptogamic epiphytes. The most abundant and conspicuous species in *Phylica* thickets are:

dominant: *Phylica arborea*
understory: *Asplenium erectum*
Blechnum palmiforme
B. penna-marina
Dryopteris aquilina
Histiopteris incisa

Epiphytes, often extending to the ground beneath the trees, where there is no understory:

Asplenium alvaradense
Elaphoglossum spp.
Hymenophyllum spp.
Nertera depressa
Vittaria vittarioides

and numerous mosses, especially:

Dicranoloma spp.
Macromitrium antarcticum
Hypnum elatum

very numerous hepaticae, especially of the genera:

Drepanolejeunea
Jamesoniella
Lepidozia
Metzgeria
Lophocolea

and several lichens, including the conspicuous plants of the genus:

Pseudocyphellaria.

Very few angiosperms occur in closed *Phylica* communities and there is probably not much seasonal variation in its general appearance.

Histiopteris incisa dominates extensive areas in the fern-bush, often in more-or-less pure stands with no associates except for *Asplenium alvaradense* and mosses (especially *Brachythecium* sp.) on the ground, and *Metzgeria* and other small hepatics on the *Histiopteris* stipes. The *Histiopteris* fronds grow thickly on the damp peat to a height of 1 m or more above the surface. It is likely that the *Histiopteris* community displays more seasonal change than the other components of the fern-bush, and that flowering plants (notably *Apium australe* and Cyperaceae) are conspicuous when the fern fronds die down in the winter, but no observations have been made on the vegetation throughout the year.

The small tree-fern *Blechnum palmiforme* dominates some remarkable communities in which it often has no associates (except for epiphytes); and on level ground it forms more-or-less evenly spaced ranks of individuals, each with the cycad-like canopies of stiff fronds about 1 m in diameter interlacing at about the same height above the ground. Such regular communities on patches of flat ground resemble pineapple plantations in appearance, but the *Blechnum palmiforme* communities are generally uneven in the gulches and on broken ground, and other species may be present in the more open field layer. The most common associates are:

Empetrum rubrum *Uncinia* spp.
Scirpus spp.

together with the ferns *Elaphoglossum* spp. and *Gymnogramma cheilanthoides* and bryophytes on the ground. The thick trunks of the tree-fern are invariably covered by a dense growth of cryptogams, notably *Asplenium alvaradense*, *Hymenophyllum* spp. and various bryophytes. *Acaena* spp. and *Nertera* spp. sometimes scramble over the outspread fern fronds, but flowering plants are generally scarce in closed *Blechnum palmiforme* communities. *B. palmiforme* has a greater altitudinal range than the other components of the fern-bush, and extensive stands of the ferns are found some way above the *Phylica* and *Histiopteris* communities in the larger islands.

The various fern-bush communities may be serally related to one another under some conditions, and a sequence involving the three principal components in a cyclical process of peat build-up and landslides has been described from steep slopes on Gough Island, where the instability of the peat is increased by the burrowing activities of ground-nesting Procellariidae.

Fern-bush is structurally the most complex type of vegetation occurring in the islands, and is most fully developed in lowland areas where the degree of slope and shelter permit an accumulation of moist peat. It is not developed where exposed to salt spray or penguin and seal breeding near the shores. It is replaced in such areas by tussock grasslands. However, *Phylica* does form some coastal communities in association with tussock grasses and other flowering plants, and with the ferns *Asplenium obtusatum* and *Rumohra adiantiformis*.

The fern-bush has been markedly affected by man on Tristan, where cutting of *Phylica* for fuel, clearance of the Coastal Strips for grazing, and possibly the burning of the whole community, has led to a marked decline in the importance of the community around the Settlement in the north of the island (see below). On the other islands, the formation has probably been little affected by man so far.

4·3. *Wet heath*

Closed communities of microphyllous woody chamaephytes and tufted perennial graminioids, growing to a height of up to 1 m above the hummocks of sphagna and other bryophytes, cover much of the island terrain above the altitudinal limits of fern-bush and tussock grassland. The communities are varied, but all agree in the predominance of tufted, or prostrate, or dwarf fruticose perennial plants, with a high proportion of the ground covered by bryophytes. Locally, pteridophytes play an important part in the wet heath communities, especially *Blechnum palmiforme* (in a very dwarfed state, with the trunk submerged in the peat and the fronds on the peat surface), *B. penna-marina* and *Lycopodium* spp. But although widespread, the pteridophytes are far less important in wet heath than in fern-bush. *Empetrum rubrum* and various grasses and sedges, with sphagna and Dicranaceae, all growing on wet (and often unstable) peat, are the most important species. A composite list of the more important plants of the wet heath formation is:

locally dominant: *Empetrum rubrum*
Deschampsia sp.
abundant: *Agrostis* spp.
Apium australe
Acaena stangii
Carex spp.
Scirpus spp.
Uncinia spp.
Blechnum penna-marina
Elaphoglossum laurifolium
E. succisifolium

Bryophytes of the genera *Dicranoloma*, *Jamesoniella*, *Rhacomitrium* and *Sphagnum* are also dominant locally or in association with the flowering plants.

Such wet heath communities are very widespread on the two larger islands (and probably on Inaccessible also). They merge into all the other formations, and contain many of the vascular species which are also found in the others. Wet heath is thus the central vegetation type of the islands, and the other formations may in a sense be considered as more specialized types which have been developed in response to particular factors of the environment:

tussock grassland: maritime influence and gregarious breeding of sea animals
fern-bush: some shelter and high humidities at low altitudes
feldmark: extreme exposure at higher altitudes
mires: topography giving rise to impeded drainage and waterlogging

Man has profoundly altered the wet heath communities on Tristan (and possibly on the smaller islands in the Tristan group also), by the introduction of *Rumex acetosella* and *Holcus lanatus* which have assumed dominance over wide areas of wet heath on the main island. Elsewhere, man's impact on these communities has probably been only small.

4·4. *Feldmark and montane rock communities*

Open communities of cushion, mat-forming and crevice plants occur over considerable upland areas of the two larger islands. *Empetrum rubrum*, small tufted grasses (notably *Agrostis carmichaelii* on Gough Island, and probably on the other islands also), *Rostkovia tristanensis*, *Grammitis billardieri* and *Lycopodium magellanicum* are the most important vascular species. *Rhacomitrium crispulum* and *R. lanuginosum* and various Dicranaceae are often found in association with the flowering plants, and *R. crispulum*, *Andreaea* spp., hepatics, and crustose and fruticose lichens (notably *Placopsis* and *Stereocaulon*) by themselves.

The distribution of the feldmark communities is clearly related to exposure and to altitude, but is also much influenced by the nature of the substratum on which it is developed. Much of the Tristan peak is almost bare of plants, or supports only scattered individuals because of the unstable nature of volcanic cinders which form the top 600 m (figure 25, plate 39). Some of the rounded rock domes which form many of the northern peaks of Gough Island are nearly bare of plants, possibly because the vegetation has not yet had time to cover them.

Man has probably had little effect on the open montane communities, except possibly to lead to some extension of them where grazing animals have been imported. It is likely that some weeds grow in the Tristan feldmark, but none is important enough to have received notice.

4·5. *Mires*

All the native vegetation types except the open montane communities are, to some extent, peat-forming, and peat accumulation is an important ecological factor in their development. Sphagna and other hygrophilous peat-forming bryophytes are widespread, especially in the fern-bush and wet heath communities: in this sense, much of the insular vegetation could be called 'blanket bog' (Tansley 1939, p. 676) because peat is able to form in the hyper-oceanic climate quite independently of waterlogging resulting from the pattern of the local drainage. But peat more than about 2 m deep, with a flat or convex surface form indicating substantial undisturbed growth *in situ*, is confined to basins of impeded drainage. Because of the small size of the coastal plains and the very steep and rugged lowland terrain of most of the islands, these basins are mostly at altitudes of over 500 m above sea-level.

Three, or possibly four, types of mire differing in their structure and their surface vegetation may be recognized in the islands:

(*a*) Valley bogs formed mainly by sphagna, but with *Empetrum* and Cyperaceae also abundant in the surface of the vegetation, in which the peat, which is up to 5 m deep, is dissected into domed mounds by the drainage streams. These bogs grade into the surrounding heath vegetation, and there is no continuous lagg surrounding them. Such valley bogs occur at several sites on Gough Island from about 500 to 700 m altitude, and in one site at 740 m on Tristan. They may be present also on the south-eastern part of the Base on Tristan, and possibly on the Inaccessible Island plateau, but do not occur on Nightingale.

Peat borings that have been carried out on these bogs in Albatross Plain, Gough Island, and Soggy Plain, Tristan (Hafsten 1951, 1960*a*, *b*) show that the bogs have developed over the uneven floors of the mountain valleys, and there is no reliable evidence to suggest that the bogs have overgrown pre-existing lake or fen vegetation.

(*b*) Plateau bogs in which the surface vegetation, mainly of Bryales and Hepaticae (although with some sphagna), is level or shallowly terraced and very wet. Although subterranean drainage channels are present, the bogs are not dissected to the same extent as the valley bogs, and most of the water drainage across them probably flows over the terraced surface. Some vascular plants line the margins of the terraces, above the usual level of the water; the important species in these bogs are:

Dicranoloma spp.
Rhacocarpus humboldtii
Sphagnum spp.
Jamesoniella grandiflora
Scirpus spp.
Tetroncium magellanicum

together with numerous small hepatics (but none associated with the sphagna as are such species as *Odontoschisma sphagni* and *Calypogeia fissa* in British bogs).

The plateau bogs differ from the valley bogs in their form, the presence of numerous pools, in their shallower peat (to only 2 m depth), in the absence of *Empetrum* and the lesser importance of sphagna. They are confined to the plateaux on Gough Island at about 600 m above sea-level, and are not known from any of the other islands. No peat borings have been carried out in the plateau bog peats, but examination of eroding peat faces suggests that they have not displaced any other type of vegetation.

(*c*) A small mire with a convex form and lagg drainage, in which hummocks of *Breutelia integrifolia* and small tussocks of *Scirpus* spp. comprise most of the surface vegetation, covers an area known as Jenny's Watron below some springs at the bottom of the cliffs on the Tristan Settlement plain. Similar mires from which sphagna are absent may occur elsewhere on Tristan or in the other islands, but none has been described.

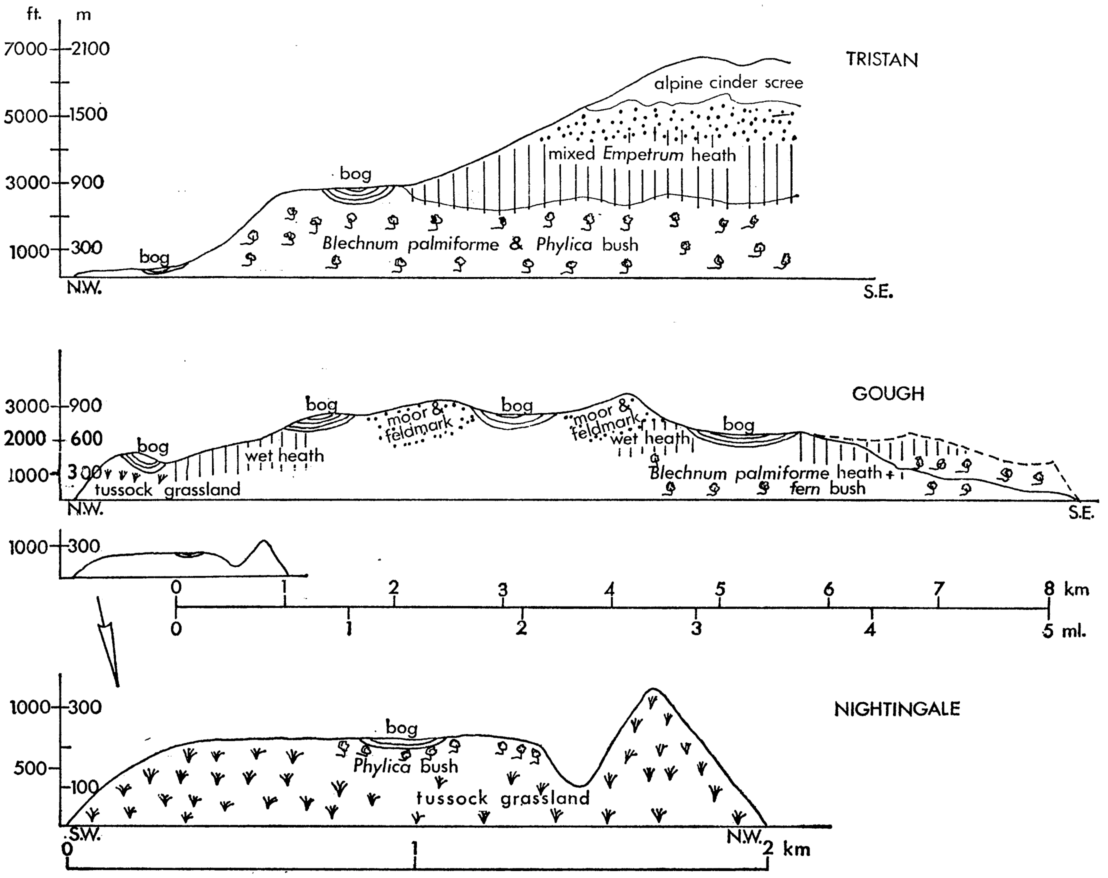

FIGURE 16. Altitudinal zonation of vegetation of Tristan, Gough and Nightingale Islands. Tristan and Gough diagrams taken from Wace (1961).

The distribution of mires in the islands is clearly controlled by topography, and the porosity of the rock types in the upland basins.

It is probable that some of the vegetation around the region of The Ponds in Nightingale Island should be recognized as a fourth type of mire. The Ponds have an almost complete and pure cover of *Scirpus sulcatus*. Further mires may remain to be discovered amongst fern-bush vegetation on the Tristan Base and at the southern end of Gough Island.

Man has had a negligible effect on the mire vegetation of the islands, except at Jenny's Watron on Tristan where some weeds from the nearby Settlement have colonized the surface.

Figure 17. *Poa flabellata* tussock grassland on stabilized boulder scree occupied by a rockhopper penguin (*Eudyptes crestatus*) rookery near West Point, Gough Island. The ground between the tussocks is almost bare of plants. The penguins stand about half a metre high. From Wace (1960).

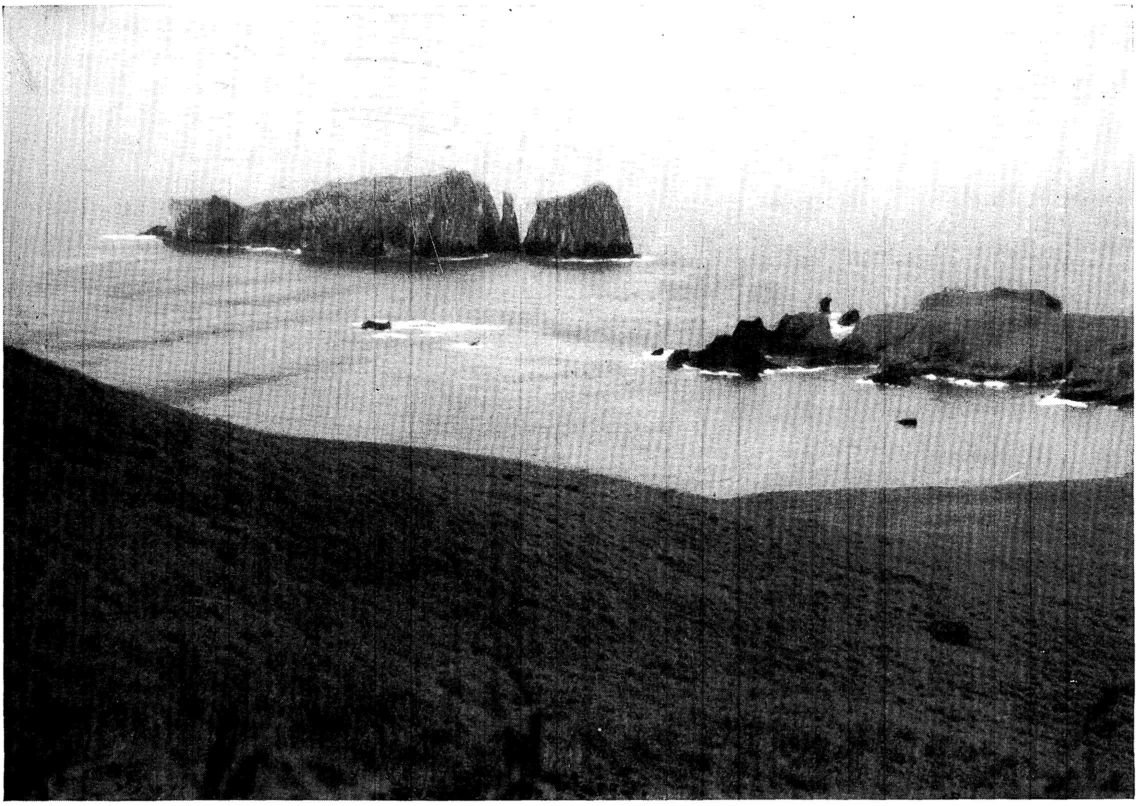

FIGURE 18. *Spartina arundinacea* tussock on the seaward slopes of the northern side of Nightingale Island; Stoltenhoff Island on the left, Middle Island on the right. The very dense, pure stand of the tussock is between 1·5 and 2 m high.

FIGURE 19. The western side of Hottentot Gulch, Tristan, showing about 6 m of downwash. Very low, overgrazed grassland on top. Tufts of *Spartina arundinacea* out of reach of domestic animals, centre.

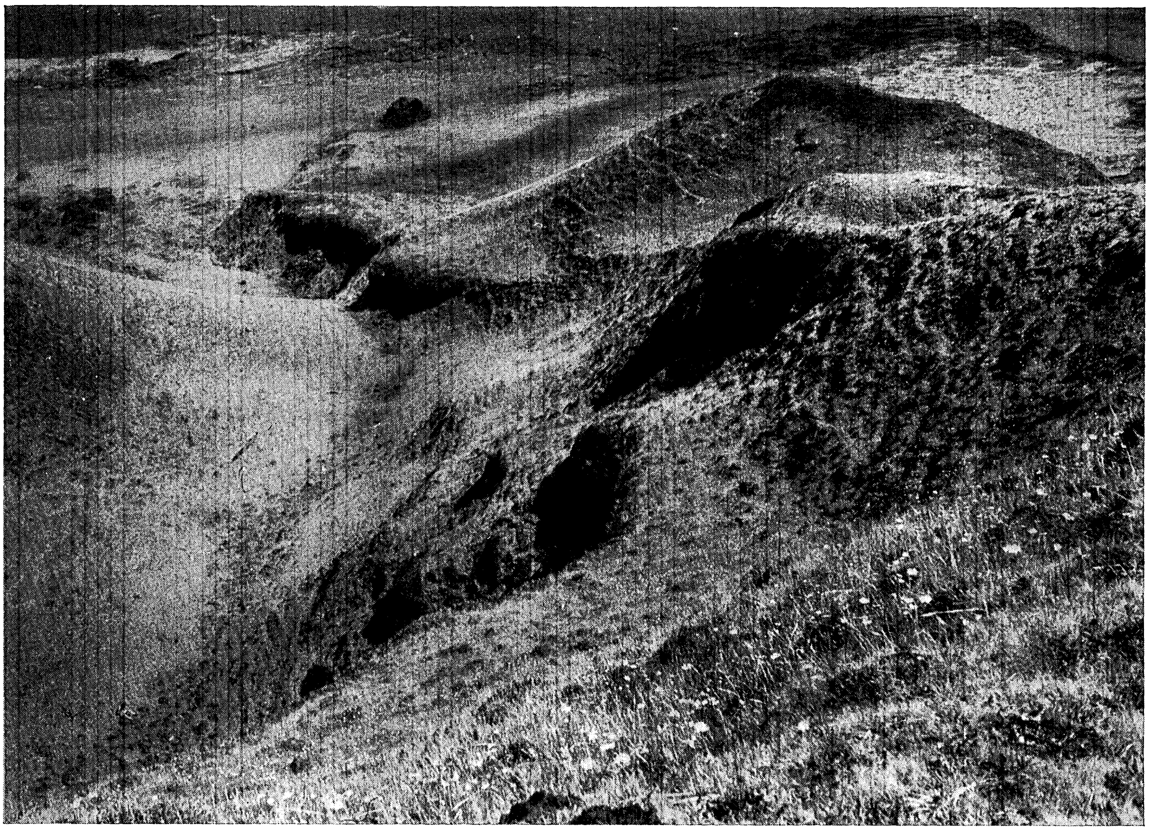

Figure 20. Overgrazed grassland at Hackel Hill, southwest Tristan. Soil at background base and eroding. Numerous inflorescences of *Chrysanthemum leucanthemum* in the foreground.

Figure 21. The Base and Peak from Burntwood, Tristan. Foreground to middle distance is dominated by *Blechnum palmiforme* with a few low bushes of *Phylica*. Many *Blechnum* plants with upright sporophylls.

FIGURE 22. The rugged topography of the edge of the Base above Sandy Point, Tristan. Top of Main Cliffs at bottom right. Dense growth of *Phylica* covers all but the steepest ground.

FIGURE 23. Oceanic heath on Gough Island at 450 m above sea level. Patches of *Empetrum rubrum* and tufts of *Deschampsia* sp. and *Agrostis media* are rooted in a bryophyte mat, mainly of *Sphagnum magellanicum*. Stunted *Blechnum palmiforme* with the fronds borne on the moss surface is also present. A more continuous mat of *Empetrum* in the left background is marked by the half metre probe. The peat is here 120 cm deep.

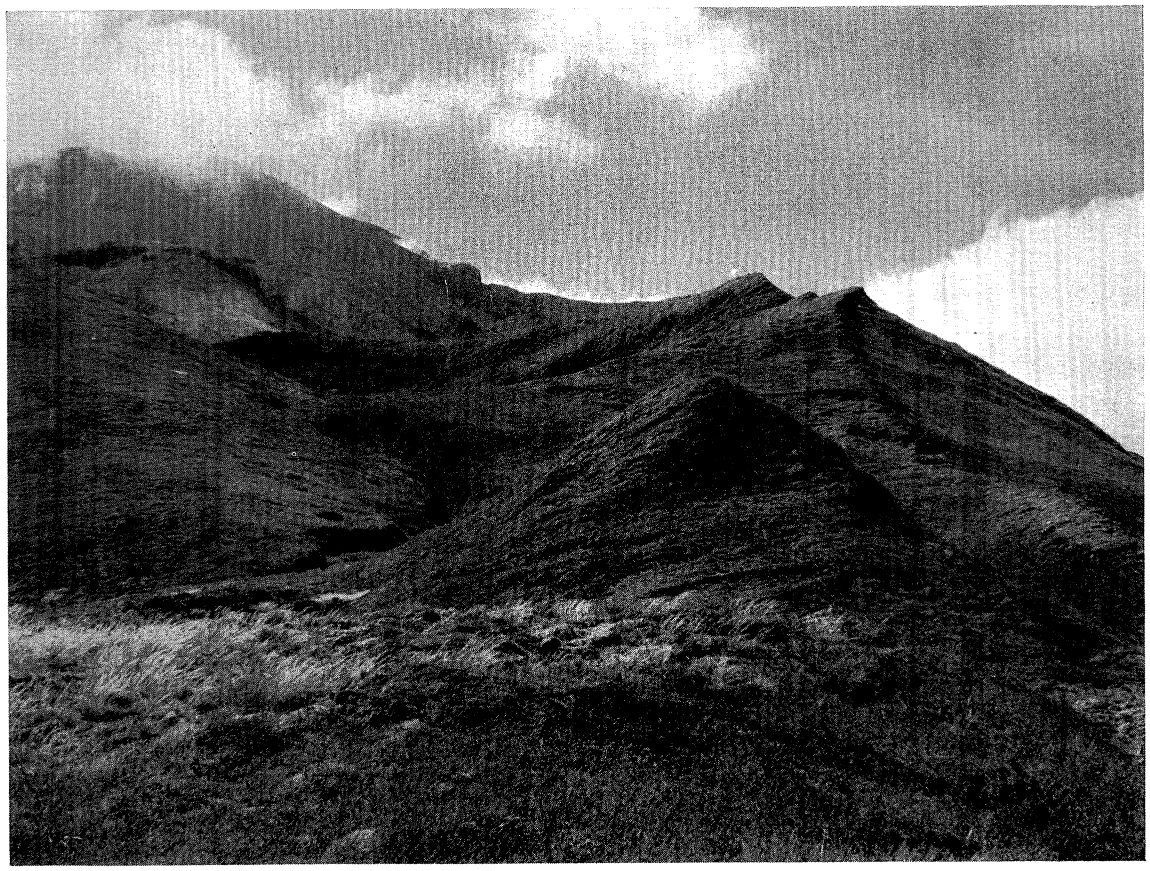

Figure 24. Green Hill on the south-west of Tristan at *ca.* 900 m. Peak at top left. Apart from small stand of *Deschampsia* sp., left foreground, the entire foreground to middle distance is covered by dense luxuriant *Rumex acetosella*.

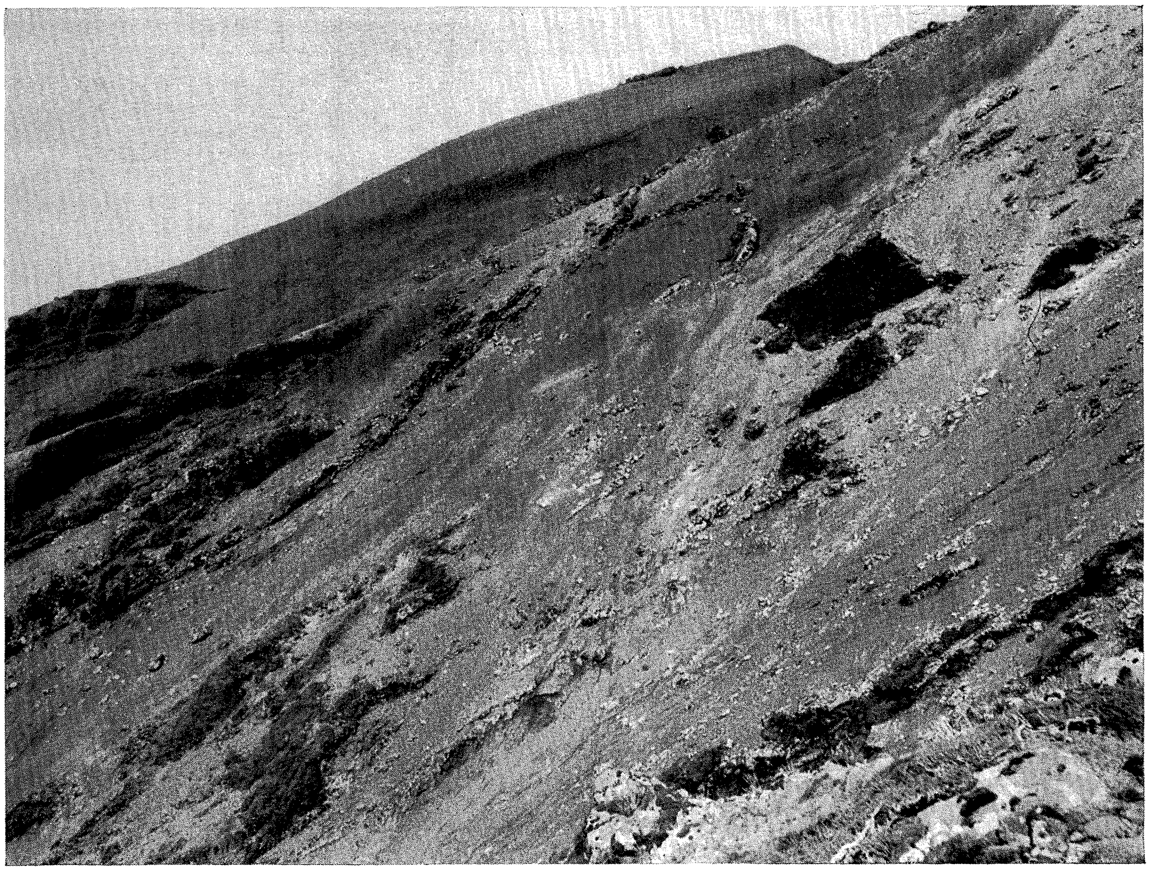

Figure 25. The Peak at *ca.* 1800 m, Tristan. Little vegetation, consisting almost solely of mosses and lichens, except on more stable ground.

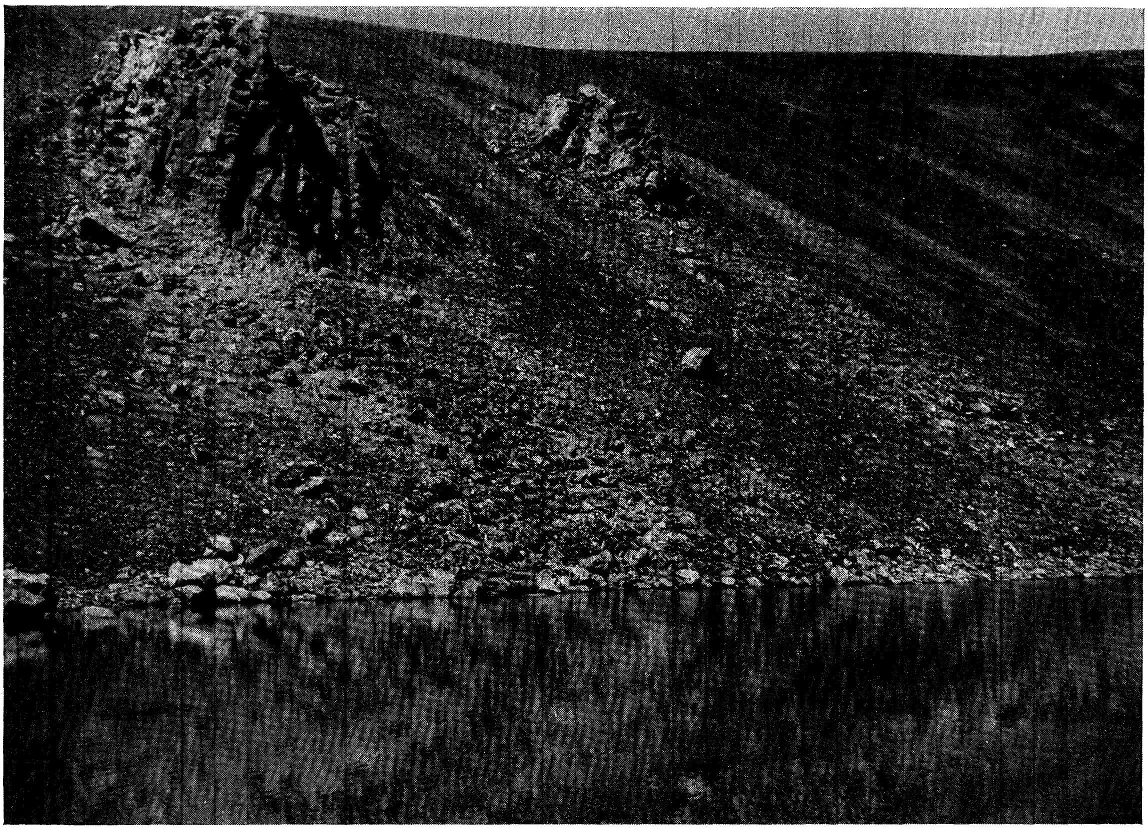

FIGURE 26. The summit crater, Tristan. Foreground is shallow lake. Stripes of vegetation on slopes. *Rhacomitrium lanuginosum*, *Andreaea* and *Cladonia* spp. abundant.

FIGURE 27. The interior of Nightingale Island. Small areas of *Phylica* bush surrounded by *Spartina*. Areas on the slopes free of *Spartina* may have been burned.

FIGURE 28. The Second Pond, Nightingale Island. *Spartina* surrounds the Pond which is covered by *Scirpus sulcatus*. *Rumex obtusifolius* beside the nearest yellow-nosed albatross chicks.

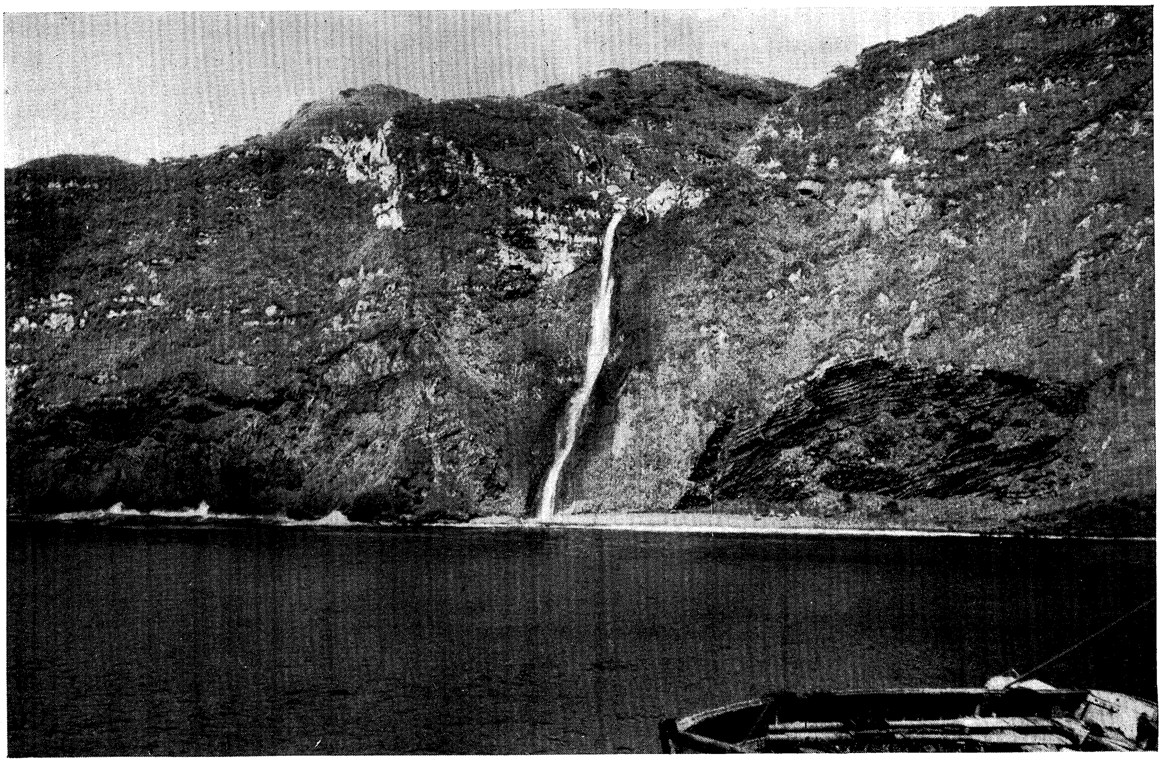

FIGURE 29. Saltbeach Waterfall, Inaccessible Island. Cliffs covered by *Spartina*. *Phylica* on distant slopes. The gully above the Waterfall is only habitat of *Peperomia tristanensis*.

FIGURE 30. *Azolla filiculoides*, bottom right and centre background on open water at West Point, Inaccessible Island. *Spartina*, *ca.* 1·5 m high, on right. *Scirpus sulcatus* on left.

FIGURE 31. Pure stand of flowering *Sonchus oleraceus* on the uppermost part of a beach on Inaccessible Island. Broken stems of *Spartina* lying in foreground.

4·6. *Vegetation of the different islands*

4·61. *Tristan da Cunha*

The vegetation of the main island shows a very clear zonation according to altitude and topography. It has been markedly affected by man. Only the principal divergences from the native formations already described as occurring throughout the island group will be noted here. Altitudinal zonation is shown in figure 16. All the following information is taken from Wace & Holdgate (1958), supplemented by recent observations on the island (J. H. D.).

The Coastal Strips, from sea-level to an altitude of about 100 m support mainly a close-cropped grassland which has been derived from the native tussock grassland and fern-bush by human clearance and firing, and the grazing of imported animals. Remains of *Spartina* and *Phylica* in the lowland mire at Jenny's Watron confirm the early accounts (Lambert 1811; Carmichael 1819) of tussock and *Phylica* on the Settlement plain. The grassland there consists almost exclusively of introduced species, of which the following are more-or-less abundant:

Agrostis stolonifera
A. simulans
Bellis perennis
Centella asiatica
Cynodon dactylon
Holcus lanatus
Plantago lanceolata
Poa pratensis
Sporobolus capensis
Veronica serpyllifolia

Of the native species, only *Blechnum penna-marina* and *Hydrocotyle capitata* are at all common in the turf. *Spartina arundinacea*, *Elaphoglossum succisifolium*, *Hymenophyllum aeruginosum*, *H. peltatum* and *Scirpus* spp. all occur on the Settlement plain, but mainly in areas out of reach of the domestic animals, for example, on the steep sides of the gulches (figure 19, plate 36). Alien species which occur in the grassland turf, but in small quantities only include:

Cerastium caespitosum
Festuca rubra
Hypochoeris glabra
Lolium perenne
Prunella vulgaris
Rumex acetosella
Trifolium dubium
T. repens

Some species in the turf which were noted as abundant in 1955 by Wace & Holdgate (1958), were not found in 1962, notably *Anthoxanthum odoratum* and *Myosotis discolor*. These differences, and the failure of the 1955 observers to record *Cynodon dactylon*, which was noted as very abundant in 1962, may be due to the visits being made at different times of the year (1955: Oct. to Nov.; 1962: Jan. to Mar.).

The Settlement Plain has a cover of outwash material brought down by streams from the Main Cliffs and Base (figure 19, plate 36). The vertical sides of the gulches exhibit sections of this material many feet thick. A soil profile, dug to a depth of 80 cm under the *Cynodon dactylon* sward between the Settlement and the western side of the new lava field, gave the following data:

0–22 cm Dark brown, highly organic soil with dense *Cynodon* rhizomes in the top 5 cm.
22–80 cm Light red brown soil with coarse gravel and fine small rounded stones which became larger and more frequent with depth. *Cynodon* roots penetrated to the bottom of the depth dug.

Another profile from the erosion face at the top of the cliff above Little Beach was similar, but showed a small iron pan at a depth of 15 cm from the surface, although the dark humus-rich soil above showed no signs of leaching. The pan was only a few millimetres thick, and overlay angular stones, pebbles and sand. It is probable that podsolization on the soils of the Settlement Plain has only been initiated following the destruction of the native vegetation there, but more observations of the soils are needed (Wace 1961).

Some strand communities, with scattered plants of *Chenopodium tomentosum*, *Rumex frutescens* and *Sonchus oleraceus* also occur on the Coastal Strips and elsewhere round the coasts. The mire at Jenny's Watron has been described above.

The Tristan cliffs, from sea-level (or the inner margins of the Coastal Strips) to about 600 m above sea-level, support four major types of vegetation:

scree and rock-face communities	fern-bush
Blechnum penna-marina sward	grassland

The open communities of scree and loose rock and rock crevices consist mainly of patches of *Empetrum rubrum*, *Rumex frutescens*, *Scirpus* spp., *Asplenium obtusatum*, *Blechnum australe* and *B. penna-marina*, but the introduced species *Chrysanthemum leucanthemum*, *Plantago lanceolata*, *Poa annua* and *Sonchus oleraceus* are also present. It is notable that all the native colonists of these open habitats are perennial plants, and that the therophytes are all adventive. Raunkiaer's (1937) insistence that the native flora of Tristan was peculiar in its high proportion of therophytes, was based on an incomplete knowledge of the plants at the time (§ 6·2).

The small fern *Blechnum penna-marina* covers large areas of the Tristan cliff-slopes, often forming more or less pure communities which may be terraced with the contours, and sometimes associated with *Elaphoglossum* spp. and other ferns. These terraced low-growing cliff communities may be deflected climax types replacing the tussock grassland which was formerly more abundant on the cliffs of Tristan. Dupetit Thouars (1811) observed that the grass to which he gave the name *Phalaris caespitosa*, and which has not been satisfactorily matched to any modern taxon from the island, was very abundant, and remarked:

'Cette plante couvre quelquefois, a elle seule, un grand espace de terrain', which describes the ecological behaviour of both *Spartina arundinacea* and *Poa flabellata* coastal tussock. Since the sealer Lambert (1811) recognized two sorts of tussock grass, and low fern sward is not developed to anything like the same extent on the uninhabited islands as it is on Tristan, it is possible that the community on Tristan has replaced either or both the tussock-forming grasses over much of the cliffs. Whether *Poa flabellata* formerly inhabited any of the three northern islands is further discussed by Wace (in preparation); an examination of Thouars's original specimens of '*Phalaris caespitosa*' and '*Phalaris mollis*' is clearly relevant to this problem.

The grassland communities on the Tristan cliff-slopes are simply extensions of the coastal plain grasslands, and do not ascend above the levels where cattle graze. The fern-bush communities are substantially similar to the native formation described above, except that *Phylica*, on the Main Cliffs skirting the Settlement Plain is kept shrubby by the cutting of the islanders, and the communities on the Main Cliffs are richer in species than those on the Base or elsewhere in the islands due to the presence of alien species. There are also fewer epiphytes on the *Phylica* trunks in the cliff communities, and *Pseudocyphellaria intricata* is largely confined to the bases of the main stems. The structure of five *Phylica* communities on Tristan is shown in figure 32 in Part IV, and the species present in the understory of ten communities are listed in table 32, Part IV. The Tristan cliffs as a whole fall within the altitudinal range of fern-bush communities, and most of the variants mentioned above can be attributed either to the steep and unstable topography or to the effects (direct or indirect) of man.

The Tristan Base, which lies between 300 and 900 m above sea-level supports mainly native vegetation which has been little affected by man. Fern-bush covers most of the ground up to about 750 m altitude, but above 450 m *Phylica* is more-or-less confined to sheltered gullies, and wide stretches of *Blechnum palmiforme* dominate the scene. Above 750 m wet heath, dominated almost exclusively by *Empetrum rubrum* stretches to the bottom of the Peak. The structure and composition of all these communities has been described previously.

The Peak of Tristan supports three major vegetation types. At an altitude of about 900 m, and probably extending all round the bottom slopes of the Peak in a belt perhaps 100 m deep, is a clearly defined zone of vegetation dominated by the introduced species *Rumex acetosella.* The species occurs in great abundance, forming pure, or almost pure, stands over extensive areas, and grows luxuriantly to a height of 40 to 50 cm (figure 24, plate 39). Various grasses (notably *Agrostis* sp., *Deschampsia* sp., and the introduced *Holcus lanatus*), native carices, and the fern *Blechnum penna-marina* are associated with the *Rumex acetosella,* in patchy communities, and the moss *Drepanocladus uncinatus* is abundant. The presence of this vegetation zone dominated by an introduced species is one of the most striking features of the vegetation of the main island, and serves to distinguish it from the other islands. *Rumex acetosella* was first gathered on Tristan in 1832, and it is possible that it became established on the island before permanent human settlement 22 years previously (Hafsten 1960 *a*, *b*). The aggressiveness and success of the species is similar to its performance in sod tussock grassland communities in New Zealand (Moore 1954), in tussock and heath communities in the Australian mountains (Costin 1954), and in Masafuera of the Juan Fernandez group (Skottsberg 1953, p. 932). As in all these areas, other introduced species (notably *Anthoxanthum odoratum*) would probably be found important in the Tristan *Rumex*-zone if observations were made throughout the year. The native community supplanted by the *Rumex acetosella* is uncertain, but it is possible that a diverse type of wet heath similar to that now found on Gough Island (where *R. acetosella* was not established in 1955–56) formerly covered the lower parts of the Peak, or possibly that tussock grassland of *Spartina arundinacea* was present. Patches of bare ground occur within the *Rumex acetosella* zone, but the remaining two vegetation types of the Tristan Peak (*Rhacomitrium–Empetrum* heath, and an alpine desert), are more open, and fall within the category of feldmark, as described above.

The instability of the volcanic cinders and the extremely exposed conditions on the upper part of the Peak are the most important factors controlling the physiognomy and distribution of the vegetation. In the flatter ground and relatively sheltered conditions of the main crater, at an altitude of about 1800 m, various bryophytes, notably *Rhacomitrium lanuginosum* and *Andreaea* spp., and a few lichens, e.g. *Cladonia* spp., are abundant (figures 25, 26, plates 39 and 40). The only vascular plant in the crater is *Empetrum rubrum*, which forms a few, very scattered and dwarfed patches. Outside the crater, the bryophytes and lichens are very largely confined to the crevices of stable rocks and scarcely colonize the mobile cinder screes.

4·62. *Nightingale Island*

Of the five native vegetation formations in the islands, three (tussock grassland, fern-bush and peat mires) are represented on Nightingale Island.

Spartina arundinacea tussock, growing luxuriantly to a height of $2\frac{1}{2}$m dominates most of the vegetation. Middle and Stoltenhoff Islands, except for the sea-cliffs, have a virtually complete cover of *Spartina* tussock (figure 18, plate 5). Over a large part of Nightingale the tussock is so dense as to exclude other species. Even bryophytes are very sparse on the peaty soil under the tussocks, and the scarcity of associated species can be further explained by the presence of huge colonies of ground-nesting sea birds, notably rockhopper penguins (*Eudyptes crestatus*) and greater shearwaters (*Puffinus gravis*). Hagen (1952) estimates that there are more than half a million burrows of the greater shearwater on the islands, and states (p. 97) that 'the ground on Nightingale was over large areas completely sapped by Petrel (greater shearwater) burrows. Exceptions were found only where rocks, soggy ground, or ground occupied by penguins (a smaller area of the north-east side) excluded the digging of burrows'. In the large penguin rookery, the ground under the tussock is covered by excreta and feathers.

Scattered trees of *Phylica* grow amongst the tussock on Nightingale, and here and there the trees occur in small groups (figures 27, 28, plates 40 and 41). In the region of the Ponds (figure 27) there are small areas of *Phylica* with a closed canopy. The trees grow to a height of 4 to 5 m and bear a luxuriant growth of epiphytes—mostly lichens of the genera *Ramalina* and *Usnea*. The species of the field layer, which is well developed only where the canopy is relatively open, include *Acaena sarmentosa*, *Asplenium obtusatum*, *Carex insularis*, *C. thouarsii* and *Nertera holmboei*. According to Hafsten (1951), *Phylica* is confined to the wetter areas on the islands, and follows the watercourses, forming only a sparse forest around the Ponds.

There is very little open water in the area known as the Ponds. According to Christophersen (quoted in Hafsten 1951, p. 21), the mire where he made a peat excavation to a depth of over 3 m, lay in a hollow which was a typical infilled and overgrown lake. The first Pond has a small central area of *Phylica*, with *Blechnum palmiforme* associated. *Scirpus sulcatus* forms an almost complete cover round about, and the edges of the open water contain *Callitriche* sp.

Empetrum rubrum, *Scirpus thouarsianus*, *Asplenium obtusatum* and various bryophytes and lichens grow on exposed rocks. Apart from *Empetrum*, all these plants and *Hypolepis rugosula*, *Vittaria vittarioides* and *Elaphoglossum succisifolium* were seen on rocks against the tussock. *Neohodsonia mirabilis* (H. Perss.) H. Perss. (Persson 1953, 1954; Campbell 1954) is one of the most conspicuous bryophytes in such a habitat, and it occurs also on the vertical sides of the nests of the yellow-nosed albatross (*Diomedea chlororhynchos*).

Of the vegetation of the three northern islands, that of Nightingale has probably suffered least from human interference, although it is visited annually by the Tristan islanders to collect shearwaters. There are at present no grazing animals on the island, and rats have not yet succeeded in establishing themselves there. Fires in the tussock have been reported (Hafsten 1951), and there was a fire a few years ago on the top of the slope overlooking the east end of Second Pond (A. Swain, personal communication). A species of *Scirpus* (perhaps *S. thouarsianus*) has invaded the burnt ground. A broad path has been cut through the tussock grass from the landing place at the north-east corner of the island to the Ponds, and *Acaena sarmentosa*, *Nertera holmboei* and *Scirpus* sp. (*S. thouarsianus*?) especially are found on the cleared areas beside the path. *Phormium tenax* has been planted at a few places along the path, and the plants were large and luxuriant, reaching a height of 3 m and fruiting freely. The few other alien species seen were *Solanum tuberosum* (at the islanders' huts only), *Poa annua* (on the path), *Rumex obtusifolius* (on the path, and with *Holcus lanatus* at the east end of the Second Pond).

4·63. *Inaccessible Island*

All the following information about Inaccessible Island vegetation is taken from the fragmentary observations of Moseley (1875), Hemsley (1885), Wild (1923), Rogers (1926), Christophersen (1940*a*), Dunne (1941), Hafsten (1951), Hagen (1952), and the observations of one of us (J. H. D.) during two brief visits in 1962.

The island, the highest point of which is about 600 m above sea-level, is surrounded by very steep cliffs, but it has one main valley which is covered with fern-bush (and in which the phytogeographically surprising *Peperomia tristanensis* has been discovered).

The vegetation of the low-lying areas and cliffs is exactly similar to that of Nightingale Island (figure 30, plate 42). *Spartina*, in luxuriant condition, is dominant. There are scattered *Phylica* bushes, especially on the upper parts of the cliffs. The plateau probably supports some wet heath with *Blechnum palmiforme*. Neither mire nor feldmark vegetation is known to be present on the island.

Feral pigs, goats and sheep are known to have been present on the island at different times (pp. 331 and table 14). Survivors from a shipwreck lived some months on the island in 1822 (Lockhart 1930). Two Germans inhabited it for several years up to 1873 (Moseley 1892), and attempts were made to settle and farm the island in 1937–38. Nevertheless, man has probably not had a very great impact on the plant life there. Around the ruined cottage at Saltbeach the following aliens are well established: *Agrostis stolonifera* L., *Brassica rapa* L., *Centella asiatica* (L.) Urb., *Gnaphalium luteoalbum* L., *Oxalis corniculata* L., *Plantago major* L. and *Poa annua* L. At both Saltbeach and Blenden Hall, *Calystegia sepium* (L.) R. Br., *Holcus lanatus* L., *Mariscus congestus* C.B. cl., *Rumex obtusifolius* L. and *Sonchus oleraceus* L. occur mostly along the littoral margin of the *Spartina* tussock. *Azolla filiculoides* Lam. abounds on wet ground under *Spartina*, and especially on open water, at Blenden Hall and West Point (figure 30, plate 42).

4·64. *Gough Island*

All five of the native vegetation formations in the group are present on Gough Island, almost completely undisturbed by man or introduced animals. The formations are very clearly zoned according to altitude, but the boundaries between the corresponding zones are about 150 to 300 m lower on Gough than their counterparts on Tristan (figure 16).

There are several other major differences in the vegetation of Gough, as compared to that of the Tristan group islands.

Although *Spartina arundinacea* tussock grassland is an important constituent of the vegetation on the Tristan group islands (especially on Nightingale), there is no ecologically important equivalent on the other islands to the widespread *Poa flabellata* coastal tussock of Gough. Since both these communities appear, at least to some extent, to be biotic climax types, it may be that this difference between the vegetation of Gough and Nightingale Islands on the one hand and Tristan and Inaccessible on the other, is a reflexion of the differing density of breeding sea birds on the islands. Whether *Poa flabellata* formerly inhabited any of the Tristan group islands has been discussed above, but tussock communities dominated by this species and its relatives are predominantly sub-Antarctic in distribution (Wace 1960), so that the absence of the species from the Tristan group islands would be in accordance with the climatic preferences of the community elsewhere.

The fern-bush vegetation on Gough Island appears to be richer in cryptogams than that on the Tristan group islands, and to be more rigidly confined to the relatively sheltered 'glens' of the eastern side of the island. Where fern-bush occurs on Gough outside the relatively sheltered conditions of the glens, more flowering plants are present as associates, and it is more similar to the Tristan community.

Both the wet heath and the mires are far more extensive on Gough Island than on Tristan, and the open montane communities are more extensive on Tristan than on Gough in relation to their total areas. These differences are probably due to the differing topographies of the two largest islands in the group. The porous and friable basalts of Tristan, and the large quantities of mobile cinders on the Peak have probably restricted the incidence of waterlogging which could lead to the development of topogenous peat and, at the same time, restricted the area over which closed wet heath communities could develop. By contrast, on Gough the wide trachyte valleys in the upper parts of the island have given many sites in which topogenous peat has developed and on which wet heath forms closed communities. Some of the larger areas of open communities on Gough, such as the Barren Dome, may be largely bare of vegetation for other than climatic reasons (see above).

In general, it can be seen that the native vegetation of the several islands in the Tristan–Gough group differs only in detail from one island to another in accordance with their differing topographies. The most conspicuous differences are associated with different biotic factors, or with the differing impact of man and his animals on the several islands.

4·7. *Vegetational history*

Deposits of peat from all the islands except Inaccessible have been sampled for pollen analysis and diagrams have been published for two sites on Tristan, one on Nightingale, and one on Gough Island (Hafsten 1951, 1960*a*, *b*). Some details of these sites are included in table 11. In addition to these sampled sites, peat monoliths have been excavated from Jenny's Watron on Tristan, and from Albatross Plain on Gough, for extraction of macroscopic fossils, and two levels of the Gough monolith have been radiocarbon dated.

Apart from the influx of weed pollen at the highest levels in the Tristan peats, the pollen frequency curves show little change over the entire depth of all the analysed profiles.

With the exception of pollen whose presence in the samples can be attributed to long-distance dispersal (*Ephedra*, *Nothofagus*) or contamination (*Alnus*, *Betula*, *Corylus*, *Pinus*), no pollen of plants which do not now inhabit the islands have been found in the peat. However, according to Hafsten (1960*b*), a single grain of what may be *Collomia* pollen possibly represents a temporary sojourn of that genus on Gough Island. Various unidentified grains were also found by Hafsten.

Radiocarbon dating of peat at a depth of 2·15 m from the surface of Albatross Plain, Gough Island, has given an age of 4720 ± 130 years B.P. (Cambridge, England; sample Q418). By comparing the pollen content of the dated peat with that of the pollen profile, Hafsten (1960*a*, *b*) concluded that the vegetation in the vicinity of Albatross Plain on Gough Island had undergone no major changes during the last 5000 years or so. Judged by the comparable depths of peat and similarly invariable profiles, this argument for vegetational and floristic stability during the last few thousand years (excluding the effects of man on Tristan), may also be applied to the other islands from which pollen profiles have been analysed.

TABLE 11. ALTITUDES, SURROUNDING VEGETATION, AND DEPTHS OF PEAT IN THE SITES FROM WHICH POLLEN PROFILES HAVE BEEN ANALYSED IN THE ISLANDS

	Tristan da Cunha			Nightingale	Gough Island
	Jenny's Watron	Soggy Plain		The Ponds	Albatross Plain
altitude (approx.)					
metres	30	740		200	600
feet	100	2400		670	2000
surrounding native vegetation	tussock and fern-bush	fern-bush and wet heath		tussock and fern-bush	wet heath
depth of peat (m)	1·55	2·45	3·75	3·4	4·5
fieldwork and date sampled	Wace & Holdgate in 1955	Christophersen in 1937	Wace & Holdgate in 1955	Christophersen in 1937	Wace in 1956

Bands of volcanic ash are present in the recent peats on Tristan, Nightingale and Gough Islands. One of these bands in the Albatross Plain monolith from Gough Island has been radiocarbon dated at 2345 ± 120 years B.P. (Cambridge, England; Q418), but other ash bands occur at shallower depths in all three islands. Almost nothing is known of the changes in the vegetation induced by this periodic volcanic activity in the islands. The formation of numerous secondary cones on Tristan may well have affected the vegetation in ways similar to, but perhaps more severe, than those described by Dickson (Part IV). The narrowness of the dated ash layer (less than 0·1 cm thickness) in the Albatross Plain peat, in an area about 1½ miles from the putative source (Edinburgh Peak, the highest part of Gough Island), may be taken to indicate that the eruption was of a very minor nature, possibly similar to the 1961 disturbance on Tristan, and that serious damage to the vegetation resulting from burial by ash was very localized indeed.

Two discoveries made by members of the Royal Society Expedition promise to yield important information about the history of the biota of the islands. Organic layers, of ages far greater than any of the deposits investigated by Hafsten were found on Tristan and Nightingale Island.

The Tristan material was discovered in Council Gulch at an altitude of about 700 m. An organic deposit had been buried by the cinders thrown out by the secondary volcano, Big Green Hill described as a scoria mound by Baker *et al.* (1964). A very recent landslide had revealed a section about 3 m wide and 5 m high. The stratigraphy was as follows:

cm	
0	Bottom of cinder agglomerate.
0–12	Light brown silt.
12–14·5	Dark brown organic silt with very abundant diatoms, radiocarbon sample NPL-47.
14·5–18·5	Light brown inorganic silt.
18·5–22·5	Dark brown organic silt with few diatoms, radiocarbon sample NPL-48.
22·5–26	Light brown inorganic silt of a coarser nature.
26–27	Very marked iron pan.
27–36·5	Dark grey gravel.
36·5–51	Gradual transition to light reddish brown silt.
51–56	Cinder.
56–61	Light reddish brown silt.
61–74	Dark brown gravel.
74	Thin layer of cinders on bed rock.

The silty nature of the material and the diatoms indicate that the deposit was laid down in a shallow pool. The iron pan and the lower organic silt ($18\frac{1}{2}$ to $22\frac{1}{2}$ cm) extended across the section and were uniform in thickness. The upper organic silt ($12\frac{1}{2}$ to $14\frac{1}{2}$ cm) was irregular in thickness and discontinuous.

Radiocarbon assays of the two organic silts were carried out by the National Physical Laboratory

NPL-47	10770 ± 156 B.P.
NPL-48	11310 ± 168 B.P.

On Nightingale Island two deposits with the following stratigraphies were found:

Hardie (sea-stack) near Sea-hen Rocks

m	
8 (approx.)	Sea-hen Tuff; coarse and fine almost unconsolidated tuff.
0·1	Organic layer, radiocarbon sample NPL-49.
0·5	Blocky lava.
15 (approx.)	Columnar-jointed trachytic lava.

On the coast of Nightingale Island opposite Sea-hen Rocks

8	Sea-hen Tuff.
5·5	Trachytic lava.
3	Fine tuff with abundant plant remains, and numerous ash partings, radiocarbon sample NPL-50 from one of the plant layers.
4·5	Raised beach deposit.
9	Weathered trachyte.

The radiocarbon dates are:

NPL-49	39160 + 6090/ − 3410 B.P.
NPL-50	> 36900 B.P.

Pollen analyses of the four radiocarbon dated horizons have been made by Dr D. M. Churchill and Dr N. T. Moar.

The Big Green Hill deposit has pollen spectra which differ in no significant way from those of the younger peats studied by Hafsten (1960*a*, *b*). This points to a high degree of floristic uniformity throughout the last 11 000 years.

The present-day flora of Nightingale Island is very poor in species. As yet, there are records of only 31 native vascular plants, compared with 61 from Tristan and 57 from Gough Island. The total numbers of pollen and spore types of native vascular plants so far recognized in all the pollen analyses from the three islands are: Nightingale 13, Tristan 23, Gough 24. The Sea-hen Rocks analyses may be taken to indicate that the flora of the Nightingale Island of 39 000 years ago was as impoverished as is the modern one.

TABLE 12. POLLEN ANALYSIS FROM BIG GREEN HILL, TRISTAN DA CUNHA, AND SEA-HEN ROCKS, NIGHTINGALE ISLAND

	Big Green Hill			Sea-hen Rocks		
	NPL-48			NPL-49		
	no.	total pollen spores (%)	NPL-47 presence	no.	total pollen spores (%)	NPL-50 presence
Cyperaceae	400	54	+	690	69	+
Gramineae	90	12	+	147	14	+
Umbelliferae	58	8	+	103	10	+
Hydrocotyle	—	—	—	1	< 1	—
Callitriche	31	4	+	1	< 1	—
Nertera	17	2	+	41	4	+
Acaena	4	1	—	—	—	—
Compositae (tubuliflorae)	2	< 1	—	—	—	—
Cotula	—	—	—	—	—	+
Phylica	2	< 1	—	—	—	—
Empetrum	1	< 1	+	—	—	—
Chenopodiaceae	+	—	—	1	< 1	+
Lycopodium insulare	57	8	+	5	< 1	+
L. magellanicum and/or *L. diaphanum*	5	1	+	—	—	—
Ophioglossum	8	1	+	—	—	—
Polypodiaceae	61	8	+	11	1	+
Gymnogramma	4	1	—	—	—	—
totals	740	100		1000	100	

A striking feature of Hafsten's diagrams is the consistent presence of such obviously exotic taxa as *Nothofagus*, *Ephedra*, *Betula*, and *Alnus*. No such grains were seen in the Big Green Hill samples. However, a three-pored grain, similar in state of preservation and stain reaction to the other grains in the preparation, was found in one of the Sea-hen Rocks samples. Insufficient detail of the pore wall has been preserved to allow a positive identification. Its superficial appearance suggests *Corylus* or *Myrica*. As Hafsten (1960*a*) has stated, the interpretation of pollen data from such remote islands as the Tristan–Gough group presents special difficulties, due to the isolation and its ecological consequences. These difficulties may be summarized as follows:

(*a*) Many species of the native plants have a very high ecological amplitude on the islands, and there are therefore few good 'indicator species' of particular vegetation types.

(*b*) Some of the best potential 'indicators' are either self-pollinating species with a floral morphology which prevents the shedding of much pollen into the air (e.g. *Phylica arborea*), or else belong to taxonomic groups in which pollen or spore discrimination between the different insular species is difficult (e.g. *Blechnum palmiforme* and other Polypodiaceae; *Poa flabellata* and other grasses; different representatives of the tubiflorous Compositae).

(*c*) The rate of establishment of new species on the islands in response to any environmental change is probably very slow, due to the remoteness of the islands; any such changes in environmental conditions may therefore be difficult to detect by corresponding changes in the flora.

The special interest of the newly discovered deposits is that they formed during the last glacial period which is tentatively considered to be broadly contemporaneous in both hemispheres (Auer 1960; Godwin 1960) and which had such marked effects on the vegetation of many regions of the world (Auer 1958; Godwin 1956; Wardle 1962). With the proviso that the difficulties listed above must be borne in mind, it can be stated that there is nothing in the new palynological data which is indicative of any major difference in the flora and composition of the vegetation of last glacial age from those of the islands of the present day. This accords with the view of Skottsberg (1942) that Quaternary climatic changes have had little effect upon the floras of remote mid-latitude islands.

Nothing is known of the effects on the vegetation of the erosion which has reduced Nightingale, Inaccessible and Gough to mere fragments of huge cones. As yet, the effects of the periodic volcanism and the Quaternary climatic changes are little understood. Detailed study of all the organic layers in the Sea-hen Rocks strata and the discovery and investigation of similar deposits will help to elucidate these problems.

4·8. *Geographical relationships of the vegetation*

The different native formations of the islands' vegetation are structurally similar to types found in the sub-Antarctic regions, in the high mountains of the tropics, and in temperate latitudes of hyper-oceanic climates. Until there is some generally accepted and relatively simple quantitative method of denoting vegetation structure, such comparisons are bound to remain somewhat subjective and superficial, but the following geographical affinities of the insular vegetation are clear. The formulae proposed by Küchler (1949) to denote different structural types are used where possible, but other criteria (functional characteristics, developmental phenomena) are used in some cases, which cannot be expressed in Küchler's formulae (Fosberg 1958).

Tussock grassland is most clearly related to sub-Antarctic vegetation types. Maritime tussock grassland dominated by large species of *Poa* are one of the most characteristic features of the southern cool temperate and sub-Antarctic insular vegetation (Wace 1960). The *Poa flabellata* tussock of Gough Island (Gtc. Hlr) is clearly an outlier of this circum-Antarctic type, and the *Spartina arundinacea* tussock of the Tristan–Gough and Amsterdam–St Paul island groups is structurally similar.

The fern-bush vegetation of the islands, particularly the elements dominated by *Phylica arborea* and *Blechnum palmiforme* (Blpe and Ylce, respectively), resemble communities which are characteristic of the upper limit of woody vegetation in the tropical mountains (Troll 1958*b*). The structural relation of the *Phylica* community in the islands to microphyll thicket vegetation elsewhere, have been discussed by Wace & Holdgate (1958) and Wace (1960, 1961): 'The general points of resemblance in all these communities are the dominance of one, or a small number of species of straggling heath-like microphyllous evergreen trees without a continuous canopy, the importance of ferns in the field layer and understory, and the abundance of cryptogamic epiphytes' (Wace 1961, p. 350). Communities with these general characteristics which have been described from different parts of the world are listed in table 13. Troll (1958*a*) has suggested that these similarities in vegetation reflect similar aseasonal and microthermal climates in the tropical tree-line and sub-Antarctic regions.

TABLE 13. THE STRUCTURAL EQUIVALENTS OF FERN-BUSH VEGETATION

locality	vegetation	dominants	authors
Atlantic Islands			
O Pico, Azores	*Ericetum azoricae*	*Erica azorica*	Tutin 1953
Fernando Po, Gulf of Guinea	ericaceous zone	*E. arborea*	Adams 1957
Tristan–Gough group	fern-bush	*Phylica arborea*	Wace & Holdgate 1958 Wace 1961
Africa			
East African mountains	ericaceous belt	*Erica arborea* *Philippia* spp.	Hedberg 1951
America			
tropical mountains	elfin woodland	various	Beard 1955
Jamaican mountains	elfin woodland	*Clethra* spp., *Clusia* spp.	Asprey & Robbins 1953
Australasia and Oceania			
Javanese mountains	elfin woodland	*Libocedrus* spp. *Vaccinium* spp.	Schimper 1903
New Guinea mountains	montane cloud forest	*Rhododendron* spp. *Vaccinium* spp.	Robbins 1961
Australian and Tasmanian mountains	microphyll mossy thicket	*Nothofagus cunninghamii*	Webb 1959
New Zealand mountains	subalpine scrub	*Libocedrus* sp. *Weinmannia* spp.	Cockayne 1928
New Zealand shelf islands	rata forest	*Metrosideros lucida*	Cockayne 1909
Hawaii	upper forest	*Cyathodes* sp. *Coprosma* spp. *Metrosideros* spp. *Sophora chrysophila*	Hartt & Neal 1940

In addition to these accounts, van Steenis (1935) and Troll (1958*a*) have compared what they have described as moss (subalpine) forest, and round-canopied mist forest ('Kugelschirmbäume Nebelwald') in different areas of the tropical high mountains.

The wet heath, mire and feldmark vegetation of the islands is structurally similar to temperate zone vegetation types, in so far as it is possible to make valid comparisons between communities that are not characterized by the dominance or importance of distinctive growth forms. The general physiognomy of the wet heath (EmpGliLcy) and feldmark communities (GhLr) in the islands (especially the importance of dwarf ericoid chamaephytes in association with moss hummocks and small tufted graminoids) is very reminiscent of the moorland and montane vegetation which is developed under extremely oceanic climates in north-west Europe. The valley bogs of Gough and Tristan appear to be closely similar in their structure to the dissected high level bogs of Britain (Pearsall 1950), the ombrosoligenous bogs of Sweden (von Post 1937), and the mixed mires of Ireland (Oswald 1949).

It is noteworthy that some of the circum-Antarctic and tropical montane vegetation types are not represented in the islands. None of the large hard cushion-plants, either of open feldmark (e.g. *Azorella*, *Hectorella*, *Pycnophyllum*) or of bog communities (e.g. *Distichia*, *Donatia*, *Gaimardia*, *Phyllachne*) which are so characteristic of sub-Antarctic and tropical montane regions is present on the islands, and none of the island plants has a comparable growth form. With the exception of *Azorella*, the cushion plants appear to be 'continental' in range (Wace 1965) and the islands lack these specialized growth forms and the communities they dominate.

5. THE GENERAL CHARACTERISTICS OF THE PLANT LIFE

In a classic paper, Hooker (1867) reviewed the general characteristics of insular floras, some of which were later discussed by Hemsley (1885), Guppy (1919) and Gulick (1932). Skottsberg (1956, pp. 351–362) has reviewed the subject fully, and some of the major characteristics of insular floras that he recognizes will be discussed in relation to the Tristan–Gough flora here. Recently Fosberg (1963) has considered some of the significant features of island ecosystems in the Pacific, which he lists as follows:

relative isolation,
limitation in size, leading to a lack of ecological 'buffering' effects found in larger land masses,
limitation in organic diversity,
reduced inter-species competition,
protection from outside competition, and the consequent preservation of archaic, bizarre, or possibly ill-adapted forms,
tendency towards climatic equability,
extreme vulnerability, or tendency towards great instability when isolation is broken down,
tendency towards rapid increase in 'entropy' when the change has set in.

Many of these features are also displayed by the Tristan–Gough ecosystems, and are discussed in the following pages.

5·1. *Impoverishment and disharmony*

The angiosperm flora of the islands is notably poor in species when contrasted with continental areas of similar size, climate and diversity; but this impoverishment may be less marked among the cryptogams. The impoverished flora is also 'disharmonic' in the sense that 'its species lack the local coherence of inter-relationships, and that the assortment of forms fails to constitute a normally balanced and diversified total flora' (Gulick 1932). Two related elements are involved in this concept of disharmony, both of which can be illustrated from the Tristan–Gough native flora: a lack of genetic diversity in the few taxa present, and a paucity of major biological types of plants as compared to continental floras.

Leaving aside the species which have undoubtedly been introduced by man (§ 6), it is clear from the figures in tables 3 and 4 that the islands have a very meagre angiosperm flora. Thus, the island of Rhum in the Scottish Hebrides, which resembles Gough Island in area, altitude, and climate, probably has about 320 species of native flowering plants (Heslop Harrison 1939), and the much smaller Clare Island near the West coast of Ireland has 312 native species (Preager 1911). This compares with 31 known native species from Gough Island. The density of native flowering plant species for the whole Tristan–Gough group (0·26 species per sq. km, or 0·67 species per sq. mile) falls within the range of that of many other oceanic islands, as listed by Good (1953, p. 144). Figures for the individual islands range from 3·75 species per sq. km (9·74 species per sq. mile) on Nightingale, to 0·37 species per sq. km (0·86 species per sq. mile) on Tristan.

The lack of genetic diversity in the native angiosperm flora is shown by the small number of species per genus, and genera per family, when compared to continental (or continental island) floras (Hooker 1867). Of the eighteen families of native angiosperms in the islands, ten are represented by only a single native genus and species:

Ranunculaceae (*Ranunculus*)
Cruciferae (*Cardamine*)
Geraniaceae (*Pelargonium*)
Rhamnaceae (*Phylica*)
Papilionaceae (*Sophora*)
Empetraceae (*Empetrum*)
Polygonaceae (*Rumex*)
Piperaceae (*Peperomia*)
Juncaceae (*Rostkovia*)
Juncaginaceae (*Tetroncium*)

Three further families, each with a single genus, have 2 or 3 species recorded from the islands:

Rosaceae (*Acaena*, 2 spp.)
Callitrichaceae (*Callitriche*, possibly 2 spp.)
Rubiaceae (*Nertera*, 3 spp.)

The more diverse families, with more than one genus in the islands, are:

Umbelliferae (*Apium*, *Hydrocotyle*)
Compositae (*Chevreulia*, *Cotula*, *Gnaphalium*, *Lagenophora*)
Chenopodiaceae (*Atriplex*, *Chenopodium*)
Cyperaceae (*Carex*, *Scirpus*, *Uncinia*)
Gramineae (*Agrostis*, *Deschampsia*, *Glyceria*, *Poa*, *Spartina*, and possibly *Festuca* and *Polypogon*)

Although the figures for generic and family sizes in table 4 are based on rather uncertain taxonomic foundations, they show that none of the islands differs markedly from the mean values for the whole group, and that these mean values of *ca.* 1·4 species per genus and *ca.* 1·7 genera per family, are in keeping with those from other remote insular floras (Hooker 1867), and are far less than the mean values of *ca.* 46 genera per family and 18 species per genus which are the world averages for the flowering plants (Good 1953).

Even though some of the insular species are extremely variable, and may be more polymorphic than their continental relatives (?*Apium australe*, *Empetrum rubrum*), such polymorphism has not received taxonomic recognition above the rank of subspecies. In those cases where several species of the same genus are native to the islands, these species are so distinct from each other as to suggest that they are due to separate arrivals from outside and not to evolutionary divergence within the group; although *Nertera*, *Scirpus* and *Agrostis* may have undergone minor radiation (see below). In most cases, time has perhaps been insufficient to enable distinct taxa to evolve from the descendants of the earliest immigrants, but the relaxation of competition in the species-poor ecosystem may allow a greater range of phenotypic expression in some genera than is present elsewhere.

The different balance of major biological types in the Tristan–Gough group compared with those of other regions is shown by a comparison of the biological spectra of the islands with climatically similar areas elsewhere (Raunkiaer 1937). The recognition that oceanic islands lack (or have very few species of) native annual flowering plants is the most striking example of the narrow range of biological types in their floras (Hooker 1867): the only undoubtedly native therophyte in the Tristan–Gough flora is *Gnaphalium pyramidale*. Raunkiaer's (1937) supposedly high proportion of therophytes in the native flora was due to the wrongful inclusion of several perennial species (e.g. *Cotula moseleyi* and *C. goughensis*) in this category. The fact that several alien therophytes are successfully invading native communities which have not been affected by man's activities shows that there is a place in the insular ecosystem for more plants of this life form, and that the native flora is disharmonic in lacking them. The paucity of phanerophytes, and of several more specialized life forms such as climbers, epiphytes, parasites and saprophytes, amongst the angiosperms, also suggests that the native flora does not 'constitute a normally balanced and diversified' whole.

The lack of a close specificity between the partners in various types of biological associations in the insular flora also suggests that many niches remain unexploited, and that host parasite relations have not had time to diversify in the islands. Jørstad (1947) stated that none of the rust fungi in the Tristan group appears to be obligatorily host-alternating. Only two rusts parasitic on native hosts (i.e. *Puccinia goughensis* on *Apium australe* in Gough Island, and *Uredo caricis-thouarsii* on *Carex thouarsii* in Nightingale) were considered to be specific to single host species and endemic to the islands. Most of the plant-feeding invertebrates in Gough Island have a wide range of food plants, although some are less catholic in their choice of hosts, and Holdgate (1960) states that it is at present 'impossible to assess how under-exploited the various habitats are' (but see Holdgate 1965; Part III this Report).

Disharmony in the flora, in contrast to that of the world as a whole, is also shown by the abnormally high proportion of cryptogams to phanerogams in the islands. The proportion of pteridophyte species in the vascular flora is exceptionally high, even for insular floras. Raunkiaer (1934, 1937), in discussing the significance of the varying proportions of pteridophytes in the floras of different regions of the world, noted the unusually high proportion in the Tristan–Gough group. Raunkiaer's 'pteridophyte quotient' is calculated on the supposedly normal world proportion of twenty-five phanerogams to every one pteridophyte, so that for any flora its pteridophyte quotient is

$$\frac{\text{number of species of pteridophytes} \times 25}{\text{number of species of phanerogams}}.$$

On this basis, he arrived at the following pteridophyte quotients for a number of island floras:

Ascension Island	35		
Tristan–Gough group	24	20·1	see table 3
Marion Island		22·5	Greene & Greene 1963
Amsterdam–St Paul group		20·8	Hemsley 1885; Werth 1928
Tahiti	12·2		
St Helena	11		
Rarotonga	9·3		

Juan Fernandez group		9·0	Skottsberg 1956
Seychelles	7·8		
South Georgia	6·6	10	Greene & Greene 1963
Fiji	6·1		
Hawaii	5·1		
Falkland Islands	3·2		
Clare Island		2·8	Preager 1911
Madeira	2·7		
Azores	2·2		

Some of Raunkiaer's calculations were based on very small numbers of species (Ascension Island), or on a very incomplete knowledge of the flora (South Georgia) or the status of the insular plants (St Helena). Figures for a few islands which are based on more complete knowledge of the island floras are given for comparison, together with the sources of information, in the right-hand column. It appears that even the revised figures for the Tristan–Gough group are high, and are approached only by those from the South Indian Ocean islands of Marion and the Amsterdam–St Paul group.

Similarly, Raunkiaer proposed 'quotients' for bryophytes, based on the following proportions. The figures given are calculated from the sources noted, or taken from Raunkiaer's (1937) paper:

	$\frac{\text{no. of mosses} \times 11}{\text{no. of phanerogams}}$	$\frac{\text{no. of hepatics} \times 25}{\text{no. of phanerogams}}$
Tristan–Gough group (see table 3)	40	137
Juan Fernandez group (Skottsberg 1956)	11	35
South Georgia	73	84
Faeroe Islands	10	12
Azores	2	3

The large cryptogam quotients of the islands are partly a reflexion of the hyper-oceanic temperate climate, but they are no doubt also related to the greater ease of dispersal of the spore-dispersed plants and the youth of the present flora.

If, as Gulick (1932), believes, disharmony in insular biota is related to age, and if floras and faunas attain an internal harmony with evolutionary diversification over long periods, then the strikingly impoverished and disharmonic flora of the Tristan–Gough group is evidence that the present plant life of the island is very young.

5·2. *Endemism and radiation*

The presence of endemic plants and animals in oceanic islands was recognized early as one of their outstanding biological features. The taxonomic confusion which has led to a poor understanding of the degree of endemism in the Tristan–Gough flora has been discussed previously (§§3·1, 3·2 and 3·3). There are no endemic families or genera, and the levels of specific endemism have been estimated at:

angiosperms	*ca.* 37%	of the native flora
pteridophytes	*ca.* 42%	
mosses	*ca.* 43%	
hepatics	*ca.* 14%	

Although these figures are subject to revision with further taxonomic work, it is clear that specific endemism among the land plants is not deep-seated: most of the insular species differ little from their continental relatives. The Tristan–Gough endemics, at least among the flowering plants, give the impression of being very young species 'newly evolved in isolation upon the islands' (Guppy 1906).

In marked contrast to many oceanic islands in lower latitudes, there are no epibiotics or relict endemics (Cain 1944) which show only distant relations to continental plants. There are no equivalents in the Tristan–Gough group to the woody Compositae of St Helena and Islas Juan Fernandez, or to the arborescent Lobeliaceae of Hawaii, or to *Pringlea* of the islands of the southern Indian Ocean. With the possible exception of *Phylica arborea* (Levyns 1964), none of the Tristan–Gough species could be considered as 'relicts of species extinct elsewhere' (Guppy 1919). The relations of *Phylica arborea* in the South Atlantic and mid-Indian Ocean islands to St Helena and South African species suggests a parallel to the lauraceous genera of the Macaronesian and Canary Islands, which Hooker (1867) considered relict genera from the Tertiary Mediterranean flora.

There appear to be no differences in the rates of endemism of terrestrial vascular plants between the various islands in the Tristan–Gough group; but more collecting of bryophytes in the lesser islands will be necessary before any statement to this effect can be made for them. Each of the four main islands has a single species of vascular plant which has not been discovered on any of the others, and is accepted as endemic:

Tristan da Cunha	*Elaphoglossum insulare*
Inaccessible	*Peperomia tristanensis*
Nightingale	*Cotula moseleyi*
Gough	*Cotula goughensis*

Evolutionary radiation in the islands may be responsible for the small numbers of species recognized in a few genera (*Nertera*, *Acaena*, *Cotula*, and possibly some sedges and grasses). With the exception of *Nertera holmboei*, which has been recorded only from Nightingale and Inaccessible, and *Cotula moseleyi* and *C. goughensis* from Nightingale and Gough, respectively, such minor radiation has not been confined to single islands or groups of islands. The numbers of endemic species within the different islands (as the distribution within the islands of the vascular plants as a whole) seems to be related more to the diversity of habitats than to any historical factors such as geological age, or even the presumed facilities for dispersal.

In our present state of knowledge concerning evolutionary rates, it is hazardous to attach any meaning to differing rates of endemism in plants and animals. However, the Tristan–Gough endemics illustrate the principle suggested by Gulick (1932) of the greater 'maturity' of insular faunas as compared to floras, judged by comparative endemism between the two kingdoms in the chain of islands north-west of Hawaii. Thirteen genera in various animal phyla, and perhaps 60 % of invertebrate species in the Tristan–Gough group have been described as endemic (Holdgate 1965, Part III this Report), whereas endemism in the plants is less widespread and less deep seated. These differences between rates of endemism in the plants and animals could be attributed to one or more of the following causes:

(*a*) a greater dispersive capacity amongst plants leading to colonization initially by larger numbers of individuals, and perhaps continued genetic exchange with continental stocks;

(*b*) the 'founder principle' (Dhobzhansky 1963) or genetic drift in the small colonist populations of animals, with initial differences being more readily perpetuated because of their differing genetic systems;

(*c*) more rigorous selection at the higher trophic levels within the insular ecosystem, due to a lack of diversity in food plants, promoting faster evolutionary rates in animals;

(*d*) differing interpretation amongst plant and animal taxonomists on the criteria for specific or generic recognition in the two kingdoms.

Skottsberg (1960, p. 455, footnote) has commented on a similar difference between rates of endemism in plants and animals in the recently immigrant biota of South Georgia.

5·3. *Age, derivation and history of the flora*

Three fields of enquiry can give an indication of the age and history of the flora in the islands. Geological and geophysical studies can indicate how long the islands have existed as suitable habitats for terrestrial plants. Palaeontology can indicate which forms have been present in the past. Biological evidence from the existing flora can suggest how long the present species have been isolated on the islands, and from what regions they are likely to have been derived.

Potassium–argon age determinations (Miller 1964) suggest that the islands began to form in late Miocene to early Pliocene times, and the estimated ages of the different islands vary from about 18 million years (Nightingale) to one million (Tristan). It is generally assumed that if continental drift has taken place, the continents lay at or near their present positions by the latter half of the Tertiary era. There is thus no geophysical support for the view of Arnell (1958) that a formerly closer proximity of the group to the continents is necessary to account for the present hepatic flora. Knowledge of the bathymetry of the South Atlantic does not provide any clear evidence of now disappeared islands between the Tristan–Gough group and any of the surrounding continents, although the Bromley Plateau (32° S, 35° W), the Discovery Table Mount (43° S, 0°) and the Walvis Ridge may possibly be the foundations on which such islands have existed. Wilson (1963) marks Tristan as a focal point from which ridges radiating to Africa and America are joined, but even if any chains of islands on these ridges were formerly present (such as his theory supposes), the distances between them must have been considerable, and a formidable obstacle to plant dispersal. There is thus little support for the view of Christophersen (1939) that the agencies of plant dispersal have been more efficient over shorter oversea distances in the past.

Pollen analyses of organic deposits have provided direct evidence of the past flora as far back as periods contemporaneous with the last glacial period. However, there is still a very long period between the assumed time of colonization of the islands by plants, and the earliest flora of which remains have been discovered.

The islands are thought to be Tertiary in age; but all the biological evidence as presented in this paper supports the contention that the flora is young and possibly of only Quaternary origin, and mostly immigrant from the west. This evidence may be summarized as follows:

(*a*) endemism, although widespread, is not deep-seated (§§3·1, 3·2, 3·3 and 5·2);

(*b*) the flora is notably impoverished, and has not yet attained an internal harmony by the local radiation of immigrant plants (§§5·1 and 5·2);

(*c*) biological associations involving plants and animals, or between different plants, are not generally specific (§5·1);

(*d*) the diaspores of the native flora mostly appear to be capable of long range dispersal (§3·9);

(*e*) the overwhelming affinity of the flora with southern South America and sub-Antarctic regions, is consistent with the present direction of the dispersing agencies, which impinge upon the islands mainly from the west and south-west (§§3·8 and 3·9);
Whether volcanic activity, or climatic fluctuations during the Quaternary, have destroyed any different floras on the islands in the past is unknown; but the extreme remoteness of the Tristan–Gough group and the consequent difficulties of long-range plant dispersal to the islands, may mean that its present vegetation is not in stable equilibrium with the present environment. Under these circumstances, the biological inertia of the insular ecosystems (Pearsall 1957) is probably low. Their ecosystems are liable to rapid change and replacement when their evolutionary isolation is broken down by man (§6).

6. The effects of man upon the plant life

The marked effects of human activities upon insular biota have been commented upon by a number of authors (e.g. Wallace (1895) on St Helena; Skottsberg (1934, 1954) on Hawaii and Juan Fernandez, respectively; Allan (1937) and many others on New Zealand). Elton (1958) has discussed some of the reasons for the extreme vulnerability of insular biota to man's actions, and a recent symposium on *Man's place in the island ecosystem* (Fosberg 1963 (Ed.)) has considered man's effects in the Pacific and tropical islands. Holdgate & Wace (1961) have given a summary of the human impact on the biota of various islands in the Southern Ocean, including those of the Tristan–Gough group.

Although it is convenient to distinguish between direct habitat alteration and the introduction of alien plants in discussing the human influence on native floras, the effects of each can scarcely be distinguished in practice because both processes almost invariably occur together, and markedly affect one another.

6·1. *Human alteration of habitats*

Man has directly affected the plant communities of the islands by clearing the vegetation, by burning, and by the importation of alien animals. The major effects of these activities on the native vegetation have been noted above (§4). Table 14 summarizes the events of major importance in this process of habitat disturbance on each island, and compares them with the rather scanty records of numbers of species of alien flowering plants that have been recorded at different times since botanical investigations started in the group.

The native plant communities of Tristan have been far more radically altered by man than those of the other islands in the group, largely due to its 150 years of continuous human settlement. Clearance of the coastal plains for tillage and grazing has led to the substitution of alien-dominated plant communities in place of the native fern-bush and tussock grassland (§4·61), and much *Phylica* has been cut from the cliffs near the Settlement Plain; but there are no records of any clearance of vegetation on the Tristan Base or above. Early accounts of firing of the coastal and cliff vegetation (Earle 1832) and some of the island place names on Tristan (e.g. Burntwood) suggests that intermittent burning has played some part in the destruction of native vegetation away from the Settlement. None of the smaller islands in the group has yet supported a permanent breeding population of man, and although some clearance of lowland vegetation by visitors and by parties living ashore (sealers, etc.) has occurred on all the smaller islands, the effects have probably been very small and localized so far. A fire on Inaccessible Island in 1909 burned for a month (Christophersen 1940*a*), and must have done considerable damage to the plant cover (although its effects have not been commented upon by later observers); but fires on Nightingale (§4·62) and Gough (Wace 1961) in the tussock grasslands have probably had only slight local effects.

The most widespread alteration of the native plant communities on the islands has undoubtedly been due to imported animals. On Tristan main island, sheep (on the Base and the Peak), and cattle, donkeys and geese (on the Coastal Strips) have had the most marked effects: plant communities dominated by alien species now cover all the Coastal Strips, and *Rumex acetosella* dominates an extensive zone round the bottom of the Peak. The distribution and extent of these alien communities is clearly related to that of the introduced herbivores. Goats and rabbits, both of which have been enormously destructive of insular vegetation elsewhere (Holdgate & Wace 1961) are not present on any of the islands today. Earle (1832) noted numerous goats on the Tristan Cliffs and Base in 1824, when they were hunted by the inhabitants, but they do not seem to have had a very pronounced effect on the vegetation, so far as can be judged by comparing the Tristan communities with those of the other islands in the group where goats were almost certainly never present. There is no justification for the statement that the goats on Tristan 'once destroyed the original flora almost completely' (Hagen 1952, p. 202). Moseley (1892) states that the goats (and pigs) on Tristan were extinct there at the time of H.M.S. *Challenger's* visit in 1873. Rabbits are said to have occurred on Tristan in 1829 (Morrell 1832), but to have been extinct there, or nearly so, by 1873 (Moseley 1892). The reasons for the failure of goats or rabbits to establish large and destructive feral populations on Tristan, as they have done elsewhere, remain obscure.

The effects of the smaller alien vertebrates (such as mice and poultry) on the native vegetation have probably been only slight; but the alien predators (notably cats, dogs and rats) must have had a considerable indirect effect through their destruction of penguins and other sea birds whose closely inhabited rookeries support a characteristic tussock vegetation (§4·1).

On the smaller islands the effects of alien animals have been relatively slight, compared to that on Tristan. No alien vertebrates are known from Nightingale, and the larger herbivores on Gough (sheep) and Inaccessible (goats, sheep, pigs) have probably always been confined to small areas near the shores, by the steep cliffs. But pigs may have been at free range on Inaccessible, where Hagen (1952, p. 210) also noted the presence of seven sheep in 1938 'probably under a certain control, and not actually wild' (?). The history of the goat population on Inaccessible Island is obscure: the small numbers noted by Moseley (1892) in 1873 were possibly the descendants of some said to have been put ashore there from Tristan in the 1820's (Munch 1946). No goats are present on the island today.

Goats landed on Gough Island in 1958 were ordered to be destroyed immediately. Although these animals may have had some effect on the Inaccessible communities, Nightingale and Gough Islands remain more or less unaffected by alien animals.

TABLE 14. IMPORTANT EVENTS LEADING TO THE DISTURBANCE OF THE NATIVE VEGETATION IN THE ISLANDS, COMPARED TO THE NUMBERS OF ALIEN FLOWERING PLANTS RECORDED AT VARIOUS TIMES

Information taken largely from Holdgate & Wace (1961). Predators are noted because of the indirect effects that they have on vegetation by their destruction of the native avifauna. Dates in parentheses indicate that the animals concerned are not now present on the islands in question.

	Tristan	Inaccessible	Nightingale	Gough
man				
discovery	1506	1506	1506	?1505*
first recorded landings	1643	1656	?1656	?1810
parties living ashore (sealers, scientific parties, weather stn., etc.)	1790–1815	1871–73	visited each year by Tristan islanders	1810–11 1888–92 1955–
settlement (i.e. breeding population)	1815–1961 1963–	none	none	none
introduction and establishment of alien vertebrate animals				
cats	*ca.* 1810–	—	—	—
cattle	pre-1824–	(1937)	—	—
dogs	pre-1824–	(occasional)	—	1959–
donkeys	(pre-1867–)	—	—	—
goats	(pre-1790– *ca.* 1870?)	(*ca.* 1820–1883)	—	1958
mice	?pre-1829–	—	—	pre-1887–
pigs	(pre-1810–?)	(1873–1938?)	—	—
poultry	1811–	—	—	1956–
rabbits	(?pre-1829– *ca.* 1873?)	—	—	—
rats	1882–	?	—	—
sheep	pre-1824–	(?–1938–?)	—	1956–
numbers of species of alien flowering plants recorded†				
1793 (Dupetit Thouars 1811)	3	—	—	—
1816 (Carmichael 1817)	3	—	—	—
1873 (Hemsley 1885)	*ca.* 10	*ca.* 5	0	—
1904 (Rudmose Brown 1905)	—	—	—	5
1909 (Phillips 1913)	*ca.* 26	—	—	—
1933 (Christophersen 1934)	—	—	—	5
1934 (Christophersen 1937)	*ca.* 34	—	—	—
1937 (Dyer 1939)	*ca.* 21 +	—	—	—
1955 (Wace 1961)	—	—	—	12
1962 (this paper, see appendix)	*ca.* 82	19	5	12

* Possibly earlier: see Uhden (1939).
† Not including cultivated species.

6·2. *Introduction of alien plants*

A list of all the alien plants recorded from each island in the group is included in the appendix. Each visit by a botanist to the islands has resulted in the discovery of alien plants not previously recorded. No terrestrial cryptogams have been considered as definitely introduced by man, but *Azolla filiculoides* is thought to be a recent arrival on Inaccessible Island (Christensen 1940), and it may be that some mosses owe their presence on the islands to man (e.g. *Ceratodon purpureus*).

Jørstad (1947) thought that five species of the Tristan rust fungi were introduced, and a few saprophytic fungi found on imported materials on Gough Island (*Aspergillus*, *Penicillium*, etc.) are probably introduced also. Baardseth (1941) considers it probable that some marine algae (*Enteromorpha*, *Ulva*) may have been transported to the islands on the hulls of visiting ships. The present discussion is confined to the alien angiosperms.

The total number of alien angiosperm species recorded from all the islands (83) is twice the known number of native species (41), but the numbers and the proportions of aliens to natives differ widely on the several islands of the group (table 4, p. 281). Although it may be that more aliens are now established on the smaller islands than here recorded, Tristan has a far larger proportion of aliens than any of the other islands, and this is undoubtedly related to the greater contact between Tristan and other regions, and to the greater disturbance of the native plant communities in the main island. Only one alien species (*Brassica rapa* L. at Saltbeach, Inaccessible Island; clearly an escape from cultivation) which does not occur on Tristan itself, is known from the smaller islands, and it is likely that Tristan acts as a pool from which aliens are distributed to the smaller islands.

A few willows (mostly *Salix babylonica* L.) and apples have been planted in various sheltered gullies on Tristan, e.g. at about 300 m in Hottentot Gulch and near West Jews Point. On Inaccessible Island a few apple trees occur in the *Spartina* tussock at Saltbeach and Blenden Hall. There are three trees of *Pinus caribaea* Morelet behind the ruined cottage at Saltbeach and a few willows (*Salix babylonica* L.) in the tussock there. As far as the authors are aware, none of these alien trees regenerates, at any rate, at all freely.

The alien species can be roughly divided into three categories, according to their success in colonizing habitats which differ in the degree of their disturbance from the pre-human conditions in the islands.

1. The majority of aliens are confined to the radically altered communities which are themselves dominated by alien plants, and subject to continual disturbance by grazing and cultivation. About half these species are therophytes and half hemicryptophytes, and almost all are confined to the Lowland Plains on Tristan. It is probable that most of them would die out in the absence of man and his animals. To this group also could be added the cultivated plants.

2. About fourteen species, or about a sixth of the alien species, are spreading into disturbed (but not necessarily radically altered) native communities away from the human settlements. About half of this group are therophytes and half hemicryptophytes, and most of them occur in at least one of the smaller islands of the groups as well as on Tristan itself. The species are almost all recognized anthropochores which include various remote archipelagoes in their wide ranges in temperate latitudes. For example, sixteen of the twenty-six species in this and the following category are recorded as adventives in the Chatham Islands (Madden & Healy 1959).

3. About twelve species of aggressive aliens are spreading into the native communities which have not been affected by man or his animals. Most of these species are hemicryptophytes (including four grasses), and about half the species are recorded from three or more islands in the group. With the exception of *Calystegia soldanella*, which may be native to the islands (see p. 279), all are widespread anthropochores, and although many are most conspicuous in coastal sites, a few are notably successful colonists inland (*Rumex acetosella*, *R. obtusifolius*, *Holcus lanatus*, *Poa annua*).

TABLE 15. THE PERFORMANCE OF THE ALIEN FLOWERING PLANTS

This division of the alien species according to their ecological behaviour in the islands is largely subjective (especially as between groups 2 and 3), but the groups 1, 2, 3 represent a series of species which are increasingly aggressive in invading the native plant communities. Some plants listed as aliens in the appendix have been omitted due to uncertainty of status or taxonomic confusion.

Life forms are indicated as follows:

P Phanaerophyte
Ch Chamaephyte
H Hemicryptophyte
Ge Geophyte
Th Therophyte

Distribution within the islands is indicated for each species by the following abbreviations:

T Tristan main island
I Inaccessible
N Nightingale
G Gough Island

1. *Species which are more or less confined to communities dominated by introduced plants* (*i.e. alien species in alien communities*)

H	T	*Ranunculus acris*
Th-Ch	I	*Brassica rapa*
Th	T	*Coronopus didymus*
?H	T	*Rorippa nasturtium-aquaticum*
Th	T	*Polycarpon tetraphyllum*
?Th	T	*Scleranthus* sp.
Th	T	*Malva parviflora*
H	T	*M. sylvestris*
H	T	*Oxalis purpurea*
H	T	*Trifolium repens*
?Th	T	*Trifolium cf. micranthum*
Th	T	*Trifolium dubium*
P	T	*Ulex europaeus*
?Th	T	*Crassula pellucida*
Th	T	*Anthemis cotula*
H	T	*Bellis perennis*
H	T	*Cotula anthemoides*
?Th	T	*Crepis* sp.
Th-H	T	*Crepis capillaris*
Th	T	*Conyza bonariensis*
?Th	T	*Gnaphalium purpureum*
Th	T	*Senecio vulgaris*
Th	T	*Sonchus asper*
Th	T	*Lobelia erinus*
Th	T	*Anagallis arvensis*
?	T	*Lithospermum* sp.
Th	T	*Myosotis discolor*
H	T	*Convolvulus* sp.
Ch	T I	*Physalis peruviana*
H	T	*Verbascum virgatum*
Th	T	*Veronica agrestis*
H	T	*Verbena officinalis*
H	T	*Leonitis leonurus*
H	T	*Prunella vulgaris*
Th	T	*Polygonum aviculare*
H	T	*Rumex crispus*
Th	T	*Euphorbia peplus*
Ge	T	*Romulea bulbocodium*
Th	T	*Juncus bufonis*
H	T	*J. effusus*
H	T	*J. macer*
H	T	*Cyperus tenellus*
H	T	*Scirpus cernuus*
H	T	*Agrostis tenuis*
Th	T	*Bromus uniloides*
H	T G	*Dactylis glomerata*
Th	T	*Digitaria sanguinalis*
?Th	T	*Eleusine indica*
H	T	*Festuca rubra*
H	T	*Lolium perenne*
H	T	*Paspalum dilatatum*
H	T	*Poa trivialis*
Th	T	*Polypogon monspeliensis*
H	T	*Sporobolus capensis*
Th	T	*Vulpia myuros*

2. *Species growing in alien communities, but also extending into native vegetation which has been affected by man or his animals* (*i.e. alien species in both alien and semi-native communities*)

Th	T I	*Oxalis corniculata*
H	T I	*Centella asiatica*
Th	T I	*Gnaphalium luteoalbum*
Th	T G	*Hypochoeris glabra*
H	T I	*Calystegia sepium*
Th	T I	*Solanum nigrum*
H	T I	*Veronica serpyllifolia*
H	T	*Plantago lanceolata*
Th	T	*Chenopodium album*
?H	T I	*Mariscus congestus*
Th	T I	*Aira caryophyllea*
H	T	*Cynodon dactylon*
H	T G	*Poa pratensis*
Th	T	*Vulpia bromoides*

3. *Species growing in alien and semi-native communities, but which are also successful invaders of native vegetation which has not been affected by man or his animals* (*i.e. alien species in alien, semi-native and fully native communities*)

Ch	T I	*Cerastium holosteoides*
Th	T G	*Stellaria media*
H	T	*Chrysanthemum leucanthemum*
H	T I N G	*Sonchus oleraceus*
H	T I	*Calystegia soldanella*
H	T I G	*Plantago major*
H	T I (G)*	*Rumex acetosella*
H	T I N G	*R. obtusifolius*
H	T I G	*Agrostis stolonifera*
H	T	*Anthoxanthum odoratum*
H	T I N G	*Holcus lanatus*
Th	T I N G	*Poa annua*

* Accidentally imported from Tristan to Gough in 1955, and Gough plant subsequently destroyed; probably re-established since then on Gough.

All the alien species in the islands seem to be confined to areas that have suffered some disturbance. Even the most aggressive aliens (group 3, above) are predominantly plants of open habitats which result from 'natural' (i.e. non-human) causes. Nesting sea birds (especially penguins), breeding sea mammals, peatslips on steep slopes (Wace 1961) and shoreline erosion all give rise to naturally open communities, but there appear to be few, if any, native species well adapted to exploit these habitats. The aggressive aliens largely fill these untenanted niches (figures 31, plate 42), and there is no evidence (at least on Gough Island) to show that they are invading closed and undisturbed native communities. Observation on the Tristan–Gough aliens thus supports the contention of Allan (1936) and Egler (1942) that the alien species in New Zealand and Hawaii, respectively, owe their success to the radical alteration of habitats by man rather than to any superior competitive ability when contrasted to the native species. Aliens are capable of penetrating native vegetation mainly because the indigenous flora lacks species adapted to exploiting disturbed habitats—an important manifestation of ecological 'disharmony' in the native biota (§5·1). The biological spectra of the native and alien flowering plants, when compared with one another, and with those of New Zealand (table 16), show the great importance of therophytes amongst the aliens in both regions, and the small numbers of this life form amongst the native plants (Hooker 1867).

TABLE 16. THE BIOLOGICAL SPECTRA OF THE NATIVE AND ALIEN FLOWERING PLANTS IN THE ISLANDS, COMPARED WITH THOSE OF NEW ZEALAND

percentage proportions of life forms	number of species	phanerophytes	chamaephytes	hemicryptophytes	geophytes	therophytes	sources of information
'normal' spectrum	1000	46	9	26	6	13	Raunkiaer 1937
Tristan–Gough indigenous species	38	5	27	63	0	5	this paper
New Zealand indigenous species	1500	33	14	39	8	6	Allan 1937
Tristan–Gough alien species	83	1	3	52	1	43	this paper
New Zealand alien species	500	10	4	41	8	37	Allan 1937

Many of the alien species in the islands now have such a wide geographical range, that it is difficult to define precisely their areas of origin. But it is clear that the majority are common European weeds, and probably native to the Palearctic region. Few native South African species seem to have established themselves as aliens in the islands (e.g. *Crassula pellucida*, *Romulea bulbocodium*) despite the fact that most of the traffic between the islands and the outside world has been with or through the Cape. There also appear to be few natives from other southern continents amongst the aliens.

APPENDIX A. THE TERRESTRIAL PLANTS OF THE TRISTAN DA CUNHA ISLANDS

The following table is intended to show the present state of plant collecting from all the islands of the Tristan–Gough group. It has been compiled from publications and herbarium collections, supplemented by a knowledge of the plants in the islands.

There is no published list of plants for the whole Tristan–Gough group. Although the vascular floras of Tristan main island and Gough are known, at least in outline, there has been no previous attempt to treat the flora of the islands as a unit. *It is emphasized that this list cannot be taxonomically precise.* Any such precision would require full-scale taxonomic revisions in the case of many genera. It is intended as a guide to present knowledge of the flora, and as a help to future workers.

The native species are numbered in sequence in the left-hand column. An asterisk against the name of any species indicates that it has probably been introduced to the islands by man, although the status of a few of these species is in doubt. The numbers in the right-hand columns refer to the collections and publications which are listed chronologically in table 1, and the letters K and BM to various unpublished collections at Kew and the British Museum (Natural History), respectively. The records for Nightingale Island include collections which have been made on the nearby Middle and Stoltenhoff Islands. Brackets around the entries enclose the islands to which the species in question have been considered endemic: some of these which were originally described as endemic to Tristan have now been found on other islands in the group, and these are therefore bracketed as group endemics here. Cultivated plants which do not persist in natural or semi-natural communities are not included.

ANGIOSPERMAE

This list includes all the flowering plants that have been recorded from the islands, with the addition of certain unpublished herbarium collections, and some recent collections made by Dickson in the Tristan group in 1962 and Stableford during 1963.

No account of the flowering plants collected by the Norwegian Expedition of 1937–38 in the Tristan group has yet been published, except for an incomplete list in Hafsten (1951). The earlier lists of Christophersen (1937) and Dyer (1939) refer only to Tristan, although the former paper includes a useful summary of all the plants recorded from the main island up to 1937. Because of the need for taxonomic revisions amongst many of the native genera, it is difficult to arrive at any list of agreed names in the phanerogams. All the names that have been used by the various authors are therefore included, but those which in the present authors' opinions refer to the same species are bracketed together, and the possibly correct names of the native species are included in heavier print. Although the earliest records of Dupetit Thouars (1811) and Carmichael (1817) introduce complications in naming, they have been included because they give a useful indication of the status of some species in the islands. Records of Gough Island plants are taken from the appendix of Wace (1961), which also includes all earlier records of flowering plants from there.

The arrangement follows Bentham and Hooker's *Genera Plantarum*.

		Tristan	Inaccessible	Nightingale	Gough
	**Ranunculus acris* L.	BM	—	—	—
1	*Ranunculus* sp.	2, 11b	—	—	—
	R. caroli Christophersen	[13c, 14a	—	—	14c]
2	*Cardamine propinqua* Carmichael	[2, 11b]	—	—	—
	G. glacialis Forst.	16	—	—	14c
	**Coronopus didymus* (L.) Sm.	BM, 16	—	—	—
	**Rorippa nasturtium-aquaticum* (L.) Hayek or *R. microphylla* × *nasturtium-aquaticum*	16, 17	—	—	—
	**Brassica rapa* L.	—	16	—	—
	* *Cerastium triviale* Link	6b	—	—	—
	C. caespitosum Gilib.	11b, 12, 13e, 14a,	13e	—	—
	C. holosteoides Fr.	16	—	—	—
	**Polycarpon tetraphyllum* (L.) L.	11b, 13e, 16	—	—	—
	**Scleranthus* sp.	BM	—	—	—
	**Stellaria media* (L.) Vill.	13e, 16	—	—	14c
	**Malva parviflora* L.	11b, 13e, 16	—	—	—
	**M. sylvestris* L.	11b	—	—	—

3	*Pelargonium acugnaticum* Thouars	[1, 2, 4a, 11b, 13e	4a, 13e]	—	—
	P. australe Willd.	6b	—	—	—
	P. grossularioides (L.) Ait.	12, 13a, 16	16	—	—
	**Oxalis corniculata* L.	4a, 6b, 11b, 12, 13e, 14a, 16	13e, 16	—	—
	**O. purpurea* L.	14a	—	—	—
	O. variabilis Jacq.	6, 11b	—	—	—
4	***Phylica arborea*** Thouars	1, 2, 3, 4a, 4b, 8, 11b, 12, 13a, 14a, 16	4a, 4b, 13e, 16	4a, 4b, 13e, 16	4b, 7, 10, 14c
	P. nitida Lam.	6b	—	—	5, 9
5	***Sophora macnabiana*** Grah.	—	—	—	14c
	S. tetraptera J. F. Mill.		—	—	7, 10
	**Trifolium dubium* Sibth.	16	—	—	—
	**T. repens* L.	6, 11b, 12, 13e, 16	—	—	—
	**Trifolium* spp. (cf. *micranthum*, *polymorphum* and *dubium*)	14a, 16	—	—	—
	**Ulex eropaeus* L.	13e, 14a, 16	—	—	—
[6]	*Acaena sanguisorbae* (L. f.) Vahl.	6, 11b	—	—	—
	A. sarmentosa (Thouars) Carmichael	[2, 3, 4a, 4b, 8, 12, 14a, 16	4a, 4b, BM, 16	4a, 4b, BM, 16	9, 14c]
	Ancistrum sarmentosum Thouars	1	—	—	—
[7]	***Acaena stangii*** Christophersen	[13d, 13e, 14a, 16	13d, 13e	—	14c]
	**Crassula pellucida* L.	BM, 14a	—	—	—
8	***Callitriche christensenii*** Christophersen	—	—	—	[10, 14c]
?	*Callitriche* sp.	14b, 16	K, 14b, 16	14b, 16	—
	Callitriche sp. (cf. *obtusangula* Heglm.)	—	—	—	14c
*	*Centella asiatica* (L.) Urb.	13e, 14a, 16	16	—	—
	Hydrocotyle asiatica L.	12	—	—	—
	Hydrocotyle cf. *asiatica*	6, 11b	—	—	—
9	***Hydrocotyle capitata*** Thouars	[1, 2, 3, 4a, 4b, 6, 8, 11b, 12, 13e, 14a, 16	4a, 13e, 16	—	9]
	H. leucocephala Cham. et Schlecht.	—	BM		5, 7, 10, 14c, 15
10	***Apium australe*** Thouars	1, 2, 4a, 4b, 6, 8, 11b, 12, 13a, 13e, 14a, 14b, 16	4, 13e, 16	13e	5, 14c, 15
	A. goughensis Wilkins	—	—	—	[7, 10]
[11]	*Erythrodanum majus* Thouars	1	—	—	—
	Nertera assurgens Thouars (pro syn.)	[2, 6, 11b, 13e, 14a, 16	4	4]	—
	N. cf. *assurgens*	6, 11b	—	—	—
12	*Erythrodanum alsineforme* Thouars	1	—	—	—
	Nertera depressa Gaert.	2, 4, 6, 8, 11b, 12, 13a, 13d, 14a, 16	13e	13e	5, 9, 10
	N. granadensis (Mutis) Druce	8, 12, 14a	—	—	14c
[13]	***N. holmboei*** Christophersen	—	[13d, 13e, 16	13d, 13e, 16]	—
	**Anthemis cotula* L.	6, 11b, 13e	—	—	—
	**Bellis perennis* L.	11b, 13e, 14a, 16	—	—	—

APPENDIX A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
14	***Chevreula sarmentosa*** (Pers.) Blake	11b, 13a, 13e, 14a, 16	13e	—	—
	C. stolonifera Cass.	2	—	—	—
	**Chrysanthemum leucanthemum* L.	6, 11b, 12, 13e, 14a, 16, 17	—	—	—
	**Cotula anthemoides* L.	14a	—	—	—
	C. australis (Less.) Hook. f.	11b, 12, 13e, 16	—	—	—
[15]	***C. goughensis*** Rudmose Brown	—	—	—	[5, 7, 10, 14c]
[16]	***C. moseleyi*** Hemsl.	—	—	[4, 11b, 16]	—
	**Crepis* sp.	11b	—	—	—
	**C. capillaris* (L.) Wallr.	16	—	—	—
	**Conyza bonariensis* (L.) Cronq.	16	—	—	—
	**Gnaphalium luteoalbum* L.	6, 11b, 12, 13e, 14a, 16, 17	13e, 16	—	—
	**G. purpureum* L.	BM, 16	—	—	—
[17]	***G. pyramidale*** Thouars	1, 2, 4, 8, 11b, 13a, 16	4, 7, 16	—	5, 7, 9, 10, 14c
	G. thouarsii (Thouars)	13e	13e	13e	—
	**Hypochoeris glabra* L.	4, 11b, 14a, 16	—	—	5, 10
18	*Calendula pusilla* Thouars	1	—	—	—
	Lagenifera magellanica (Willd.) Cass.	2	—	—	—
	Lagenophora nudicaulis (Comm. ex Lam.) Dus.	11b, 12, 13e, 16	13e	—	14c
	**Senecio vulgaris* L.	6, 11b, 12, 13e, 16	—	—	—
	**Sonchus asper* (L.) Hill	16	—	—	—
	**S. oleraceus* L.	2, 4, 6, 11b, 12, 13e, 14a, 16	4, 13e, 16	13e	5, 10, 14c
	**Lobelia erinus* L.	BM, 14a	—	—	—
19	*Empetrum nigrum* L.	1, 6	—	—	5, 7
	E. medium Carm.	2, 4	—	—	—
	E. rubrum Vahl	3, 8, 12, 11b, 13a, 13c, 13d, 14a, 16	4, 13e, 16	4, 13e, 16	10, 14, 15
	**Anagallis arvensis* L.	6, 11b, 13e, 14a, 16	—	—	—
	**Lithospermum* sp.	11b	—	—	—
	**Myosotis discolor* Pers.	14a, 16	—	—	—
	**Calystegia sepium* (L.) Roem. et Schult.	6, 11b	16	—	—
	**C. soldanella* (L.) R. Br.	2, 6, 11b, 13a, 13c, 16	—	—	—
	**Convolvulus* sp.	11b	—	—	—
	**Physalis peruviana* L.	14	13e	—	—
	**Solanum nigrum* L.	6, 11b, 13e, 14a, 16	13e, 16	—	—
	**S. tuberosum* L.	BM, 16	16	16	14c
	**Verbascum virgatum* Stokes	6, 11b, 16	—	—	—
	**Veronica agrestis* L.	16	—	—	—
	**V. serpyllifolia* L.	6, 12, 13e, 14a, 16	16	—	—
	**Verbena officinalis* L.	6, 11b, 13e, 16	—	—	—
	**Leonitis leonurus* (L.) R. Br.	13e	—	—	—
	**Prunella vulgaris* L.	13e, BM, 16	—	—	—
	**Plantago major* L.	8, 12, 13e, 16	BM, 16	—	5, 10, 14c
	**P. lanceolata* L.	6, 11b, 12, 13e, 14a, 16	—	—	—

20	*Chenopodium ambrosioides* L.	13e	13e	13e	—
	C. tomentosum Thouars	[1, 2, 3, 4, 6, 8, 11b, 14a, 16	4, 16	4	7, 10, 14c]
	**C. album* L.	1	—	—	—
	**C. murale* L.	6, 11b	—	—	—
21	***Atriplex plebeia*** Carmichael	2, 11b	—	—	—
	**Polygonum aviculare* L.	12, BM, 16	—	—	—
	**Rumex acetosella* L. sens. lat.	K†, 3, 6, 11b, 12, 14a, 16, 17	4	—	14c
	**R. crispus* L.	6, 11b, 16	—	—	—
22	***R. frutescens*** Thouars	1, 2, 4, 6, 11b, 12, 13a, 13e, 14a, 16	13e, BM, 16	—	5, 7, 10, 14c=
	**R. obtusifolius* L.	14a, 16	13‡, 16	16	5, 7, 10, 14c
[23]	***Peperomia tristanensis*** Christophersen	—	[13d, 13e]	—	—
	**Euphorbia peplus* L.	16	—	—	—
	**Romulea bulbocodium* (L.) Seb. et Maur.	6, 11b	—	—	—
	**Phormium tenax* J. R. & G. Forst.	13e, 14a, 16	—	16	—
	**Juncus bufonius* L.	12, 13e, 14a	—	—	—
	**J. effusus* L.	13e	—	—	—
	**J. macer* S. F. Gray	13e	—	—	—
	J. tenuis Willd.	6, 11b, 12, 16	—	—	—
[24]	*J. tristanensis* Hemsley	4b	—	—	—
	Rostkovia tristanensis Christophersen	[13d	—	—	14c]
25	***Tetroncium magellanicum*** Willd.	—	—	—	14c
[26]	***Carex insularis*** Carmichael	[1, 2, 4, 11b, 13e, 14a, 16	4a, 13e, 16	13e, 16	14c]
[27]	***C. thouarsii*** Carmichael	[1, 2, 4, 11b, 12, 13d, 13e, 14a, 16	13e, 16	4b, 13e, 16	14c]
28	***Uncinia brevicaulis*** Thouars	[1, 2, 4, 11b, 12, 13e, 14a, 16	13e, 16	—	14c]
29	***U. compacta*** R. Br.	16	—	—	14c
	U. gracilis Thouars	1, 13e	13e	13e	—
	**Cyperus congestus* Vahl	11b, 13e	13e	—	—
	Mariscus congestus (Vahl) C. B. Clarke	6, 12, 16	16	—	—
	**Cyperus tenellus* L.	12, 13e, 14a, 16	—	—	—
	**Scirpus cernuus* Vahl	6, 11b, 14a, 16	—	—	—
[30]	*S. moseleyanus* Boeck.	11b	—	—	5, 10
	S. sulcatus Thouars	1, 2, 6, 11b, 12, 14a, 16	16	16	5, 10, 14c
[31]	*S. oliveri* Boeck.	11b, 14a	—	—	—
	S. thouarsianus Schult.	11b, 12, 14a, 16, 17	16	16	5, 10, 14c
	S. virens Boeck.	12	—	—	—
	Scirpus spp. and *Isolepis* spp.§	+	+	+	+
[32]	***Agrostis media*** Carmichael	[2, 4, 11b, 16	—	—	7, 10, 14c]
[33]	***A. carmichaelii*** J. A. et J. H. Schult.	[2, 4, 11b	—	—	14c]
	A. ramulosa Carmichael	—	—	—	7, 10]

APPENDIX A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
34	***Agrostis*** sp. (nr. *A. bergiana* Trin.)§	6, 11b	—	—	—
35	***Agrostis*** sp. (nr. *A. magellanica* Lam.)§	—	—	—	14c
	**A. simulans* Hemsley	4b, 12, 13e, 16	—	—	—
	**A. stolonifera* L.	13e, 14a, 16	16	—	14c
	**A. tenuis* Sibth.	13e	—	—	—
	**Aira caryophyllea* L.	13e, 16	13e	—	—
	**Anthoxanthum odoratum* L.	11b, 13e, 14a	—	—	—
	**Bromus uniloides* Humb., Bonpl. & Kunth	14, 16	—	—	—
	**Cynodon dactylon* (L.) Pers.	12, BM, 16, 17	—	—	—
	**Dactylis glomerata* L.	BM, 16	—	—	14c
36	***Deschampsia*** sp.	BM, 16	BM	—	14c
	D. kingii (Hook. f.) E. Desv.	14a	—	—	—
	**Digitaria sanguinalis* (L.) Scop.	16	—	—	—
	**Eleusine indica* (L.) Gaertn.	16	—	—	—
37	***Festuca*** sp. (nr. *F. erecta*)§	14a	—	—	—
	**F. rubra* L.	16	—	—	—
38	***Glyceria*** sp. indet.	—	K	—	14c
	**Holcus lanatus* L.	6, 11b, 12, 13e, 14a, 16	16	13e, 16	14c
	**Loium perenne* L.	13e, 14a, 16	—	—	—
	**Paspalum dilatatum* L.	16	—	—	—
39	? *Phalaris mollis* Thouars‖	1, 11b	—	—	—
	Poa flabellata (Lam.) Hook. f.	—	—	—	14c
	**P. annua* L.	11b, 12, 13e, 14a, 16, 17	13e, 16	13e, 16	5, 10, 14c
	**P. pratensis* L.	6, 4b, 12, 13e, 16	—	—	14c
	**P. trivialis* L.	13e	—	—	—
	**P. infirma* Humb., Bonpl. & Kunth	13e	—	—	—
40	? ***Polypogon intermedius*** Carmichael	2, 11b	—	—	—
	Phalaris caespitosa Thouars‖	1, 11b	—	—	—
	**Polypogon monspeliensis* (L.) Desf.	6, 11b	—	—	—
41	*Ponceletia arundinacea* Thouars	1	—	—	—
	Spartina arundinacea Carmichael	2, 4, 11b, 12, 13a, 13e, 14a, 16	4, 13e, 16	4, 13e, 16	5, 7, 9, 10, 14c
	* *Sporobolus capensis* (Beauv.) Kunth	12, 13e	—	—	—
	S. indicus (L.) R. Br.	6, 11b, 16	—	—	—
	**Vulpia bromoides* (L.) Dumort.	6, 11b, 12, 13e, 14a	13e	—	—
	**V. myuros* (L.) Gmel.	11b	—	—	—

† Unnamed collection, dated 1832. ‡ In Hagen (1952). = Accidentally imported from Tristan 1955; subsequently destroyed.

§ Various other species of *Isolepis* (*bicolor*, *prolifer*, *squarrosa*) and *Scirpus* (*prolifer*) are listed from Tristan by Thouars and Carmichael. Their relationships and/or status are uncertain. The identities of the native species of *Agrostis* and *Festuca* are also in doubt (see p. 278).

‖ Relationships of Thouars' species hardly to be determined without reference to his herbarium (see text, p. 314).

PTERIDOPHYTA

This list is based on C. Christensen's (1940) full account of the collections made in the Tristan group by the Norwegian Expedition of 1937–38; and the late A. G. H. Alston's naming of Wace's collections from Tristan and Gough Island made in 1955–56. We are indebted to Dr E. A. Schelpe for advice over some of the names.

The list includes all pteridophytes that have been recorded from the islands, with the addition of some unpublished herbarium material, and recent collections made by Dickson in the Tristan group in 1962. Synonyms recognized in Christensen's paper are not listed, but a few of his names are bracketed together, now that additional collecting in the islands has suggested that they may refer to the same species. (The possibly correct name in these cases is in heavier print.) The records of Hafsten (1951) are not included, being only repetitions of Christensen's identifications. We consider that all the pteridophytes listed here are native to the islands, including *Azolla filiculoides* (cf. Christensen 1940).

		Tristan	Inaccessible	Nightingale	Gough
[1]	***Lycopodium diaphanum*** Sw.	[1, 2, 4, 8, 11b, 12, 13b, 16	13b	—	7, 10, 14c]
2	{***L. insulare*** Carmichael	[2, 11b, 13b, 14a, 16	13b	13b	7, 10, 14c]
	{*L. saururus* Hemsley	4	—	4	14c
3	***L. magellanicum*** Sw.	2, 4, 11b, 13b, 14a, 16	—	—	14c
4	***Ophioglossum opacum*** R. Br.	2, 4, 11b	—	—	14c
5	***Azolla filiculoides*** Lam.	—	13b, 16	—	—
6	***Adiantum poiretii*** Wikström	1, 2, 4, 6, 11b, 13b, 14a, 16	13b	—	5, 7, 9, 10, 14c
[7]	***Asplenium alvaradense*** Rudmose Brown	[13b	13b	—	5, 10, 14c]
8	{***A. erectum*** Bory	4, 11b, 13b	4, 13b, 16	4, 13b, 16	—
	{*A. insulare* Carmichael	2	—	—	14c
9	***A. monanthes*** L.	2, 4, 11b, 13b, 16	—	—	—
[10]	***A. obtusatum*** Forst. f.	[1, 2, 3, 4, 6, 8, 11b, 12, 13b, 14a, 16	4, 13b, 16	4, 13b, 16	5, 7, 10, 14c]
11	***A. platybasis*** Kze.	—	13b	—	—
[12]	***Athyrium medium*** (Carmichael) Moore	[2, 4, 11b, 13b, 16	13b]	—	—
13	{***Blechnum australe*** L.	1, 2, 3, 4, 6, 8, 11b, 12, 13b, 16	13b, 4	—	—
	{*B. punctulatum* Sw.	14a	—	—	14c
[14]	***B. palmiforme*** (Thouars) C. Chr.	[1, 2, 3, 4, 8, 11b, 12, 13b, 14a, 16	4, 13b, 16	13b, 16	5, 7, 10, 14c]
15	***B. penna-marina*** (Poiret) Kuhn	1, 2, 3, 4, 6, 8, 11b, 12, 13b, 14a, 16	13b, 16	13b, 16	5, 10, 14c
[16]	***Dryopteris aquilina*** (Thouars) C. Chr.	[1, 2, 3, 4, 6, 8, 11b, 12, 13b, 14a, 16	4, 13b	4, 13b	5, 7, 9, 10, 14c]
17	***D. paleacea*** (Sw.) C. Chr.	—	—	—	14c
[18]	***Elaphoglossum insulare*** C. Chr.	[13b, 16]	—	—	—
19	***E. hybridum*** (Bory) Moore	1, 2, 4, 11b, 13b, 14a, 16	13b	—	14c
[20]	***E. laurifolium*** (Thouars) Moore	[1, 2, 4, 6, 11b, 12, 13b, 14a, 16	13b, 16	13b, 16	5, 10, 14c]
[21]	***E. obtusatum*** (Carmichael) C. Chr.	[2, 4, 13b, 16	13b]	—	—
[22]	***E. succisifolium*** (Thouars) Moore	[1, 2, 3, 4, 11b, 12, 13b, 14a, 16	4, 13b, 16	4, 13b, 16	14c]
23	{*Grammitis billardieri* Willd.	14a	—	—	14c
	{***G. magellanica*** Desvaux	2, 4, 11b, 13b, 16	13b	13b	5, 10
[24]	***Gymnogramma cheilanthoides*** (Sw.) Kaulfuss	[2, 4, 6, 11b, 12, 13b, 14a, 16	BM, 13b	—	14c]
25	***Histiopteris incisa*** (Thunb.) J. Sm.	2, 3, 4, 6, 11b, 13b, 14a, 16	4, 13b, 16	13b	5, 9, 10, 14c
26	***Hypolepis rugosula*** (Labill.) J. Sm.	11b, 13b	13b, 16	13b, 16	14c

APPENDIX A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
27	***Polystichum mohroides*** (Bory) Presl.	—	—	—	7, 10
28	*P. adianteforme* (Forst. f.) J. Sm.	8, 11b, 12, 13b	13b	—	10
	Rumohra adiantiformis (Forst. f.) Ching	14a, 16	16	—	14c
[29]	***Thelypteris tomentosa*** (Thouars) O. Kuntze	[1, 2, 4, 11b, 13b, 14a, 16	13b, 16	13b	14c]
[30]	***Vittaria vittarioides*** (Thouars) C. Chr.	[1, 2, 4, 11b, 12, 13b, 14a, 16	13b	13b, 16	14c]
[31]	***Hymenophyllum aeruginosum*** (Poiret) Carmichael	[1, 2, 3, 4, 6, 11b, 12, 13b, 14a, 16	13b	13b	14c]
32	***H. peltatum*** (Poiret) Desvaux	11b, 12, 13b, 14a, 16	13b	—	14c
	H. tunbridgense (L.) Sm.	—	—	—	7, 10
33	***Trichomanes angustatum*** Carmichael	2, 3, 4, 6, 11b, 13b, 14a, 16	13b, 16	—	—

BRYOPHYTA

MUSCI

The following table is based on H. N. Dixon's posthumus (1960) account of the mosses collected by the Norwegian Expedition of 1937–38 in the Tristan group. Dixon's paper includes (pp. 5–7) a list of all the mosses recorded in Christophersen (1937) and Dyer (1939), which Dixon also named, from the three northern islands. Earlier records from the Tristan group (Dupetit Thouars 1811; Hemsley 1885; Geheeb & Herzog 1910) are not included here, but they probably add nothing to Dixon's lists. The mosses recorded from Gough Island by Wright (1905), Cardot (1912), Wilkins (1925), Christophersen (1934) and Bartram (1959) are included. We are much indebted to Dr D. H. Dalby and to Mr A. H. Norkett of the British Museum (Natural History) for allowing us to add their unpublished identifications of some of the mosses collected by Wace on Gough Island and Tristan in 1955–56 (these records are numbered 14 in the table). A bryophyte collection of 400 packets made by Dickson has yet to be studied.

Families have been arranged in sequence according to Brotherus' treatment of the mosses in the second edition of *Natürlichen Pflanzenfamilien* (1924–25), but genera are listed alphabetically within families. Doubtful records are not included, and no attempt has been made to allow for synonomy except in a few cases noted in Dixon's paper. Species which are considered to be endemic, either to single islands or to parts of the Tristan–Gough group, have their records enclosed within brackets: a number of species which were thought by Dixon to be endemic to Tristan have now been found on Gough Island, and are therefore bracketed as group endemics.

		Tristan	Inaccessible	Nightingale	Gough
1	*Sphagnum fimbriatum* Wils.	—	—	—	10b, 14, 15
2	*S. magellanicum* Brid.	—	—	—	14, 15
3	*S. recurvum* P. Beauv.	13	13	—	15
4	*S. scotiae* Card.	—	—	—	5, 10b, 15
5	*Andreaea aquatica* R. Br. ter.	13	—	—	—
[6]	*A. atlantica* Dix.	[13]	—	—	—
7	*A. grimmioides* Dus.	13, 14	—	—	14
8	*A. loricata* Dus.	—	—	—	14
9	*A. parallela* C. Muell	13	—	—	14
10	*A. regularis* C. Muell	13, 14	—	—	—
[11]	*A. squarrifolia* Dix.	[13]	—	—	—
[12]	*Ceratodon plano-marginatus* Dix.	—	—	[13]	—
13	*C. purpureus* (Hedw.) Brid.	11b, 13	—	13	—
14	*Ditrichum conicum* (Mont.) Par.	11b, 12, 13	—	—	—
15	*D. flexifolium* (Hook.) Hampe.	13	13	13	—

16	*D. hyalinum* (Mitt.) Par.	13	—	—	—
17	*D. strictum* (H. f. & W.) Hampe.	13, 14	13	—	14
[18]	*D. tenuinerve* Dix.	[13]	—	—	—
[19]	*Pseudodistichium altanticum* Dix.	[11b, 12, 13]	—	—	—
[20]	*Blindia brachystegia* Dix.	[12, 13]	—	—	—
[21]	*B. subcapillifolia* Dix.	[13]	—	—	—
[22]	*Campylopus alienus* Dix.	[13	13	13]	—
[23]	*C. alvarezianus* Card.	—	—	—	[5, 10b]
24	*C. arcuatus* Mitt.	11b, 13	—	—	—
[25]	*C. calvatus* (Mitt.) Dix.	[13]	—	—	—
26	*C. introflexus* (Hedw.) Brid.	11b, 12, 13, 14, 16	13	13	14
[27]	*C. luscinialis* Dix.	—	[13	13	14]
28	*C. vesticaulis* Mitt.	11b, 13, 14, 16	—	13	14, 15
[29]	*Dichodontium opacifolium* Dix.	[13]	—	—	—
30	*Dicranella fuegiana* Broth. & Card.	13	—	—	14
31	*D. hookeri* (C. Muell) Card.	13	—	—	15
32	*D. vaginata* (Hook.) Card.	13	—	—	—
[33]	*Dicranodontium insularum* Bartr.	—	—	—	[15]
[34]	*D. tristanense* Dix. et Thér.	[13	—	—	14]
[35]	*Dicranoloma atlanticum* Bartram	—	—	—	[15]
36	*D. harioti* (C. Muell) Par.	12, 13, 14, 16	13	—	14, 15
37	*D. imponens* (Mont.) Broth.	12, 13, 14	13	—	14, 15
[38]	*D. perdecurrens* Dix.	[13]	—	—	—
39	*Dicranoweisia antarctica* (C. Muell) Par.	12, 13	—	—	—
[40]	*D. falcifolia* Dix.	[13]	—	—	—
41	*Dicranum aciphyllum* H. f. & W.	12, 13	13	—	—
42	*Oncophorus fuegianus* Card.	—	—	—	10b, 14
43	*Thysanomitrium richardii* Schwaegr.	—	—	—	14
[44]	*Trematodon intermixtus* Card.	[13	13	—	5, 10b, 14]
45	*Fissidens asplenoides* Hedw.	11b, 13	13	—	14
[46]	*F. fluitans* Dix.	[13]	—	—	—
47	*F. leptochaetae* Dus.	—	13	—	—
[48]	*F. subobtusus* Dix.	—	[13]	—	—
[49]	*Syrrhopodon atlanticus* Dix.	[13	—	13	14]
50	*Barbula validinervia* C. Muell	13	—	—	—
51	*Didymodon austro-alpigena* (C. Muell) Broth.	13	—	—	—
52	*Gymnostomum calcareum* Nees. et Hornsch.	11b, 13	—	—	—
53	*Leptodontium interruptum* (Mitt.) Broth.	12, 13, 14	—	—	—
54	*Tortula kunzeana* (C. Muell) Mitt.	13	—	—	—
55	*Trichostomum aequatoriale* Spr.	13	—	—	—
56	*Grimmia kerguelensis* Card.	14	—	—	14
[57]	*G. stenobasis* Dix.	[13]	—	—	—
[58]	*Rhacomitrium breutelioides* Dix.	[13]	—	—	—
59	*R. crispulum* (H. f. & W.) H. f. & W.	11b, 12, 13, 14 ,16	—	13	14
[60]	*R. decurrens* Dix.	[13]	—	—	—

Appendix A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
61	*R. symphyodontum* (C. Muell) Jaeg.	—	—	—	5
[62]	*R. gracillimum* Dix.	[13]	—	—	—
63	*R. heterostichoides* Card.	13	—	—	—
64	*R. lamprocarpum* (C. Muell) Jaeg.	13	—	—	—
65	*R. lanuginosum* (Hedw.) Brid.	12, 13, 14	13	—	14, 15
66	*R. loriforme* Dus.	—	—	—	14
67	*R. nigritum* (C. Muell) Jaeg.	13	—	—	—
68	*R. subnigritum* (C. Muell) Par.	13	—	—	10b
[69]	*Funaria euryloma* Dix.	[13	13]	—	—
70	*F. hygrometrica* Hedw.	16	—	—	—
[71]	*Physcomitrium auberti* Besch.	[11b, 13	13]	—	—
72	*Anomobryum filiforme* (Dicks.) Husn.	11b, 13	—	—	—
73	*Brachymenium megalachrion* (Schwaegr.) Jaeg.	11b, 13	—	—	—
[74]	*B. amplifolium* Dix.	[13]	—	—	—
[75]	*B. cymbifoliellum* Dix.	[13]	—	—	—
[76]	*B. flacidifolium* Dix.	[12, 13]	—	—	—
[77]	*B. fluitans* Dix.	—	[13]	—	—
78	*B. incurvifolium* C. Muell	13	—	—	—
[79]	*B. subantarcticum* Dix.	[13	13]	—	—
[80]	*B. subulinerve* Card.	—	[13	—	5, 10b]
[81]	*B. tenellicaule* Card.	[13	13	—	5, 10b, 15]
[82]	*B. tristanense* Dix.	[13]	—	—	—
83	*B. truncorum* Brid.	11b, 13	13	13	—
84	*Mniobryum wahlenbergii* (Web. & Mohr.) Jennings	13	—	—	5
85	*Pohlia elongata* Hedw.	13	—	—	—
[86]	*P. excurrens* (Dix.) Bart.	[13	13	—	10b]
87	*P. nutans* Hedw.	13	—	—	5, 10b
88	*Eustichia longirostris* (Brid.) C. Muell	11b, 12, 13, 16	—	—	14
89	*Rhizogonium spiniforme* (Hedw.) Bruch	13, 14	—	13	15
[90]	*Bartramia inconspicua* Mitt.	[13]	—	—	—
[91]	*B. obscura* Dix.	[13]	—	—	—
92	*B. patens* Brid.	13	13	—	—
[93]	*B. radicosa* Mitt.	[13]	—	—	—
[94]	*B. stenobasis* Card.	[13	—	—	5, 10b]
95	*Breutelia dumosa* Mitt.	—	—	—	10b
96	*B. integrifolia* (Tayl.) Jaeg.	13, 14	—	—	—
97	*B. propinqua* Kaalaas	13	13	—	—
[98]	*B. tenuifolia* (Mitt.) Par.	[12, 13, 14, 16	13	—	15]
[99]	*Philonotis capillata* Mitt.	[11b, 13	—	—	5, 10b, 15]
100	*P. scabrifolia* (H. f. & W.) Mitt.	13	—	—	—
101	*P. tenuis* (Tayl.) Jaeg.	11b, 13, 14	13	—	14
102	*P. vagans* (H. f. & W.) Mitt.	13	—	—	10b
[103]	*Macromitrium acutirameum* Mitt.	[12]	—	—	—
[104]	*M. antarcticum* C. H. Wright	[11b, 13, 14	13	13	5, 7, 10b, 14]

105	*M. fimbriatum* Schwaegr.	11b, 12, 14	—	—	—
[106]	*Schlotheimia atlantica* Dix.	[11b]	—	—	—
[107]	*Zygodon insularum* Dix.	[13, 14	—	—	14]
108	*Orthostichopsis subimbricata* (Hampe.) Broth.	12, 13	—	—	—
109	*Rhacocarpus humboldtii* (Hook.) Lindb.	—	—	—	14
110	*Ptychomnion densifolium* (Brid.) Jaeg.	11b, 12, 13, 14, 16	13	—	14, 15
[111]	*Lepyrodon alaris* Dix.	[13	—	—	14, 15]
112	*Phyllogonium fulgens* (Sw.) Brid.	—	—	—	14
113	*P. viscosum* (P. Beauv.) Mitt.	11b, 13	—	—	—
[114]	*Porotrichum atlanticum* Dix.	[12, 13]	—	—	—
115	*Cyclodictyon laetevirens* (Hook. & Tayl.) Mitt.	13, 14, 16	16	—	5, 10b, 14
[116]	*Daltonia tristanensis* Dix.	[13	—	—	14]
117	*Distichophyllum fasciculatum* Mitt.	13	—	—	—
[118]	*Thuidium alvarezianum* Card.	—	—	—	[5, 7, 10b]
119	*T. curvatum* Mitt.	11b, 12, 13, 14, 16	13	13	14, 15
120	*Amblystegium excurrens* Broth. & Card.	13	—	—	—
[121]	*A. patenti-flexuosum* Dix.	—	[13]	—	—
[122]	*A. stricto-serpens* Dix.	[13]	—	—	—
[123]	*Calligeron acuminatum* Dix.	[13]	—	—	—
124	*Campylium polygamum* (B. S. & G.) Bryhn	11b, 13	—	—	—
125	*Drepanocladus uncinatus* (Hedw.) Warnst.	11b, 12, 13, 14, 16	—	—	14
126	*Hygroamblystegium fuegianum* (Besch.) Reimers	—	13	—	—
[127]	*Brachythecium pallidiflavens* Card.	—	—	—	[5, 10b]
128	*B. subpilosum* (H. f. & W.) Jaeg.	13	—	—	10b, 15
129	*B. subplicatum* (Hampe.) Jaeg.	—	—	—	14
[130]	*Meiothecium urceolatum* (Schwaegr.) Broth.	[11b, 13]	—	—	—
131	*Pleuropus bonplandii* (Hook.) Broth.	11b, 13	13	—	—
[132]	*Rhynchostegium irriguum* Dix.	[13]	—	—	—
[133]	*R. isopterygioides* Card.	[13, 16	13	13	5, 10b, 15]
[134]	*Rigodium crassicostatum* (Dix.) Bartr.	[12, 13, 16]	—	—	—
135	*Leptotheca gaudichaudii* (Spreng.) Schwaegr.	—	—	—	14
136	*Sematophyllum crassiusculum* (Brid.) Broth.	11b, 13	13	13	—
137	*Catagonium nitidum* (H. f. & W.) Broth.	13	—	—	—
138	*Hypnum cupressiforme* Hedw.	11b, 12, 13, 16	13	—	15
[139]	*H. elatum* Dix.	[13, 16	13	13	14]
[140]	*Isoptergyium ambiguum* Card.	[13	—	13	5, 10b]
141	*I. brownii* Card.	—	—	—	[5, 10b]
[142]	*I. tristanense* Dix.	[13	—	13]	—
[143]	*Oligotrichum tristanense* Dix.	[13]	—	—	—
144	*Polytrichadelphus magellanicus* (Hedw.) Mitt.	13, 14	13	—	5, 10b, 14, 15
145	*Polytrichum gracile* Sm.	—	—	—	14
146	*P. juniperinum* Hedw.	11b, 12, 13, 16	13	13	14
147	*Psilopilum antarcticum* (C. Muell) Par.	13	—	—	—
[148]	*P. laxifolium* Dix. & Thér.	[13	13]	—	—
[149]	*P. tristanense* Dix.	[13]	—	—	—

APPENDIX A (*cont.*)

HEPATICAE

This list of hepatics is based on Mr S. Arnell's (1958) account of the collections made by the Norwegian Expedition of 1937–38 in the Tristan group. Several species collected by Wace on Tristan in 1955 (which are listed in an appendix to Arnell's paper) and by Dickson in 1962 (named by Mr Arnell) are also included here. We are much indebted to Mr Arnell for allowing us to incorporate all his unpublished identifications of Wace's collections on Gough Island in 1955–56: these unpublished records are numbered 14 in the right-hand column of the table. Mr Arnell has made a few taxonomic revisions since his 1958 paper. The following are deleted: *Lophocolea stronglyophylla* (Tayl.) Hodgson, *L. minima* Arnell and *Frullania serrata* G. *Clasmatocolea heterostipa* Spr. is reclassified as *C. vermicularis* (Lehm.) Grolle and *Frullania lindenbergii* Lehm. as *F. stipatiloba* Jack and Steph. The species of *Mylia* are reclassified as *Mylia chiloscyphoides* (Ldbg.) Herz.; *Leptoscyphus expansus* (Lehm.) Grolle and *L. cuneifolius* (Hook.) Mitt. subsp. *fragilis* (Jack and Steph.) Grolle. *Lophocolea sapuletorum* (H. f. et T.) G., L. et N. is added.

The genera are arranged alphabetically. Doubtful records and uncertain identifications are excluded.

		Tristan	Inaccessible	Nightingale	Gough
1	*Acrobolus excisus* (Mitt.) Schiffn.	13, 14	13	—	—
2	*Adelanthus magellanicus* (Ldbg.) Spr.	16	—	—	14
3	*A. unciformis* (Tayl.) Mitt.	13, 14, 16	13	—	14
4	*Anastrophyllum crebrifolium* (Tayl.) Steph.	13, 14, 16	—	—	14
[5]	*A. incumbens* (Lehm. et Ldbg.)	[13, 16	13]	—	—
6	*Anthoceros plicatus* Mitt.	11b	—	—	—
7	*Aphanolejeunea microscopica* (Tayl.) Evans.	13, 14	13	13	14
8	*Bazzania creberrima* Steph.	—	13	—	—
9	*B. peruvianum* (Lehm. et Ldbg.) Trevis.	13	13	13	—
10	*B. skottsbergii* (Steph.) Fulf.	13, 16	13	13	14
11	*Blepharidophyllum densifolium* Ångstr.	—	—	—	14
12	*Blepharostoma quadripartita* (Hook.) Steph.	13	13	—	14
13	*Calypogeia bidentula* (Web.) Nees.	13	13	—	14
14	*C. fusca* (Lehm.) Steph.	13	13	—	—
15	*Cephalozia bicuspidata* (L.) Dum. sens. lat.	13	—	—	—
16	*C. crassicaulis* Steph.	13	—	—	—
17	*C. kirkii* Steph.	13	13	—	—
18	*C. turbulata* (Tayl.) Spr.	13	—	—	—
[19]	*Cephaloziella tristaniana* Arnell	[13, 16]	—	—	—
20	*C. varians* (G.) St.	13	—	—	14
21	*Chiloscyphus granditextus* Steph.	13	13	—	14
22	*Clasmatocolea vermicularis* (Lehm.) Grolle	13, 16	13	—	14
[23]	*Cololejeunea olivaceoviridis* Arnell	[13]	—	—	—
24	*Colura calyptrifolia* (Hook.) Dum.	13	—	—	—
25	*Drepanolejeunea araucariae* Steph.	13, 14	13	—	14
26	*D. lancifolia* Mass.	—	—	—	14
[27]	*D. tristaniana* Arnell	[13, 14, 16	13	—	14]
28	*Dumortiera hirsuta* (Sw.) Nees.	13	13	—	—
29	*Fossombronia fernandeziana* Steph.	13	13	—	—
30	*Frullania stipatiloba* Jack and Steph.	13, 14, 16	13	13	14
31	*F. magellanica* Web. et Nees.	13, 14	—	—	—
[32]	*F. tristaniana* Arnell	[13, 14, 16]	—	—	—
33	*Gymnomitrium stygium* Hook. et Tayl.	13	—	—	14

34	*Harpalejeunea parasitica* Tayl.	13, 14	—	13	—
35	*Herberta oldfieldianum* (St.)	—	—	—	14
36	*Hymenophytum flabellatum* (Labill.) Dum.	13	—	—	—
37	*Isotachis georgensis* Steph.	13	—	—	—
38	*I. halleana* Steph.	13	—	—	—
39	*I. madida* (Tayl.) Mitt.	13, 14	—	—	14
40	*I. nordenskjoldii* Steph.	—	—	—	14
41	*I. quadriloba* Steph.	—	13	—	—
42	*I. spegazziana* Mass.	—	—	—	14
43	*I. striolata* Steph.	13, 16	—	—	—
44	*Jamesoniella colorata* (Lehm.) Spr.	11b, 13	13	—	5, 7, 10b, 14
45	*J. grandiflora* (Lehm. et Ldgb.) Spr.	13, 16	13	—	14
46	*J. ligulifolia* Steph.	13	—	—	—
47	*J. oenops* (L. et G.) Steph.	13, 14	—	—	14
48	*J. paludosa* Steph.	13	—	—	—
49	*Jungermannia rostrata* (St.) Arnell	—	—	—	14
[50]	*J. tristaniana* Arnell	[13]	—	—	—
51	*Lejeunea flava* (Sw.) Spr.	—	13	13	14
52	*L. holtii* Spr.	—	13	—	—
53	*L. lamacerina* St.	—	—	—	14
[54]	*L. longicollis* Arnell	[13	13	—	14]
55	*L. patagonica* Steph.	14	—	—	—
56	*Lepicolea ochroleuca* (Spr.) Spr.	13, 14	13	—	14
57	*Lepidozia bicuspidata* Mass.	13	—	—	—
58	*L. breviseta* (Herz) Arnell	13	—	—	—
59	*L. fusca* Steph.	13	—	—	—
60	*L. halleana* St.	—	—	—	14
61	*L. oligophylla* Ledbg.	—	—	—	14
62	*L. procumbens* Mitt.	11b, 13, 14, 16	13	13	14
63	*L. saddlensis* Besch. et Mass.	13, 14	13	13	14
64	*L. setiformis* De Not.	—	—	—	14
65	*Leptoscyphus expansus* (Lehm.) Grolle	13	13	—	14
66	*L. cuneifolius* (Hook.) Mitt. ssp. *fragilis* (Jack et Steph.) Grolle	13	13	—	14
[67]	*Lethocolea prostrata* Mitt.	[13	13	—	14]
[68]	*Leucolejeunea tristaniana* Arnell	—	[13	13	14]
69	*Lophocolea abnormis* (Besch. et Mass.) Steph.	13	—	—	—
70	*L. aequifolia* (Nees. et Mont.) Steph.	13	13	—	—
71	*L. anomoda* (Mont.) Steph.	13, 14, 16	—	—	—
72	*L. austrigena* Hook. f. et Tayl.	13	13	—	—
73	*L. bidentata* Dum.	—	—	—	5, 10b
74	*L. chiloensis* St.	16	—	—	14
[75]	*L. christophersenii* Arnell	[13]	—	—	—
76	*L. cuspidata* L. sens. lat.	13	13	13	—
77	*L. diverstipa* St.			—	14

APPENDIX A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
[78]	*L. gracillima* Arnell	[13]	—	—	—
79	*L. humilis* (Hook. f. et Tayl.) Steph.	13	13	—	14
80	*L. inconspicua* Mitt.	11b	—	—	—
81	*L. irregularis* Steph.	13	—	—	—
82	*L. monoica* St.	—	—	—	14
83	*L. muricata* Nees.	14	—	—	14
84	*L. novae-zelandiae* (L. et L.) Nees.	—	—	—	14
85	*L. obvoluta* (Tayl.) Mass.	—	—	—	14
86	*L. patulistipa* Tayl.	—	—	—	14
87	*L. puccioana* (De Not.) Mass.	13, 16	—	—	14
88	*L. sapuletorum* (H. f. et T.) G. L. et N.	13	—	—	—
89	*L. serrata* Mitt.	11b	—	—	—
90	*L. skottsbergii* Steph.	13	—	—	—
91	*L. subcapillaris* Steph.	13	—	—	14
92	*L. submuricata* Herz.	13, 16	13	13	14
93	*L. textilis* Tayl.	—	—	—	14
[94]	*L. tristaniana* Arnell	—	[13]	—	—
95	*L. undulata* Mont.	—	—	—	14
96	*L. vasculosa* (Tayl.) Nees.	—	—	—	14
[97]	*L. wacei* Arnell ined.	—	—	—	[14]
[98]	*Lophozia squarrosa* Arnell	[13]	—	—	—
99	*Marchantia berteroana* Lehm. et Ldbg.	—	13	13	—
100	*M. polymorpha* L.	11b, 13	—	13	5, 10b, 14
101	*Marsupidium brevifolium* Steph.	—	13	—	—
102	*Metzgeria epiphylla* Evans.	13	13	—	—
103	*M. hamata* Ldbg.	13	—	—	—
104	*M. multiforme* (Mass.) Schiffn. et Gottsche.	13	13	13	14
105	*M. violacea* (Ach.) Dum.	—	—	—	14
106	*Microlejeunea ulicina* Spr.	13, 14, 16	13	13	14
107	*Mylia chiloscyphioides* (Lebg.) Herz.	13, 16	13	13	14
108	*M. ligulata* (St.) Herz.	—	—	—	14
109	*M. repens* (Mitt.) Herz. ?	—	—	—	14
110	*Neohodgsonia mirabilis* (H. Perss.) H. Perss.	13, 16	13, 16	16	14
111	*Noteroclada confluens* Tayl.	—	—	—	14
112	*Phaeoceros chiloensis* Steph.	13	13	—	—
113	*P. laevis* (L.) Proskauer.	—	—	—	14
114	*Plagiochila ansata* (Tayl.) Hook. et Tayl.	—	13	13	—
115	*P. equitans* G.	13	—	—	—
[116]	*P. fragifolia* Arnell	[13, 14	13]	—	—
117	*P. fusco-brunnea* Steph.	13, 14, 16	13	—	—
[118]	*P. infuscata* Mitt.	[11b, 13, 16	13]	—	—
119	*P. lechlerii* G.	—	—	13	—
120	*P. remotioides* Steph.	—	13	—	—
121	*P. robusta* Steph.	—	13	—	—

122	*P. rufescens* Steph.	13	13	—	—
[123]	*P. wacei* Arnell ined.	—	—	—	[14]
124	*Porella chilensis* (Lehm. et Ldbg.) Herz.	—	13	—	—
125	*Pseudomarsupidium piliferum* (Steph.) Herz.	—	13	13	14
126	*Radula diversifolia* Steph.	14	—	—	—
127	*R. fernandeziana* Steph.	13, 16	13	—	—
128	*R. hastata* Steph.	—	13	—	—
129	*R. striata* Mitt.	13	—	—	—
130	*Reboulia hemisphaerica* (L.) Raddi.	11b, 13	—	—	—
131	*Riccardia alcicornis* (Hook. et Tayl.) Trevis.	—	—	—	14
132	*R. autoica* (Steph.) Evans	—	13	—	—
[133]	*R. christophersenii* Arnell	[13]	—	—	—
134	*R. crassicrispa* (Steph.) Evans	13	13	—	—
135	*R. diversiflora* Evans	13	—	—	14
136	*R. floribunda* (Steph.) Evans	—	13	—	—
[137]	*R. mejlandii* Arnell	[13]	—	—	—
138	*R. mycophora* Evans	—	—	—	14
139	*R. nudimitra* (Steph.) Evans	—	—	—	14
140	*R. pallidovirens* (Steph.) Evans	—	—	—	14
141	*R. savatieri* (Steph.) Evans	13, 14, 16	13	—	14
142	*R. stolonifera* Steph.	—	—	—	14
[143]	*R. tristaniana* Arnell	[13]	—	—	—
144	*Schistochila pachyla* Tayl.	—	13	—	—
145	*S. pachyphylla* (Lehm.) Steph.	13	—	—	14
146	*S. splanchnophylla* (Tayl.) Steph.	13	13	13	—
147	*Solenostoma crassulum* Mont.	13	13	—	—
148	*Sphenolobus peridonialis* Tayl.	13	—	—	—
149	*Strepsilejeunea gayana* Steph.	—	—	—	14
150	*Symphogyna circinnata* Nees. et Mont.	13	13	—	14
151	*S. crassifrons* Sull.	—	—	—	14
152	*S. hockstetteri* Nees. et Mont.	13	—	—	—
153	*S. hymenophylla* (Hook.) Nees. et Mont.	13, 16	13	13	14
[154]	*S. tristaniana* Arnell	[13, 14]	—	—	—
[155]	*Syzygiella tristaniana* Arnell	[13	—	—	14]
156	*Telaranea sejuncta* (Ångstr.) Arnell	13, 14, 16	13	13	14
157	*Trichocolea verticillata* Steph.	13	13	—	14
158	*Tylifmanthus hallei* Steph.	13	13	—	—
159	*T. silvaticus* Steph.	13	13	—	—
160	*T. viridis* Mitt.	13	13	—	

APPENDIX A (*cont.*)

FUNGI

The list of fungi has been taken from all publications which include records of fungi gathered in the islands, except Dupetit Thouars (1811) (who listed four genera from Tristan island). Most records are from the papers describing collections made in the Tristan group by the Norwegian Expedition of 1937–38 (for authors, see table 7). We are indebted to Mrs Balfour-Browne of the British Museum (Natural History), for allowing us to publish her identifications of Wace's collections from Gough Island, which are numbered 14 in the right-hand column.

No Myxomycetes or Phycomycetes are known from the islands, and the present list gives no indication of the total number of species which must be present. The individual islands of the Tristan group in which many Agaricales have been found are not indicated in the paper by Singer (1955): these group records are indicated by the symbol + against all three islands. Hosts of various parasites described by Jørstad (1947) are listed in brackets after the names.

		Tristan	Inaccessible	Nightingale	Gough
ASCOMYCETES					
1	*Catacuma acaenae* (Henn.) Theiss. et Syd. (on *Acaena stangii*)	13	13	—	—
2	*Claviceps purpurea* (Fr.) Tul. (on *Spartina arundinacea*)	—	13	—	—
3	*Daldinia concentrica* (Bolt. ex Fr.) Ces. et de Not.	13	—	—	—
4	*Eutypella macowani* Doidge	13	—	—	—
5	*Hypoxylon exutans* Cke.	13	13	—	—
6	*H. glomeratum* Cke.	13	—	—	—
7	*H. placentaeforme* Berkl. et Curt.	11	—	—	—
8	*H. sclerophaeum* Berkl. et Curt.	13	—	13	—
9	*H. serpens* (Pers. ex Fr.) Fr.	13	—	—	—
10	*Melanomma ? fuscidulum* Sacc.	13	—	—	—
11	*Rosellinia subiculata* (Schw.) Sacc.	—	13	—	—
12	*Ustulinia deusta* (Hoffm. ex Fr.) Petrak	13	—	—	—
13	*Xylaria anisopleura* (Mont.) Mont.	13	—	—	—
14	*X. castorea* Berk.	—	—	—	14
15	*X. cubensis* (Mont.) Mont.	13	13	—	—
16	*X. hypoxylon* (Fr.) Grev.	—	—	—	14
17	*Calycella sulfurina* (Quel.) Bond.	13	—	—	—
18	*Chlorociboria versiformis* (Pers. ex Fr.) Seaver	13	—	—	—
19	*Ciliaria scutellata* (Fr.) Boud.	—	—	—	14
20	*Cistella incrustata* (Ell.) Dennis	13	—	—	—
21	*Coryne sarcoides* (Jacq. ex Fr.) Tul.	13	—	—	—
22	*Corynella atrovirens* (Pers. ex Fr.) Boud.	13	—	—	—
23	*Hyaloscypha australis* Dennis	13	—	—	—
24	*Farlowiella australis* Dennis	13	—	—	—
25	*Karschia stygia* (Berk. et Curt.) Massee	13	—	—	—
26	*Ombrophila* sp. (nr. *O. pellucida* A. L. Smith)	13	—	—	—
27	*Orbilia leucostigma* (Fr.) Fr.	13	—	—	—
28	*Peziza vesiculosa* Bull. ex Fr.	13	—	—	—
29	*Plectania coccinea* (Scop. ex Fr.) Fuckel	13	—	—	—
30	*Stictis radiata* (L.) Pers. ex Fr.	13	—	—	—

FUNGI IMPERFECTI					
31	*Ascochyta* sp. (cf. *A. graminicola* Sacc.)	—	—	—	14
32	*Aspergillus niger* van Teig.	—	—	—	14
33	*Cercospora apii* Fres. (on *Apium australe*)	—	13	—	—
34	*Cladosporium herbarum* Link. ex Fr.	—	—	—	14
35	*Coniothryium nerterae* Jørst. (on *Nertera depressa*)	—	—	13	—
36	*Darluca filum* (Biv. Bern.) Cast. (on various *uredosori*)	13	13	13	10
37	*Fusarium graminum* Corda	—	—	—	14
38	*Penicillium* sp.	—	—	—	14
39	*Septoria apicola* Speg. (on *Apium australe*)	—	13	—	—
40	*S. geranii* Rob. et Desm. (on *Pelargonium grossularioides*)	—	13	—	—
41	*Xiphomyces caricis* Jørst. (on *Carex insularis*)	13	—	—	—
USTILAGINALES					
42	*Entyloma crastophilum* Sacc. (on **Holcus lanatus*)	13	—	—	—
43	*Farysia olivacea* (DC) Syd. (on *Carex insularis* and *C. thouarsii*)	—	13	13	—
44	*Ustilago striaeformis* Niessl. (on **Holcus lanatus*)	13.	—	—	—
UREDINALES					
45	*Puccinia gnaphalii* (Speg.) Henn. (on *Gnaphalium pyramidale*)	13	—	—	—
46	*P. goughensis* Jørst. (on *Apium australe*)	—	—	—	10
47	*P. hieracii* (Schum.) Mart. (on **Hypochoeris glabra*)	13	—	—	—
48	*P. hydrocotyles* (Link) Cooke (on *Hydrocotyle capitata*)	13	13	—	—
49	*P. poae-sudeticae* (West.) Jørst. (on **Poa pratensis*)	13	—	—	—
50	*Uredo caricis-thouarsii* Jørst. (on *Carex thouarsii*)	13	—	13	—
51	*U. scirpi-nodosi* McAlp. (on *Scirpus bicolor*)	13	13	—	—
52	*Uromyces nerviphilus* (Grogn.) Hots. (on **Trifolium repens*)	13	—	—	—
53	*U. planisculus* (Mont.) Jørst. (on *Rumex frutescens*)	13	13	—	—
54	*U. striatus* Schroet. (on **Trifolium dubium*)	13	—	—	—
55	*U. tenuicutis* McAlp. (on **Sporobolus capensis*)	13	—	—	—
APHYLLOPHORALES					
56	*Corticium ochraceo-fulvum* Bourd. et Galz.	13	—	—	—
57	*Hydnum mucidum* (Fr.) Fr.	—	—	—	14
58	*Inonotus jamaicensis* Murrill	13	—	—	—
59	*Leptoporus rufoflavus* (Berk. et Curt.) Pilát	13	—	—	—
60	*Merulius ambiguus* Berk.	—	—	—	5, 10
61	*M. corium* Fr.	—	—	13	—
62	*Odontia arguta* (Fr.) Quel.	13	—	13	—
63	*Peniophora argillacea* (Bres.) Sacc. et Syd.	13	—	—	—
64	*P. cremea* (Bres.) Sacc. et Syd.	13	—	—	—
65	*P. incarnata* (Fr.) Karst.	—	—	—	14
66	*Solenia candida* Fr.	13	—	—	—

APPENDIX A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
AGARICALES					
67	*Agaricus* aff. *campestris* L. ex Fr.	13	—	—	—
68	*Agrocybe cylindracea* (DC ex Fr.) R. Marie	13	—	—	—
	Pholiota phylicegena (Berk.) Sacc.	11	—	—	14
69	*Agrocybe pediades* (Fr.) Fayod	+	+	+	—
70	*A. praecox* (Pers. ex Fr.) Fayod	+	+	+	—
71	*Alnicola bohemica* (Vel.) Singer	+	+	+	—
72	*Conocybe* sp. (cf. *C. marginospora* (Murrill) Singer)	+	+	+	—
73	*Coprinus silvaticus* Peck.	—	—	—	14
74	*Coprinus* sp.	+	+	+	—
75	*Deconcia* sp. (or ?*Psilocybe* sp.)	+	+	+	—
76	*Galerina* sp.	+	+	+	—
77	*Hemimycena fibula* (Bull ex Fr.) Singer	+	+	+	14
78	*Hydropus frater-niger* Singer	+	+	+	—
79	*Inocybe* sp.	—	—	—	14
80	*Laccaria tetraspora* Singer	13	—	—	—
81	*Marasmius* sp.	—	—	—	14
82	*Mycena* sp.	+	+	+	—
83	*Omphalia umbellifera* (Fr.) Quel.	—	—	—	14
84	*Paneolus* sp.	+	+	+	—
85	*Psathyra* sp.	—	—	—	14
86	*Psathyrella* sp. 1	13	—	—	—
87	*Psathyrella* sp. 2	13	—	—	—
88	*Psathyrella* sp. 3	13	—	—	—
89	*Pleuroflammula flammea* (Murrill) Singer	+	+	+	—
90	*Stropharia semiglobata* (Batsch. ex Fr.) Quel.	13	—	—	—
GASTEROMYCETALES					
91	*Lycoperdon depressum* Bon.	13	—	—	—
	Approximate numbers of species recorded from the islands.	*ca.* 60	*ca.* 20	*ca.* 15	*ca.* 20

LICHENS

The following names have been taken from all publications listing lichens collected in the islands, with the exception of Dupetit Thouars (1811). There has been little attempt to allow for synonymy, except in the case of several equivalent names quoted in Christophersen (1937), and the inclusion of early records for *Sticta intricata* under *Pseudocyphellaria*. The total number of lichens derived from this list is therefore probably an overestimate of the number of separate species which have been recorded from the islands.

Since no lichenologist has ever visited any of the islands, and only the genera *Cladonia* (des Abbayes 1940) and *Placopsis* (Mackenzie Lamb 1940) from the Tristan group have been thoroughly examined by specialists, the list gives little idea of the total lichen flora of the group, which must be very much larger than these few names suggest. We are much indebted to Mr Peter James of the British Museum (Natural History) for allowing us to include his unpublished identifications of collections made in 1955–56 on Gough Island and in 1962 on the Tristan group.

		Tristan	Inaccessible	Nightingale	Gough
1	*Buellia acunhana* (Nyl.) Zahlbr.	11	—	—	14
2	*Cladonia balfourii* Cromb.	13	—	13	—
3	*C. capitellata* (Tayl.) Babingt. f.	13	—	—	—
4	*C. ceratophylla* (Sw.) Spreng.	—	—	13	—
5	*C. coccifera* Willd.	13, 14, 16	—	—	14
6	*C. didyma* (Fée) Wain	—	—	13	—
7	*C. fallax* des Abb.	13	—	—	—
8	*C. gracilis* (L.) Willd.	13	—	—	—
9	*C. macilenta* Nyl.	13	—	—	—
10	*C. mitis* Sandst.	13	—	—	—
11	*C. ochrochlora* Flk.	—	13	13	—
12	*C. pityrea* (Flk.) Fr.	13	—	—	—
13	*C. pyxidata* (L.) Fr.	12, 13, 14	13	—	—
14	*C. scabriuscula* (Del.) Sandst.	13, 14	—	—	—
15	*C. squamosa* Hoffm.	—	—	—	5, 10
16	*Lecanora subfusca* Ach.	11	—	—	—
17	*Leceidea* sp.	—	—	—	14
18	*Parmelia cetrata* Ach.	11	—	—	5, 7, 10
19	*P. perforata* (Wulf.) Ach.	11	—	—	—
20	*P. perlata* (Huds.) Ach.	11, 14	—	7	14
21	*P. proboscidea* Ach.	—	—	7	—
22	*P. revoluta* Floerke	—	—	—	14
23	*P. revolutella* Nyl.	11	—	—	—
24	*P. saxatilis* (L.) Ach.	—	—	—	10
25	*P. sphaerosporella* Muell.	—	—	—	5, 10
26	*Physcia stellaris* Nyl.	—	—	—	5, 10
27	*Placopsis cribellans* (Nyl.) M. Lamb	13, 14	—	—	14
28	*P. fuscidula* M. Lamb	13	—	—	14
29	*P. gelida* (L.) Linds.	11, 13, 14	—	—	14
30	*P. parellina* (Nyl.) M. Lamb	13, 14, 16	13	—	14
31	*P. perrugosa* (Nyl.) Nyl.	13	13	—	14
32	*P. rhodophthalma* (Müll. Arg.) Räs.	13	—	—	—
33	*Pseudocyphellaria aurata* Wain.	—	—	—	14

Appendix A (*cont.*)

		Tristan	Inaccessible	Nightingale	Gough
34	*P. intricata* (Del.) Wain	11, 16	—	—	14
35	*Ramalina intermedia* Del.	11, 16	—	—	14
36	*R. scopulorum* Ach.	—	—	—	5, 10
37	*R. yemenensis* (Ach.) Nyl.	11	—	—	14
38	*Stereocaulon antarcticum* Vain.	11	—	—	—
39	*S. implexum* Th. Fr.	—	—	—	14
40	*S. mixtum* Nyl.	11, 14, 16	—	—	—
41	*Sticta fuliginosa* Nyl.	—	—	—	5, 10
42	*S. ambivallaria* Ach.	14	—	—	—
43	*Teloschistes flavicans* (Ew.) Norm.	14, 16	—	7	—
44	*Usnea articulata* Hoffm.	—	—	7	—
45	*U. barbata* (L.) Wigg. wm. Mot.	—	—	—	5, 10
46	*U. plicata* (L.) Wigg.	—	—	7	—
47	*U. rubiginea* Stirt.	14, 16	—	—	—
48	*Lepraria* sp.	14	—	—	—
49	*Peltigera polydactyla* (L.) Hoffm.	—	—	—	14
	Total number of species recorded from the islands.	31	4	9	24

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Note added in proof, 21 *July* 1965.

Guppy records finding 'a small hard seed' in the gizzard of *Daption capensis* taken about 550 miles east of Tristan da Cunha. Although common in Tristan waters, this bird does not breed in the Tristan–Gough group, nor in South Africa: therefore the seed was presumably transported at least 2000 km from its nearest known breeding grounds in the Scotia Arc islands, the Crozet group, or Kerguelen (see Hemsley 1885, p. 258).

FIGURE 17. *Poa flabellata* tussock grassland on stabilized boulder scree occupied by a rockhopper penguin (*Eudyptes crestatus*) rookery near West Point, Gough Island. The ground between the tussocks is almost bare of plants. The penguins stand about half a metre high. From Wace (1960).

FIGURE 18. *Spartina arundinacea* tussock on the seaward slopes of the northern side of Nightingale Island; Stoltenhoff Island on the left, Middle Island on the right. The very dense, pure stand of the tussock is between 1·5 and 2 m high.

FIGURE 19. The western side of Hottentot Gulch, Tristan, showing about 6 m of downwash. Very low, overgrazed grassland on top. Tufts of *Spartina arundinacea* out of reach of domestic animals, centre.

FIGURE 20. Overgrazed grassland at Hackel Hill, southwest Tristan. Soil at background base and eroding. Numerous inflorescences of *Chrysanthemum leucanthemum* in the foreground.

FIGURE 21. The Base and Peak from Burntwood, Tristan. Foreground to middle distance is dominated by *Blechnum palmiforme* with a few low bushes of *Phylica*. Many *Blechnum* plants with upright sporophylls.

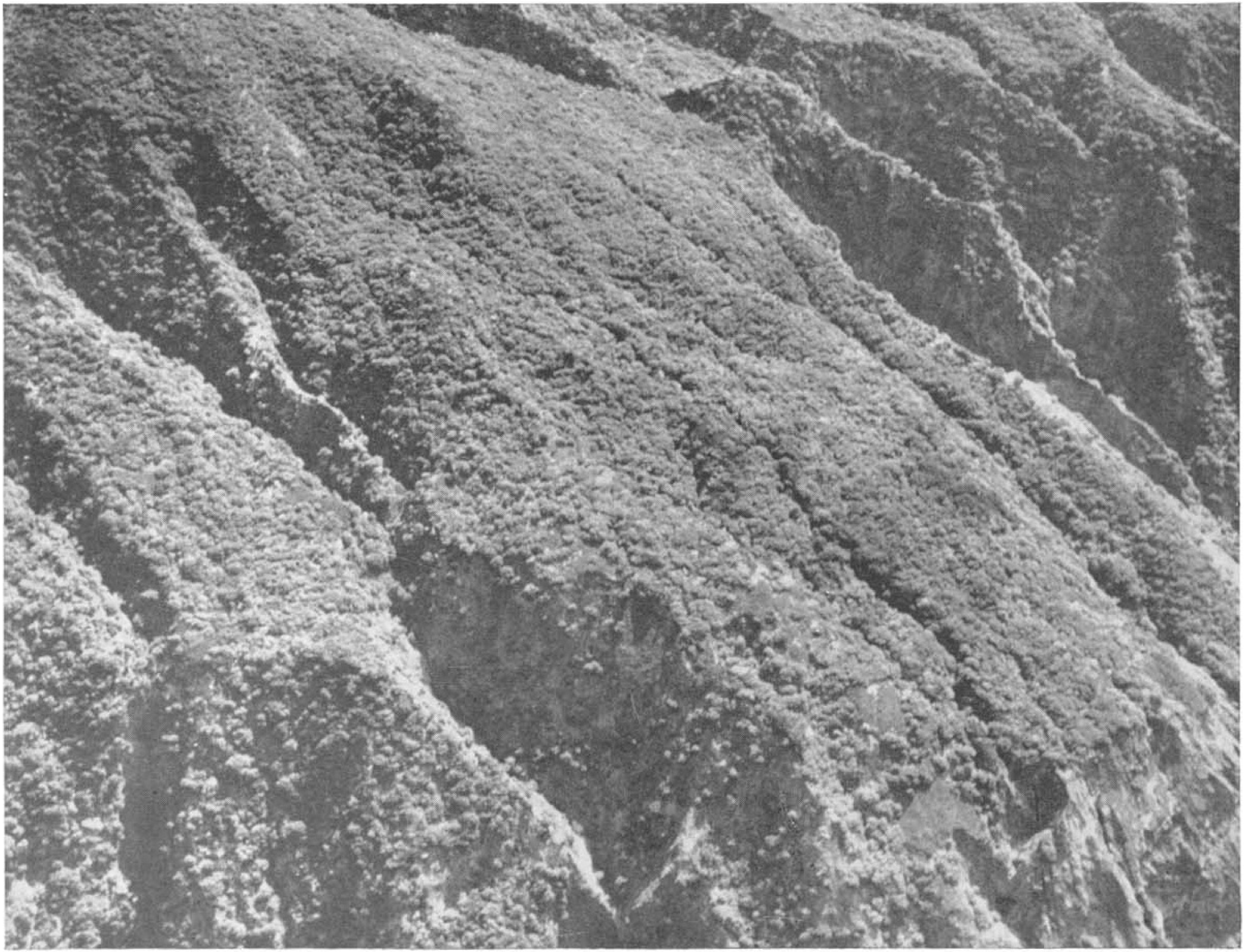

FIGURE 22. The rugged topography of the edge of the Base above Sandy Point, Tristan. Top of Main Cliffs at bottom right. Dense growth of *Phylica* covers all but the steepest ground.

Figure 23. Oceanic heath on Gough Island at 450 m above sea level. Patches of *Empetrum rubrum* and tufts of *Deschampsia* sp. and *Agrostis media* are rooted in a bryophyte mat, mainly of *Sphagnum magellanicum*. Stunted *Blechnum palmiforme* with the fronds borne on the moss surface is also present. A more continuous mat of *Empetrum* in the left background is marked by the half metre probe. The peat is here 120 cm deep.

FIGURE 24. Green Hill on the south-west of Tristan at *ca.* 900 m. Peak at top left. Apart from small stand of *Deschampsia* sp., left foreground, the entire foreground to middle distance is covered by dense luxuriant *Rumex acetosella*.

FIGURE 25. The Peak at *ca.* 1800 m, Tristan. Little vegetation, consisting almost solely of mosses and lichens, except on more stable ground.

FIGURE 26. The summit crater, Tristan. Foreground is shallow lake. Stripes of vegetation on slopes. *Rhacomitrium lanuginosum*, *Andreaea* and *Cladonia* spp. abundant.

FIGURE 27. The interior of Nightingale Island. Small areas of *Phylica* bush surrounded by *Spartina*. Areas on the slopes free of *Spartina* may have been burned.

FIGURE 28. The Second Pond, Nightingale Island. *Spartina* surrounds the Pond which is covered by *Scirpus sulcatus*. *Rumex obtusifolius* beside the nearest yellow-nosed albatross chicks.

FIGURE 29. Saltbeach Waterfall, Inaccessible Island. Cliffs covered by *Spartina*. *Phylica* on distant slopes. The gully above the Waterfall is only habitat of *Peperomia tristanensis*.

FIGURE 30. *Azolla filiculoides*, bottom right and centre background on open water at West Point, Inaccessible Island. *Spartina*, *ca.* 1·5 m high, on right. *Scirpus sulcatus* on left.

FIGURE 31. Pure stand of flowering *Sonchus oleraceus* on the uppermost part of a beach on Inaccessible Island. Broken stems of *Spartina* lying in foreground.